Bilateral age-related atrophy in the planum temporale is associated with vowel discrimination difficulty in healthy older adults

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Abstract: In this study we investigated the association between age-related brain atrophy and behavioural as well as electrophysiological markers of vowel perception in a sample of healthy younger and older adults with normal pure-tone hearing. Twenty-three older adults and 27 younger controls discriminated a set of vowels with altered second formants embedded in consonant-vowel syllables. Additionally, mismatch negativity (MMN) responses were recorded in a separate oddball paradigm with the same set of stimuli. A structural magnet resonance scan was obtained for each participant to determine cortical architecture of the left and right planum temporale (PT). The PT was chosen for its function as a major processor of auditory cues and speech. Results suggested that older adults performed worse in vowel discrimination despite normal-for-age pure-tone hearing. In the older group, we found evidence that those with greater age-related cortical atrophy (i.e., lower cortical surface area and cortical volume) in the left and right PT also showed weaker vowel discrimination. In comparison, we found a lateralized correlation in the younger group suggesting that those with greater cortical thickness in only the left PT performed weaker in the vowel discrimination task. We did not find any associations between macroanatomical traits of the PT and MMN responses. We conclude that deficient vowel processing is not only caused by pure-tone hearing loss but is also influenced by atrophy-related changes in the ageing auditory-related cortices. Furthermore, our results suggest that auditory processing might become more bilateral across the lifespan.

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HIGHLIGHTS

Discriminating differing formants in vowels is more difficult for older participants

Volume and area in the planum temporale favor the detection of deviant formants

Auditory processing by the planum temporale is less lateralized in the elderlies

Bilateral age-related atrophy in the planum temporale is associated with vowel discrimination difficulty in healthy older adults

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Abstract

In this study we investigated the association between age-related brain atrophy and behavioural as well as electrophysiological markers of vowel perception in a sample of healthy younger and older adults with normal pure-tone hearing.
Twenty-three older adults and 27 younger controls discriminated a set of vowels with altered second formants embedded in consonant-vowel syllables. Additionally, mismatch negativity (MMN) responses were recorded in a separate oddball paradigm with the same set of stimuli. A structural magnet resonance scan was obtained for each participant to determine cortical architecture of the left and right planum temporale (PT). The PT was chosen for its function as a major processor of auditory cues and speech.
Results suggested that older adults performed worse in vowel discrimination despite normal-for-age pure-tone hearing. In the older group, we found evidence that those with greater age-related cortical atrophy (i.e., lower cortical surface area and cortical volume) in the left and right PT also showed weaker vowel discrimination. In comparison, we found a lateralized correlation in the younger group suggesting that those with greater cortical thickness in only the

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left PT performed weaker in the vowel discrimination task. We did not find any associations between macroanatomical traits of the PT and MMN responses. We conclude that deficient vowel processing is not only caused by pure-tone hearing loss but is also influenced by atrophy-related changes in the ageing auditory-related cortices. Furthermore, our results suggest that auditory processing might become more bilateral across the lifespan.

Keywords: presbycusis; vowel perception; neural atrophy; mismatch negativity; spectral processing; planum temporale

1. Introduction

In our steadily ageing society, age-related hearing loss (presbycusis) is one of the most common health problems in both normal and pathological ageing. Particularly in industrial and urban societies with their constant acoustic noise emissions, the prevalence of age-related hearing loss is increasing (Alberti, 1992; Saunders et al., 1991). Approximately half the population over the age of 75 display symptoms of hearing loss that affect daily life (Lin et al., 2011a). Notably, the effects of presbycusis are not limited to impaired hearing in communicative situations, but can extend in the long-term to social deprivation, isolation, loneliness, and depression (Strawbridge et al., 2000; Kramer et al., 2002). Further, some scholars have reported considerable loss in quality of life (Ciorba et al., 2012), increased risk for neurodegenerative disease (Lin et al., 2011b; Livingston et al., 2017), and a rise in mortality and morbidity due to loss of hearing (Karpa et al., 2010; Deal et al., 2019; Besser et al., 2018).

To this day, presbycusis is primarily understood as a loss of inner ear sensory structures, and is clinically assessed using pure-tone audiometry. Consequently, presbycusis is often treated with hearing aids, prescribed mainly to amplify sounds. Within this context, however, it is important to emphasise that the structure and function of the auditory cortices change across the lifespan as well (Peelle et al., 2011; Lin et al., 2014; Pichora-Fuller et al., 2016; Vermeire et al., 2016; Loughrey et al., 2018; Glick and Sharma, 2020), for example as a function of age-related cortical atrophy and sensory deafferentiation (Lin et al., 2014; Giroud et al., 2018a, 2019; Neuschwander et al., 2019). This indicates that age-related alterations in the auditory cortices, for example in their cortical morphology, may also be an essential feature of speech processing difficulties in older adults. In fact, in a previous study by our group, Giroud and colleagues (2018a) observed an association between cortical thinning in auditory-related areas and lower performance in a speech-in-noise (SIN) perception task, namely the *Oldenburger Satztest* (OLSA), in which participants must comprehend spoken sentences in a simulated noisy environment (Wagener et al., 1999c,a,b). Further, an association between cortical thinning in the planum temporale (PT) and the performance in a supra-threshold frequency discrimination task in older participants with no pure-tone hearing loss could be established. They concluded that older individuals whose cortex has altered due to age-related atrophy are

performing worse in speech perception in irrelevant background noise and show difficulties in auditory processing such as frequency selectivity.

However, the link between cortical atrophy and age-related differences in the neurophysiological processing of speech remains largely unknown. This present lack of knowledge pertaining to the specific impact of structural cortical alterations on neurofunctional speech processing prompted us to combine structural, functional, and behavioural data in the current study. In a previous study from our lab in which data on brain structure, function, and behaviour were combined to investigate speech processing in older adults, we demonstrated that prosodic speech perception becomes less lateralised across the lifespan as a function of age-related structural decline in auditory areas (Giroud et al., 2019). Also, despite the fact that existing data cannot yet be used to draw a consistent picture, it is likely that age-related changes in both brain function and structure may attenuate the division of labour between left and right peri-auditory regions during initial stages of speech perception (Keller et al., 2019).

A better understanding of the mechanisms underlying impaired speech processing therefore requires a knowledge of recent neurobiological frameworks of speech and language. For a long time, human language has been considered a monolithic entity that resides in the left hemisphere (Tremblay and Dick, 2016). The view that the left hemisphere is dominant for expressive and receptive language tasks has been challenged in various ways. And it is currently undisputed that the contralateral hemisphere, namely the right perisylvian cortex, also accommodates neural components that mediate speech processing (Hickok and Poeppel, 2007; Zatorre and Gandour, 2008; Friederici, 2011; Vigneau et al., 2011; Meyer et al., 2018; Flinker et al., 2019; Rogalsky et al., 2020). However, the computational as well as the functional differences between the two hemispheres in relation to auditory processing are incompletely understood (McGettigan and Scott, 2012). By the framework established by Zatorre and Belin cortical areas in the left posterior perisylvian region, are preferentially driven by rapidly changing acoustic cues that represent (sub-)segmental phonetic and temporal fine-structure information (Zatorre and Belin, 2001; Zaehle et al., 2004; Ocklenburg et al., 2018), while the contralateral homologues primarily subserve the processing of slow acoustic modulations, namely prosody, intonation, speech rhythm, and metre (Poeppel, 2003; Meyer et al., 2018). Thus, right peri-auditory areas also contribute significantly in the initial stages of speech perception through the processing of suprasegmental cues, a process which can be understood as an essential structuring prerequisite to group and segment phrasal constituents.

Applying the "asymmetric sampling in time" hypothesis (AST) in auditory language processing, the inflowing auditory signal is cut into temporal integration windows of different sizes. These chunks are asymmetrically processed in the left and right PT, where short windows are preferentially processed in the left hemisphere (Poeppel, 2001, 2003). The PT has been described as a key area for the processing of inflowing auditory signals, incorporating spectral and temporal cues in non-speech sounds and spoken language (Griffiths and Warren,

2002). Because of its anatomical leftward asymmetry as well as its functional lateralisation it has been the centre of attention in multiple studies (Ocklenburg et al., 2018). The PT is a region of the superior temporal plane, caudal to the Heschl's gyrus, asymmetrical in its size and architecture between the left and the right hemisphere (Galaburda and Sanides, 1980). Because of its overlap with Wernicke's area, it has been viewed as language processor (Wise et al., 2001; Griffiths and Warren, 2002) whereas today it is assumed that PT is involved in a number of functions: Speech perception, speech production, music processing, tone sequence perception, spatial processing of auditory signals, and auditory motor integration (Isenberg et al., 2012; Adank et al., 2012). Based on the dorsal and ventral stream framework by Hickok and Poeppel, a dorsal stream critical for auditory-motor integration, located within the posterior portion of the PT (area Spt i.e., Sylvian-parietal-temporal) (Hickok et al., 2003, 2009) gives reason to support the view for a separation between an anterior spatial hearing region of the PT (Buchsbaum et al., 2005; Isenberg et al., 2012). A recent study showed recruitment of dorsal stream areas in the PT when performing speech discrimination tasks (Rogalsky et al., 2020), while Warren et al. showed activation of anterolateral PT while changing spectral envelope or the pitch of a sound. In previous studies, the PT showed to be of importance in early auditory processing such as pitch perception (Binder et al., 1996).

Further a division of labor between the two hemispheres is discussed by many scholars: Applying the above mentioned framework by Zatorre and Belin the left PT preferably processes rapidly changing acoustic patterns; that is, short temporal phonetic information on the sub-syllabic level (Zaehle et al., 2004; Ocklenburg et al., 2018), whereas the right PT is more proficient in processing slowly changing acoustic cues (Meyer et al., 2002; Liem et al., 2012; Poeppel, 2003). Giroud and colleagues (2018a) found evidence for a relationship between the thickness of the PT and the performance in a supra-threshold frequency discrimination task. To further investigate these findings our focus was set on the influence of atrophy-related changes of the PT on processing frequency changes in consonant vowel syllables in older adults and younger controls. For our study, we manipulated the second formant frequency in the set of experimental stimuli. This manipulation allowed us to analyse neural processes underlying the computation of spectral resolution (Zaehle et al., 2009; Zatorre and Belin, 2001).

The event-related potential (ERP) technique is a particularly useful technique to analyze effects on central processing in aging and other clinical conditions (Näätänen et al., 2012). A particular ERP for auditory feature processing is resembled in the mismatch negativity (MMN) paradigm: A change detection process in the bilateral auditory cortices generates the auditory MMN response (Näätänen and Escera, 2000; Näätänen et al., 2011). A widely accepted theory proposes that the MMN reflects the short-lived memory trace of a repeated standard stimulus that is compared to a current deviating stimulus (Näätänen et al., 2012).

The aim of the present study was therefore to investigate age-related differences in both brain structure and function related to vowel discrimination ability. Younger and older peripherally normal-for-age hearing participants, as defined

by pure-tone audiograms, performed a syllable discrimination task. Syllables containing vowels of varying spectral deviancy, namely varying second formant frequencies, served as speech stimuli. Additionally, we recorded mismatch negativity (MMN) responses in a separate, passive oddball paradigm presenting the same stimuli. A T1-weighted structural magnetic resonance image (sMRI) was obtained for each participant to determine established neuroanatomical traits (cortical volume, CV; cortical surface area, CSA; cortical thickness, CT) by means of surface-based morphometry using FreeSurfer (Chiarello et al., 2016; Winkler et al., 2010; Athinoula A. Martinos Center for Biomedical Imaging, 2011).

Our hypothesis was that older adults would perform worse in the syllable discrimination task, and show weaker MMN responses in EEG compared to younger adults. Furthermore, we predicted that we would find indications of cortical atrophy in the left and right PT, namely less CT and CV in older adults. Based on the assumption that age-related cortical atrophy influences the ability of spectral discrimination of speech syllables (Profant et al., 2014; Giroud et al., 2018a), we expected that a worse performance in actively (behavioural) and passively (MMN) detecting small deviations between vowels would be related to thinner cortical structures (i.e., more atrophy) of the PT (Lin et al., 2014; Wong et al., 2010). Furthermore, we expected the older adults to show a bilateral pattern with respect to potential correlations between cortical atrophy in the left and right PT and behavioural performance. Whereas in the young group we expect to find a correlation between the morphological traits of the right PT and behavioural performance given that the spectral differences in the vowels are expected to be related to the right planum temporale (Zatorre and Belin, 2001).

2. Materials and methods

2.1. Participants

In this study, 24 healthy older adults (OA, age range = 67 - 84 years, M_{age} = 72.29 years, 11 females) participated. Twenty-seven younger adults served as controls (YA, age range = 19 - 29 years, M_{age} = 23.74 years, 10 females). The OA were tested with the Mini-Mental State Examination (MMSE) (Folstein et al., 1975) and scored higher than 24 points indicating that they did not have cognitive impairment. The participants confirmed that they did not have a past or present neurological or psychiatric disease. Furthermore, no tinnitus symptoms, dyslexic problems, or language disorders were reported by the participants. The study participants were all native speakers of (Swiss-) German. Professional musicians were excluded. Additionally, none of the subjects learnt a second language before the age of 7, hence no early bilinguals were included in this study. Assessment using the Annett Hand Preference Questionnaire (Annett, 1970) assured that participants were all right-handed. Younger and older

volunteers were matched for several cognitive abilities (i.e., working memory and inhibition) to exclude potential confounding effects of cognition on vowel processing abilities. Cognitive skills were assessed by the TAP test battery (*Testbatterie zur Aufmerksamkeitsprüfung*) (Bühner et al., 2006; Zimmermann and Fimm, 2002). Inhibition was measured with the go/no-go task, while working memory was assessed with the n-back task ($t(39) = .59$, $p = .56$; $t(39) =$ -.38, $p = .70$, respectively).

All volunteers met the safety requirements for MRI scanning, gave their written informed consent for participation, and received compensation. The ethics committee of the Canton Zurich approved the study.

2.2. Pure-tone thresholds

To assess pure-tone hearing loss, the pure-tone average (PTA) of each participant was assessed (500, 1000, 2000, and 4000 Hz). A PTA below 25 dB is usually classified as normal hearing according to the World Health Organization (WHO) whereas a PTA between 26 and 40 dB is classified as mild hearing loss. To ensure that the participants would hear all the test items used in this study, those participants with a PTA greater than 30 dB were excluded therefore only leaving participants with normal hearing or very slight pure-tone hearing loss in the study. We also excluded individuals with an asymmetrical hearing loss (i.e., >15 dB difference between right and left ears). Pure-tones were presented for 250 ms using a probe-detection paradigm.

A licenced audiologist performed the audiometry in a sound-attenuated, double-walled booth. The presentation of pure-tone audiometry was controlled through a custom-made Matlab script and played over circumaural headphones (Sennheiser HD 280 – 13300 Ω). During the assessment, the subjects answered using a touch screen (ELO AccuTouch, version 5.5.3.6.). The younger subjects were tested using the MAICO ST20 Screening System (Maico-Diagnostics, 2013).

2.3. Stimulus material

The natural German syllable [tuː] was recorded by a trained speaker resulting in a [t] of 0.1 s and a [uː] of 0.32 s. This stimulus was altered by means of a sound manipulation software (Praat, Version 5.3.47) (Weenink, 2013). In a first processing step, the consonant /t/ was separated from the vowel /u/. In a further step, a semi-artificial syllable was created by convolving pitch and amplitude values of the original syllable. This syllable was used as the standard stimulus (Standard) in the oddball paradigm to record mismatch negativity responses. We increased the second formant frequency by 500 Hz (Deviant 1), 1000 Hz (Deviant 2), 1500 Hz (Deviant 3), and 2000 Hz (Deviant 4), thus changing the perception of the vowel perception from /tu/ to /ty/ to /ti/ for German listeners leading to four stimuli which were used as deviants in the oddball paradigm. Our manipulation procedure is particularly fruitful in that it enables us to produce a semi-artificial consonant-vowel syllable continuum with fully controlled physical features, such as duration, pitch, timbre, and formant transitions. For

better understanding, the spectrograms of the stimuli are depicted in the figures 1 - 5.

— insert Figure 1 about here —
— insert Figure 2 about here —
— insert Figure 3 about here —
— insert Figure 4 about here —
— insert Figure 5 about here —

2.4. Vowel discrimination task

To assess the ability to discriminate the five produced vowels, a behavioural forced-choice syllable discrimination task was created. The five different syllables were set in random order in groups of two, while one was always the standard stimulus, with the presentation controlled by Presentation software (http://www.neurobs.com, version 14.9). Stimuli were presented with 72 dB sound pressure level (SPL) via in-ear headphones (Sennheiser CX271). The participants had to indicate whether the two stimuli were the same (indicated with a left-click) or different (indicated with a right-click) after listening to each stimulus pair. Every possible combination of stimuli (i.e., 5 different combinations) was presented six times, with the sequence of the first and second syllable balanced across trials, and including trials with same stimuli to check for the rate of false-positives. Thus, stimuli pairs could differ in the second formant frequency of 0 Hz, 500 Hz, 1000 Hz, 1500 Hz, or 2000 Hz depending on their combination with the standard stimulus in the stimulus pairs. The interstimulus interval was 300 ms with an additional jittered delay of 3000 ms after each stimulus pair. Discrimination accuracy as well as reaction times were recorded.

2.5. EEG recording and processing

Participants were seated in a comfortable chair at a distance of about 75 cm in front of a computer screen and were presented with an auditory oddball paradigm controlled by Presentation software (http://www.neurobs.com, version 14.9) using the same five stimuli as for the behavioural discrimination task, while electrophysiological activity (i.e., the MMN) was recorded. During recording, the participants were asked to focus on a silent video showing nature and animals. The standard stimulus was presented 950 times ($p = .76$), while the four deviants were each presented 75 times ($p = .06$ each). The stimuli followed at jittered intervals of 1000 ms, 1200 ms and 1400 ms respectively. Using a 128 electrode system (BioSemi ActiveTwo, Amsterdam NL), EEG was continuously recorded and digitised at an online sampling rate of 512 Hz. The recording was band-pass filtered between 0.1 - 100 Hz, and impedance was kept below 5 kΩ for all electrodes. For the preprocessing steps, Brain Vision Analyzer Software (Version 2.1.0, Brainproducts, Munich, Germany) was used. A 50 Hz notch-filter with a 0.1 - 80 Hz bandpass was used to filter the data offline. To remove blinking and other eye movements, an independent component analysis (ICA) (Jung et al., 2000) was applied and noisy channels were interpolated (Perrin

et al., 1987). Any remaining artifacts were then semi-automatically removed during a raw data inspection. The data were then set to the new reference of two bilateral mastoid channels (B10 and D32). A narrower filter between 0.1 Hz and 20 Hz was then applied to the data before segmentation into epochs of 1100 ms time-locked to between -500 ms and 600 ms to the onset of the stimulus. Further, the baseline was corrected relative to the -150 ms baseline. All segments were averaged for each participant and stimulus type, separately (Standard, Deviant 1, Deviant 2, Deviant 3, Deviant 4). To detect the MMN, difference waves for all deviants respective to the standard stimulus were generated for each participant. Furthermore, grand averages of the difference waves for the four deviants were generated and then visually inspected. This inspection showed that the greatest negative deflections of the MMN occurred in the centre skull area (cf. Fig. 1) leading us to pool these central channels (C11, C12, C2, C21, C22, C23, C24, C25, D2). The MMN was defined as the largest negative deflection within the latency window of 100 - 400 ms. Amplitude and respective latency were exported separately with ±20 ms around the peak for each difference wave for all participants (Cooper et al., 2006; Duncan et al., 2009).

— insert Figure 6 about here —

2.6. T1-weighted MR image processing

To collect the anatomical MR scans, a 3.0 T Philips Ingenia scanner (Philips Medical Systems, Best, The Netherlands) with a 12 channel head-coil was used. The sequence applied was a high resolution T1-weighted anatomical 3D Turbo-Field-Echo (TFE) sequence with echo time (TE) = 3.79 ms, repetition time (TR) = 8.18 ms, acquisition matrix = 256 x 256, 160 slices per volume, field of view (FOV) = 240 x 160 x 240 mm, flip angle (α) = 90° and isotropic voxel size = 0.94 x 0.94 x 1 mm. Two T1-weighted images were obtained for all participants, except for four older participants for whom only one scan each was acquired. Using the two images, an averaged single image volume with high contrast-to-noise was created (Reuter et al., 2010).

For the cortical surface reconstruction, the FreeSurfer image analysis suite (version 5.1.0.) was used. This software is freely available (http://freesurfer.net) and documented online (Athinoula A. Martinos Center for Biomedical Imaging, 2011). The FreeSurfer routines contain several processing steps (Dale et al., 1999; Dale and Sereno, 1993; Fischl and Dale, 2000; Fischl et al., 2001, 2002, 2004a, 1999a,b, 2004b; Reuter et al., 2010; Ségonne et al., 2004). The software generates individual, high precision cortical surface models. We controlled all brains for segmentation precision. One participant from the older group had to be excluded because the surface reconstruction of the T1-weighted image was unsuccessful.

The cortical thickness (CT) and the cortical surface area (CSA) were calculated using FreeSurfer at each vertex of the surface. CT is defined as the minimal distance between the pial surface and the grey-white matter border at each surface vertex (Fischl and Dale, 2000). CSA defines the mean area of the region at

the respective vertex and, when multiplied by the CT, yields the measurement for cortical volume (CV). To get a more comprehensive surface measure, the mean of the grey-white matter surface area and the mean of the pial surface area was entered as the values of CSA. CT has been validated by using manual segmentations (Cardinale et al., 2014; Kuperberg et al., 2003; Salat et al., 2004) and histological analysis (Rosas et al., 2002). In addition, this method has been established to generate reliable results in healthy adults (Liem et al., 2015). The aparc.a2009s annotation (Destrieux et al., 2010) was used to index the cortex into regions of interest (ROIs). By Destrieux et al. (2010), the PT is defined as "part of the superior aspect of the superior temporal gyrus, posterior to the transverse temporal sulcus. Since the posterior segment of the lateral sulcus – which is the medial limit of the planum temporale - curves postero-superiorly, the planum temporale followes this angulation." Because the cytoarchtectonics are the same in the subsegments, the segments were grouped (Shapleske et al., 1999). Based on the findings of Giroud and colleagues, our analysis focused on the features of the bilateral PT (2018a). Other authors too have reported structural-behavioural relationships in this particular region in a paradigm investigating pre-lexical speech processing (Liem et al., 2014).

2.7. Statistical analyses

An analysis plan was established under supervision of the Research Methods Consulting Service of the University of Zurich. All analyses were performed using SPSS® 25.0 for Windows (IBM® SPSS® Statistics)

First, to compare effects of group and stimuli combination, a 4 x 2 repeated measures ANOVA with the factor stimulus (i.e., second formant frequency difference between standard stimulus and respective deviant of 500, 1000, 1500, or 2000 Hz, respectively) and between-subject factor age group (YA, OA) was conducted. To compare potential response-bias in the discrimination task between the young and the older participants an independent t-test was conducted for the accuracy of detecting two similar stimuli.

Second, for the MMN amplitude and latency, 4 x 2 repeated measures ANOVA with factors stimuli (i.e., difference waves for Deviant 1, Deviant 2, Deviant 3 and Deviant 4) and between-subject factor age group (YA, OA) were computed. For each ANOVA, the assumption of sphericity was assessed using Mauchly's test of sphericity and post-hoc t-tests were conducted when appropriate. Unless otherwise indicated, an alpha level of $\alpha = .05$ was accepted and effect sizes were indicated by partial eta-squares η_p^2.

Third, age-related differences in CT, CSA, and CV of the left and right PT were compared between the younger and the older group by independent samples t-tests.

Fourth, correlations between the left and right neuroanatomical metrics, namely CT, CSA, and CV of the PT, and the accuracy in the most difficult behavioural discrimination condition (i.e., when discriminating the standard stimulus and Deviant 1 which only differed by 500 Hz in the second formant) were analysed using a Kendall's tau-b correlation coefficient was chosen to test the strength and direction of the association between the accuracy and the morphological

measurements for the two groups.
Visual inspection of the boxplots revealed two outliers in the CV of the left PT in the younger group and, in the older group, one outlier in CT in the right PT, as well as three outliers in CSA of the left PT. The outliers were kept in the analyses because their exclusion did not affect the outcome.
Further, no significant associations between neuroanatomical and electrophysiological measurements were discovered. These analyses are therefore not reported further here in detail; however, the possible reasons behind this lack of results are discussed in what follows.

3. Results

3.1. Pure-tone hearing

The audiograms of the younger and older individuals are shown in Figure 7. The thresholds of the younger control group were within normal limits (i.e., $\leq$ 20 dB HL) throughout all the tested frequencies. In the older participants, audiometric thresholds at low frequencies (500 and 1000 Hz) on average amounted to 6.18 and 5.52 dB HL, respectively. At frequencies above 1000 Hz, the threshold increased on average to 12 dB HL at 2000 Hz and 25 dB HL at 4000 Hz. The averaged PTA thresholds for the older subjects over all four assessed frequencies was 12.3 dB HL. Thus, for all subjects, hearing thresholds were within normal limits at lower frequencies (up to and including 2000 Hz) which meant that their hearing levels were sufficient to complete the tasks given that the vowel differed only in the second formant frequency which did not go beyond 3000 Hz.

— insert Figure 7 about here —

3.2. Vowel discrimination task

The results of the accuracy for the consonant-vowel syllable discrimination in our behavioural experiment are depicted in Figure 8.
We found a main effect of stimulus ($F(2.22, 97.62) = 74.67$, $p < .001$, $\eta_p^2 = .63$) indicating that participants performed better the stronger the acoustic difference between two vowels. For both the older and younger individuals, the most difficult difference to detect was the pair with the smallest acoustic difference of 500 Hz in the second formant (i.e., standard stimulus vs. Deviant 1), while all individuals, regardless of age group, were able to distinguish the strongest difference (i.e., standard stimulus vs. Deviant 4) with a high average accuracy of 93%.
Furthermore, we found a main effect of age group ($F(1,44) = 22.24$, $p < .001$, $\eta_p^2 = .336$) showing that OA performed significantly worse across all stimuli pairs than YA. While on average the younger individuals mastered detecting the 1000 Hz deviant in 84% (SD = 21%) of the trials, the older participants needed a stronger acoustic deviation (1500 Hz) to reach similar average detection rates of 78% (SD = 10%).
Moreover, we found an interaction ($F(2.22,97.62) = 14.74$, $p < .001$, $\eta_p^2 =$

.25) between group and stimuli. The pattern of observed behavioural results is in line with our expectations. An independent t-test for accuracy on trials which presented two similar vowels was run to assess response-bias: There was no statistically significant difference between false-positive answers in the older group and the younger group $t(45) = .196$, $p = .846$.

(Table A1 about here)

— insert Figure 8 about here —

3.3. Mismatch negativity

Figures 9 and 10 (younger group) and 11 and 12 (older group) illustrate the mean ERP difference waves and the ERPs time-locked to each stimulus, respectively. As expected, the younger participants showed a clear mismatch negativity (MMN) in response to all deviants at an averaged amplitude of -4.12 μV ($SD = 1.9$) with an averaged latency of 233 ms ($SD = 50.9$) time-locked to the start of the syllable (not the vowel). In the group of the older participants a repeated measures ANOVA showed no difference in the ERP between the standard stimulus and the deviations ($F(3.580, 82.341) = 2.473$, $p = .057$, $\eta_p^2 = .097$).

Amplitude

Figure 13 illustrates the group and stimulus differences for the amplitudes. The repeated measures ANOVA showed a main effect group revealing that the amplitude between the age groups differed significantly ($F(1,47) = 45.23$, $p < .001$, $\eta_p^2 = .490$) across all stimuli. This result could be expected, considering no MMN was derivable in the older group. No main effect stimulus was observed ($F(3, 141) = 1.096$, $p = .353$, $\eta_p^2 = .023$) and no significant interaction between group and stimulus was obtained ($F(3, 141) = .316$, $p = .813$, $\eta_p^2 = .007$).

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— insert Figure 10 about here —

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— insert Figure 12 about here —

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— insert Figure 14 about here —

Latency

Figure 14 shows the latency differences between younger and older subjects for all stimuli. No significant main effect for group was found, meaning that the two groups did not differ significantly ($F(1, 47) = 2.842$, $p = .098$, $\eta_p^2 = .057$) in latency. Also, the ANOVA did not show a main effect stimulus ($F(3, 141) = 1.382$ $p = .251$, $\eta_p^2 = .029$) and no significant interaction between group and stimulus was obtained ($F(3, 141) = .751$, $p = .523$, $\eta_p^2 = .016$).

3.4. Surface-based morphometry

Age-related differences in cortical macroanatomy were assessed using measurements of CV, CT, and CSA of the PT bilaterally. Means, standard deviations and statistical values of independent t-tests comparing the young and older adults are shown in Table A2.

Cortical volume

The younger participants showed on average significantly greater CV (right hemisphere: 1502.84 mm^3 ± 257.23; left hemisphere: 2078.08 mm^3 ± 307.73) than the older subjects (right hemisphere: 1222.75 mm^3 ± 165.61; left hemisphere: 1693.79 mm^3 ± 225.39; (95% CI [155, 405]), $t(41.19) = 4.55$, $p = .000$***, for the right and 384.29 mm^3 (95% CI [229, 540]), $t(43.99) = 5.00$, $p = .000$*** for the left hemisphere).

Cortical thickness

In the right PT, the younger group had significantly thicker cortex on average (2.67 mm ± 0.20) than the older subjects (2.36 mm ± 0.16) ((95% CI [0.21, 0.42]), $t(47) = 6.06$, $p = .000$***). A similar finding could be established for the left PT: The younger group had significantly thicker cortex on average (2.66 mm ± 0.16) than the older subjects (2.43 mm ± 0.12)((95% CI [0.21, 0.42]), $t(47) = 5.66$, $p = .000$***.). These results together with the results on CV suggest age-related atrophy in the PT bilaterally in our sample of older adults.

Cortical surface area

The analysis revealed a small significant difference of 43.99 mm^2 (95% CI [4.19, 83.78]), $t(47) = 2.22$, $p = .03$* on the right hemisphere and of 84.06 mm^2 (95% CI [21.90, 146.22]), $t(47) = 2.72$, $p = .009$** on the left hemisphere) suggesting that the older participants had lower average surface area (515.83 mm^2 ± 61.69) than the younger subjects (559.82 mm^2 ± 75.73).

(Table A2 about here)

3.5. Association between anatomical traits of PT and vowel discrimination accuracy

Using a Kendall's tau-b correlation, we found positive correlations between the traits of the PT and accuracy in the most difficult (500 Hz difference) stimulus comparison in the older adults as depicted in Table A3 revealing that those who have greater atrophy (i.e., lower CSA and lower CV) in the PT also show weaker vowel discrimination abilities. In the younger group, a negative correlation could be established between the CT of the left PT and the accuracy in the most difficult discrimination condition.

(Table A3 about here)

4. Discussion

As the projected life-span of our society increases, so does the importance and salience of age-related diseases. The problem that hearing loss presents to older people is often underestimated; associated difficulties extend beyond the audibility of sounds to deficiencies in speech perception, and the standard treatment of a prescribed hearing aid may not adequately alleviate these problems in understanding speech. Recent findings have suggested that even those older individuals with normal pure-tone thresholds or corrected hearing still demonstrate difficulties processing speech, in particular during adverse listening conditions (Giroud et al., 2018b; Profant et al., 2019). This handicap to communication may limit social interaction and thus have a profound impact on the quality of life, perhaps leading to isolation and depression (Strawbridge et al., 2000; Kramer et al., 2002; Ciorba et al., 2012; Karpa et al., 2010).

This bleak outlook makes a better understanding of the interaction between hearing loss and age-related changes in the brain both urgent and relevant. The present study adds new findings to the current understanding of hearing loss by presenting evidence for an association between non-primary auditory cortex (i.e., the PT) atrophy and lower accuracy in the processing of spectral speech information which is also reflected in lower and slower electrophysiological responses to the speech stimuli as evident in the MMN differences between the younger and older participants. Furthermore, in the older group, we also show bilateral correlations between brain atrophy and behavioural performance in that lower cortical volume and surface area of the left and the right PT were associated with lower vowel discrimination abilities. In the younger group, we only found one association indicating that greater cortical thickness of the left PT was associated with lower performance thus indicating that speech processing might become more bilateral across the lifespan.

4.1. Auditory perception in aging: More than pure-tone hearing loss

In line with our hypotheses, the older participants showed a significantly lower performance in vowel discrimination than the younger participants, despite having age-appropriate audiograms. Previous studies have found corresponding results in similar tasks (Füllgrabe, 2013; Füllgrabe et al., 2014; Hopkins and Moore, 2011; Vermeire et al., 2016; Giroud et al., 2018a).

In older participants with age-appropriate pure-tone hearing, factors like age-related changes of the auditory cortex, such as atrophy, may have a greater influence on how they manage to process subtle acoustic differences available in spoken language. With our findings in mind, we believe that this concept might be important for clinics and future research. Specifically, it might not be sufficient to assess the hearing ability using only pure-tone threshold audiograms. In the future, the diagnosis and treatment of age-related changes in auditory perception could contain discrimination of relevant speech signals such as vowels, sentence or word comprehension tests, and speech-in-noise assessment. Note

that the relevance for each of those tests for real-world daily-life speech understanding remains to be studied and should be a priority for future research. Importantly, both groups were also assessed in cognitive skills, inhibition and working memory and no significant group difference could be established, indicating only minimal influence of cognitive capacities in this examination. Answering bias was countered by false-positive analysis. No significant group difference between the older and young group was found, suggesting that both groups had very few false-positives in the same range. However, evidence provided by behavioural tasks alone do not allow for the drawing of firm conclusions regarding the underlying neural mechanisms. For this reason, we also analysed neurophysiological and neuroanatomical data.

4.2. Age-related differences in MMN responses to acoustic differences in vowels

The MMN is a highly selective ERP and a relatively automatic response to an auditory stimulus that is different from foregoing standard stimuli (Näätänen and Escera, 2000; Näätänen et al., 2011). It is believed that the MMN reflects the comparison of the short-lived memory trace of the current stimulus with the standard stimulus (Näätänen et al., 2012). The activity primarily originates in both left and right auditory-related cortices (Zaehle et al., 2009), but contributions from the right inferior frontal gyrus (rIFG) have also been reported (Opitz et al., 2002). Due to the bottom-up nature of the MMN, it is less prone to be influenced by individual differences in attention and explicit task demands. However, this does not mean the complete absence of top-down modulation of high-level cognition on the MMN which may differ between younger and older individual.

According to our ERP data, the younger group showed a clear MMN. This observation suggests that the younger adults' auditory system was able to distinguish between all the varying spectral cues in the vowels. For the older group, we were not able to derive a clean MMN in all deviants. Previous studies have shown similar difficulties in MMN in older adults. It is known that, in those individuals, there is a significant delay in peak MMN amplitude (Cooper et al., 2006), and that the MMN amplitude is smaller (Czigler et al., 1992). Generally, the weaker MMN in the older participants indicates an impaired mechanism of automatic subtle deviance detection in acoustic cues. One reason for an attenuated MMN amplitude in the participants of the older group could be a shortened auditory sensory-memory duration in age (Pekkonen et al., 1996). According to Cooray et al. (2014, p. 1781), "age-related changes of MMN are due to reduced modulation of intrinsic connectivity at rIFG together with changes in temporal-frontal connectivity and an imbalance in excitatory-inhibitory frontal cortical activity". These circumstances may have resulted in the missing MMN as indicated by the significantly lower amplitude in the older group. Nevertheless, the recorded MMNs and the pertaining statistical analyses indicate that the younger individuals recognised all the deviants.

It is questionable that we could not find a significant correlation between morphological traits and parameters of the MMN (latency, amplitude), particularly

given the fact that we noticed a significant association between the morphological and behavioural data. Here, it should be noted that the MMN was recorded during a passive oddball paradigm which means that the participants were not required to respond to stimuli actively. In addition, our behavioural data were collected separately from the EEG study which means that the higher task-related demands during the behavioural paradigm may have influenced the processing mode and hence the outcome. Alternatively, yet another reason may account for the missing correlation. As mentioned above, the MMN is driven by auditory and frontal circuits which may undergo different age-related alterations. Hence, it is unlikely that neurophysiological processes which are partly driven by inferior frontal regions would correlate with alterations in the auditory-related PT, which is situated at the caudal portion of the superior temporal plane. However, it should be noted that a relationship between parameters of the MMN and behaviour has been observed in other studies (Giroud et al., 2019). Further research is needed to clarify the reasons for these differences.

4.3. Age-related differences in morphometry of the PT

For the morphometric analysis of the auditory cortex, our subjects underwent a structural neuroimaging procedure. Giroud and colleagues (2018b) found evidence for a positive correlation between cortical thickness in the right PT and auditory spectral discrimination performance in older adults. This is in line with the model by Zatorre and Belin (Zatorre and Belin, 2001), in which they postulate that the auditory regions of the right hemisphere are specialised in the processing of spectral information. Consequently, our focus here was on the morphological features, namely CV, CSA, and CT, of the PT; that is the caudalmost part of the supratemporal plane. This region is a central element of the auditory association cortex, and is thus vital for the auditory reception and processing of non-speech sounds as well as of spoken language (Griffiths and Warren, 2002; Liem et al., 2014). Once the acoustic signal has passed the primary and secondary auditory cortex, it enters the auditory-related region in the bilateral PT where it is subjected to further steps of spectro-temporal signal decoding. Due especially to the difference in the histological architecture of the PT compared to the primary auditory cortex, the PT is believed to support complex auditory analyses (Fullerton and Pandya, 2007). Previous research has found evidence that, "the left PT is preferentially driven by rapidly changing acoustic cues (temporal resolution). The identification of such cues is essential for speech processing, for example, perceiving the difference between the syllables /da/ and /ta/" (Zaehle et al., 2004; Meyer et al., 2012, p.117). The contralateral right PT, however, appears to host frequency processing mechanisms that are also important for decoding spoken language, namely the distinction between spectral cues (e.g., /ta/ vs. /to/). It should be mentioned that Zatorre and Belin's model was based on findings with younger adults. Unexpectedly, the correlations in our data of young adults suggest a leftward lateralization of the association between thinner CT in the left PT and better formant discrimination of our syllables. This result was somewhat unexpected.

According to recent research, the right PT supports the processing of sentence-level prosody (Meyer et al., 2002, 2004; Liem et al., 2014). These observations concur with the AST hypothesis, in which it is postulated that the processing of rapidly changing cues occurs preferentially in the left auditory cortex while the contralateral brain areas are more strongly driven by prosodic modulations at the level of syllable rates.

In our data of the young participants, we found a correlation between the CT of the left PT and behavioural performance in the vowel discrimination task contradicting the AST hypothesis and the predictions made by Zatorre and Belin given that 320 ms of spectral differences in the vowels would be considered slow acoustic transitions and spectral speech cues and therefore expected to be right-lateralized. A large number of scholars were able to reproduce the findings summarized by Zatorre and Belin. Nevertheless some failed to reproduce this finding (Hall et al., 2002; Scott and Wise, 2004). Interestingly, sounds containing continuums of spectral information, such as vowels, tend to be perceived more categorically (Liebenthal et al., 2005; Healy and Repp, 1982). Thus, it is possible that a correlation with the CT of the left PT could reflect the functional specialization in left dorsal temporal auditory regions for spectrally dynamic sounds and their categorization (Liebenthal et al., 2005). A similar, but bilateral, correlation was found in older adults with CV of the PT, which was, however, not in the same direction. In younger adults, it has been discussed, that a thicker auditory cortex may not necessarily be advantageous for its functioning and can also reflect expertise. In other words a thinner cortex might resemblance of efficient neural organization as consequence of learning dependent plasticity. (Hyde et al., 2007; Bermudez et al., 2009; Liem et al., 2012; Meyer et al., 2014). Thus, it is possible that younger and older adults, who already experienced age-related atrophy, may have different associations between brain structure and behaviour (Giroud et al., 2018a).

Our previous work however implies that this "division of labour" attenuates in older age in that phonetic and prosodic processing becomes more bilaterally distributed which also agrees with our results showing correlations between the MMN and the structure of the PT in both hemispheres, particularly in older adults (Keller et al., 2019; Giroud et al., 2018a, 2019). Indeed, with respect to the present work, we found associations between neuroanatomical traits of the PT and behavioural performance in both hemispheres. This finding is in line with the HAROLD model, where lateralization decreases during life due to age-related processes of compensation and dedifferentiation (Cabeza, 2002). This model is based on findings during tests on cognitive performance where older adults would use more regions on both hemispheres compared to younger participants. A very recent study showed support with reservations for the HAROLD model for auditory semantic function where poorer performers in the older showed less lateralization compared to their peers (Liu et al., 2020). It is of great interest to further investigate the appliance of the HAROLD model in terms of auditory functions.

4.3.1. Age-related differences between neuroanatomical traits and their association with behaviour

We discovered a relationship between CV and CSA of both the left and the right PT and behaviour (cf. Table A3). No significant correlation was observed for cortical thickness and behavioural accuracy in the OA. This finding suggests that a larger surface area of the bilateral PT is associated with better performance in the ability to detect deviant formants, but only for our sample of older participants. With due restraint, we interpret this relationship as evidence that the amount of remaining PT CSA predicts the observed performance in the processing of spectral information. To date, the specific hereditary and/or plastic properties of CT and CSA are still unsettled; "cortical volume is the product of surface area and thickness that have independent biological bases" (Chiarello et al., 2016, p. 366). According to the Radial Unit Hypothesis (Rakic, 1988), there is reason to assume that CT is more strongly indicative of plastic changes following life-span learning and training-dependent alterations, whereas CSA appears to be attributed to genetically determined maturation. However, previous research so far has not only provided evidence that corroborates this hypothesis (Chiarello et al., 2016; Winkler et al., 2010). It rather seems that both CT and CSA can be subject to age-related alterations in that CT atrophy is characterised by cortical thinning (Fjell et al., 2009) while loss in surface area is caused by non-specific, global grey matter loss (Dickerson et al., 2009; Fotenos et al., 2005). However, more research is needed with other auditory tasks to investigate potential correlations between CSA and auditory performance to fully understand the differential role of CT and CSA in auditory processing. (Storsve et al., 2014)

4.4. Limitations

This study was designed to examine differences in anatomical and functional organisation during vowel processing in ageing. In more detail, structural MRI and EEG (i.e., MMN) measurements were combined with behavioural tasks to further explore functional and morphological changes in the brain and its contribution to speech processing difficulties in older adults.

Due to the cross-sectional nature of this study, it is not feasible to draw conclusions about the direction of effects. Future research should systematically investigate the interaction between cortical atrophy, electrophysiology, and speech perception over a period of several years.

The PT entails two zones; an posterior portion for auditory-motor integration (area Spt) and an anterior spatial hearing region (Hickok et al., 2003, 2009). In our study we analyze the PT as whole entity. In future morphological studies this should be taken into account.

Younger and older subjects were assessed using pure-tone audiometry thresholds. The exclusion of subjects with pure-tone thresholds indicating over 30 dB HL was in accord with the references from the WHO. This convention is based on the assumption that individuals with a PTA less than 30 dB HL do

not have impaired hearing. Although we desired younger and older subjects with comparable thresholds, the audiogram revealed PTA differences between the two groups. Hence, we had to accept that it was not possible to find older individuals with PTA thresholds that were exactly equivalent to those of our younger individuals. This age-related difference in pure-tone thresholds might have influenced the outcome of our examination. As Peelle and Wingfield point out, even mild levels of hearing loss may lead to a decline in speech comprehension, memory performance, and perceptual outcomes.

Eventually, we cannot rule out that morphological symptoms of brain aging, namely atrophy per se may account for differences in the absolute amplitude when two samples of young and older individuals are considered. The putative differences are difficult to quantify and interpret. Hence, we think it is not unlikely that differences between difference waves comparing younger and older participants are caused by differential neurophysiological responses to the standard stimulus rather than by differences between neural responses to the deviant stimuli.

4.5. Conclusions

The present study supports the assumption that poorer auditory performance in older age is not solely explainable by elevated pure-tone hearing thresholds. Additionally, differences in cortical morphology due to ageing seem to have an impact on processing of spectral speech cues irrespective of pure-tone hearing loss. Evidently, general age-related atrophy affects the neuroarchitecture of the bilateral PT in that we noticed a decrease of CV, CSA and CT. Our findings suggest that the remaining CSA and CV in older individuals grow of importance in speech perception in higher age. Furthermore, in older adults only, integrity of the the left and right PT was associated with better vowel discrimination performance suggesting less lateralized mediation of auditory processing in aging by the PT.

This new insight invites new developments in the diagnosis and treatment of age-related changes in speech perception. It highlights the necessity to expand the assessment of age-related hearing loss by combining it with speech perception and understanding tasks, while age-related atrophy of relevant brain areas may be taken into account. This approach will uncover a new extent of presbycusis that has been neglected to date.

5. Conflicts of interest

We state that none of the authors and collaborators of the study have competing interests.

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Appendix A. Tables

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stimulus pairs	***M* (YA)**	***SD* (YA)**	***M* (OA)**	***SD* (OA)**
500 Hz difference	.63	.34	.13	.22
1000 Hz difference	.85	.22	.68	.32
1500 Hz difference	.89	.11	.79	.11
2000 Hz difference	.94	.14	.94	.08

Table A.1: The accuracy of the syllable discrimination task discriminating between second formant frequency differences of 500 Hz (Standard stimulus vs. Deviant 1), 1000 Hz (Standard stimulus vs. Deviant 2), 1500 Hz (Standard stimulus vs. Deviant 3), and 2000 Hz (Standard stimulus vs. Deviant 4), respectively. Mean values and the standard deviation (SD) of the younger individuals indicated with (YA) and of the older individuals indicated with (OA).

	Left planum temporale				Right planum temporale			
	M	***SD***	***t***	***p***	***M***	***SD***	***t***	***p***
YA CV [in mm^3]	2078.08	307.73			1502.84	257.23		
OA CV [in mm^3]	1693.79	225.39	$t(47) = 4.97$	.000***	1222.75	165.61	$t(41.19) = 4.55$	.000***
YA CSA [in mm^2]	774.56	113.08			559.82	75.73		
OA CSA [in mm^2]	690.50	102.72	$t(47) = 2.72$	.009**	515.83	61.69	$t(47) = 2.22$	.031*
YA CT [in mm]	2.66	.16			2.67	.20		
OA CT [in mm]	2.43	.12	$t(47) = 5.66$	.000***	2.36	.16	$t(47) = 6.06$	.000***

*$p < .05$, **$p < .01$, ***$p < .001$

Table A.2: Age group (i.e., younger (YA) versus older (OA) adults) differences in cortical architecture (Cortical volume, CV, cortical surface area, CSA, and cortical thickness, CT) of the planum temporale (PT) for the right and left hemispheres. *M* = mean, *SD* = standard deviation.

	Planum temporale		CV	CT	CSA
OA	**right**	correlation coefficient	.257**	0.112	.244**
		Sig. (2-tailed)	.001	0.134	.001
		N	126	126	126
	left	correlation coefficient	.211**	0.010	.207**
		Sig. (2-tailed)	.005	0.895	.006
		N	126	126	126
YA	**right**	correlation coefficient	-0.098	-0.056	-0.123
		Sig. (2-tailed)	.160	0.419	.077
		N	144	144	144
	left	correlation coefficient	-0.060	-.205**	0.022
		Sig. (2-tailed)	.390	0.003	.755
		N	144	144	144

*$p < .05$, **$p < .01$, ***$p < .001$

Table A.3: This table shows the correlational coefficients of the Kendall's tau-b correlation between neuroanatomical traits (cortical volume, CV, cortical surface area, CSA, and cortical thickness, CT) of the left and right planum temporale (PT) and vowel discrimination accuracy of pairs of consonant-vowel syllables differing only in 500 Hz in the second formant frequency for the young (YA) and the older (OA) participants separately.

Appendix B. Figure Captions

Figure 1: Spectrogram of the standard stimulus
The spectrogram and the waveform of the standard stimulus.

Figure 2: Spectrogram of deviant 1
The spectrogram and the waveform of the 1st deviant.

Figure 3: Spectrogram of deviant 2
The spectrogram and the waveform of the 2nd deviant.

Figure 4: Spectrogram of deviant 4
The spectrogram and the waveform of the 4th deviant.

Figure 5: Spectrogram of deviant 5
The spectrogram and the waveform of the 5th deviant.

Figure 6: Topography of MMN responses averaged across deviants
The mapping view of the MMN averaged across the difference waves of the four deviants in the time interval between 100 and 400 ms after stimulus onset. Note that the scaling for the topography for the younger and older adults is different due to the higher amplitudes in the younger participants. The red electrodes depict the cluster used for pooling the signal. The blue colours indicate the areas with negative voltage during the indicated time period.

Figure 7: Pure tone audiogram
Pure-tone audiograms are shown averaged for all participants of the older (green) and younger (blue) group for the left and right ear separately.

Figure 8: Accuracy in the consonant-vowel discrimination task
This graph shows that older adults performed consistently worse than younger adults in the discrimination task. The graph also depicts the difficulty to discriminate 500 Hz acoustic difference in the second formant between two vowels. The stronger acoustic deviations (i.e., 1000, 1500, 2000 Hz) were easier to distinguish. The error-bars indicate the standard error.
$^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$

Figure 9: MMN difference waves for the young group
Figure 4 shows the difference waves of the four deviants compared to the standard stimulus, averaged for the younger group. Zero marks the onset of the syllable. There is a clear MMN visible between 200 and 260 ms for all four deviants.

Figure 10: The ERPs for the young group
This figure shows the ERPs of all presented syllables (standard stimulus and

four deviants) in the younger group.

Figure 11: MMN difference waves for the older group
Figure 6 depicts the difference waves of the four deviants minus the standard, averaged for the older group. There is an adumbrated MMN visible between 220 and 280 ms for all four deviants.

Figure 12: The ERPs for the older group
The ERPs time-locked to all syllables (Standard and four deviants) are shown averaged for the older group.

Figure 13: The amplitude of the MMN peaks of the difference waves
The amplitudes of the MMN peaks of the difference waves are shown for the younger group (blue) which show a significantly higher amplitude than the older group (green) in the MMN peaks of all four deviants.
$^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$

Figure 14: The latency of the MMN peaks of the difference waves
The latency of the MMN peaks of the difference waves. The younger group (blue) shows a similar latency to the older group (green) in the MMN peak of all four deviants. There was a tendency for later MMNs in the older group.

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Kind regards,

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