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RESEARCH REPORT

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Different neuroanatomical correlates for temporal and spectral supra-threshold auditory tasks and speech in noise recognition in older adults with hearing impairment

Pia Neuschwander[1] | **Raffael Schmitt**[2] | **Laura Jagoda**[1] | **Ira Kurthen**[3] | **Nathalie Giroud**[2] | **Martin Meyer**[4,5,6]

[1]Division of Neuropsychology, Department of Psychology, University of Zurich, Zurich, Switzerland

[2]Neuroscience of Speech & Hearing, Department of Computational Linguistics, University of Zurich, Zurich, Switzerland

[3]Developmental Psychology: Infancy and Childhood, Department of Psychology, University of Zurich, Zurich, Switzerland

[4]Evolutionary Neuroscience of Language, Department of Comparative Language Science, University of Zurich, Zurich, Switzerland

[5]Center for the Interdisciplinary Study of Language Evolution (ISLE), University of Zurich, Zurich, Switzerland

[6]Cognitive Psychology Unit, Alpen-Adria University of Klagenfurt, Klagenfurt, Austria

Correspondence

Martin Meyer, Evolutionary Neuroscience of Language, Department of Comparative Language Science, University of Zurich, Zurich, Switzerland.
Email: martin.meyer@uzh.ch

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Abstract

Varying degrees of pure-tone hearing loss in older adults are differentially associated with cortical volume (CV) and thickness (CT) within and outside of the auditory pathway. This study addressed the question to what degree supra-threshold auditory performance (i.e., temporal compression and frequency selectivity) as well as speech in noise (SiN) recognition are associated with neurostructural correlates in a sample of 59 healthy older adults with mild to moderate pure-tone hearing loss. Using surface-based morphometry on T1-weighted MRI images, CT, CV, and surface area (CSA) of several regions-of-interest were obtained. The results showed distinct neurostructural patterns for the different tasks in terms of involved regions as well as morphometric parameters. While pure-tone averages (PTAs) positively correlated with CT in a right hemisphere superior temporal sulcus and gyrus cluster, supra-threshold auditory perception additionally extended significantly to CV and CT in left and right superior temporal clusters including Heschl's gyrus and sulcus, the planum polare and temporale. For SiN recognition, we found significant correlations with an auditory-related CT cluster and furthermore with language-related areas in the prefrontal cortex. Taken together, our results show that different auditory abilities are differently associated with cortical morphology in older adults with hearing impairment. Still, a common pattern is that greater PTAs and poorer supra-threshold auditory performance as well as poorer SiN recognition are all related to cortical thinning and volume loss but not to changes in CSA. These results support the hypothesis that mostly CT undergoes alterations in the context of auditory decline, while CSA remains stable.

KEYWORDS

ageing, auditory perception, pure-tone hearing loss, speech in noise recognition, surface-based morphometry

1 | INTRODUCTION

Communication through spoken language is one of the most important means of cultivating social relationships in daily life. With ageing, the emergence of hearing loss often impairs this ability. According to the World Health Organization (WHO, 2021), approximately one third of people over 65 years of age experience an age-related hearing loss over 40-dB SPL. This makes age-related hearing loss the third most chronic condition in adults over the age of 65 years (Yueh et al., 2003). It mostly occurs because of age-related decreased functioning in the inner ear and the auditory nerve, which results in difficulty understanding speech and partaking in conversations and, hence, in reduced quality of life (Ciorba et al., 2012). For affected individuals, the reduced sensitivity to auditory information almost always results in social isolation, frustration, and loneliness (Ciorba et al., 2012). In the context of a steadily ageing population, it is therefore important to investigate the different aspects of hearing loss and its associations with difficulties in speech perception and comprehension and to gain new knowledge, which may inform a more comprehensive diagnosis of speech comprehension challenges as well as novel possibilities to combat its associated adverse effects, thus raising the quality of life of affected persons.

So far, age-related hearing loss has mostly been considered a problem to do with the outer hair cells that are situated peripherally within the spiral organ of Corti on the thin basilar membrane in the cochlea of the inner ear (Humes et al., 2012; Peelle & Wingfield, 2016). Once these hair cells are damaged, for example, due to noise exposure, stress, or simply ageing, they can neither regenerate nor be replaced artificially, and a decline in hearing sensitivity occurs (Eggermont, 2017). To date, hearing sensitivity is usually measured and clinically diagnosed using pure-tone audiometry (i.e., by pure-tone averages [PTA]; Pickles, 2012).

However, recent research has shown that age-related decline of communication through speech must not be considered an isolated problem resulting from age-related decline in hearing sensitivity (Humes et al., 2012; Wingfield et al., 2015). In a seminal position paper, Humes et al. (2012) emphasize that speech perception and comprehension rely on a network ("triangular relationship") that incorporates good pure-tone thresholds (referred to as "peripheral hearing"), good auditory perceptual abilities (referred to as "central hearing"), and high cognitive abilities. While audibility can be linked to the auditory periphery that encompasses the cochlea, middle ear, and outer ear, supra-threshold auditory perception (e.g., frequency specificity (FS) or temporal compression (TC)) and speech in noise (SiN) recognition can additionally be linked to the central auditory system (Giroud et al., 2018), namely, the auditory core, adjacent areas, and additional cognitive systems recruited for working memory and attentional capacity (therefore, also often referred to as central hearing). Note that a decline in FS is strongly related to outer hair cell loss, which leads to lower sensitivity on the one hand, but also to less sharp tuning on the other hand (resulting in lower FS) (Liberman & Kujawa, 2017). Thus, certain aspects of supra-threshold perception are likely to originate in the periphery but have neurostructural and neurofunctional correlates in auditory cortex regions. Further, the mentioned cognitive systems help listeners cope with adverse listening conditions such as those simulated in SiN paradigms (Humes et al., 2012).

The contribution of the central auditory system and cognition is probably one reason why older adults often experience increased difficulties in understanding speech in adverse environments (CHABA Working Group on Speech Understanding and Aging, 1988), even in the absence of a (clinically relevant) pure-tone hearing loss (Dubno et al., 2002; Füllgrabe et al., 2015; Giroud et al., 2018; Goossens et al., 2017). Interestingly, evidence suggests that those three factors leading to decline of speech perception and comprehension in older adults may interact. For example, longitudinal studies show that elevated pure-tone thresholds are associated with accelerated central atrophy, namely in peri-auditory regions, the hippocampus, and entorhinal cortex in the human brain (Lin et al., 2014; Xu et al., 2019).

Considering these results together, it seems reasonable to focus more attention on the relationship between pure-tone hearing loss and neurostructural plasticity but additionally also between supra-threshold measures of auditory perception as well as speech in noise comprehension and anatomical correlates in older adults, particularly in those who have pure-tone hearing impairment. Further, as shown by a previous study, a significant correlation between greater pure-tone thresholds and thinner cortical thickness of auditory cortex regions can already be found in participants without pure-tone hearing loss (below 25 dB) (Neuschwander et al., 2019). This association found in individuals with clinically (near-to) normal hearing thresholds suggests that age-related atrophy may affect parts of the cortex that accommodates functions of spoken language, which may impair spoken communication even in the absence of clinically impaired audibility. Thus, in the current work, we extend our previous work (Giroud et al., 2018) in which we investigated age-related differences in neuroanatomical traits of supra-threshold auditory perception in normal hearing participants and include healthy older adults with a broader range of PTAs starting at 8.5-dB HL ranging up to 51.4-dB HL, measured over the five octave frequencies between 500 and 8000 Hz. This allowed us to gain a more comprehensive view over a broader spectrum of age-related hearing loss severity and gave us the opportunity to extend the findings of Giroud et al. (2018), who solely included normal hearing participants in their study (PTA below 30-dB HL). In those participants, we assessed supra-threshold auditory perceptual abilities (i.e., FS and TC) (Giroud et al., 2018; Lecluyse et al., 2013; Lecluyse & Meddis, 2009) as well as speech in noise recognition.

Actually, FS and TC represent the two most important cues in any acoustic signal, namely, the acoustic variation in the frequency and in the time domain. Hence, they are indirectly linked to initial stages of auditory and potentially speech perception and thus represent an adequate measure for "central" hearing acuity. Further, the adaptive procedure used in this study, first introduced by Lecluyse and Meddis (2009), is a participant friendly (no training is needed because there is no complex task, and good acceptability is shown in previous studies; e.g., Giroud et al., 2018) as well as a fast procedure to assess supra-threshold auditory perceptual abilities, because of the limited number of trials given the adaptive algorithm (see also Section 2 for more details), which is especially important for the ageing population due to fatigue. Additionally, these tasks are reliable (e.g., response bias is taken care of by catch trials) and, compared with other methods (e.g., forced choice), they revealed similar threshold measures, but in a more efficient manner, due to lower number of trials (Lecluyse et al., 2013; Lecluyse & Meddis, 2009).

Because pure-tone hearing loss and speech in noise comprehension difficulties have been associated with changes in brain morphology in normal hearing older adults (e.g., Alfandari et al., 2018; Eckert et al., 2012, 2019; Giroud et al., 2018; Giroud, Keller & Meyer, 2021; Husain et al., 2011; Lin et al., 2014; Neuschwander et al., 2019; Peelle et al., 2011; Peelle & Wingfield, 2016; Ren et al., 2018; Rigters et al., 2017; Schneider et al., 2009; Slade et al., 2020; Wong et al., 2009) as well as in older individuals with (risk for) neurodegeneration (Giroud, Pichora-Fuller, et al., 2021), we extracted the morphology of auditory-related, language-related, and cognitive-related brain areas from the MR-images of older adults with varying degrees of pure-tone hearing loss ranging from normal hearing to moderate hearing loss.

So far, most studies investigating the association between brain anatomy and age-related decline of speech perception and comprehension focused on pure-tone audiometry. For example, several studies showed an association between increasing severity of pure-tone hearing loss and reduced grey matter (GM) volume in auditory cortex areas in older adults (e.g., Eckert et al., 2012; Husain et al., 2011; Peelle et al., 2011; Ren et al., 2018; Rigters et al., 2017; Schneider et al., 2009). These findings were reported across several studies involving different sample sizes, age distributions, and severity of pure-tone hearing loss and are further supported by evidence from longitudinal studies showing that pure-tone hearing loss is associated with accelerated GM atrophy in peri-auditory regions, the hippocampus and entorhinal cortex in the human brain (Lin et al., 2014; Xu et al., 2019). However, these findings could not be replicated by a more recent study that found no longitudinal evidence that pure-tone hearing loss does directly affect brain morphology (Eckert et al., 2019). The authors showed that participants with increased high-frequency pure-tone thresholds exhibited larger increases in ventricle size, but this effect could not be found for associations between high-frequency pure-tone thresholds and auditory cortex morphology.

A study investigating the association between speech in noise recognition and brain anatomy, showed that better performance in these tasks correlated with higher cortical volume (CV) in the left pars triangularis and the cortical thickness (CT) of the left superior frontal gyrus in older adults (Wong et al., 2010). Further, one other study by Giroud et al. (2018) showed a positive relationship between the CT of the left pars orbitalis and the left pars triangularis as well as cortical surface area (CSA) of the left pars opercularis and SiN performance in older adults with normal (pure-tone) hearing. Also, Giroud, Keller and Meyer (2021) recently showed that increased cortical thinning in the left superior frontal lobe is disadvantageous for SiN understanding in older adults compared with younger adults, which further emphasizes the importance of the frontal lobe for SiN processing in older adults.

In the study of Giroud et al. (2018), it was also observed that reduced CT may be associated with supra-threshold perceptual difficulties in older adults. The authors showed that older adults suffering from "central" but not pure-tone hearing loss evidenced reduced CT in auditory-related areas, as well as in frontal areas when compared with a normal-hearing, younger control group (Giroud et al., 2018). Compelling arguments that the audiogram only tells a limited story of age-related auditory perceptual difficulties has been made repeatedly, especially in recent years (Füllgrabe et al., 2015; Humes et al., 2013; Kiessling et al., 2003; Kricos, 2006). However, the neural substrates of supra-threshold processing yet remain unknown to a large extent. Therefore, the main goal of this study was to investigate threshold and supra-threshold auditory perception as well as SiN recognition and their association with brain anatomy in a sample of healthy older adults with varying degrees of pure-tone thresholds, ranging from mild up to moderate hearing loss. For this purpose, we applied an established surface-based morphometry (SBM) approach, using the FreeSurfer analysis software suite (Dale et al., 1999, 2000; Fischl, 2012). This software allows for the separate examination of CT and CSA, the two independent constituents of CV (Meyer et al., 2014; Panizzon et al., 2009; Winkler et al., 2010), thus resulting in a more differentiated and detailed picture of the association between age-related hearing loss and cortical anatomy than is possible with voxel-based morphometry (VBM) approach.

So far, the specific neuroplastic characteristics of CT and CSA have not been fully clarified and the association between differential aspects of age-related perceptual auditory difficulties and alterations in cortical architecture remain unclear. As previous research already showed, it seems that CT is especially sensitive to the dynamic modulations associated with training and experience over the lifespan when compared with CSA or CV (Bermudez et al., 2009; Engvig et al., 2010; Schneider et al., 2009; Storsve et al., 2014). This makes CT an interesting and promising trait to investigate morphological changes following age-related changes in supra-threshold auditory perceptual acuity and speech recognition abilities. Existing research, however, has not only provided evidence that supports this hypothesis (Chiarello et al., 2016; Winkler et al., 2010). In fact, it appears that both CT and CSA may be undergoing age-related alterations, in that CT atrophy may be characterized by cortical thinning (Fjell et al., 2009), whereas loss of area seems to be a result of a nonspecific, global loss of GM (Dickerson et al., 2009; Fotenos et al., 2005).

1.1 | Hypotheses

We hypothesized that threshold and supra-threshold auditory perception as well as SiN comprehension abilities are differently related to CT and CV differences in auditory-related brain areas ([extra]-perisylvian region), such as Heschl's gyrus (HG), Heschl's sulcus (HS), superior temporal gyrus and sulcus (STG/STS), planum polare (PP), and planum temporale (PT), as these are the most likely cortical regions to be associated with age-related changes in auditory perception (Giroud et al., 2018; Profant et al., 2014). For the more demanding SiN task (not only "simple" tone perception but also the perception of speech, inhibition of background noise and the processing of a generally more complex signal), we additionally hypothesized an association between task performance and neuroanatomy of extra-auditory language-related regions, most probably the bilateral prefrontal cortex (PFC), pars triangularis (PTRI), pars orbitalis (POR), and pars opercularis (POP), as these regions are (amongst other functions) related to increased task demand and verbal working memory during spoken language comprehension (Best et al., 2010; Fiez et al., 1995; Gabrieli et al., 1998; Giraud et al., 2004; Hickok & Poeppel, 2007; Meyer et al., 2000, 2004; Sheppard et al., 2011). We also expected this association to extend to the precuneus as it has been observed to be involved in speech recognition in noise tasks (Giroud et al., 2018; Wong et al., 2009). A further assumption was, that we would find an association between CT and age-related hearing loss because CT appears to be especially sensitive to age-related change (Bermudez et al., 2009; Engvig et al., 2010; Schneider et al., 2009; Storsve et al., 2014).

2 | MATERIAL AND METHODS

2.1 | Participants

In total, 59 healthy older adults (32 males, 27 females; M age = 69.88 years, age range: 64–78 years, SD = 3.49 years) participated in the study. All participants had clinically relevant symmetrical mild to moderate pure-tone hearing impairment (>25-dB HL and <60-dB HL averaged across 500, 1000, 2000, and 4000 Hz; <20-dB interaural difference). For screening only, audiograms were measured with a MAICO ST 20 Audiometer using air conduction. Further, none of the participants used hearing aids. All participants were native Swiss-German speakers. The Annett Hand Preference Questionnaire (Annett, 1970) indicated that all participants were right-handed. All participants scored at least 26 points on the Montreal Cognitive Assessment (MOCA) (Nasreddine et al., 2005). Exclusion criteria were the use of psychotropic medication, a history of a neurological or psychiatric disease, ear, or brain surgery, reading problems (e.g., dyslexia), tinnitus, early bilingualism (i.e., a second language learned in preschool age), practice of more than 6 hours of music per week, and having metal in the body or claustrophobia, either of which would contraindicate MRI scanning. All participants provided written informed consent and the study was approved by the Ethics Committee of the Canton of Zurich (BASEC-NR, 2017-00284). Participants were paid for their participation.

2.2 | Pure-tone thresholds and supra-threshold auditory perception and speech in noise comprehension

To assess participants' hearing and auditory perceptual abilities, we used four different procedures to measure threshold and supra-threshold auditory perception as well as speech in noise comprehension.

In a first step, we measured the participants' absolute pure-tone thresholds. To do so, a probe-detection paradigm with pure-tones presented for 250 ms at 500, 1000, 2000, 4000, and 8000 Hz was used (Lecluyse et al., 2013). The audiograms for all participants are shown in Figure 1a and the PTAs, averaged over all five measured frequencies (M = 26.19-dB HL, SD = 9.90, range: 8.5- to 51.4-dB HL), are depicted in Figure 1b. PTAs did not correlate significantly with age over the 24-year age range investigated in the present study ($r = 0.112$, $p = 0.403$).

In a second step, participants then performed two supra-threshold auditory tasks to obtain frequency selectivity (FS) and temporal compression (TC) (Lecluyse et al., 2013; Lecluyse & Meddis, 2009). FS can be described as the ability to detect small frequency differences between two sine-wave tones, while TC can be conceived as the ability to detect small temporal gaps between the presentation of two pure tones. Hence, these two approaches test not merely audibility of acoustic signals but rather the ability to perceive essential acoustic features underlying spoken language. Following Lecluyse et al. (2013), we used a forward-masking paradigm to assess participants' FS (see Figure 2a) and TC (see Figure 3a) performance for five frequencies between 500 and 8000 Hz. Additionally, a cue, presented at the start of each trial, directed the participants attention to the start of the task.

The paradigm used to measure FS consisted of a 108-ms masker (i.e., the test masker) followed by a 16-ms probe tone (i.e., the test probe) presented at 10 dB above the individual absolute threshold, with a 10-ms gap between the masker and the probe (see Figure 2a). With this task, we identified the lowest level of the masking tone that was able to prevent the perception of the probe tone. To adapt the level of the masker between trials, a single-interval adaptive tracking procedure was used. The start level of the masker was set at a low level so that only probe tones were heard in the first few trials. The level of the masker was then increased in 10-dB steps from trial to trial. As soon as the participant made the first mistake, the paradigm continued with 2-dB steps of the masker level. This adaptive procedure was applied to all five probe frequencies (500, 1000, 2000, 4000, 8000 Hz), for which the masker frequencies varied in relation to the respective probe frequency (0.7:1, 0.9:1, 1:1, 1.1:1, 1.3:1). To make the task as user-friendly as possible, a cue masker and a cue probe were presented 500 ms before the test masker and the test probe. The cue masker was always presented 10 dB below the sound level of the test masker, making the detection of the cue probe easier. Participants had to indicate whether they did not hear a tone or heard one or two probe tones. The mean masker threshold averaged over the five probe frequencies is shown in Figure 2b. As a parameter for statistical analysis, the depth between masker levels at the highest and the lowest frequency obtained during testing was

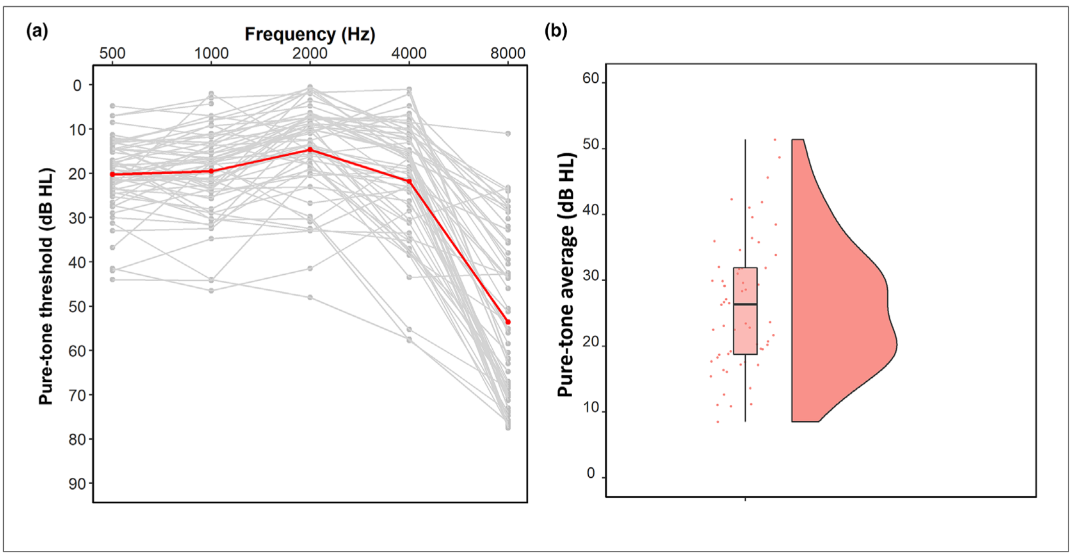

FIGURE 1 (a) Pure-tone thresholds at the octave frequencies between 500 and 8000 Hz. Red line shows the group average, light grey lines show the pure-tone thresholds for each participant. (b) Pure-tone averages in dB HL (0.5–8 kHz). Dots represent single participants.

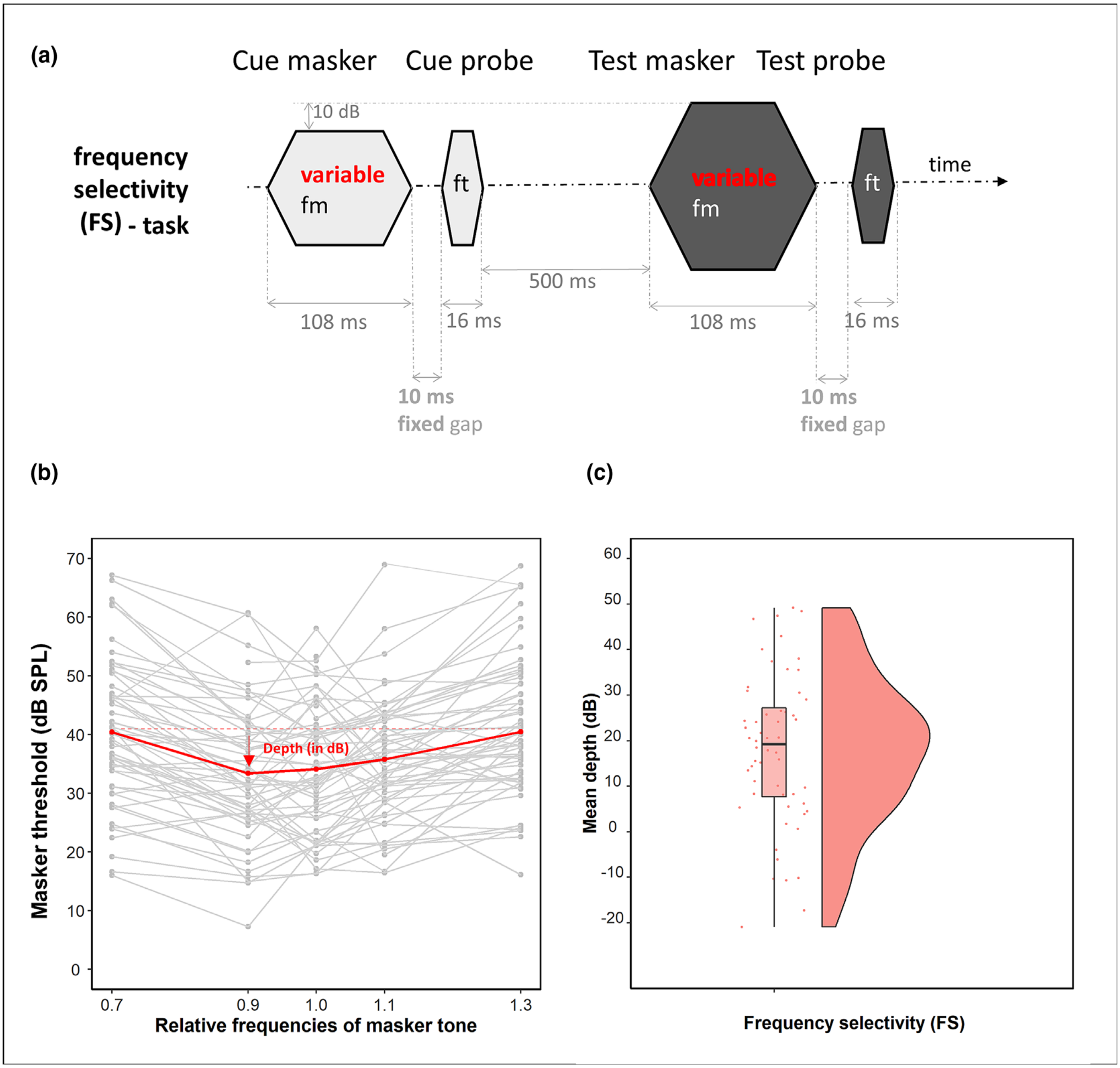

FIGURE 2 (a) Design of the supra-threshold task to assess frequency selectivity (FS) according to Lecluyse et al. (2013). (b) The task was used to identify the lowest level of the masking tone that was able to prevent the perception of the probe tone for each probe frequency (500, 1000, 2000, 4000, 8000 Hz). The masker frequencies were varied in relation to the respective probe frequency (0.7:1, 0.9:1, 1:1, 1.1:1, 1.3:1; see x-axis). For this figure, the mean masker threshold was averaged over the five probe frequencies. (c) As a parameter for statistical analysis, the depth between masker levels at the highest and the lowest frequency was obtained for each probe frequency and then averaged across the five probe frequencies. The higher the mean depth (in dB), the better the frequency selectivity. Mean FS depth across all participants (each participant is represented with a dot) was 17.94 dB (SD = 16.72, range = −20.9–49.2).

calculated for each probe frequency, and then averaged across the five probe frequencies (see Figure 2c). This calculation has been shown to be a valid parameter for the description of FS in adults with normal hearing and with hearing impairment (see Lecluyse et al., 2013, for more details). In general, the higher the mean depth (in dB), the better the frequency selectivity. Mean FS depth across all participants was 17.94 dB (SD = 16.72, range = −20.9–49.2).

To measure TC, a similar approach to that used for assessing FS was used. Again, a forward-masking task with a masker and a probe tone, presented at 10 dB above the individual absolute threshold was used, while an adaptive procedure was applied to assess the lowest level of the masking tone, which prevented the perception of the probe (see Figure 3a). Here, the gap between the masker and the probe varied between 10, 30, 50, and 70 ms while, as before, five masker frequencies were used (500, 1000, 2000, 4000, 8000 Hz). As in the FS task, a quieter cue masker and a cue probe preceded the test masker and test probe. The mean masker threshold averaged over the five probe frequencies for each of the four gaps is shown in Figure 3b. In this task, the steepness of the slope as a function of gap duration for each frequency tested indicates the temporal compression. Here, the slope was measured for each frequency and then averaged (see Figure 3c), to obtain a parameter that best describes TC (see Lecluyse et al., 2013, for more details). The higher this value, the better the temporal compression of the participant. Mean TC slope was 3.17 dB/100 ms (SD = 8.66, range = −12.7–25.1).

In a last step, we used a speech in noise (SiN) sentence recognition task, the Oldenburger Sentence Test (OLSA). This task was used to measure the signal-to-

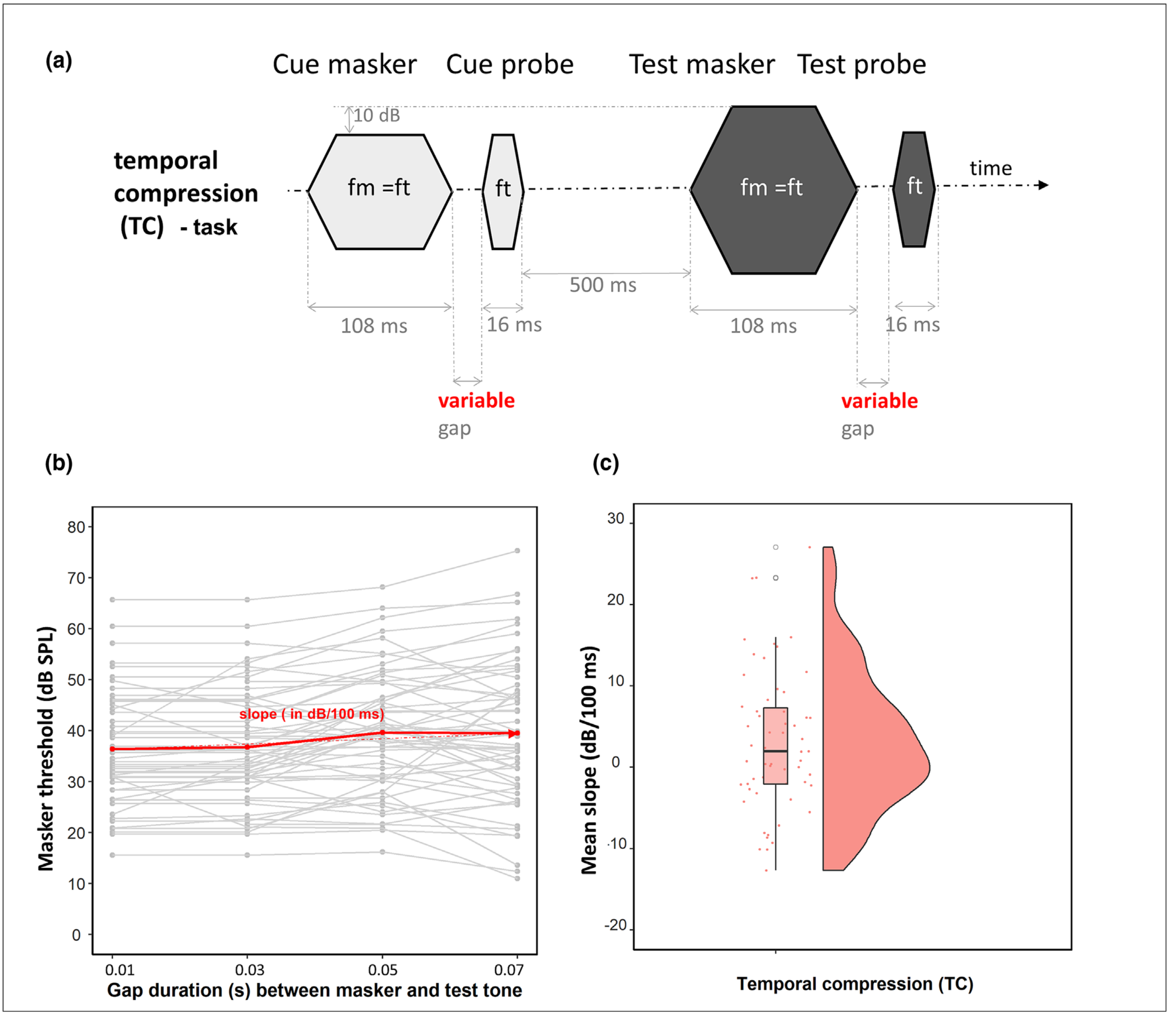

FIGURE 3 (a) Design of the supra-threshold task to assess temporal compression (TC) according to Lecluyse et al. (2013). (b) The lowest level of the masking tone preventing the perception of the probe tone was assessed for different gaps between the masker and the probe (i.e., 10, 30, 50, and 70 ms) for five different masker frequencies (500, 1000, 2000, 4000, 8000 Hz). The mean masker threshold averaged over the five probe frequencies for each of the four gaps is shown in this figure. (c) In this task, the steepness of the slope as a function of gap duration for each frequency tested indicates the temporal compression. Here, the slope was measured for each frequency and then averaged. The higher this value, the better the temporal compression of the participant (represented by the dots). Mean TC slope was 3.17 dB/100 ms (SD = 8.66, range = −12.7–25.1).

noise ratio (SNR) at which the participant was able to correctly repeat 50% of the words in a sentence that was presented within background noise. The OLSA (Wagener et al., 1999) uses matrix sentences in which each sentence follows the same structure: name–verb–number–adjective–object. For each trial, the individual words are randomly selected from a large list of words, resulting in a series of meaningless sentences, which makes guessing the words based on contextual information impossible. The noise used during the test was generated by 30 random overlays of the whole test material, leading to a noise with low amplitude modulations and of the same spectrum as the test sentences.

The loudspeaker was positioned 1 m away (0° azimuth) from the seated subject's head. Sentences and noise were initially presented at 65-dB SPL each (i.e., an SNR of 0). While the sentence level was adaptively varied depending on the participant's response, the sound level for the masking signal was kept constant at 65-dB SPL. Participants were instructed to repeat as many words as possible after each sentence. Responses were recorded by a microphone and sent to the investigator, who sat outside the sound attenuated booth and documented the participant's responses. The adaptive procedure followed the rule that the sentence level remained constant when two or three words were correctly understood. With four correctly repeated words, the sentence level decreased by 1 dB and with five correct words (i.e., when the whole sentence was correctly understood) by 2 dB. If only one word was recognized, the sentence level increased by 1 dB; if no word was understood at all, the sentence level increased by 2 dB. A total of 30 sentences were presented,

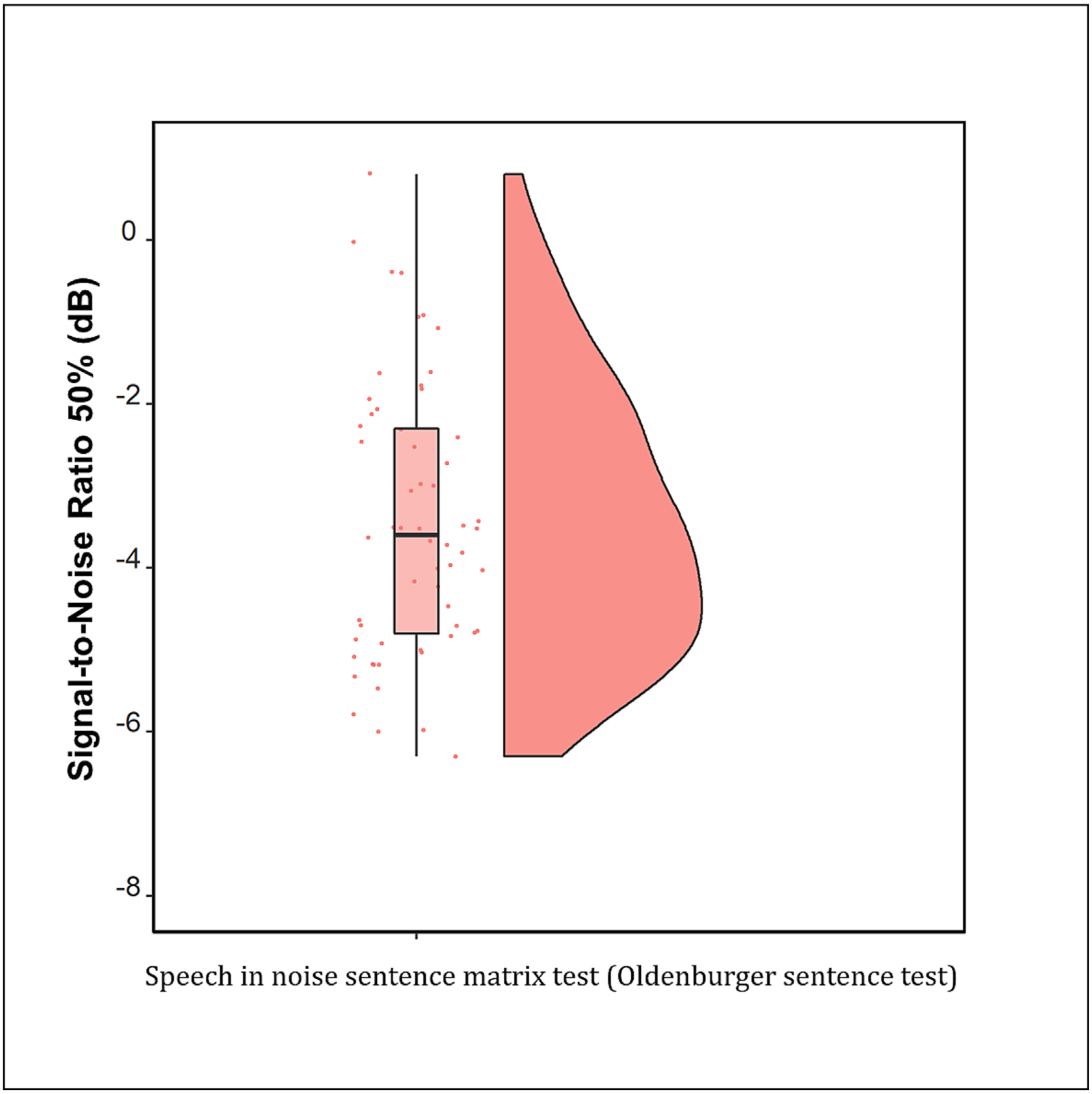

FIGURE 4 Results of the Oldenburger speech in noise matrix sentence test. The figure depicts the mean signal-to-noise ratio (SNR) in dB for 50% correct word recognition in the matrix sentences. Dots represent individual participants.

with the average SNR of the last 20 sentences representing the 50% threshold. The mean SNR was −3.68 dB (SD = 1.81, range = −6.3–0.6; see Figure 4).

All stimuli used and the procedure have already been successfully applied and comprehensively described in previous studies (Giroud et al., 2018; Lecluyse et al., 2013; Wagener et al., 1999). All tests were performed in a sound attenuated booth and administered by trained lab personnel. The acoustic stimuli were presented over a Genelec (8030B) speaker inside the cabin while a custom-written Matlab software controlled the stimulus presentation. The participants were seated inside the cabin in front of a computer screen and indicated their answers through mouse button press.

2.3 | MRI data acquisition

High-resolution T1-weighted images were obtained for each participant from a 3.0 T Philips Ingenia scanner (Philips Medical Systems, Best, The Netherlands) with a 12-channel head coil using an anatomical 3D Turbo-Field-Echo sequence with echo time = 3.7 ms, repetition time = 8.2 ms, field of view = 240 × 240 × 160 mm, acquisition matrix = 240 × 240, 160 slices per volume, and isotropic voxel size = 1 × 1 × 1 mm, flip angle (α) = 90°. Total scan time was approximately 6 min.

2.4 | Surface-based morphometry analysis

For the reconstruction of the cortical surface and the volumetric segmentation, the FreeSurfer image analysis suite (version 6.0; Fischl, 2012) was used. The software is documented online and freely available for download (https://surfer.nmr.mgh.harvard.edu/). The surface-based morphometry analysis implemented in the FreeSurfer pipeline comprises several pre-processing steps. These pre-processing steps have already been described in detail in previous publications (Dale et al., 1999; Dale & Sereno, 1993; Fischl et al., 2001; Fischl & Dale, 2000; Ségonne et al., 2004). The automatic parcellation of the cerebral cortex into units based on gyral and sulcal structure was performed using Destrieux's aparc.a2009s annotation (Destrieux et al., 2010). To ensure quality of the conducted pre-processing steps, the implemented quality assessment tools within FreeSurfer were used. Finally, morphometric parameters such as the total CV, mean CSA, and the mean CT were extracted. For the statistical analysis, the reconstructed images were morphed to an average spherical surface template (fsaverage) and were then spatially smoothed with a 10-mm full-width-half-maximum Gaussian kernel. The resulting surface models were not manually edited.

2.5 | Statistical analyses

2.5.1 | FreeSurfer vertex-wise correlation analysis with auditory task performance

A vertex-wise partial correlation analysis was performed between morphometric parameters (CV, CT, and CSA) and auditory task performance (PTA, TC, FS, and SiN) across all participants within the 12 bilateral predefined regions-of-interest (ROIs) (see Figure 5). PTA, TC, FS, and SiN were used as continuous variables fitted to the general linear models (GLM) separately. Age and gender were included in the model as covariates of no interest. For supra-threshold auditory perception and SiN recognition, PTA was included in the GLM as an additional covariate. After fitting the GLMs with the built-in function in FreeSurfer, 5000 Monte-Carlo simulations were run to correct for multiple comparisons at cluster level (Nichols & Hayasaka, 2003). For the simulations, the initial cluster-forming threshold was set to $p = 0.05$. Statistical analysis was conducted vertex-wise within the defined ROIs (see Figure 5). The ROIs were chosen according to previous studies that have demonstrated associations of these regions with auditory processing in older adults (Giroud et al., 2018; Meyer et al., 2014; Profant et al., 2014). Further, these regions were defined using the aparc.a2009s annotation (Destrieux et al., 2010). This labelling procedure allows for the annotation of separate regions for Heschl's gyrus (HG), Heschl's sulcus (HS), superior temporal gyrus/sulcus (STG/STS), planum polare (PP), planum temporale (PT), the angular gyrus (AG), pars triangularis (PTRI), pars orbitalis (POR), pars opercularis (POP), prefrontal cortex (PFC), and the precuneus (PCUN). For a better overview, only significant clusters are shown in Section 3.

3 | RESULTS

3.1 | Associations between pure-tone averages and brain anatomy

The conducted vertex-wise partial correlation analysis between the morphometric parameters and pure-tone averages within the defined ROIs revealed a cluster in the right superior temporal lobe (CWP = 0.008, $r = -0.44$). For this cluster, higher pure-tone averages were associated with reduced CT (see Table 1). According

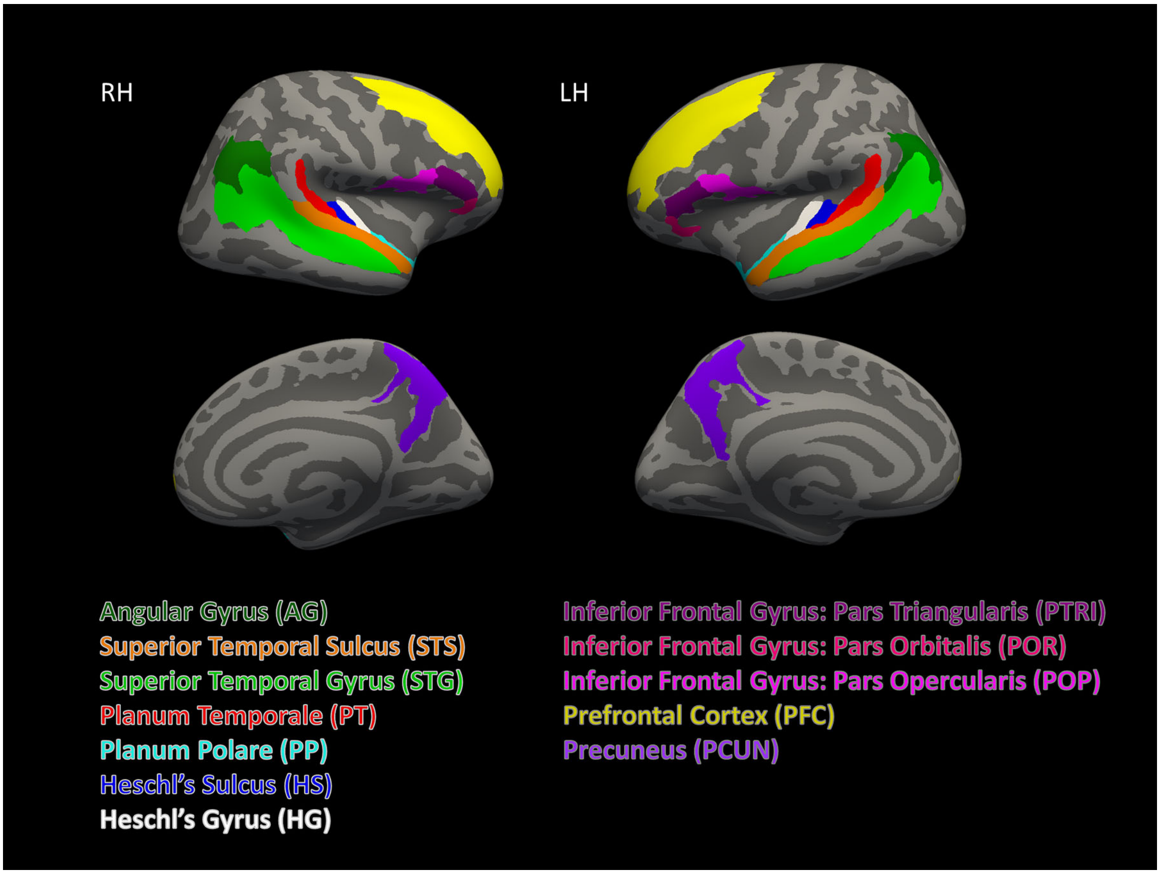

FIGURE 5 Twelve bilateral predefined anatomical regions-of-interest (ROIs) for the vertex-wise analysis using FreeSurfer.

TABLE 1 Negative correlation between pure-tone averages (PTA) and CT in right STS.

					MNI				
Measure	**Annotation**	**Max**	**NVts**	**Size (mm^2)**	***X***	***Y***	***Z***	**CWP**	***r***
RH thickness	STS upper bank	−2.9	975	346.8	46	−37	5	0.008	−0.44

Note: RH: right hemisphere; Max: log10(p) at peak vertex; NVts: number of vertices above threshold; CWP: cluster-wise *p* value of Monte Carlo simulation; *r*: effect-size.

to Destrieux's (2010) aparc.a2009s atlas, this right hemisphere (RH) cluster includes parts of the STS and parts of the STG (see Figure 6a). The association between CT in this cluster and PTA is depicted with a scatterplot in Figure 6b.

3.2 | Associations between supra-threshold auditory perception and brain anatomy

The conducted vertex-wise partial correlation analysis between the morphometric parameters and the two supra-threshold auditory perception tasks, TC and FS, for the defined ROIs revealed several clusters in which poorer auditory performance was associated with reduced CV or CT (see Figures 7a and 8a for TC and FS, respectively) in auditory regions as described below separately for TC and FS.

3.2.1 | Temporal compression

The vertex-wise analysis for TC revealed one cluster in the right superior temporal region, in which poorer temporal performance (i.e., a shallower masking function in TC) was significantly associated with reduced CV (CWP = 0.044, $r = 0.34$) (see Table 2). According to Destrieux's aparc.a2009s atlas (2010), this RH cluster includes parts of the planum temporale and parts of

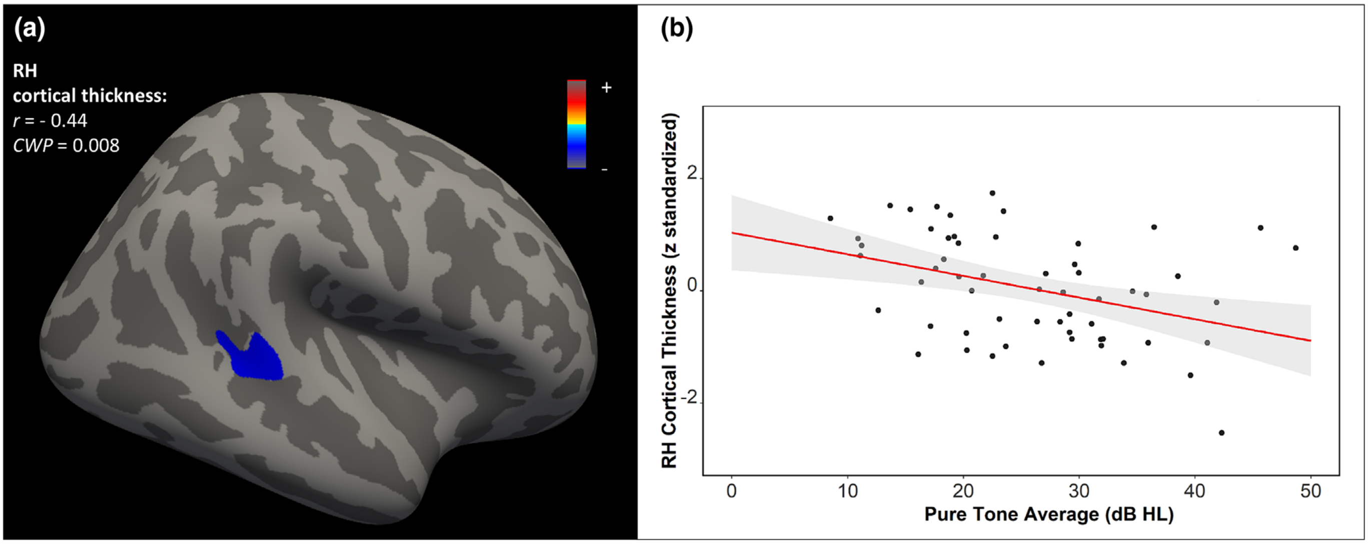

FIGURE 6 (a) Cluster in the right STS upper bank region, the cortical thickness of which correlated significantly negatively with pure-tone averages (dB HL). Negative (blue) values represent a negative correlation between cortical thickness and PTA. RH = right hemisphere, r = correlation coefficient, CWP = cluster-wise p value. (b) Correlation between cortical thickness of the right STS upper bank region and pure-tone averages (500, 1000,2000, 4000, and 8000 Hz). The 95% confidence interval around the linear trend is plotted in grey.

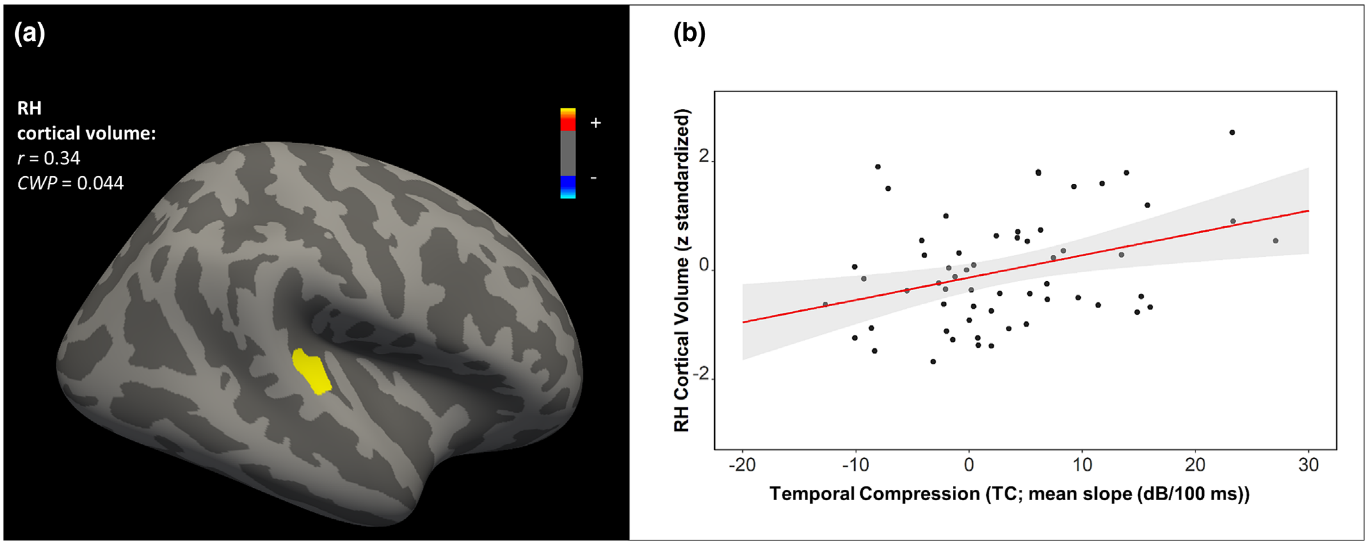

FIGURE 7 (a) Cluster in the right superior temporal region, the cortical volume of which correlates significantly positively with varying degrees in supra-threshold temporal perception measured by temporal compression (TC). Positive (yellow) values represent a positive correlation between cortical volume and TC. RH = right hemisphere, r = correlation coefficient, CWP = cluster-wise p value. (b) Relationship between cortical volume of the right superior temporal region and TC performance. The 95% confidence interval around the linear trend is plotted in grey.

Heschl's sulcus (see Figure 7a). The association is depicted with a scatterplot in Figure 7b.

3.2.2 | Frequency selectivity

The vertex-wise analysis for FS revealed four clusters in the left temporal lobe, in which poorer FS was significantly associated with reduced morphometric parameters: two clusters for CV (a: CWP = 0.002, $r = 0.42$; b: CWP = 0.028, $r = 0.33$) and two clusters for CT (c: CWP = 0.002, $r = 0.40$; d: CWP = 0.002, $r = 0.38$) (see Table 3). According to Destrieux's aparc.a2009s atlas (2010), clusters b and c encompass parts of Heschl's gyrus, parts of the planum polare and a small part of the superior temporal gyrus, while clusters a and d encompass parts of Heschl's sulcus, planum temporale and parts of the superior temporal sulcus and gyrus (see

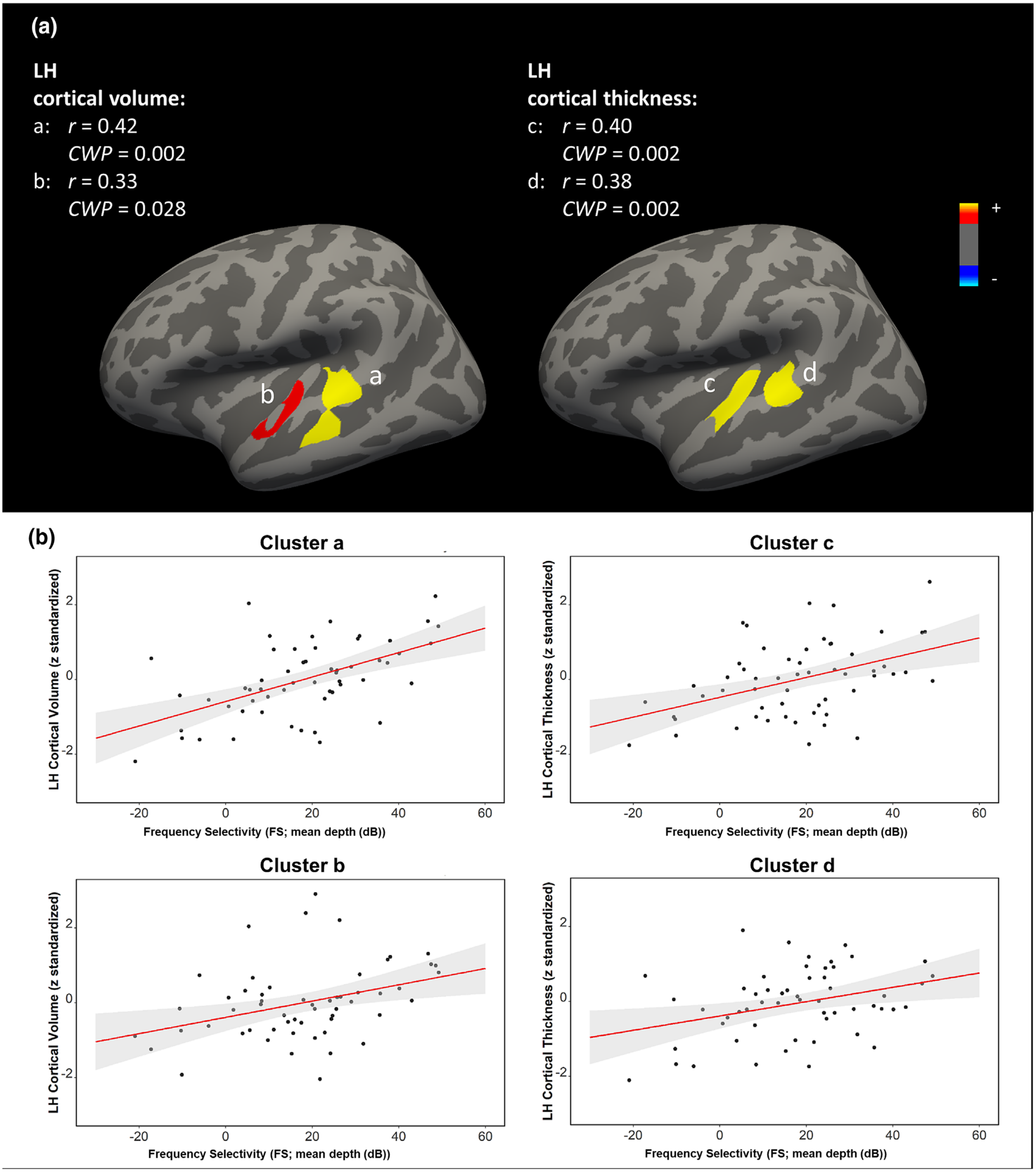

FIGURE 8 (a) Clusters in the left middle and superior temporal region, the cortical volume and thickness of which correlates significantly positively with varying degrees of supra-threshold spectral perception measured by frequency selectivity (FS). Positive (yellow and red) values represent a positive correlation between morphometric parameters and TC. LH = left hemisphere, r = correlation coefficient, CWP = cluster-wise p value. (b) Relationships between morphometric parameters of the significant clusters and TC performance. The 95% confidence interval around the linear trend is plotted in grey.

TABLE 2 Positive correlation between supra-threshold temporal perception (TC) and right STR CV.

Measure	Annotation	Max	NVts	Size (mm^2)	MNI *X*	MNI *Y*	MNI *Z*	CWP	*r*
RH volume	Superior temporal region	1.8	592	299.4	57	−30	8	0.044	0.34

Note: RH: right hemisphere; Max: log10(p) at peak vertex; NVts: number of vertices above threshold; CWP: cluster-wise *p* value of Monte Carlo simulation; *r*: effect-size.

TABLE 3 Clusters that correlate positively in terms of cortical volume and cortical thickness with supra-threshold spectral perception (FS) revealed by ROI analyses with FreeSurfer.

Measure	Annotation	Max	NVts	Size (mm^2)	MNI *X*	MNI *Y*	MNI *Z*	CWP	*r*
LH volume	Middle temporal (a)	45	1714	779.4	−58	−24	−14	0.002	0.42
	Superior temporal (b)	2.4	780	361.2	−57	−12	2	0.028	0.33
LH thickness	Superior temporal (c)	3.8	1158	505.4	−57	−13	2	0.002	0.40
	Superior temporal (d)	3.1	1032	486.9	−62	−31	2	0.002	0.38

Note: RH: right hemisphere; Max: log10(p) at peak vertex; NVts: number of vertices above threshold; CWP: cluster-wise *p* value of Monte Carlo simulation; *r*: effect-size.

TABLE 4 Significant correlations between cortical thickness and SiN reception thresholds revealed by ROI analyses with FreeSurfer.

Measure	Annotation	Max	NVts	Size (mm2)	MNI *X*	MNI *Y*	MNI *Z*	CWP	*r*
RH thickness	Superior temporal (a)	−4.0	1029	565.4	57	4.4	−11	0.002	−0.33
	Pars triangularis (b)	−3.0	754	428.3	53	23	9	0.014	−0.32
	Rostral middle frontal (c)	−3.1	466	360.9	19	62	−1	0.048	−0.26

Note: RH: right hemisphere; Max: log10(p) at peak vertex; NVts: number of vertices above threshold; CWP: cluster-wise *p* value of Monte Carlo simulation; *r*: effect-size.

Figure 8a). The associations between morphometric parameters of these clusters and FS are depicted with scatterplots in Figure 8b.

3.3 | Associations between brain anatomy and speech in noise comprehension

The vertex-wise analysis for the SiN task revealed three clusters in the right hemisphere, in which poorer SiN recognition (i.e., a higher signal-to-noise ratio) was significantly associated with reduced cortical thickness (a: CWP = 0.002, $r = 0.33$; b: CWP = 0.014, $r = 0.32$; c: CWP = 0.048, $r = 0.26$) (see Table 4). According to Destrieux's aparc.a2009s atlas (2010), cluster a encompasses parts of the right superior temporal gyrus and the planum polare, cluster b covers the triangular gyrus, and cluster c encompasses parts of the transverse frontopolar gyrus and sulcus (see Figure 9a). The association between morphometric parameters of these clusters and the signal-to-noise ratio in the SiN task are depicted with scatterplots in Figure 9b.

4 | DISCUSSION

The main objective of this study was to investigate brain anatomical correlates of auditory pure-tone thresholds and supra-threshold auditory perceptual abilities as well as speech in noise recognition in a sample of healthy older adults with mild to moderate pure-tone hearing loss ($N = 59$). For this purpose, we used an established morphometric analysis approach that allows the separate consideration of CV, CT, and CSA within and outside the auditory pathway to examine the interplay between threshold and supra-threshold auditory as well as speech in noise perception and neuroanatomical metrics. In the following, we first discuss the neuroanatomical correlates of pure-tone thresholds, followed by those for temporal

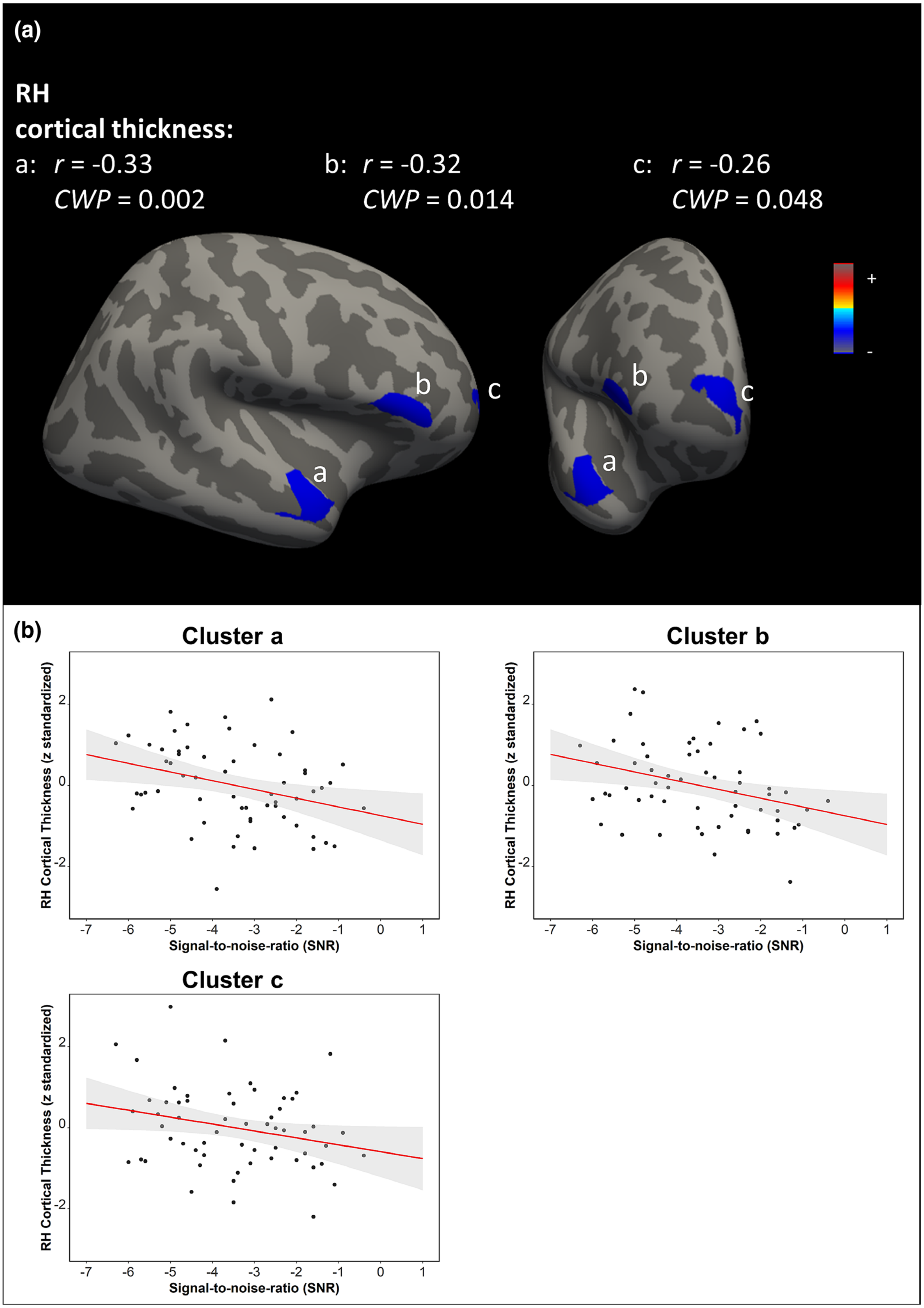

FIGURE 9 Legend on next page.

FIGURE 9 (a) Clusters in which cortical thickness correlate significantly negatively with speech in noise recognition in the Oldenburger sentence test. Negative (blue) values represent a negative correlation between morpho-metric parameters and speech in noise recognition. RH = right hemisphere, r = correlation coefficient, CWP = cluster-wise p value. (b) Relationships between morphometric parameters of the significant clusters and speech-in-noise performance. The 95% confidence interval around the linear trend is plotted in grey.

and spectral supra-threshold auditory perception and, in a last section, the results for speech in noise recognition.

4.1 | Associations between pure-tone thresholds and brain morphometry

The conducted vertex-wise partial correlation analyses between the morphometric parameters of the predefined ROIs and auditory measures revealed several significant clusters. For pure-tone averages, we found a significant correlation with the CT of a right hemisphere cluster encompassing parts of the STS and STG. In this cluster, greater pure-tone hearing loss was significantly associated with decreased CT. This finding is in line with the results reported by Lin et al. (2014). In their longitudinal study, they showed accelerated rates of decline in GM volume in the right temporal lobe, especially in the STG region, for older adults suffering from pure-tone hearing loss. Because Lin et al. (2014) used a VBM approach to analyse their data, our results can be seen as a complement and extension to these results. As such, we assume that the found longitudinal decline of CV in the study of Lin et al. (2014) may emerge from changes in CT in these regions through auditory deprivation caused by pure-tone hearing loss. Further, our results are in line with several cross-sectional studies showing the association between increased pure-tone hearing loss and decreased neuromorphometric parameters in auditory-related brain areas (e.g., Eckert et al., 2012; Husain et al., 2011; Peelle et al., 2011; Rigters et al., 2017). Our study thus contributes to the existing literature on the association between pure-tone hearing loss and brain plasticity in a sense that sensory deprivation through elevated hearing thresholds might lead to GM decline (sensory deprivation hypothesis; for review articles, see Golub, 2017; Peelle & Wingfield, 2016; Slade et al., 2020). Nevertheless, besides this auditory deprivation hypothesis, there are further potential mechanisms discussed in the literature, which may lead to neuroanatomical alterations in combination with age-relate hearing loss and cognitive decline. Amongst others, the common-cause hypothesis (e.g., Christensen et al., 2001) suggests a general age-related decline in the nervous system, which manifests both peripherally and centrally and is attributable to a common neurodegenerative pathology. Further, the social isolation hypothesis proposes that reduced social interaction associated with social isolation and depression may influence the association between hearing loss, cognitive decline and neurodegeneration. For a more comprehensive overview, see, for example, Slade et al. (2020), Peelle and Wingfield (2016), and Golub (2017).

4.2 | Associations between supra-threshold auditory perception and brain morphometry

Regarding supra-threshold auditory perception, we found different neuroanatomical characteristics in association with TC and FS. While TC showed a significant positive correlation with a CV cluster situated in the right planum temporale as well as parts of the right Heschl's sulcus, FS showed significant positive correlations with CV and CT in several left hemisphere clusters encompassing parts of Heschl's gyrus and sulcus, parts of the planum polare and temporale, and a small part of the superior temporal gyrus and sulcus (for more details, see Figures 7 and 8). These results are partly in line with previous work from Giroud et al. (2018), who used the same FS and TC tasks as we did in our study. In their study, Giroud et al. (2018) investigated age effects between normal hearing younger and older adults (PTA < 30-dB HL for 0.5, 1, 2, and 4 kHz) and revealed a significant moderation of age in the association between TC performance and CT of the right Heschl's sulcus suggesting that neuromorphometric integrity in the right Heschl's sulcus was only correlated with TC in the older participants. Their result is therefore like the current findings and extends to the importance of right auditory-related areas for temporal perception specifically in older adults (as compared with younger) with and without hearing impairment (i.e., PTAs up to 60-dB HL). Further, the results of Giroud et al. (2018) showed age-related differences in the association between FS and CT of the left dorsolateral prefrontal cortex and CT of the right planum temporale, namely, that the associations were only significant in the older adults, but not the younger. In the current study, we found different significant associations in a left auditory-related cluster with FS in older hearing impaired. This discrepancy between the results of an older population without hearing impairment (from the study by Giroud et al., 2018) and one with hearing impairment (the current study) suggests that different neural mechanisms support FS in ageing and in hearing impairment. Neuroanatomical integrity of left auditory-related areas might be more relevant for spectral auditory processing in hearing impaired, while structural integrity of right auditory-related areas might be more important for spectral auditory processing in older compared with younger adults without hearing impairment. Further, Giroud and colleagues extracted only mean values for the regions of interest while we used a vertex-wise analysis. These methodological differences could have further impacted differences between the results of the two studies. Still, common in all mentioned results is that higher pure-tone thresholds and lower supra-threshold perceptual abilities correlated with decreased cortical volume or thickness across all tasks and older study populations.

Interestingly, when comparing the observed neuroanatomical characteristics of auditory pure-tone thresholds and supra-threshold measures of auditory perception, it is also noticeable that the significant correlations between supra-threshold measures and brain anatomy in our study are more spread over the primary and adjacent auditory-related cortex areas, while the correlation for pure-tone audiometry is relatively restricted to a small part of the STS/STG region. This might support the assumption that supra-threshold perception difficulties might partially emerge through structural decline in mainly primary and adjacent auditory-related areas such as the left Heschl's gyrus and bilateral Heschl's sulcus as well as left planum polare and temporale (lateralization depending on task). Unlike supra-threshold auditory perceptual deficits, pure-tone hearing loss is associated with cortical thinning in a secondary auditory area, possibly due to sensory deprivation. However, because of the cross-sectional nature of this study, it is not feasible to draw conclusions about the direction of the found effects. Therefore, longitudinal studies are needed to investigate these assumptions and to examine how different aspects of ageing and age-related hearing loss and their association with neuroanatomy develop over a longer time period.

4.3 | Speech in noise recognition and brain morphometry

The results for the association between speech in noise recognition and neuroanatomy revealed several significant clusters in the right hemisphere. Here, poorer speech in noise performance was significantly associated with reduced cortical thickness of parts of the right superior temporal gyrus, parts of the planum polare, the triangular gyrus and parts of the transverse frontopolar gyrus and sulcus. As expected, the performance on the SiN task was not only related to core auditory regions, but also to anatomical markers of higher-order audiomotor areas, namely, the pars triangularis and the transverse frontopolar gyrus and sulcus. These regions have already been described as relevant to speech and higher-order language processing in previous, functional studies (Friederici, 2012; Gabrieli et al., 1998; Hickok & Poeppel, 2007; Sheppard et al., 2011; Vigneau et al., 2011). Akin to our study, also Wong et al. (2010) showed a correlation between SiN performance and the left pars triangularis as well as PFC anatomy. These findings suggest that, in addition to age-related changes in the inner ear, cortical circuits also contribute to the ability to perceive SiN and support the assumption, that in older adults an age-related decline in CT frontal areas may be a crucial factor for speech perception in adverse listening environments. This assumption is further supported by a recent study of Giroud, Keller and Meyer, (2021), who showed that increased cortical thinning in the left superior frontal lobe is disadvantageous for SiN understanding in older adults without hearing impairment compared with younger adults which further emphasizes the importance of the frontal lobe for SiN processing in older adults. Further, these results also speak for the decline-compensation hypothesis, which states that an age-related decrease in sensory processing may be associated with an increase in the recruitment of more general cognitive areas as a means of compensation (Wong et al., 2010). Further, our results are partly in line with the findings from Giroud et al. (2018), who showed a significant correlation between SiN performance and the CT of right Heschl's sulcus and the left pars triangularis. The pars triangularis is part of the ventrolateral frontal lobe, which has been shown to be active during SiN processing especially in older adults. This is also often related to cognitive compensation mechanisms in a way that additional cognitive resources (e.g., working memory and attention) must be recruited to compensate for the ineffectively processing of speech sounds due to the background noise or hearing impairment, thus boosting SiN understanding in difficult listening situations (Bidelman & Howell, 2016; Rudner et al., 2019; Wong et al., 2009). Additionally, Giroud et al. (2018) also showed a bilateral correlation with the CT of the pars orbitalis in older adults without hearing impairment, which we did not find with our older adults who have a larger degree of hearing impairment (up to 60-dB HL), perhaps suggesting that ageing leads to thinning in the pars orbitalis, but not necessarily hearing impairment. Still, it cannot be ruled out that different degrees in PTA in those with clinically not relevant slightly elevated pure-tone thresholds might influence the results. However, as mentioned above, to fully disentangle cause and effect, longitudinal data would be needed, ideally in combination with functional data.

One may wonder whether the different findings of right and left hemisphere changes are meaningful and should be further discussed. We are reluctant with respect to this issue because the pattern of data we report does not demonstrate a clear hemisphere bias. We should also emphasize that we are discussing neuroanatomical data and not functional brain responses. Hence, we do not think that we can interpret our results with the same strength and "verve" as would be possible for a relationship between behavioural and functional responses because the relationship between structural and behavioural data is probably not as densely related. Taking this into account, we have some evidence from previous studies of our own group that the right hemisphere is more strongly affected by age-related decay which corresponds to a reorganization of language functions, specifically in terms of lateralization (Giroud et al., 2018, Keller et al. 2019). Once more evidence (especially combined functional and structural data) becomes available, it will be important to discuss our results in the light of present frameworks about a division of labour between the right and left superior temporal regions during language comprehension (e.g., AST-hypothesis by Poeppel, 2003, or Friederici, 2012).

Comparing the results of SiN recognition with those for TC and FS, it appears that all three are indirectly associated with different patterns of morphological traits in different brain regions. Although they may all be associated with related or similar causes such as cochlear (nerve) degeneration, the difference between the "simple" perceptions of tones (TC and FS tasks) compared with the recognition of speech (SiN task) also manifests itself in differences of involved brain areas. In addition to the perception of auditory cues during a SiN recognition task, also speech and thus a more complex signal must be processed. In addition, the background noise must be suppressed, and the listener must concentrate on the speech signal. We assume that, because of these additional tasks, we found other correlates for SiN recognition with an involvement of areas outside the core auditory cortex, compared with TC and FS.

Compared with the results for the pure-tone thresholds, our findings imply that supra-threshold auditory perception and SiN recognition are more strongly related to the integrity of cortex morphology than pure tone thresholds, simply because supra-threshold auditory perception requires more complex cognitive processing. Nevertheless, based on our results, we can assume that the different correlates for the different types of thresholds and supra-threshold auditory perception and SiN recognition suggest that the separate consideration of these measures is necessary, because even if they are related or have similar causes (e.g., cochlear degradation), they seem to have different effects on auditory processes and the brain. This also suggests that different therapies should be considered for different auditory perceptual difficulties.

4.4 | The role of CT and CSA in auditory processing

In sum, our study shows that auditory thresholds and supra-threshold auditory perception as well as SiN recognition are indirectly associated with differential patterns of morphological traits in different brain regions. All our results show that greater pure-tone thresholds and poorer performance in temporal and spectral supra-threshold auditory perceptual tasks as well as SiN recognition is related to reduced CT and CV in primary, secondary and tertiary auditory regions of the human brain, as well as higher-order language regions.

As expected, we only found an association between hearing and perception with CT, not CSA. As mentioned before, the specific neuroplastic characteristics of CT and CSA have not yet been fully clarified. As previous research already showed, it seems that CT is especially sensitive to the dynamic modulations associated with training and experience over the lifespan when compared with CSA or CV (Bermudez et al., 2009; Engvig et al., 2010; Schneider et al., 2009; Storsve et al., 2014). Thus, our results are in line with the radial unit hypothesis of Rakic (1988, 1995) and other previous views that suggest different genetic trajectories for CT and CSA (Panizzon et al., 2009). Whereas CSA has been shown to be related to the number of cortical columns, CT has been related to the number, packing density, and size of cells within a column (Rakic, 1988, 1995, 2007). In other words, ageing may lead to a loss of neuropil and dendritic branching in the auditory and higher areas involved in language while the number of columns remains relatively stable across the lifespan. Our results, therefore, emphasize the importance of discriminating between CT and CSA in future studies when investigating age-related hearing loss (Amlien et al., 2016; Lee et al., 2016; Lyall et al., 2015; Panizzon et al., 2009; Rakic, 1988, 1995). Nevertheless, existing research has not only provided evidence that supports the hypothesis but that also only CT is subject to age-related alterations as the results of our study would let suggest (Chiarello et al., 2016; Winkler et al., 2010). In fact, other studies also showed that both CT and CSA may be undergoing age-related alterations, in that CT atrophy may be characterized by cortical thinning (Fjell et al., 2009), whereas loss of cortical surface area seems to be a result of a nonspecific, global loss of GM (Dickerson et al., 2009; Fotenos et al., 2005).

However, even though our results clearly move CT to the forefront in the context of age-related alterations associated with hearing loss, further studies with additional auditory tasks and functional data are needed to fully assess the differential role of CT and CSA in auditory processing (Storsve et al., 2014).

4.5 | Limitations

Based on the present cross-sectional data, we cannot determine whether the degraded perception of auditory input due to hearing loss leads to alterations in brain structures or vice versa, namely, whether people with reduced CT/CV are more vulnerable to hearing loss, tone perception difficulties, and speech in noise recognition decline. While it is plausible that reduced sensory input due to pure-tone hearing loss may have led to neuroanatomical alterations (sometimes referred to as the auditory deprivation hypothesis; Ren et al., 2018) as already shown by longitudinal data (see Lin et al., 2014), potential longitudinal effects of supra-threshold auditory perception and SiN recognition remain unclear. Therefore, longitudinal studies with a large group of older adults and the assessment of age-related hearing loss, auditory, and speech perception, as well as cognitive functioning, combined with structural and functional data are needed to confirm our interpretations.

In future cross-sectional designs, the detailed assessment of the potential origin of hearing impairment (e.g., noise exposure, ototoxic events, and family reasons) as well as onset to estimate potential causes and effects should added. However, usually such reports are highly subjective and many study participants do not remember when they first noticed their hearing impairment and it also is unclear whether such reports truly correlate with the physiological onset of changes in the inner ear.

Even though one of our previous studies showed good acceptability of the used auditory tasks (Giroud et al., 2018), some of our participants reported that the tasks were quite tiring and exhausting over time. Since we performed four different listening tasks in the same afternoon, it is probably useful to divide the number of tasks in future studies so as not to unnecessarily overwhelm older participants. Since these tasks seem to challenge not only the auditory system but also require a certain amount of attention, the assessment of participant cognitive functions (e.g., attention and working memory) should be an additional objective in the future. This would also allow to better investigate the potential triangular association between age-related hearing, cognition, and brain morphology (Humes et al., 2012).

5 | CONCLUSION

Our vertex-wise partial correlation analysis with FreeSurfer of neuroanatomy and pure-tone thresholds as well as tone and speech in noise perception showed different significant correlations for independent neuroanatomical traits, namely, CT, CSA, and CV. While pure-tone thresholds significantly correlated with CT in a right hemisphere STS/STG cluster (mostly auditory association cortex), supra-threshold auditory perception additionally showed significant correlations with CV and CT in left (spectral perception) and right (temporal perception) primary and adjacent auditory region clusters including Heschl's gyrus and sulcus, the planum polare and temporale.

These results indirectly support the view of a possible hemispheric preference for the processing of temporal and spectral information that contrasts with the hemispheric preference shown in younger adults (Giroud et al., 2019; Meyer et al., 2018). This finding shows that the (functional) architecture underlying hemispheric preferences for acoustic cues is far more complex than previously suggested (Zatorre & Belin, 2001) and might change across the lifespan. This complexity has also been shown by a recent study observing that cortical neuronal responses to temporal features of an acoustic stimulus depend not only on the hemisphere but also on the type of the stimulus (modulated noise, modulated tones, clicks), and age (Bures et al., 2021). Taken together, our results lead to the assumption that age-related plasticity combined with hearing loss, may lead to a variation of hemispheric preferences over the lifespan and a further understanding of this lateralization plasticity could help to better understand how the ageing brain tries to counteract hearing loss. But it will take longitudinal studies to see if neuroplasticity is really the consequence of hearing loss/ageing.

For speech in noise recognition, as expected, we found not only a significant correlation with a CT cluster situated in auditory-related areas (STG and PP), but also the involvement of higher order language-related areas in the PFC region (transverse frontopolar gyrus and sulcus), which further emphasizes the importance of the frontal lobe for SiN processing especially in older adults with and without hearing impairment (see, e.g., also Giroud et al., 2018). Taken together, our results let assume that different kinds of supra-threshold auditory measures as well as SiN recognition are differently associated with alterations in brain structure in a way that higher pure-tone thresholds and poorer supra-threshold auditory perception as well as SiN recognition are all related to cortical thinning and volume loss but not related to alterations in surface area. These findings underline the hypothesis that it is especially CT that undergoes age-related alterations in the context of auditory processing and that it seems to be more sensitive to age-related changes compared with CSA. Furthermore, our results support the proposed differential associations between different measures of tone and speech processing (i.e., thresholds, supra-threshold measures, and SiN recognition) and morphological metrics, suggesting that these different measures lead to potentially different consequences in the brain (e.g., involving different brain areas) although they arise in part from damage in hair cells (e.g., higher PTA, lower frequency selectivity), which, however, should be further investigated in longitudinal studies. Moreover, the results emphasize the importance of looking at age-related hearing loss much more broadly than just on the basis of pure-tone thresholds, as it has often been done in the past. Based on these results, it can be assumed that higher auditory thresholds and supra-threshold measures of auditory perceptual difficulties might require different treatment approaches. Thus, hearing aids, which mostly address deficits in audibility (by amplifying sounds), could be combined with training approaches that focus on supra-threshold auditory processing and speech comprehension in adverse listening conditions.

Further, our results show that the separate consideration of CV, CT, and CSA provides additional information when investigating brain structure and hearing acuity in old age and is crucial to further clarify the specific plastic characteristics of CT and CSA that have not yet been elucidated.

AUTHOR CONTRIBUTIONS

Pia Neuschwander conducted the experiments, analysed the data, and wrote the first version of the manuscript. Raffael Schmitt assisted in the experiments, contributed to the data analyses, and edited the manuscript. Laura Jagoda and Ira Kurthen helped with data collection. Nathalie Giroud and Martin Meyer designed the experiment, supervised the project, wrote part of the manuscript, and edited the rest of the manuscript. All authors contributed to data interpretation and have read the manuscript.

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CONFLICT OF INTERESTS STATEMENT

We state that there are no competing interests.

DATA AVAILABILITY STATEMENT

All data will be made available upon reasonable request.

PEER REVIEW

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ORCID

Pia Neuschwander https://orcid.org/0000-0003-0897-7265
Nathalie Giroud https://orcid.org/0000-0002-9632-5795

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