



Audio-visual speech processing in age-related hearing loss: Stronger integration and increased frontal lobe recruitment

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ABSTRACT

Hearing loss is associated with difficulties in understanding speech, especially under adverse listening conditions. In these situations, seeing the speaker improves speech intelligibility in hearing-impaired participants. On the neuronal level, previous research has shown cross-modal plastic reorganization in the auditory cortex following hearing loss leading to altered processing of auditory, visual and audio-visual information. However, how reduced auditory input effects audio-visual speech perception in hearing-impaired subjects is largely unknown. We here investigated the impact of mild to moderate age-related hearing loss on processing audio-visual speech using functional magnetic resonance imaging. Normal-hearing and hearing-impaired participants performed two audio-visual speech integration tasks: a sentence detection task inside the scanner and the McGurk illusion outside the scanner. Both tasks consisted of congruent and incongruent audio-visual conditions, as well as auditory-only and visual-only conditions. We found a significantly stronger McGurk illusion in the hearing-impaired participants, which indicates stronger audio-visual integration. Neurally, hearing loss was associated with an increased recruitment of frontal brain areas when processing incongruent audio-visual, auditory and also visual speech stimuli, which may reflect the increased effort to perform the task. Hearing loss modulated both the audio-visual integration strength measured with the McGurk illusion and brain activation in frontal areas in the sentence task, showing stronger integration and higher brain activation with increasing hearing loss. Incongruent compared to congruent audio-visual speech revealed an opposite brain activation pattern in left ventral postcentral gyrus in both groups, with higher activation in hearing-impaired participants in the incongruent condition. Our results indicate that already mild to moderate hearing loss impacts audio-visual speech processing accompanied by changes in brain activation particularly involving frontal areas. These changes are modulated by the extent of hearing loss.

Introduction

Age-related hearing loss (presbycusis) is characterized by a loss of hearing abilities for high frequencies. Therefore, hearing-impaired people have difficulties understanding speech rather than a general hearing inability (Cardin, 2016; Lin, 2012). Speech perception, however, rarely occurs under perfect conditions but rather in the presence of background noise or multiple speakers, which is especially challenging in older people (Helfer and Freyman, 2008; Wong et al., 2009, 2010). In general, speech perception is multisensory and includes the integration of auditory and visual input. There is clear evidence that the visual input in audio-visual speech can facilitate speech understanding (Campbell,

2008; Driver and Noesselt, 2008; Grant and Seitz, 2000; Irwin and DiBlasi, 2017; Rosenblum, 2008; Ross et al., 2007; Sumbly and Pollack, 1954) and working memory for speech (Frtusova and Phillips, 2016). Hence, the visual information in audio-visual speech conveyed by lip-movements seems to be particularly important for hearing-impaired listeners to improve speech intelligibility (Auer and Bernstein, 2007; Bishop and Miller, 2009; Grant et al., 1998; Moradi et al., 2016).

Hearing loss does not only affect the sensory processing of speech itself, but impacts on the available neural resources that are needed for cognitive control (Cardin, 2016; Humes et al., 2013; Lin et al., 2011). Several cognitive abilities such as working memory, attention switching and interference control decline with increasing age (Cardin, 2016;

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Wingfield et al., 2005). Therefore, the increased effort in understanding speech may further decrease cognitive capacities in hearing-impaired elderly participants (Peelle and Wingfield, 2016; Moradi et al., 2014; Rönnberg et al., 2013; Tun et al., 2009). Hearing loss also negatively impacts long-term memory (Rönnberg et al., 2011). Linguistic knowledge and verbal intelligence quotient may, on the other side, lead to an effective compensation (Wingfield et al., 1995; Thiel et al., 2016). Furthermore, an increased working memory capacity was found to improve speech intelligibility in hearing-impaired people with or without hearing aids (Anderson et al., 2013; Arehart et al., 2013; Moradi et al., 2014; Rönnberg et al., 2013; Souza and Arehart, 2015).

Likewise, several neural changes have been described in the hearing-impaired. An additional recruitment of frontal areas is related to the increased listening effort and therefore supposed to compensate for the decreased auditory input due to the hearing loss (Berding et al., 2015; Campbell and Sharma, 2013; Erb and Obleser, 2013; Davis and Johnsrude, 2003; Hervais-Adelman et al., 2012; Lee et al., 2016; Peelle et al., 2011; Reuter-Lorenz and Cappell, 2008; Tyler et al., 2010; Wong et al., 2009). Most studies focused however on cross-modal plasticity and found increased neural responses to visual input in the auditory cortex comprising Brodmann areas 41, 42 and 22, after complete loss of function (Allman et al., 2009; Lambertz et al., 2005; Lazard and Giraud, 2017; Lomber et al., 2010; Merabet and Pascual-Leone, 2010; Meredith et al., 2012; Rettenbach et al., 1999; Schierholz et al., 2015) but recently also in subjects with moderate hearing-impairment (Campbell and Sharma, 2013, 2014). As a consequence, the cortical processing of auditory, visual and audio-visual information is affected (Champoux et al., 2009; Musacchia et al., 2009; Peelle et al., 2011; Sandmann et al., 2012). We have previously shown that even mildly to moderately hearing-impaired listeners rely more on additional visual information than normal-hearing listeners during an auditory stimulus categorization task, which led to higher distraction by nonmatching visual input (Puschmann et al., 2014). In a subsequent brain imaging study in the same population, the extent of hearing loss was related to a changed cross-modal connectivity between visual and auditory cortex when processing audio-visual input, as well as to an altered resting-state connectivity between auditory and visual cortex (Puschmann and Thiel, 2017).

In patients with cochlear implants, cross-modal plasticity in the temporal cortex was shown to correlate with poor speech perception outcome (Chen et al., 2016; Kim et al., 2016; Lazard and Giraud, 2017; Sandmann et al., 2012). On the other hand, cross-modal reorganization correlated with good visual speech-reading abilities in deaf patients (Lee et al., 2007) and with good face recognition and lip reading abilities in cochlear implant users (Stropahl et al., 2015). Additionally, patients with a cochlear implant showed an increased benefit for congruent audio-visual speech due to an increased coupling between visual and auditory cortex (Song et al., 2015; Strelnikov et al., 2015). A recent

electroencephalography study showed a relationship between cross-modal activation in the auditory cortex and audio-visual integration strength in cochlear implant patients (Stropahl and Debener, 2017). Cross-modal plasticity was mostly found in the right temporal cortex (Kim et al., 2016; Lazard and Giraud, 2017; Lee et al., 2007; Sandmann et al., 2012; Stropahl et al., 2015; Stropahl and Debener, 2017), but there are also studies showing cross-modal plasticity in the left hemisphere (Chen et al., 2016) or in both hemispheres (Sandmann et al., 2012).

Up to now, however, the influence of reduced auditory input on audio-visual speech processing in hearing-impaired subjects is largely unknown. Therefore, we investigated neural processing of audio-visual speech in mild to moderate hearing-impaired subjects. We used functional magnetic resonance imaging (fMRI) while subjects performed an audio-visual sentence task with congruent and incongruent audio-visual conditions as well as unimodal conditions at individually matched speech intelligibility thresholds (auditory speech intelligibility of 80%). In addition, outside the scanner, subjects performed a widely-used assay for audio-visual integration, the McGurk task. In this task incongruent audio-visual syllables are presented leading to an illusory percept, e.g. an auditory 'ba' and a visual 'ga' lead to the perception of a 'da' sound (Irwin and DiBlasi, 2017; MacDonald and McGurk, 1978; McGurk and MacDonald, 1976).

Our main aim was to answer the question, whether hearing-impaired subjects show stronger audio-visual integration when processing audio-visual speech. If this was the case we would expect i) an increased McGurk effect, ii) differences in neural activity in the congruent audio-visual condition, e.g. increased coupling of auditory and visual cortex and iii) increased distraction-related brain activity with incongruent audio-visual speech in the hearing-impaired as a function of hearing loss.

Methods

Participants

Twenty hearing-impaired subjects with a mean age of 63.5 ± 5.4 years and nineteen normal-hearing participants with a mean age of 63.2 ± 5 years participated in this study. The group of hearing-impaired subjects showed a uniformly varying degree of age-related hearing loss. The hearing loss was mild to moderate, symmetrical and affected the high frequencies. The group of healthy subjects showed no hearing impairment defined by 30 dB HL or better for octave frequencies between 125 and 3000 Hz as well as less than 30 dB HL for the mean value over 2000, 4000, 6000 and 8000 Hz (cf. WHO, 2001 definition of hearing loss; von Gablenz and Holube, 2015). None of the participants reported current or previous use of a hearing aid. Individual pure tone audiograms averaged over both ears for the two groups are depicted in Fig. 1. Mean values for the high frequencies (2 to 8 kHz) were 39.52 ± 10.25 dB for

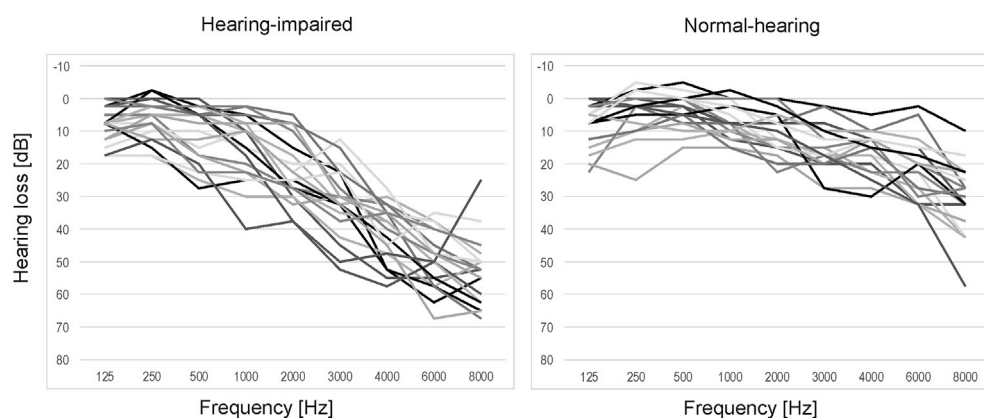


Fig. 1. Individual pure tone audiograms for hearing-impaired (left) and normal-hearing (right) subjects averaged over both ears. For each subject the individual high-frequency hearing loss (average hearing threshold between 2 and 8 kHz) was used for further analysis.

the hearing-impaired group and 18.92 ± 5.63 dB for the normal-hearing group. Mean values for the low frequencies (125–1000 Hz) were 6.14 ± 6.93 dB for the hearing-impaired group and 6.52 ± 5.16 dB for the normal-hearing group.

All participants were right-handed. Several of the volunteers also participated in other studies, in which they performed the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005), a screening instrument for mild cognitive impairment. From these measurements we have values for 18 of our participants (8 hearing-impaired and 10 normal-hearing participants) with mean values of 26 for each group (26.13 for hearing-impaired and 26.6 for normal-hearing participants), indicating normal cognitive functioning and no significant difference between both groups.

Exclusion criteria for participation were previous or current psychiatric or neurological disorders. The study was approved by the local ethics committee of the University of Oldenburg “Kommission für Forschungsfolgenabschätzung und Ethik” (Committee for research outcome assessment and ethics) and carried out in accordance with the Declaration of Helsinki. All subjects signed a written informed consent form and were paid for participation.

Stimuli

Audio-visual sentence task

The audio-visual stimulus material consisted of the *Oldenburg Linguistically and Audiologically Controlled Sentences* (OLACS; Uslar et al., 2013). In this study 128 randomly selected seven-word-sentences (declarative or relative clauses with either subject-before-object or object-before-subject structure) were used.

The stimulus material was recorded in the recording studio of the Department of Media Production at the University of Oldenburg. A male speaker was recorded with a Nikon D800 DSLR camera and a directional Sennheiser ME 66 microphone in front of a dark grey background. After recording, the videos were separated into a visual and an auditory file. Noise removal was conducted with Audacity® audio editor (<http://audacityteam.org>).

The experiment consisted of four different stimulation conditions: auditory-only, visual-only, congruent and incongruent audio-visual stimulation. All sentences were presented for 4000 ms. In the auditory-only condition, a dark grey fixation cross was presented on a moderately grey background while the speaker's voice was heard. In the visual-only condition, the speaker was visible but no auditory input was given. In the audio-visual stimulation, the speaker was both visible and audible. During the incongruent condition, the auditory and visual stimuli did not belong to the same sentence, but no stimulus was presented twice. The matching of the incongruent stimuli was done with respect to the duration and number of syllables of the sentence. In congruent conditions, both auditory and visual stimuli belonged to the same sentence. All sentences were only presented once.

After sentence presentation two nouns were presented for 3000 ms on the screen (one on the left and one on the right side). The task for the participants was to identify which of the nouns was present in the previous sentence (two-alternative forced-choice task). Answers were given via button press (index finger for the left word and middle finger for the right word). In the audio-visual incongruent condition, the target word was always coming from the auditory input, we excluded that the distractor word appeared in the visual input. Participants were instructed to fixate the fixation cross during auditory stimulation and to look at the center of the speaker's face during visual and audio-visual presentation.

The different conditions were presented intermixed, while the presentation order was the same for all participants. Each condition consisted of 32 trials, leading to 128 trials in total. The inter-trial-interval was 1000 ms. The whole experiment lasted for 18 min. Stimulus presentation was controlled by Presentation® software (Version 18.3, Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com).

Visual stimuli were presented by a projector (DLA-G15E, JVC

Professional, Japan) on a screen which was mounted in the rear of the scanner bore at a distance of 50 cm from eye to screen. Participants lied in the scanner with lights off and they were able to look at the stimuli via a mirror attached to the head coil. Auditory stimuli were presented via MR compatible headphones (Opto Active, Optoacoustics Ltd, Israel). For the presentation over headphones, the active noise-cancelling feature to cancel out the MR EPI main gradient noise was used. The mean sound level presentation for this task was $71.35 (\pm 4.7)$ dB in the hearing-impaired group and $72.53 (\pm 5.7)$ dB in the normal-hearing group. The lowest value was 61.4 dB, the highest 83.1 dB.

McGurk task

Stimuli for the McGurk test were also recorded in the recording studio of the Department of the Media Production at the University of Oldenburg with the same speaker. The experiment included presentation of congruent audio-visual, auditory-only, visual-only and the typical McGurk illusion (incongruent audio-visual) syllables. Syllables to measure the McGurk illusion were auditory ‘ba’/visual ‘ga’, leading to the fusion percept of ‘da’, auditory ‘ba’/visual ‘ta’ leading to the fusion percept of ‘da’ and auditory ‘pa’/visual ‘ka’ leading to the fusion percept of ‘ta’. These combinations were chosen based on their probability to induce a fusion effect in healthy, German speaking volunteers (Stropahl et al., 2016). For the McGurk illusion, fifteen trials per ‘illusion syllable’ were presented (45 trials in total). For the congruent audio-visual, auditory-only and visual-only conditions, 42 trials for each condition were presented leading to 171 trials for the whole experiment, which comprised approx. 15 min. Each trial began with a blank screen (grey background; 1000 ms) followed by a jittered fixation phase (600–800ms). After stimulus presentation (2000 ms), four different syllables were presented on the screen from which the answer had to be chosen (four-alternative-forced choice). The response options alternated across trials and conditions. In the McGurk trials the possible illusion, the auditory input and the visual input were always included in the response options. Syllables were provided with numbers one to four which had to be pressed on the keyboard to choose the respective syllable. The next trial only started after a response was given. Note that these stimuli were presented outside the MRI at a constant loudness level of 68 dB.

Experimental procedure

The study consisted of two magnetic resonance imaging (MRI) measurement sessions separated by a 10 min break. Before that, a short practice of the main experiment – in which each condition was presented once – was conducted. To ensure that all subjects were able to understand the auditory input in the adverse environment of the scanner we first performed a well validated matrix sentence test (Oldenburger Satztest, OLSA; Wagener et al., 1999a; b; c) to assess the individual's 80% speech intelligibility threshold under scanner noise (same sequence as in main experiment). This test lasted for 10 min, and the determined loudness level was then used for the following presentation of the auditory, visual and audio-visual stimuli to avoid that possible differences in neural activity are confounded by individual differences in speech intelligibility. Subsequently the audio-visual sentence detection task followed presented at the respective loudness level determined by the auditory matrix sentence test. Subjects were subsequently removed from the scanner for a break and filled out questionnaires about the experiment, a handedness inventory (Oldfield, 1971) and a listening effort questionnaire (“Höranstrengungsbogen”; Schulte et al., 2015). After the break, a resting state MRI, an anatomical MRI and a diffusion tensor imaging (DTI) were measured. After the two MRI sessions, subjects performed the Size comparison span (SICSPAN; Sörqvist et al., 2010) as a measure of working memory and the McGurk test to gauge audio-visual integration. Finally, a pure tone audiometry of the frequencies 125, 250, 500, 1000, 2000, 4000, 6000 and 8000 Hz was conducted.

Data acquisition

A 3T whole-body Siemens Magnetom Prisma MRI machine with a 20-channel head coil was used. Functional images were acquired with an ascending echo-planar imaging (EPI) sequence (TR = 1500 ms, TE = 30 ms, flip angle = 75°, df = 40, slice thickness: 3 mm, 25 slices). Structural images were acquired with a 3-D T1-weighted sequence (MP-RAGE, TR = 2300, TE = 4.16, slice thickness 1 mm, 176 sagittal slices).

fMRI data analysis

We analyzed the imaging data with the Statistical Parametric Mapping software package (SPM12, Wellcome Department of Imaging Neuroscience, London, UK) based on Matlab 2015b. Preprocessing of each dataset included slice-timing offset correction, realignment estimation, normalization to the Montreal Neurological Institute (MNI) stereotactic space using normalization parameters obtained from a segmentation of the anatomical T1-weighted image, and Gaussian smoothing (full width half maximum = 8 mm). In the first level analysis, a temporal high pass filter (128s) was applied and temporal autocorrelations across scans were modeled with an AR (1) model. Head movement parameters were entered as additional regressors and the four different conditions (congruent audio-visual, incongruent audio-visual, auditory-only and visual-only) were individually modeled with the canonical hemodynamic response function. The general linear model was used to calculate regression coefficients (betas) for each regressor at each measured voxel in the brain and linear contrasts between these betas. The following contrast estimates were taken to the between subjects level ("second level") to calculate within- and between-group effects using one- or two-sample t-tests respectively: congruent audio-visual input vs. baseline, incongruent audio-visual input vs. baseline, auditory-only input vs. baseline, visual-only input vs. baseline, and incongruent vs. congruent audio-visual input. Peak beta values from these contrasts were extracted for a correlational analysis with high-frequency hearing loss and behavioral data. To test the hypotheses of an increased coupling between auditory and visual cortex for congruent versus incongruent audio-visual speech in hearing-impaired participants, a functional connectivity analysis as in Puschmann and Thiel (2017) was applied. Seeds in visual cortex (MNI coordinates: -10, -100, 12) and auditory cortex (MNI coordinates: -56, -10, 2) were selected based on their highest peak of visual and auditory evoked BOLD activation. On the group level, between-subject comparisons were computed (hearing-impaired > normal-hearing participants), in addition a multiple regression analysis with high-frequency hearing-loss, listening effort values, and McGurk illusion was performed across both groups. For the fMRI data, effects were determined to be significant when passing a threshold of $p < 0.05$ (FWE cluster size inference with $p = 0.001$ cluster-forming threshold). Peak coordinates are reported in MNI space.

Behavioral data analysis

For each subject the individual high-frequency hearing loss (average hearing threshold between 2 and 8 kHz) was used for further analysis (correlation with fMRI and behavioral data). In each subject, performances in all four conditions in the audio-visual sentence detection task and in the McGurk test were analyzed. In addition, responses in the McGurk incongruent (illusion) trials were scored according to the three possible answers: responses to the auditory input ("ba", "ba", "pa"), responses to the visual input ("ga", "ta", "ka") or the resulting fusion responses ("da", "da", "ta" respectively). Percentage values for each possible condition were then computed involving the percentage of answers for fusion, auditory and visual responses in the incongruent (illusion) trials. Differences between conditions and groups in the McGurk and sentence task were assessed using repeated measures ANOVA and group differences in working memory and listening effort were assessed by two-tailed t-tests. Pearson's correlation served to assess the relationship between

hearing loss, task performance and measures of listening effort and working memory capacity (two-tailed; Bonferroni-corrected). All figures include mean values and the standard error which was chosen to indicate the standard deviation of the mean, i.e. the precision of the measurement.

Results

Behavioral data

Performance in the audio-visual sentence task was best for the congruent audio-visual condition, followed by the auditory-only condition, audio-visual incongruent condition and visual-only condition [main effect of condition $F(3; 111) = 283.294$, $p < 0.001$, $\eta^2 = 0.884$; Fig. 2]. Post-hoc paired t-tests revealed that all conditions significantly differed from each other: audio-visual congruent stimulation differed from incongruent ($T(38) = 10.906$; $p < 0.001$; $d = 1.166$), auditory ($T(38) = 7.347$; $p < 0.001$; $d = 0.668$) and visual stimulation ($T(38) = 22.269$; $p < 0.001$; $d = 4.009$), incongruent audio-visual stimulation differed from auditory ($T(38) = -3.835$; $p = 0.001$; $d = 0.422$) and visual stimulation ($T(38) = 16.615$; $p < 0.001$; $d = 2.868$), and auditory and visual stimulation significantly differed from each other ($T(38) = 17.172$; $p < 0.001$; $d = 3.129$). Performance in hearing-impaired subjects did not differ from performance in normal-hearing participants (main effect of group $p = 0.866$; $\eta^2 = 0.001$), nor was there an interaction between group and condition ($p = 0.609$, $\eta^2 = 0.016$). Performance data in the hearing-impaired did not correlate with the extent of high-frequency hearing loss, listening effort or working memory (all correlations $p > 0.1$). Hence, even though we found a clear benefit of congruent audio-visual speech, this benefit was present to a similar extent in normal-hearing and hearing-impaired subjects when auditory stimuli were presented at 80% speech intelligibility threshold.

In the McGurk task a significant effect of presentation condition was also evident [main effect of condition $F(3; 111) = 95.195$, $p < 0.001$; $\eta^2 = 0.72$], although post-hoc paired comparisons revealed no clear benefit of congruent audio-visual syllables as compared to auditory syllables ($T(38) = 0.636$; $p = 0.545$; $d = 0.03$). The improvement of visual to auditory ($T(38) = -14.939$; $p < 0.001$; $d = 2.402$) and visual to congruent audio-visual ($T(38) = -15.414$; $p < 0.001$; $d = 2.428$) conditions was significant. Obtained mean values for the visual condition were 44% ($\pm 14\%$) for the hearing-impaired and 44% ($\pm 13\%$) for the normal-hearing participants, in the auditory condition 85% ($\pm 24\%$) for the hearing-impaired and 89 ($\pm 19\%$) for the normal-hearing participants

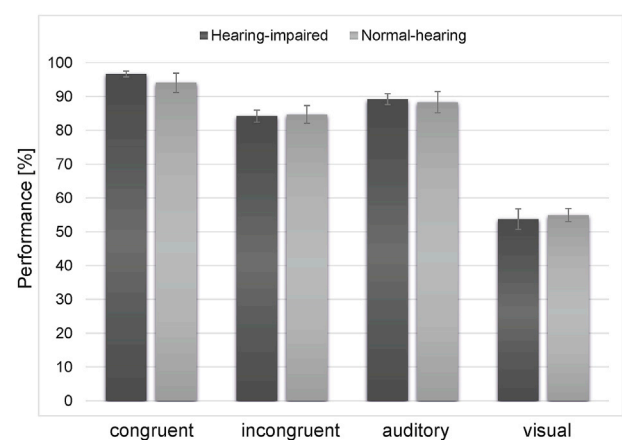


Fig. 2. Performance in the audio-visual sentence-detection task for the different conditions (congruent and incongruent audio-visual, auditory-only and visual-only). A significant main effect of presentation condition was obtained ($p < 0.001$), with all four conditions significantly differing from each other. No significant differences between hearing-impaired and normal-hearing subjects were observed ($p > 0.1$). [Mean values with standard error].

and 86% ($\pm 25\%$) for the hearing-impaired and 90% ($\pm 19\%$) for the normal-hearing participants in the congruent McGurk condition. The main analysis in this task is however the McGurk effect that occurs in incongruent audio-visual trials which can either lead to an illusion response (integration of visual and auditory syllable resulting in perception of a third syllable), or a response relying on the auditory syllable or visual syllable (Fig. 3). Hearing-impaired participants chose significantly more often the illusion response (50.1%) compared to normal-hearing subjects (23.5%; [T (37) = 3.574; $p = 0.001$; $d = 1.145$]). Hearing-impaired participants chose the auditory response only in 31.6% of trials whereas normal-hearing participants chose that response in 58.6% of the incongruent trials (T (37) = -3.167; $p = 0.003$; $d = 1.011$), showing a stronger auditory bias. The extent of hearing loss correlated positively with the McGurk illusion response ($r = 0.574$; $p < 0.001$) and negatively with the McGurk auditory response ($r = -0.517$; $p = 0.001$). Visual responses in McGurk trials were given in 9.7% in the hearing-impaired and 11.5% in the normal-hearing subjects and did not significantly differ between groups (T (37) = -0.508; $p = 0.614$; $d = 0.162$). In all congruent audio-visual, auditory-only and visual-only conditions no significant difference between both groups was obtained (main effect of group $p = 0.315$; $\eta^2 = 0.027$). Hence, the hearing-impaired participants showed stronger audio-visual integration indicated by a significantly higher McGurk illusion. Across both groups, increasing hearing loss increased audio-visual integration and reduced the auditory bias.

Measures of working memory capacity did not significantly differ between hearing-impaired and normal-hearing subjects (T (37) = -0.364; $p = 0.718$, $d = 0.117$), nor was there a correlation with performance in the audio-visual sentence or McGurk task ($p > 0.1$). Listening effort was significantly higher in the hearing-impaired group than in the normal-hearing participants (T (36) = 2.302; $p = 0.027$; $d = 0.747$), but did not correlate with performance in the audio-visual sentence or McGurk task (all correlations $p > 0.1$).

Neural activity in audio-visual and unimodal sentence conditions

A first analysis focused on comparing neural activity in the audio-visual sentence task between normal-hearing and hearing-impaired subjects. Fig. 4 displays neural activity as a function of condition (congruent, incongruent, auditory, and visual) in hearing-impaired and normal-hearing participants as well as the difference between both groups (hearing-impaired > normal-hearing participants) in these conditions. In normal-hearing participants, the different stimulation conditions primarily activated visual, including fusiform face area, and auditory cortices. In the audio-visual conditions, parts of the left premotor cortex also showed an increased activation. Hearing-impaired subjects presented not only a more widespread activation pattern including visual and auditory cortices, but also precentral gyrus, premotor and motor cortices, medial and middle frontal gyri and the

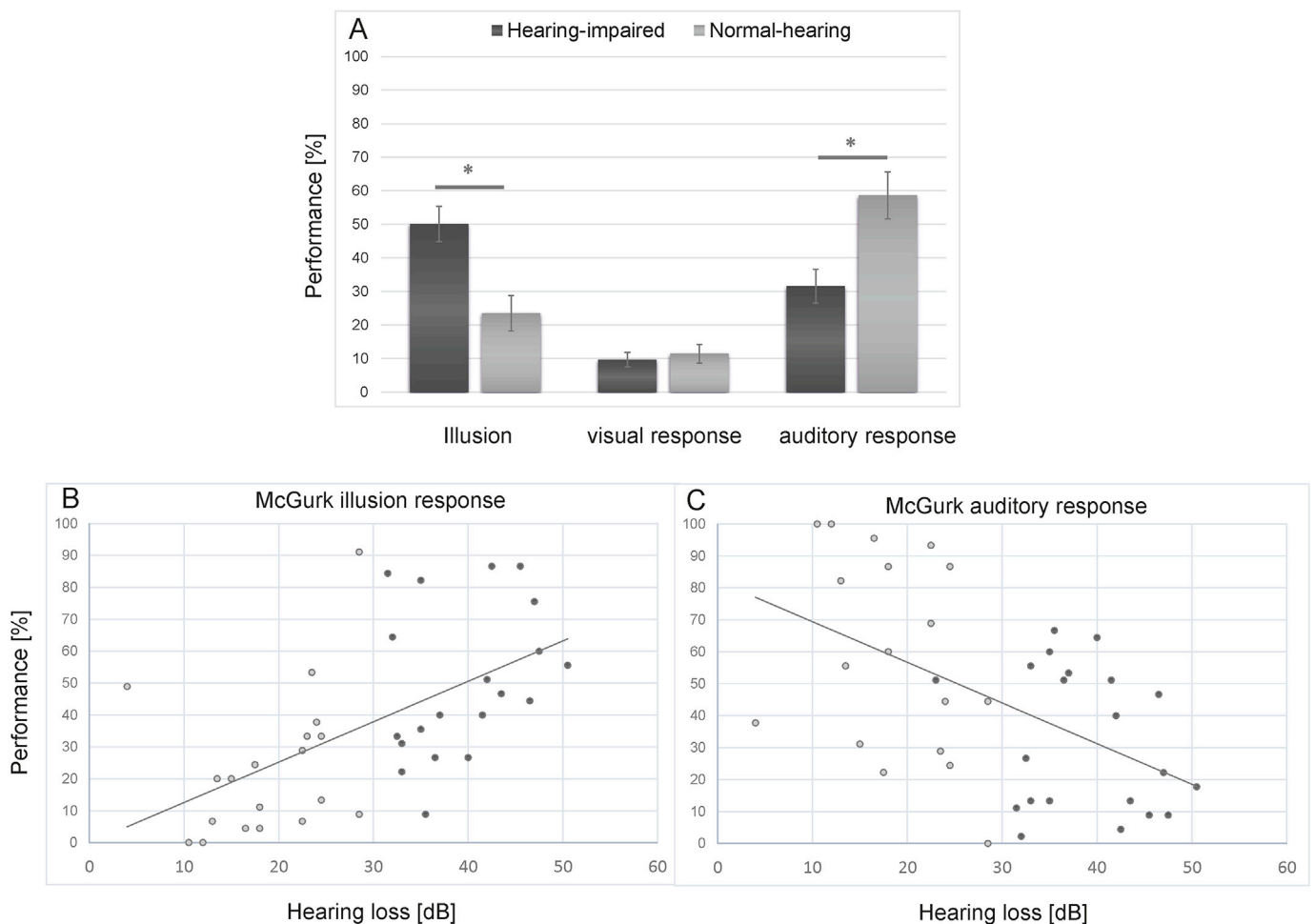


Fig. 3. Performance in the McGurk incongruent (illusion) trials. (A): Possible answers were the illusion (integration of auditory and visual syllable), the auditory or the visual input. Hearing-impaired subjects were significantly more prone to the illusion and relied significantly less on the auditory input. (* $p < 0.05$). [Mean values with standard error]. (B) and (C): Correlation between hearing loss and McGurk illusion and auditory response. A significant positive correlation between hearing loss and McGurk illusion response (B) as well as a negative correlation between hearing loss and the McGurk auditory response (C) was observed ($p < 0.05$; Bonferroni-corrected). Bright dots depict data of normal-hearing subjects while dark dots represent data of hearing-impaired subjects.

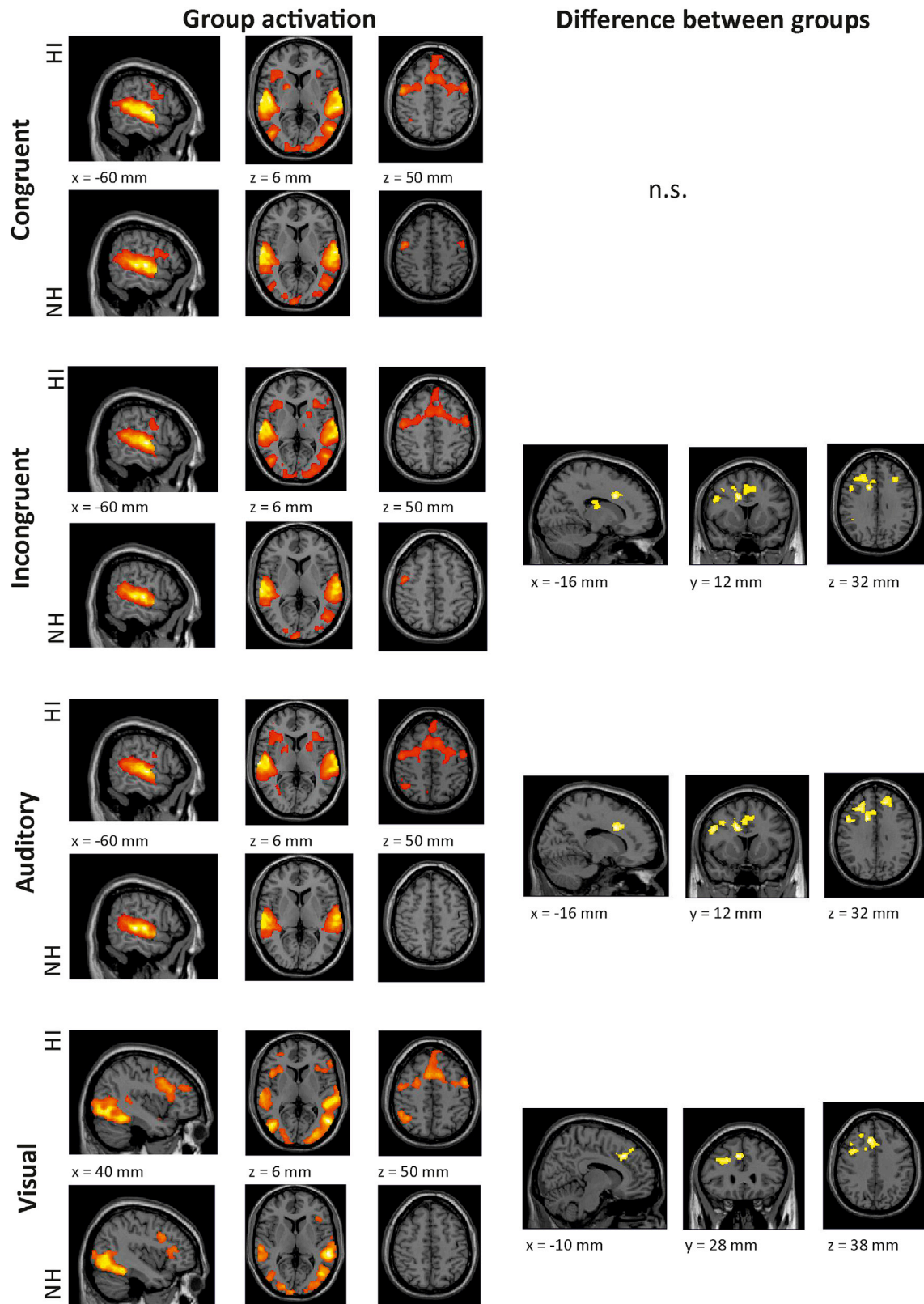


Fig. 4. Activation patterns for all four stimulation conditions for each group and difference in activation between groups. Left: Activation patterns for congruent, incongruent, auditory and visual input for each group. Hearing-impaired subjects (HI) presented on top and normal-hearing subjects (NH) presented on bottom of each condition. Activated areas include visual and auditory cortices, fusiform face area, precentral gyrus, premotor and motor cortices, medial and middle frontal gyri and the cingulate cortex [$p < 0.05$; FWE corrected on the cluster level]. Right: Results of comparison of both groups (two-sample t-test: Hearing-impaired > normal-hearing participants) were only significant for incongruent, auditory and visual input, showing higher activation in medial, middle and inferior frontal gyri, as well as cingulate cortex [$p < 0.05$; FWE corrected on the cluster level].

cingulate cortex under all conditions including the unimodal ones. Visual activation was more prominent in the right hemisphere in both groups. Peak coordinates for both groups under different stimulation conditions are displayed in Table 1.

Contrary to our hypothesis, we found no significant differences in neural activity in the congruent audio-visual condition between normal-hearing and hearing-impaired subjects. A post hoc performed functional connectivity analysis did also not provide any evidence for changed coupling between auditory and visual regions. Our results revealed however striking differences in frontal activity in the visual, auditory and incongruent audio-visual condition. Hearing-impaired subjects showed higher brain activation in medial, middle and inferior frontal gyri, as well as cingulate cortex. Additionally, higher activation in the lateral nucleus of the thalamus in the auditory condition and higher activation in the pulvinar in the incongruent condition was obtained.

To investigate whether these group differences are modulated by the extent of hearing loss, we correlated mean high frequency hearing loss with peak beta values in these regions. We found a hearing loss related modulation of brain activation in the cingulate cortex ($r = 0.591$; $p < 0.001$), medial frontal gyrus ($r = 0.619$; $p < 0.001$) and the lateral nucleus of the thalamus ($r = 0.482$; $p = 0.002$) for the auditory condition. In the incongruent audio-visual condition hearing loss was positively correlated with brain activation in the pulvinar nucleus ($r = 0.564$; $p < 0.001$), cingulate gyrus ($r = 0.591$; $p < 0.001$) and middle frontal gyrus ($r = 0.562$; $p < 0.001$). Note that increasing hearing loss was also related to these prefrontal activity increases in the visual condition (medial frontal gyrus: $r = 0.579$; $p < 0.001$; middle frontal gyrus:

$r = 0.511$; $p = 0.001$; inferior frontal gyrus $r = 0.535$; $p < 0.001$). Neural activity in these regions also correlated with the McGurk task illusion (number of fusions). Correlation values were: cingulate cortex ($r = 0.448$; $p = 0.004$), medial frontal gyrus ($r = 0.407$; $p = 0.01$) and the lateral nucleus of the thalamus ($r = 0.339$; $p = 0.035$) for the auditory condition; pulvinar nucleus ($r = 0.332$; $p = 0.039$), cingulate gyrus ($r = 0.384$; $p = 0.016$) and middle frontal gyrus ($r = 0.51$; $p = 0.001$) for the incongruent condition; and medial frontal gyrus ($r = 0.429$; $p = 0.006$), middle frontal gyrus ($r = 0.445$; $p = 0.005$) and inferior frontal gyrus ($r = 0.529$; $p = 0.001$) in the visual condition.

Comparison of neural activity for the incongruent as compared to the congruent audio-visual sentence condition

To investigate whether higher audio-visual integration in the hearing-impaired may induce higher distractibility by incongruent audio-visual input we assessed BOLD response differences when processing incongruent compared to congruent audio-visual speech in the hearing-impaired as compared to normal-hearing subjects. Differences between both groups were found in the left ventral postcentral gyrus, with higher activation obtained in the hearing-impaired group, especially in the incongruent audio-visual condition (Fig. 5A). Extraction of beta values from this peak (MNI coordinates: $-62, -16, 24$) illustrates this effect (Fig. 5B). To investigate whether this activation is related to the extent of hearing loss, we extracted the beta values of the difference contrast and entered these into a correlation analysis which provides evidence for a significant positive correlation ($r = 0.507$; $p = 0.001$; Fig. 5C). Two one-

Table 1
Peak MNI coordinates for different stimulation conditions for each group.

Condition	Group	Peak coordinates (x,y,z)	Z-value	Cluster size	Brain region		
Audio-visual congruent	Hearing-impaired	(-64, -18, 6)	7.03	27855	Auditory cortex		
		(-12, -24, -2)	4.25	729	Midbrain		
	Normal-hearing	(-60, -14, 2)	7.19	5289	Auditory cortex		
		(62, -16, 6)	7.08	8949			
		(-44, -2, 48)	5.42	324	Premotor cortex		
		(48, 0, 48)	4.49	191			
		(0, 34, -22)	4.09	590	Orbitofrontal cortex		
		(42, 24, 14)	4.05	407	Inferior frontal gyrus		
		(12, -22, 32)	3.93	478	Cingulate cortex		
		(-10, 54, 30)	3.93	202	Superior frontal gyrus		
		Audio-visual incongruent	Hearing-impaired	(-58, -10, 2)	7.47	14295	Auditory cortex
				(60, -6, 2)	7.41	11541	
				(-6, -26, -8)	4.14	437	Midbrain
				(6, -32, 34)	3.86	331	Cingulate cortex
Normal-hearing	(-58, -14, 2)		7.26	3923	Auditory cortex		
	(52, -24, 0)		6.9	3532			
	(20, -92, 18)		5.7	1300	Visual cortex		
	(4, -80, -2)		5.5	270			
	(42, -44, -18)		5.24	1509	Fusiform gyrus		
	(-44, -2, 48)		5.19	210	Premotor cortex		
	(24, -40, 30)		4.33	398	Sub-Gyral		
	Auditory		Hearing-impaired	(-56, -10, 2)	7.51	19463	Auditory cortex
				(60, -6, 2)	7.44	5877	
				(6, -34, 32)	4.2	619	Cingulate cortex
Normal-hearing		(-60, -28, 2)	7.25	5416	Auditory cortex		
		(54, -22, 0)	6.58	3511			
		(24, 30, -16)	4.4	384	Middle frontal gyrus		
		(50, -64, 6)	6.35	7446	Middle temporal gyrus		
		(-46, -72, 6)	5.86	1789	Middle occipital gyrus		
Visual		Hearing-impaired	(-48, -6, 44)	5.25	4136	Motor cortex	
			(-66, -20, 4)	5.16	1487	Auditory cortex	
			(50, 2, 44)	4.95	2306	Middle frontal gyrus	
			(-28, -54, 28)	4.88	1282	Sub-Gyral	
			(-36, 54, -6)	4.51	380	Middle frontal gyrus	
			(56, -32, 4)	6.21	5545	Auditory cortex	
	(-62, -42, 10)		5.55	1115			
	(-10, -100, 12)		4.94	705	Visual cortex		
	(-48, -8, 44)		4.36	166	Precentral gyrus		
	(-48, -76, 0)		4.76	312	Middle occipital gyrus		
	(44, 16, 30)		4.45	258	Middle frontal gyrus		
	(42, 26, 12)		4.32	225	Inferior frontal gyrus		
	Normal-hearing						

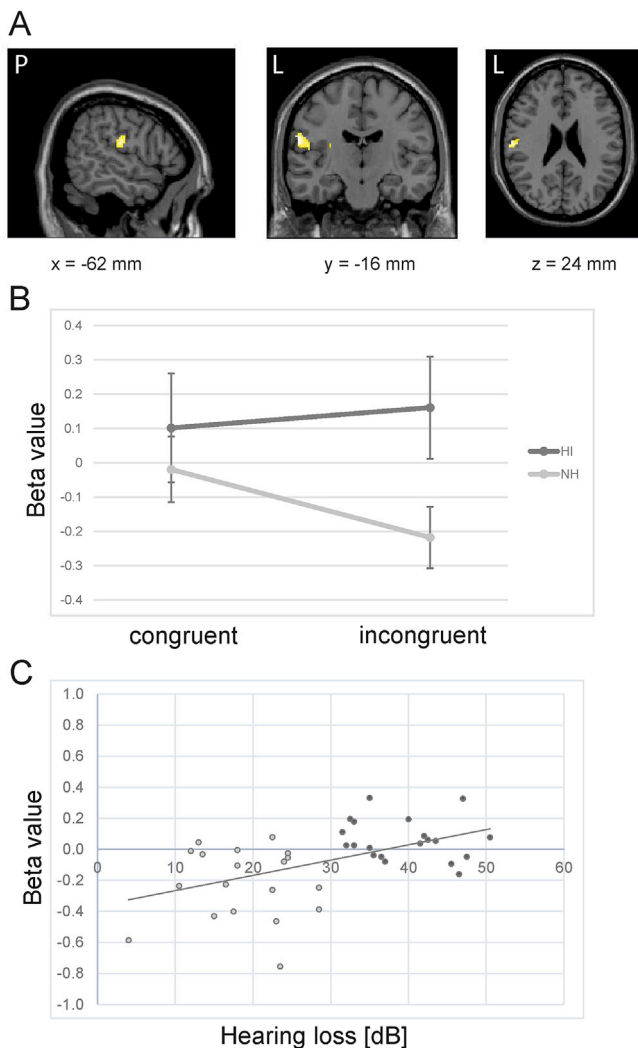


Fig. 5. Activation for incongruent vs. congruent audio-visual input. (A): Group differences (hearing-impaired > normal-hearing participants) in the contrast incongruent vs. congruent were significant in the left ventral postcentral gyrus (MNI coordinates = -62 , -16 , 24). (B): Interaction effect between group \times stimulation condition for incongruent and congruent stimulation (HI = Hearing-impaired subjects, dark line; NH = Normal-hearing subjects, bright line). Both the increase in activation in the HI as well as the decrease in activation in the NH were significant ($p < 0.05$). Mean values with standard error. (C): Correlation between beta value extracted from peak (A) and hearing loss ($r = 0.507$; $p = 0.001$). Bright dots depict data of normal-hearing subjects while dark dots represent data of hearing-impaired subjects.

sided t-tests showed that the increase in activation for the incongruent audio-visual input in the hearing-impaired group ($T = -2.010$; $p = 0.03$) as well as the decrease in activation in the normal-hearing group ($T = 3.736$; $p = 0.001$) were significant. Note that the activation of the left postcentral gyrus did not appear in Fig. 4 where single conditions are compared to rest, because this effect was not strong enough to survive after correcting for multiple comparisons.

Multiple regression analysis

We calculated different multiple regression analyses to test for linear modulatory effects on activation patterns observed for the different contrasts. In the first instance, these included high-frequency hearing-loss and listening effort as regressors. The regression with high-frequency hearing-loss revealed the same results already obtained for the group differences (3.2). Listening effort did not turn out to be a significant

modulator of the BOLD response. Because we found the strong behavioral difference in McGurk illusions between both groups, we performed a third multiple regression, including the amount of McGurk illusions as a regressor. This analysis revealed a significant correlation with brain activation obtained in the auditory-only contrast. Brain regions, whose activity showed a significant correlation with the McGurk illusion, were right and left supramarginal gyrus, middle frontal gyrus and cingulate cortex (Fig. 6).

Discussion

The present study investigated the influence of mild to moderate age-related hearing loss on audio-visual speech processing. For that aim, BOLD response amplitudes elicited by audio-visual speech processing in a sentence task were compared between hearing-impaired and normal-hearing subjects. In addition, a widely-used assay for audio-visual integration, the McGurk effect, was investigated behaviorally. We expected that hearing-impaired subjects show, as a function of hearing loss, i) increased audio-visual integration evident in an increased McGurk effect, ii) differences in neural activity in the congruent audio-visual sentence condition and iii) increased distraction-related brain activity in the incongruent audio-visual sentence condition. Our results confirmed hypotheses one and three, but not hypothesis two.

The behavioral data showed a significantly stronger audio-visual integration (McGurk illusion) in the hearing-impaired subjects. Moreover, there was a significant positive correlation between the extent of high-frequency hearing loss and audio-visual integration with higher hearing loss leading to stronger audio-visual integration. Hearing loss did not modulate neural activity in the congruent audio-visual condition when auditory stimuli were presented at 80% speech intelligibility threshold. We found, however, a hearing loss induced modulation of brain activation in frontal areas when processing auditory-only, visual-only as well as incongruent audio-visual speech, showing higher brain activation with increasing hearing loss. In addition, higher brain activity in supramarginal, cingulate and middle frontal gyri during auditory-only stimulation was associated with stronger audio-visual integration (McGurk illusion). Further, an interaction between audio-visual speech presentation condition (incongruent versus congruent) and group (hearing-impaired versus normal-hearing participants) was obtained in the ventral postcentral gyrus showing an increase in activation in the hearing-impaired group for the incongruent input, whereas the normal-hearing participants showed a decrease in activation for the incongruent audio-visual speech input compared to congruent input.

McGurk effect in age-related hearing loss

A common assay used to investigate audio-visual speech integration is the McGurk illusion (MacDonald and McGurk, 1978; McGurk and MacDonald, 1976). The McGurk illusion here served to investigate audio-visual speech integration skills in age-related hearing loss. As hypothesized, there was an increased audio-visual integration in hearing-impaired subjects, who showed a significantly increased response to the McGurk illusion. Normal-hearing subjects, in contrast, significantly more often chose the auditory response, i.e. the option driven by the auditory input of the McGurk stimuli. Both response behaviors significantly correlated (either positively or negatively) with hearing loss. These results indicate a significant shift from the auditory component to the illusory percept in McGurk stimuli. At the neural level, a whole brain multiple regression revealed a correlation between the McGurk illusion and brain activity in the auditory-only condition in the supramarginal gyri, cingulate cortex and middle frontal gyrus. Further, brain activity in frontal brain areas (see 4.2) was correlated with the increased McGurk illusion in hearing-impaired participants.

Stevenson et al., (2017) found a decrease in McGurk illusion rates in older adults compared to younger adults. Our data support this claim, since we also found illusion rates of about 50% in our hearing-impaired

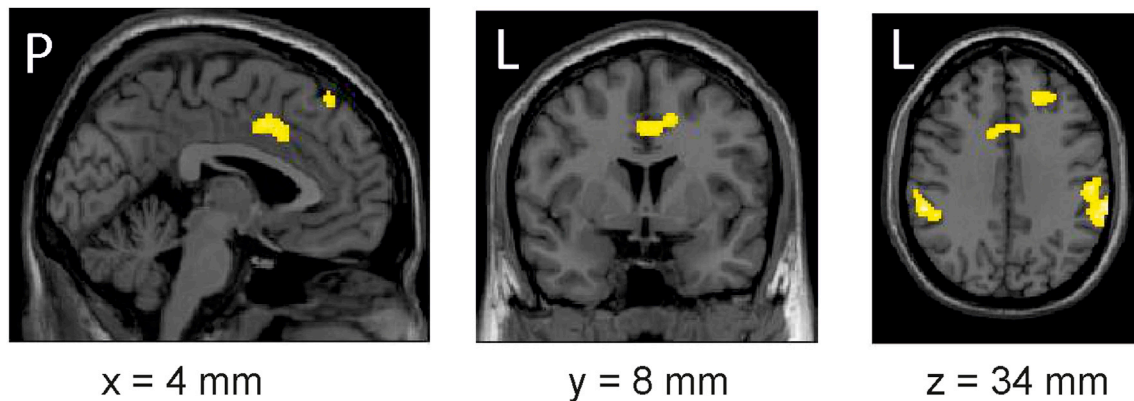


Fig. 6. Brain regions whose response to auditory stimulation correlates with the McGurk illusion. Brain activation in right and left supramarginal gyrus, middle frontal gyrus and cingulate cortex during auditory-only stimulation was significantly positively correlated with the McGurk illusion response [$p < 0.05$; FWE corrected on the cluster level].

group and even less in the normal-hearing group. In addition, our sample of normal-hearing participants showed a tendency for the auditory input of the McGurk stimuli and not to the visual input, as in the original McGurk paper. Cultural and language differences in the McGurk illusion can explain this auditory dominance, which was also found in another German sample (Stropahl and Debener, 2017), and in Japan (Hisanaga et al., 2016; Sekiyama and Burnham, 2008; Sekiyama and Tohkura, 1991), but also in a study with Canadian subjects (Tremblay et al., 2010).

Stropahl and Debener (2017) found a similar pattern of results like in our mild to moderate hearing-impaired subjects: moderately hearing-impaired participants showed an increased audio-visual integration as measured by significantly more McGurk illusions than normal-hearing participants. Cochlear implant recipients, however, showed no higher illusion rates than normal-hearing listeners but were more prone to choose the visual response in McGurk trials since in CI patients vision is the more reliable sense than audition (Rouger et al., 2007, 2008; Stropahl and Debener, 2017; Tremblay et al., 2010). Grant et al. (1998) investigated audio-visual speech recognition and the audio-visual gain in hearing-impaired individuals. They found that better audio-visual consonant integrators showed more audio-visual benefit. In cochlear implant users, enhanced audio-visual binding was found, possibly because of compensatory mechanisms developed due to the decreased auditory input (Schierholz et al., 2015). Auer and Bernstein (2007) showed that particularly hearing-impaired subjects rely more on the visual input of audio-visual speech. In line with these studies are results from Frtusova and Phillips (2016), which were found using an audio-visual digit span task to evaluate working memory effects and demonstrated that hearing-impaired individuals showed a more robust multisensory interaction. These results are in contrast to Musacchia et al. (2009), who showed decreased integration effects in hearing-impaired participants. It is possible that Musacchia and colleagues did not find integration effects as no active integration was necessary and therefore no benefit for speech perception occurred. From other studies, we already know that the visual input in audio-visual speech can facilitate speech understanding (Campbell, 2008; Grant and Seitz et al., 2000; Driver and Noesselt, 2008; Irwin and DiBlasi, 2017; Rosenblum, 2008; Ross et al., 2007; Sumbly and Pollack, 1954).

Our results complement previous findings by showing increased audio-visual speech integration in hearing-impaired subjects who do not yet wear a hearing aid and whose susceptibility to the McGurk illusion significantly correlated with hearing loss (indicating a shift from the auditory response to the illusion response with increasing hearing loss). To combine these findings, one could suggest that in healthy aging the McGurk illusion decreases (Song et al., 2015), but that the illusion

response increases if auditory abilities are degraded due to hearing loss and therefore leads to stronger integration in hearing-impaired compared to normal-hearing participants (our study and hearing-impaired participants in Stropahl and Debener, 2017). If the auditory signal is restored by a cochlear implant, the McGurk illusion rate seems to approach the one in normal-hearing listeners although now highly driven by an enhanced visual response (Rouger et al., 2007, 2008; Stropahl and Debener, 2017; Tremblay et al., 2010).

In addition, Stropahl & Debener showed a relationship between cross-modal reorganization in cochlear implant users and audio-visual integration strength in the McGurk task. The altered integration abilities in our sample seem to be related to changes in underlying brain processes as well, similar to studies in cochlear implant users. Although, we were not able to show a relation between cross-modal reorganization of the auditory cortex and the McGurk illusion, we found a correlation to increased frontal lobe recruitment (see 4.2). Correlations were highest for medial, middle and inferior frontal gyri, but also obtained for the cingulate gyrus. Additionally, a multiple regression revealed a correlation between the amount of McGurk illusions and brain activity in the supramarginal gyri, cingulate cortex and middle frontal gyrus in the auditory-only condition. From other studies, we know that these frontal areas, supramarginal gyrus and cingulate cortex, among others, are involved in the McGurk perception in healthy volunteers (Benoit et al., 2010; Erickson et al., 2014b; Jones and Callan, 2003; Skipper et al., 2007; Szyck et al., 2012). Besides, the supramarginal gyrus is involved in a wide range of multimodal sensory, speech-related and attentional functions, as well as detection of auditory or visual targets and audio-visual speech perception (Jones and Callan, 2003). It seems that the increased perception of the McGurk illusion only relates to processing of auditory input at the neural level, because the multiple regression only revealed a correlation between McGurk illusion and brain activity obtained in the auditory-only condition, but not for the visual-only or audio-visual conditions. Since we were not able to confirm cross-modal changes in our sample, the mild to moderate hearing loss may serve as a reasonable explanation for both effects. Changes in underlying brain processes may just have started and first influenced the affected modality, which is the degraded auditory input in our case.

Our results suggest that an altered processing of audio-visual information occurs early in the course of hearing loss and not only after severe hearing impairment (e.g. in cochlear implant patients with severe deafness), and increases with increasing extent of hearing loss. We further confirm a correlation between McGurk illusion and activity in frontal brain areas, as well as supramarginal gyrus. To entangle these processes, further studies exploring visual and auditory abilities as well as integration strengths are needed.

Increased frontal lobe recruitment

Hearing-impaired subjects showed a significantly increased recruitment of frontal areas when processing auditory-only, visual-only as well as incongruent audio-visual speech, compared to normal-hearing subjects. This higher brain activation included areas in medial, middle and inferior frontal gyri, as well as cingulate cortex and visual thalamic nuclei. Note that the increases in frontal activity were unconfounded by performance since sentences were presented at an individually matched intelligibility level of 80%. Furthermore, hearing-impaired participants showed significantly higher listening effort, but no correlation with performance in the McGurk task or audio-visual sentence test.

Previous research on degraded speech and hearing loss has shown similar results. They provided evidence that when speech perception becomes difficult, an additional recruitment of frontal areas takes place which is related to an increased listening effort (Berding et al., 2015; Campbell and Sharma, 2013; Campbell and Sharma, 2014; Erb and Obleser, 2013; Driver and Noesselt, 2008; Hervais-Adelman et al., 2012; Lee et al., 2016; Peelle et al., 2011; Reuter-Lorenz and Cappell, 2008; Tyler et al., 2010; Wong et al., 2009). This additional recruitment is supposed to be a compensatory mechanism to increase cognitive control due to the decreased auditory input. The increased frontal recruitment was even shown in hearing-impaired participants engaging in a passive listening task requiring no attentional resources (Campbell and Sharma, 2013). Frontal brain regions such as the cingulo-opercular network (Erb et al., 2013; Vaden et al., 2013, 2015), the premotor cortex (Hervais-Adelman et al., 2012), the anterior cingulate cortex (Erb et al., 2013; Erb and Obleser, 2013; Harris et al., 2009), left inferior frontal cortex (Campbell and Sharma, 2013; Lee et al., 2016; Hervais-Adelman et al., 2012), middle frontal gyrus (Erb and Obleser, 2013), but also the insula (Erb et al., 2013; Erb and Obleser, 2013; Hervais-Adelman et al., 2012) have been described to show this increased activity and were suggested to reflect effortful listening. The anterior cingulate cortex, the insula and pre-supplementary motor area are part of the so-called salience network (Cardin, 2016), which is responsible for detection of salient events, control of behavior and attention switching (Menon and Uddin, 2010). This network seems to be particularly influenced by age and hearing loss (Cardin, 2016; Wingfield and Grossman, 2006). Evidence comes from studies showing decreased neural resources, e.g. working memory capacity, attention switching and interference control, due to the increased effort in understanding speech in hearing-impaired subjects (Cardin, 2016; Humes et al., 2013; Lin et al., 2011; Moradi et al., 2014; Peelle and Wingfield, 2016; Rönnberg et al., 2013; Tun et al., 2009). Another study presented evidence of a shift from a primary left hemisphere fronto-temporal system to a bilateral functional language network as a consequence of age-related compensation to preserve language understanding (Tyler et al., 2010).

In line with these findings, the increased frontal activation in auditory-only, visual-only and incongruent audio-visual speech perception speaks for an effective compensatory mechanism in age-related hearing loss. Hearing-impaired subjects performed equally well in all conditions in the audio-visual speech detection task but showed increased frontal activation compared to normal-hearing subjects – even in the visual-only condition. In addition, there was a significant difference between both groups in the listening effort questionnaire, in which the hearing-impaired participants reported a higher listening effort than the normal-hearing participants. However, possibly due to a low variability in the listening effort questionnaire, this measure did not correlate with performance in the sentence test nor the obtained brain activation. The increased frontal brain activation was modulated by hearing loss, with higher hearing loss showing stronger frontal recruitment. Keeping in mind, that the loudness levels, although matched to an auditory speech intelligibility of 80%, did not differ between groups, one could suggest that the increased frontal recruitment could be a sign of the increased listening effort to perform the task, which the hearing-impaired participants experienced. This is in line with previous work in this area showing

increased frontal activation in hearing-impaired participants due to an increased listening effort (Campbell and Sharma, 2013; Campbell and Sharma, 2014; Erb and Obleser, 2013; Peelle et al., 2011). Therefore, this additional frontal recruitment during adverse listening seems to be related to more widespread changes in dynamic brain networks (Cardin, 2016). These changes might not only affect auditory speech perception but general speech perception mechanisms, as changes were also found in the visual contrast where no auditory input was present. With these results, we were able to extend previous findings to hearing-impaired participants confronted with incongruent audio-visual speech as well as auditory-only and visual-only speech.

Regarding the increased activation in the pulvinar nucleus in the hearing-impaired group during incongruent audio-visual speech perception, there is previous evidence of its relation to the adaptation to degraded speech (Erb et al., 2013). Erb and colleagues found that grey matter volume in the pulvinar positively correlated with vocoded-speech learning, i.e. better learners had an increased grey matter volume. The pulvinar is connected to both the auditory and prefrontal cortices and, therefore, seems to be highly involved in transferring auditory information to frontal areas. We here show its involvement in hearing-impaired participants engaging in effortful listening situations (incongruent audio-visual speech).

In contrast to our expectation, we were not able to find changes in neural activity in neither the congruent audio-visual condition nor any data indicative of increased cross-modal responses to visual input in the auditory cortex of hearing-impaired subjects. Previous research showed cross-modal reorganization after sensory deprivation, which lead to an increased response to visual stimuli in the auditory cortex. These changes were not only shown in cochlear implant patients (Chen et al., 2016; Kim et al., 2016; Lazard and Giraud, 2017; Lee et al., 2007; Sandmann et al., 2012; Song et al., 2015; Strelnikov et al., 2015; Stropahl et al., 2015; Stropahl and Debener, 2017) but also in moderately hearing-impaired subjects (Campbell and Sharma, 2014). On the other hand, Puschmann and Thiel (2017) found no hearing loss induced cross-modal reorganization of the auditory cortex either, but an increased functional and resting state connectivity between auditory cortex and visual motion area MT + for congruent audio-visual input. This functional and resting state connectivity was modulated by hearing loss and led to our hypothesis of neural activity changes in audio-visual conditions between normal-hearing and hearing-impaired participants. Additionally, Lazard and Giraud (2017) found an altered functional connectivity between auditory and visual cortex in cochlear implant patients that was associated with poor speech perception. However, we found neither increased cross-modal responses nor an increased functional connectivity in hearing-impaired participants. One reason for the absence of effects might be that Campbell and Sharma (2013, 2014) investigated participants with earlier onset of deafness than in our sample. They found significant auditory reorganization but also increased frontal recruitment in hearing-impaired participants. One might conclude, that cross-modal reorganization in early onset deafness and in severe deafness (as in cochlear implant users), is stronger than in mild to moderate late-onset hearing loss (as in Puschmann and Thiel, 2017; and present study) and therefore the hearing loss in our sample was too mild to induce cortical reorganization. Bishop and Miller (2009) showed that different networks are engaged in speech understanding compared to speech hearing. They further showed an increased connectivity between left lateral temporal-occipital boundary and left middle temporal gyrus, but not with the superior temporal sulcus, when participants understood speech as compared to when they heard the stimulus. This study may also explain our absence of connectivity changes, because due to our auditory loudness matching to 80% speech intelligibility, we made sure that all participants understood the stimuli. However, since we used seeds in visual and auditory cortex based on the highest evoked BOLD response, and these are different from the ones in Bishop & Miller, we cannot directly compare both studies.

The increased frontal activation in hearing-impaired participants,

however, may suggest a top-down mechanism as a first step of plasticity, which may lead to reorganization in the auditory cortex in later/more severe stages of hearing loss (Wingfield and Grossman, 2006). This view, of a top-down mechanism as a means to increase cognitive control due to increased listening effort, is supported by previous studies in hearing-impaired participants (Campbell and Sharma, 2013, 2014; Lazar and Giraud, 2017). Further evidence is given by a study in blind individuals who show cross-modal reorganization, possibly established via top-down feedback (Bedny et al., 2011). Future studies in this context are needed to explore cross-modal reorganization in age-related hearing-impaired humans.

Processing of incongruent vs. congruent audio-visual stimuli

We found a significant interaction between stimulus condition (congruent and incongruent audio-visual) and group. While hearing-impaired participants showed an increased activation for incongruent input, normal-hearing subjects showed a decrease for the incongruent audio-visual speech input. This interaction was obtained in the left ventral postcentral gyrus.

No differences between hearing-impaired and normal-hearing participants were obtained in areas suggested to be involved in processing conflicting audio-visual speech, like temporal regions, inferior frontal gyrus, supplementary motor area, precentral gyrus or inferior parietal lobule (Erickson et al., 2014). Nor did brain areas like the cingulate cortex, dorsolateral prefrontal cortex, posterior parietal cortex or the anterior insula show different brain activation patterns between hearing-impaired and normal-hearing participants. These areas are important in other conflict- and distraction-related tasks, e.g. Stroop or flanker tasks (Durstun et al., 2003; Nee et al., 2007; Roberts and Hall, 2008; Spielberg et al., 2015). Thus, differences between the hearing-impaired and normal-hearing participants seem not to evolve from these typical distraction-related brain areas but from a specific region in the ventral postcentral gyrus.

The ventral postcentral gyrus is a heterogenous region that has often been linked to somatosensory processing, pain, olfaction and gustation (Benuzzi et al., 2008; Grabski et al., 2012; Kareken et al., 2004), therefore, it is surprising that it seems to be involved in incongruent compared to congruent speech perception. However, although the exact function of this region is not fully known, there is some evidence of its involvement in speech perception. Gabrieli et al., (1998) showed an increased activation in ventral postcentral gyrus during a semantic memory task and Job et al. (2011) showed its involvement in middle ear functions. Greater activity in the ventral postcentral gyrus was also shown in a speech rhythm task (Geiser et al., 2008), in an auditory oddball task (Job et al., 2012), in speaking tasks (Behroozmand et al., 2015; Bouchard et al., 2013) and in an articulation imagery task (Tian et al., 2016). Another study showed grey matter reorganization related to tinnitus in this brain area (Krick et al., 2015). Kemmerer et al. (2012) presented that lesions in the ventral postcentral gyrus lead to an impaired conceptual knowledge of actions tested by a verb comprehension task.

We here show that the ventral postcentral gyrus is engaged in multi-modal processing since our stimuli were audio-visual. In addition, it seems that the ventral postcentral gyrus may differentially contribute to audio-visual speech perception in hearing-impaired and normal-hearing subjects, suggesting a hearing loss induced plasticity leading to increased activation for incongruent input in the hearing-impaired participants. Normal-hearing participants, on the other hand, showed a decrease for incongruent compared to congruent input. Tian et al., (2016) showed an increased activation in the postcentral gyrus for an articulation imagery task. Postcentral gyrus activation was further demonstrated in speaking tasks (Behroozmand et al., 2015; Bouchard et al., 2013). Therefore, it seems that the postcentral gyrus is involved in the speech-motor-control network. Within the framework of our study, one could suggest that hearing-impaired participants used inner speech to solve the task in the incongruent condition, because this one was more difficult than the

congruent condition. Differences in underlying integration processes may also explain these different activation patterns between both groups. Since hearing-impaired participants showed stronger integration in the McGurk, they may have tried to integrate auditory and visual input in the sentence task as well and therefore the activation in this area increased. Normal-hearing participants may not rely on the visual input that much and may have suppressed the integration of the incongruent input which led to a decrease in activation in this area (similar to audio-visual suppression found in Erickson et al., 2014b, and van Atteveldt et al., 2004). Thus, it is possible that the ventral postcentral gyrus is involved in audio-visual speech integration processes, with underlying differences in normal-hearing and hearing-impaired listeners. However, the exact role of the left ventral postcentral gyrus needs to be determined in future studies, especially its role in audio-visual speech processing.

Conclusion

Our results indicate that mild to moderate hearing-impaired subjects are more prone to the McGurk illusion (incongruent audio-visual speech) than normal-hearing subjects, which indicates an altered processing of audio-visual information. Additionally, auditory-only and visual-only speech as well as incongruent audio-visual speech elicited an increased frontal activation pattern in hearing-impaired individuals compared to normal-hearing subjects, which may be related to the recruitment of additional neural resources due to the increased effort to perform the task. Hearing loss modulated both the audio-visual speech integration strength and brain activation in frontal areas, showing stronger integration and higher brain activation with increasing hearing loss. However, we did not find cross-modal plasticity in the auditory cortex at that stage (mild to moderate age-related hearing loss). We here present data from the first fMRI study investigating audio-visual speech processing in mild to moderately hearing-impaired participants and we conclude that already mild to moderate hearing loss leads to changes in the integration of auditory and visual speech stimuli and to altered brain activation patterns particularly involving frontal cortices. We furthermore conclude that these changes are related to the extent of hearing loss.

Acknowledgements

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