Decline of auditory-motor speech processing in older adults with hearing loss

Muriel TN Panouillères[1], Riikka Möttönen[1]

[1] Department of Experimental Psychology, University of Oxford, United-Kingdom

Corresponding author: Muriel TN Panouillères

Address: Oxford Centre for Human Brain Activity

Warneford Hospital

Oxford OX3 7JX

United Kingdom

Phone: +44 (0)1865 271 374

Email: muriel.panouilleres@psy.ox.ac.uk

Running title: Auditory-motor speech processing in ageing and age-related hearing loss

Abstract

Older adults often struggle in understanding speech, partly because of age-related hearing loss. In young adults, activity of the left articulatory motor cortex is facilitated and interacts with the auditory cortex via the left-hemispheric dorsal stream during speech processing. Although it is unknown how ageing and age-related hearing loss affect the articulatory motor cortex, it has been proposed that the enhanced activation of the frontal motor system in older adults would compensate for auditory deficits. The aim of the present study was to investigate the effects of ageing and age-related hearing loss on the excitability of the tongue motor cortex during listening to spoken sentences using transcranial magnetic stimulation and electromyography. Our results show that the facilitation of the tongue motor cortex during speech processing was not modified with ageing but was impaired in age-related hearing loss. These findings suggest that auditory-motor processing of speech declines with age-related hearing loss.

Introduction

Ageing is often associated with a progressive decline in hearing, also known as presbycusis (Ries 1994; Frisina and Frisina 1997; see for review: Cardin 2016), which leads to difficulties in perceiving speech (Stewart and Wingfield 2009; Tun et al. 2010; see for review: Humes and Dubno 2010). However, hearing loss is not the only factor affecting speech perception deficits in ageing. Indeed, older adults with normal hearing also experience difficulties in understanding speech in adverse listening conditions compared to young individuals (Frisina and Frisina 1997; Wingfield et al. 2006; Stewart and Wingfield 2009). Moreover, older adults with hearing deficits do not perceive speech as well as young adults with matching hearing deficits (Dubno et al. 1984; Wingfield et al. 2006). This suggests that an interaction between hearing loss and ageing compromise speech understanding. These changes in speech perception skills are associated with alterations in the structure, function

and connectivity of the auditory cortex (see for recent reviews: Cardin 2016; Peelle and Wingfield 2016). Ageing itself is associated with a decrease of grey matter volume in the temporal lobe regions, known to be responsive to speech (Eckert et al. 2008; Profant et al. 2014). A further reduction of grey matter volume in the temporal lobe areas was detected with age-related hearing loss (Harris et al. 2009; Husain et al. 2011; Lin 2011; Eckert et al. 2012; Yang et al. 2014). Interestingly, the grey matter volume of this region was able to predict for older adults' hearing abilities (Peelle et al. 2011; Eckert et al. 2012; Lin et al. 2014). In addition to these structural changes, older adults also show less activity in the temporal auditory regions when listening to speech stimuli compared to young adults (Hwang et al. 2007; Wong et al. 2009). Older adults with hearing loss similarly present reduced activation in bilateral superior temporal gyri, including auditory cortex (Peelle et al. 2011). Finally, age-related hearing loss has been shown to be associated with reduced fractional anisotropy, a measure of white matter tract integrity, in right superior and inferior longitudinal fasciculi, corticospinal tract, inferior fronto-occipital tract, superior occipital fasciculus, and anterior thalamic radiation (Husain et al. 2011).

In young adults, the articulatory motor cortex is involved in speech perception, together with the auditory cortex (see for reviews: Möttönen and Watkins 2012; Schomers and Pulvermüller 2016; Skipper et al. 2017). Models of spoken language processing suggest that a dorsal stream would serve as an auditory-motor interface. This interface maps speech sounds onto motor representations via neural projections toward the left posterior temporo-parietal junction, left supramarginal gyrus, left premotor and motor cortices and left inferior frontal gyrus (Scott and Johnsrude 2003; Hickok and Poeppel 2007; Rauschecker and Scott 2009). In agreement with this model, neuroimaging studies in young adults have consistently shown activation of a left frontal speech motor network including inferior frontal gyrus (IFG), premotor cortex and primary motor cortex during speech perception (Wilson et al. 2004; Skipper et al. 2005; Pulvermüller et al. 2006; Callan et al. 2010; Londei et al. 2010; Osnes et al. 2011; Adank 2012; Hervais-Adelman et al. 2012; Szenkovits et al. 2012; Du et al. 2014). Moreover, accumulating evidence from Transcranial Magnetic Stimulation (TMS) studies have

shown that the articulatory regions of the primary motor cortex, important for accurate speech production, enhance their excitability during speech perception (Fadiga et al. 2002, 2002; Watkins et al. 2003; D'Ausilio et al. 2009; Murakami et al. 2011, 2013, 2015, Nuttall et al. 2016, 2017). Modulating the activity of the articulatory motor areas using TMS influence performance in both demanding speech discrimination tasks and easy word-to-picture matching tasks (Meister et al. 2007; D'Ausilio et al. 2009; Möttönen and Watkins 2009; Bartoli et al. 2015; Schomers et al. 2015; Smalle et al. 2015). These findings demonstrate that the articulatory motor regions play a causal role in speech processing in young adults. A recent TMS study investigated the effect of disrupting nodes of the dorsal stream on both speech perception and the articulatory motor cortex excitability (Murakami et al. 2015). TMS-induced virtual lesions in the posterior regions of the dorsal stream, including the posterior superior temporal sulcus and the sylvian parieto-temporal areas, led to speech perception deficits and a reduced facilitation of the articulatory motor cortex in young adults. This shows that an impaired auditory-motor transformation in the dorsal stream result in the reduced recruitment of the articulatory motor cortex during speech perception in young adults. Whether age-related hearing loss and/or ageing itself would affect the auditory-motor transformation in the dorsal stream and could lead to a reduced excitability of the articulatory motor cortex remains to be determined.

A recent neuroimaging study investigated the involvement of the frontal speech motor network in speech perception in older adults (Du et al. 2016). Older adults showed an enhanced activation of the frontal speech motor areas relative to young adults when listening to speech in noise. Moreover, this increased activation correlated with speech discrimination performance as older individuals with stronger activity of the articulatory sensorimotor regions also had a better accuracy in the speech perception task. The authors proposed that the up-regulation of activity in speech motor regions compensates for the deficient auditory processing in older adults and allows the successful decoding of speech in adverse listening conditions. Because the older adults had elevated hearing thresholds relative to the young adults and that six out of sixteen participants had mild-to-moderate hearing

loss at a frequency relevant for speech perception (4KHz – Frisina and Frisina 1997), it is unclear whether the enhanced activation of the speech motor network was caused by ageing, hearing loss or an interaction of both factors.

The aim of the present TMS study was to investigate the effect of ageing and age-related hearing loss on the involvement of the articulatory motor cortex during speech perception with and without noise. Older adults were considered to have hearing loss when their hearing threshold was above 25dB (Schoof and Rosen 2014) for any of the tested speech frequencies (Frisina and Frisina 1997). The excitability of the tongue motor cortex while passively listening to sentences in noise or to clear sentences was assessed using TMS combined with electromyography (EMG) recordings of the tongue and of the hand (control condition) muscles. The motor-evoked potentials (MEP) elicited by the TMS pulses when listening to sentences in noise, to clear sentences and to speech-correlated noise (SCN) were normalised as z-scores relative to the baseline condition where participants listened to white noise (WN). First, we investigated whether ageing affected the recruitment of the articulatory motor cortex during speech perception by comparing the excitability of the tongue motor cortex between young and older adults with normal hearing. Second, we examined whether age-related hearing loss modified the auditory-motor transformation in the dorsal stream by assessing the differences in facilitation of the tongue motor cortex when listening to speech between older adults with normal hearing (NH) and older adults with hearing loss (HL). We had two alternative hypotheses regarding the effect of age-related hearing loss on the involvement of the articulatory motor cortex in speech perception. On one hand, “the motor compensation hypothesis” predicts that age-related hearing loss will increase the recruitment of the articulatory motor cortex during speech perception, which will compensate for auditory deficits. On the other hand, “the auditory-motor decline hypothesis” predicts that age-related hearing loss will impair auditory-motor processing in the dorsal stream and consequently reduce the recruitment of the articulatory motor cortex during speech perception.

Results

Participants' characteristics

The characteristics of the three groups of participants (young adults, older adults with NH and older adults with HL) are presented in Table 1. All three groups were matched in their total numbers of years of education and their level of depression (one-way ANOVA: $F[2,36]<1$, $p>0.39$). Only older adults with normal cognitive abilities were included in the present study (MOCA≥26). However, older adults with HL had slightly lower cognitive abilities than the young adults and the older adults with NH ($F[2,36]=5.18$, $p<0.05$; Bonferroni post-hoc tests: young vs HL: $p<0.01$ and NH vs HL: $p<0.05$ respectively). The young adults had received overall more musical training than the NH and HL older adults group ($F[2,36]=4.90$, $p<0.05$; Bonferroni post-hoc tests: young vs NH: $p<0.05$ and young vs HL: $p<0.01$ respectively). Although there was a tendency for the older adults to have lower performances in the reading span task assessing working memory, this difference was not statistically significant ($F[2,36]=2.22$, $p=0.12$).

Participants' hearing abilities and speech perception performance

The results of the pure tone audiometry averaged across both ears for all the tested frequencies are plotted in Fig. 1A. The young adults had normal hearing thresholds at all tested frequencies. For the older adults with NH, pure-tone thresholds were in the normal range in the speech frequencies range (250 Hz to 4 KHz), but these participants had moderate hearing impairments at the highest frequency (8 KHz). The hearing thresholds of the older adults with HL were in the normal range from 250Hz to 2KHz (below 25dB), but they were in the moderate and moderately severe hearing loss range for the 4KHz and 8KHz frequencies, respectively. Examination of hearing thresholds across groups (Fig. 1B), measured by pure tone averages (PTA) from 500 Hz to 4 KHz, revealed a significant differences between the groups ($F[2,36]=45.60$, $p<0.001$). Indeed, both groups of older adults,

including the group with normal hearing, had higher PTA than the young adults (Bonferroni post-hoc tests, $p<0.01$). As expected, the older adults with HL had higher PTA than the older adults with NH (Bonferroni post-hoc test, $p<0.01$).

With the Quick Speech-In-Noise (QuickSIN) test, we measured the signal-to-noise ratio (SNR) loss of each participant, which is defined as the dB increase in SNR required to understand speech in noise relative to someone with normal hearing (Fig. 1C). Older adults with HL had a higher SNR loss scores than young adults and older adults with NH (Group effect: $F[2,36]=20.02$, $p<0.001$; Bonferroni post-hoc tests: $p<0.001$). The older adults with NH had similar SNR loss score as the young adults (Bonferroni post-hoc test: $p=0.10$). The normal range for this test is considered to be below 2dB of SNR loss (Killion et al. 2004), so both the young adults and the older adults with NH were in the normal range, while the SNR loss of the older adults with HL was outside the normal range. These results show that perception of speech in noise was impaired in older adults with HL, but not in older adults with NH.

Speech perception skills were also tested using a “speech report task”, in which participants listened to clear sentences or to sentences in noise at SNR of0dB. After each sentence, participants had to verbally report as many words as they had understood. The sentences were similar to the ones the participants passively listened to during the TMS part of the experiment. The proportion of correctly reported words was reduced for the 0dB stimuli compared to the clear stimuli (Fig. 1D – Stimulus effect: $F[1,36]=24.03$, $p<0.001$). The performance of the groups of participants differed for sentences in noise, but not for clear sentences (Group effect: $F[2,36]= 3.12$, $p=0.06$; Stimulus × Group interaction: $F[2,36]=3.75$, $p<0.05$) as the older adults with HL reported the sentences in noise slightly less accurately than the other groups (Fig. 1D).

No effect of age on the excitability of motor cortex when listening to speech

To investigate the effect of ageing on the excitability of the primary motor cortex when listening to speech and non-speech sounds, we compared the MEP z-scores between the young adults and the older adults with NH, separately for the hand and tongue stimulation (Fig. 2 A and 2B). The facilitation of the hand motor cortex was similar for both sentences and SCN for both age groups (Stimulus effect: $F[2,42]<1$, $p=0.52$; Group effect: $F[1,26]=1.52$, $p=0.23$; Stimulus × Group interaction: $F[2,42]<1$, $p=0.96$), suggesting that the modulation of hand motor excitability was not specific to speech (Fig. 2B). In contrast, the facilitation of the lip motor excitability was stronger for the sentences than for the SCN (Fig 2A – Stimulus effect: $F[2,52]=7.29$, $p<0.01$; Bonferroni post-hoc tests: speech in noise versus SCN: $p<0.05$; clear speech vs SCN: $p<0.01$, speech in noise versus clear speech: $p = 1$). Finally, there were no differences in the tongue motor excitability between young adults and older adults with NH (Group effect: $F[1,26]=1.04$, $p=0.32$; Stimulus × Group interaction: $F[2,52]=2.21$, $p=0.12$).

Because the older adults with NH had higher hearing thresholds relative to the young adults, we ran a complementary analysis in which the PTA of the older adults with NH was matched with a sub-group of young adults. This was done by including in this sub-group the young adults (N=10) with a PTA that was superior or equal to the median of the group (3.75dB). This sub-group of young adults had a mean PTA of 6.2 ±1.2dB, similar to the PTA of the NH group (9.8 ±1.6dB; Bootstrap for independent samples t-test: $p=0.11$). We again compared the hand and tongue excitability of these two groups for the three types of stimuli and found no effect of group or interactions involving this factor ($F[1,19]<2.85$, $p>0.11$). Our results demonstrate that the recruitment of the tongue motor cortex during speech perception is similar in young and older adults with normal hearing.

Age-related hearing loss reduces the excitability of the tongue motor cortex during listening to speech

To investigate the effect of age-related hearing loss on the motor excitability, when listening to speech and non-speech sounds, we compared the MEP z-scores between the older adults with HL and the older adults with NH, separately for the hand and tongue stimulation (Fig. 2A and 2B). The facilitation of the hand motor excitability was similar for both sentences and SCN and for the two groups of older adults (Fig. 2B – Stimulus effect: $F[2,28]<1$, $p=0.93$; Group effect: $F[1,19]<1$, $p=0.88$; Stimulus × Group interaction: $F[2,28]<1$, $p=0.59$). The facilitation of tongue motor cortex was reduced in older adults with HL compared to the older adults with NH as a function of the stimuli (Fig 2A – Stimulus effect: $F[2,27]=4.92$, $p<0.05$; Group effect: $F[1,19]=7.90$, $p<0.05$; Stimulus × Group interaction: $F[2,27]=6.47$, $p<0.01$). More specifically, the excitability of the tongue motor cortex was diminished in the HL group relative to the NH group for the clear sentences and the sentences in noise (Bonferroni post-hoc tests: speech in noise and clear speech: $p<0.05$, SCN: $p=0.47$). Because the z-scores were normalised to the WN MEPs, we assessed whether there could be any difference between older adults with HL and older adults with NH in this baseline condition. The WN MEPs were similar between the two groups (independent samples t-test: $t[19]=-1.09$, $p=0.29$), showing that the decreased excitability of the tongue was not a general decreased of excitability but was specific to listening to speech. We finally assessed whether the MEPs may differ from the WN baseline in the older with HL by comparing the z-scores for the tongue session with 0. We did not find any differences from 0 ($t[10]=[-0.67; -0.22]$, $p>0.52$), confirming the lack of facilitation of the tongue motor cortex when listening to speech and SCN relative to WN. Thus, our results show that listening to speech does not enhance the excitability of the tongue motor cortex in adults with age-related hearing loss.

Correlation between tongue excitability when listening to speech and hearing thresholds

To further explore the relationship between motor excitability when listening to speech and hearing thresholds, we ran correlational analyses for the young and older adults separately (Figure 2C and 2D). The tongue MEP z-scores did not show any significant correlation with hearing thresholds in the young adult group (Fig. 2C – Spearman rho=-0.05, p=0.84). However, there was a significant negative correlation between tongue excitability when listening to speech and hearing thresholds in the older adults group (Fig. 2D – Spearman rho=-0.50, $p<0.05$). There was no significant correlation between hearing thresholds and tongue MEP z-scores when listening to SCN. There were also no significant correlation between hand MEP z-scores and hearing thresholds in either age group (Spearman $|rho|<0.16$, $p>0.47$). Thus, the older adults with the least sensitive hearing– characterised by high PTA – had the lowest tongue motor excitability when listening to speech (relative to WN baseline).

Discussion

In this study, we demonstrate that older adults with normal hearing recruit the articulatory motor cortex in speech perception to the same extent as young adults. This suggests that ageing itself does not affect the recruitment of the articulatory motor cortex in speech perception. However, in older adults with hearing loss, the recruitment of the articulatory motor cortex during listening to speech is reduced. The present findings disagree with the motor compensation hypothesis and support the auditory-motor decline hypothesis.

The sample of older adults tested in the present study was divided into two subgroups based on whether their hearing threshold for each frequency composing the speech frequency range (250Hz to 4 KHz) was in the normal range (≤ 25dB). The group of older adults with HL had strong difficulties perceiving speech when simultaneously presented with a multi-babble noise (QuickSIN task) and mild difficulties for speech presented in speech-correlated noise (speech report task). This reduced

ability to understand speech in age-related hearing loss is in agreement with previous reports (Dubno et al. 1984; Wingfield et al. 2006; Stewart and Wingfield 2009; Tun et al. 2010). The skill to understand speech in noise was preserved in the group of older adults with NH. Previous studies have demonstrated that ageing with normal hearing can lead to a reduced capacity to perceive speech in challenging listening conditions (Dubno et al. 1984; Rajan and Cainer 2008; Wong et al. 2009; Jin et al. 2014; Schoof and Rosen 2014; Füllgrabe et al. 2015; Goossens et al. 2017). However, in the aforementioned studies, the level of noise was higher than the one used in the present study and the type of noise was often a multi-babble talker noise, leading to enhanced impairments in speech understanding. In studies in which speech was presented in non-speech noise or at approximately the same SNR (~0dB) as the one used in the present study, older adults with NH processed speech similarly as young adults (Frisina and Frisina 1997; Eckert et al. 2008; Schoof and Rosen 2014). Altogether, these results demonstrate that the ability to perceive speech in noise is impaired in older adults with HL while it is preserved in older adults with NH, at least in mildly challenging listening conditions.

Hearing ability is not the only factor involved in speech perception. Indeed, cognitive functions and working memory are crucial for comprehending speech (Schneider et al. 2002). Moreover, musical training can have a beneficial effect on perceptual and cognitive skills, including speech perception in noise, both in young and older adults (see for review: Alain et al. 2014). Therefore, we assessed the musical, cognitive and working memory performance of all participants. Young adults had more musical training and better working memory performance than both groups of older adults. However, older adults with normal hearing perceived speech similarly as the young adults. This then suggests that none of these factors contributed to speech understanding in the present study, probably because of the low level of difficulty of the tasks. Despite selecting participants based on their normal cognitive abilities (MOCA ≥26), older adults with HL had decreased cognitive functions compared to the other two groups of participants. It has been reported in several occasions that hearing impairment is independently associated with poorer cognitive performance (Tay et al. 2006;

Lin 2011; Lin et al. 2011) and accelerates the rate of cognitive decline (Lin et al. 2013). The hearing loss of older adults in the present study was mild compared to the aforementioned studies (estimated based on mean PTA for 0.5 to 4 KHz above normal) but was still associated with reduced cognitive performance. This suggests that even very mild hearing modifications could be associated with subtle modification of cognitive functions. Although it is possible that the speech perception deficits of the adults with HL could partly be due to these slightly reduced cognitive abilities in the current study, we believe that this effect is minimal compared to the effect of hearing loss.

Our finding that facilitation of the tongue motor cortex when listening to speech did not differ between young and older adults with normal hearing suggests that ageing itself does not modify the recruitment of the articulatory motor cortex during speech processing. As previously demonstrated in young adults (Watkins et al. 2003; Murakami et al. 2011, 2015; Panouillères et al. 2017), we confirmed that the facilitation of the articulatory motor cortex was specific to speech as the excitability of the tongue motor cortex was enhanced during listening to spoken sentences relative to speech-correlated noise and white noise. Despite recent studies suggesting that the articulatory motor cortex would be more facilitated in challenging listening conditions (Murakami et al. 2011; Nuttall et al. 2016, 2017), we found that the articulatory motor cortex excitability was similar for clear sentences and sentences in mild noise, replicating the results from our previous study (Panouillères et al. 2017). Finally, we also determined that the facilitation of the motor cortex for speech stimuli relative to non-speech stimuli is specific to the articulators and no other effectors, such as the hand (Watkins et al. 2003; Panouillères et al. 2017). Thus, our results confirm previous findings about the recruitment of the articulatory motor cortex in speech perception in young adults and extend them to older adults with normal hearing.

We found a correlation between hearing sensitivities and facilitation of the tongue motor cortex during speech perception only in older adults, but not in young adults. Two previous TMS studies in young adults with normal hearing found a relationship between hearing abilities and facilitation of

the articulatory motor cortex during speech perception (Nuttall et al. 2016, 2017). In these studies, young adults received single-pulse TMS to elicit lip MEPs while they listened to clear speech or speech in challenging conditions. The challenging conditions consisted of spoken syllables that were either presented in background noise or pronounced while a depressor was applied onto the tongue of the speaker. The results showed that there is a stronger facilitation of the lip motor cortex when individuals listened to speech in challenging conditions than to clear speech. Correlational analyses were then performed to evaluate the relationship between hearing abilities (measured as PTA) and the excitability of the lip motor cortex. In one study (Nuttall et al. 2016), there was a greater motor facilitation when listening to the challenging condition than to clear speech for individuals with less sensitive hearing, while there was an opposite finding in the other study (Nuttall et al. 2017). The authors suggested that the type of perturbation affected the direction of the correlation. Because Nuttall et al. did not use a non-speech baseline; the direct comparison with the current findings is difficult. Nevertheless, in the present study, no significant correlation was found between hearing abilities and the facilitation of the tongue motor cortex during listening to clear and noisy sentences (relative to non-speech baseline) in the young adult group. Thus, our results do not support the earlier studies suggesting that small individual differences in hearing abilities would modulate the recruitment of the articulatory motor cortex in speech perception in young adults.

We found that in older adults with HL the facilitation of the tongue motor cortex when listening to speech was reduced compared to the older adults with NH. In fact, no speech-induced facilitation was observed in older adults with HL. This suggests that age-related hearing loss is associated with a lack of recruitment of the articulatory motor cortex during speech processing. This finding disagrees with both the motor compensation hypothesis and the results from the previous functional Magnetic Resonance Imaging (fMRI) study by Du et al (2016). In this previous study, the authors found, in a mixed group of older adults (with and without hearing loss), an enhanced activation of the frontal speech motor network correlating with improved speech discrimination performance. However, because the syllable discrimination task used in this study included a button press with the

right hand on each trial, the left frontal activations could also reflect the button press, decision related processes or responses selection/preparation (see: Schomers and Pulvermüller 2016 for discussion of this point). Interestingly, some neuroimaging studies have demonstrated an increased activity in prefrontal regions associated with cognitive control when older adults process speech under challenging listening conditions (Wong et al. 2009; Peelle et al. 2010; Tyler et al. 2010; Erb and Obleser 2013). The activity in frontal areas or a higher volume of frontal areas were associated with better speech perception performance (Wong et al. 2009; Tyler et al. 2010; Wong et al. 2010). This increased activation and volume of more general cognitive areas could reflect a compensatory strategy of the ageing brain to counteract the decline in sensory input. Thus, the frontal compensatory mechanisms for age-related hearing loss during speech perception may be cognitive rather than motoric.

The negative correlation between hearing abilities and facilitation of the tongue motor cortex during speech perception shows that the older adults with the most severe hearing loss recruit the articulatory motor cortex the least. This is in agreement with our auditory-motor decline hypothesis and suggests that the auditory deficits weaken the auditory-motor transformations during listening to speech. As mentioned in introduction, age-related hearing loss is associated with a reduced grey matter volume and a decreased activation of the auditory cortex (Harris et al. 2009; Husain et al. 2011; Peelle et al. 2011; Eckert et al. 2012; Lin et al. 2014; Yang et al. 2014). One of these studies also demonstrated that high frequency hearing loss in older adults was associated with a reduced grey matter volume in the left primary somatosensory cortex (Eckert et al. 2012). The authors proposed that if the primary auditory and somatosensory cortices are part of a functional network, then anatomical changes in one region could affect another region of the network. We propose that the structural and functional changes in the auditory cortex that are associated with age-related hearing loss reduce the interactions with the articulatory motor cortex via the dorsal stream, leading to a reduced recruitment of the articulatory motor cortex during speech perception.

To conclude, this study provides novel evidence for the differential effects of ageing and age-related hearing loss on the recruitment of the articulatory motor cortex during speech perception. Older adults with NH did not differ from the young adults in terms of speech perception abilities and facilitation of the tongue motor cortex, whereas older adults with HL showed diminished speech comprehension in noise and no facilitation of the tongue motor cortex during speech perception. These findings demonstrate that age-related hearing loss is associated with impaired auditory-motor processing in the left dorsal stream, resulting in the disengagement of the articulatory motor cortex during speech perception.

Materials and Methods

Participants

A total of twenty-one young participants and twenty-four older adults were recruited for the present research. The data of three young adults was excluded because of the tongue recordings failing for one participant, the behavioural performance on the 0dB sentence report being below 50% accuracy in another participant and the MOCA (Montréal Cognitive Assessment) score being smaller than 26 in one last participant. The data of three older adults was also rejected as their score on the MOCA was below 26. Thus, we report the data of eighteen young adults (mean age: 21.9 ±2.9, range: 18-26 years; 10 females) and twenty-one older adults (mean age: 68.7 ±3.2, range: 63-74 years; 8 females). All participants were right-handed and native-English speakers with no known neurological, psychiatric or language impairment. All participants gave their written informed consent and were screened prior inclusion for contraindications to TMS. Experimental procedures conformed to the Code of Ethics of the World Medical Association (Declaration of Helsinki) and were approved by the Central University Research Ethics Committee (CUREC) at the University of Oxford (CUREC Reference: R45417/RE001).

Participants' musical abilities were evaluated using the training sub-scale of the Goldsmiths Musical sophistication index (Müllensiefen et al. 2014), which is a self-report inventory assessing individual differences in musical sophistication. Depression was evaluated via the Beck Depression Inventory (BDI-II). Participants had minimal to mild depression (min: 0 – max: 19).

Experimental design

All subjects received one block of single-pulse TMS to the tongue area of left primary motor cortex and one block of single-pulse TMS to the hand area of left primary motor cortex as a control site, while listening to clear speech, speech in noise, speech-correlated noise or white noise. We recorded from the tongue muscle and not from the lip muscle as we did in previous studies, because stimulating the lip area can be challenging for a number of reasons. First, lip stimulation may lead to unreliable motor-evoked potentials (MEPs - Möttönen and Watkins 2009; Swaminathan et al. 2013; Rogers et al. 2014; Panouillères et al. 2017). Second, the intensity of the stimulation required to induce an MEP in the relaxed lip muscle is usually quite high (ranging from 60 to 70% of the maximum intensity output of the Magstim 200). This level of intensity can lead to a certain discomfort that is not always tolerated by participants (Möttönen and Watkins 2009; Rogers et al. 2014; Adank et al. 2017). Thus, to minimise the participants' exclusion rate based on unreliable MEPs as well as discomfort, we targeted the motor representation of the tongue. The order of the hand and tongue blocks was counterbalanced across participants. Following the two TMS blocks, participants completed a short task in which they verbally reported sentences in clear speech and sentences in noise. Their hearing thresholds and speech-in-noise abilities were then assessed using respectively pure-tone audiometry and QuickSIN (Etymothics). Finally, participants' depression, cognitive abilities and musical training were assessed using various questionnaires (see above) and the study was concluded with a working-memory task.

Electromyography

Electromyography (EMG) activity from the right first dorsal interosseous (FDI) muscle was recorded by placing a pair of electrodes (22 × 30 mm ARBO neonatal electrocardiogram electrodes) on the belly and tendon of the muscle. In order to record MEPs from tongue muscles, two disposable EEG cup electrodes (Unimed, UK) were mounted to a nose-clip (Cressi, Italy). Participants placed this device into their mouth so that the two electrodes were above and below the right side of the tongue. The ground electrode was attached to the right wrist. The raw EMG signal was amplified (gain: 1000), band-pass filtered (1-1000Hz) and sampled (5000Hz) via a CED 1902 four-channel amplifier, a CED 1401 analog-to-digital converter and a computer running Spike2 (Cambridge Electronic Design). This EMG signal was stored on the computer for off-line analysis.

Transcranial Magnetic Stimulation

All TMS pulses were monophasic, generated by Magstim 200 (Magstim, Whitland, UK) and delivered through a 70-mm figure of eight coil. The position of the coil over the left motor cortex was adjusted until a robust MEP was observed in the contralateral target muscle (either hand or tongue). Single-pulse TMS was delivered for every trial to allow recording MEPs from the resting target muscle. The intensity of the stimulation was set in order for reliable MEPs to be consistently produced in the resting muscle. The mean intensity used for the tongue muscle was of 59.7% (±SE:2.4%) for the young participants and of 61.8% (±SE: 2.3%) for the older adults. For the hand stimulation, the averaged intensity was of 51.5% (±SE: 2.9%) and of 55.2 (±SE: 2.7%) respectively in the young and the older adults groups. The stimulation intensity significantly differed between the two stimulation sites ($F[1,37]=13.30$, $p<0.001$) but not between the two age groups (group effect: $F[1,37]<1$, $p=0.34$; group × site interaction: $F[1,37]<1$, $p=0.68$).

Speech stimuli

The stimuli used in the present study was a set of sentences generated in previous studies (Rodd et al. 2005; Davis et al. 2011). The set comprised 100 declarative sentences between 6 and 13 words in length that were semantically coherent. All 100 sentences (1.2 to 3.5 seconds in duration, speech rate 238 words/minute) were produced by a male speaker of British English and digitized at a sampling rate of 44.1 KHz. For the speech in noise condition, the sentences were degraded by adding speech-spectrum signal-correlated noise (SCN) at a signal-to-noise ratio (SNR) of 0dB using Praat software (Davis et al. 2011). Fourteen pure SCN stimuli and fourteen white noise (WN) stimuli were also used in the present study as control stimuli.

Design of the TMS blocks

Participants sat in front of a computer presenting the stimuli using Presentation® software (Neurobehavioral Systems, Inc., Berkeley, CA, USA). Audio stimuli were presented to the participants through insert earphones (Etymotic, Elk Grove Village, IL, USA). For each TMS site (hand and tongue), participants were exposed to 20 different sentences in clear speech, 20 different sentences in noise, 30 SCN stimuli and 30 WN stimuli. For each block, the order of the 100 stimuli was randomized. Altogether, the two TMS blocks (tongue and hand) led to the presentation of 40 sentences in clear speech, 40 sentences in noise, 60 SCN stimuli and 60 WN stimuli. Participants were instructed to listen to the stimuli while keeping both their tongue and hand muscles relaxed. For each stimulus (clear speech, speech in noise, SCN or WN), a single-pulse of TMS was delivered to elicit an MEP. For the sentence stimuli, it was delivered 150 ms after the onset of the final content word. This was chosen as a reliable way of matching the point at which TMS was delivered across sentences, as the final content word was likely to be the most predictable. For the WN and SCN stimuli, the pulse was delivered close to the end of the stimuli, matching the timing of the pulses for the sentence stimuli.

The average inter-trial interval was set at 5s (range: 4.02s - 5.99s). Each block lasted ~7 minutes and within each block, a short break occurred every 33-34 trials.

Speech report task

After the completion of the two TMS blocks, participants completed a speech report task to assess their ability to perceive speech. Participants were asked to listen to 10 sentences in clear speech and to 10 sentences in noise (SNR of 0dB), randomly presented, and after each of them, they were asked to repeat the sentence. The accuracy of the response was evaluated during the task by the experimenter, and off-line using the audio-recordings of the responses. Once the participants were finished repeating a sentence, they could move on to the next trial by pressing the space bar.

Pure-tone audiometry and QuickSIN

Pure-tone audiometric hearing thresholds were established using a diagnostic audiometer (Avant A2D+, MedRX International, Germany) across 250 Hz, 500 Hz, 1000 Hz, 2000 Hz, 4000 Hz and 8000 Hz for both ears. Older participants were divided into two sub-groups based on their hearing thresholds upon the range necessary for speech perception going from 250 Hz to 4 KHz (Frisina and Frisina 1997). The normal hearing (NH) older adult group had normal thresholds ≤ 25dB from 250 Hz to 4000 Hz, while the older adult group with hearing loss (HL) had mild-to-moderate hearing impairment, with thresholds > 25dB on these same frequencies. Pure-tone average (PTA) audiometric thresholds were computed across frequencies from 500 Hz to 4000 Hz for each ear.

The Quick Speech-In-Noise (QuickSIN) test was administered to the participants' to assess speech perception in noise (Killion et al. 2004). This test is composed of lists of low-context sentences spoken by a female talker presented in a four-talker babble background. The test was presented binaurally through the Avant A2D+audiometer, with the speech levels set to 70 dB HL. Each list

contains 6 sentences with a SNR decreasing from 25 dB to 0dB in 5dB steps. Following each sentence, participants were instructed to repeat to the experimenter as many words as possible. Each sentence is scored based on the correct recognition of five "target" words (e.g. Crouch before you jump or miss the mark). The test score, called SNR loss, represents the SNR required for the listener to repeat 50% of the words correctly. It is calculated for each list as the difference between 25.5 and the total number of words correctly reported for that list. One practice list and four test lists were presented per participants, the order of the test lists being counterbalanced across participants. The SNR loss for the four test lists was averaged to obtain the final score.

Working-Memory reading span task

We administered the shortened version of the reading span task, which has been verified to retain the psychometric properties of the longer version (Foster et al. 2015; Oswald et al. 2015). The task was automated, presenting stimuli onscreen and collecting the responses via mouse click (task downloaded from: http://englelab.gatech.edu/tasks.html). Participants were presented with a set of sentences of ~10 to 15 words and had to decide whether the semantic of the sentence was correct or not. After each sentence, participants were presented with a letter for recall at the end of the set. Set sizes ranged from 4 to 6, with two administrations for each set size. Participants practiced each task (remembering the letters and judging the semantic content of the sentence) separately, then two trials of the two tasks combined before starting with the main test. Participants score was obtained by averaging the proportion of correctly recalled element in each trial.

MEPs analysis

MEPs were analysed on a trial-by-trial basis using in-house software written in Matlab (Mathworks Inc, Natick, USA). Maximal and minimal peaks of the MEPs were automatically detected using a fixed

time window following the TMS pulse: [15-40ms] for the hand and [12-35ms] for the lip. The detection was checked manually by the experimenter. The absolute value of the background muscle activity was averaged across the 100ms preceding the TMS pulse and trials with a mean absolute value of background muscle activity higher than 2 standard-deviations of the average for each TMS block were excluded. Outliers MEP with values above or below 2 standard-deviations of the mean for each experimental condition (clear speech, speech in noise, SCN and WN) were removed. We calculated MEP z-scores for each experimental condition relative to the WN in each participant, separately for the hand and the tongue blocks.

Statistical analysis

Statistical analyses were performed with the SPSS Statistics software package (IBM, Armonk NY, USA). Participants' level of depression, years of education, MOCA, musical training, working memory, PTA and SNR loss (QuickSIN) were compared with separate one way ANOVAs with the between subjects factor group (young vs NH vs HL). Performance on the speech report task was submitted to a mixed design ANOVA with the between-subject factor group (young vs NH vs HL) and the within-subject factor noise level (clear speech vs speech in noise). To investigate the effect of age on the recruitment of the primary motor cortex on speech perception, separate ANOVAs for the hand and tongue stimulation were performed on the MEP z-scores with the between-subject factor group (young vs NH) and the within-subject factor stimulus (speech in noise vs clear speech vs SCN). Similar ANOVAs were ran to compare the MEP z-scores between NH and HL groups. Significant main effects or interaction in the ANOVAs were followed by bootstrapping for independent samples t-test (1000 sampling), and corrected for multiple comparisons (Bonferroni).

Correlational analyses were ran separately for the young and older adults and for the hand and tongue stimulation between the MEP z-scores (averaged for the speech in noise and clear speech

stimuli) and participants' PTA. Similar correlations were performed between the z-scores for the SCN stimuli and the PTA. Significance was set at $p<0.05$.

Acknowledgements

We thank Dr. Matt Davis and Dr. Ingrid Johnsrude for the stimulus material. We also thank Dr Jennifer Chesters, Dr Saloni Krishnan, Dr Daniel Lametti, Charlie Wiltshire and Atakan Acar for assisting with the TMS and Daniel Drew for his invaluable help in recruiting the older adults. We are grateful to the participants for contributing with their time and effort to this study. This study was funded by the Medical Research Council, UK (G1000566).

Corresponding author address: Muriel Panouillères, Oxford Centre for Human Brain Activity, Warneford Hospital, Oxford OX3 7JX, United Kingdom

Competing interests

The authors declare that there is no financial competing interests.

References

Adank P. 2012. The neural bases of difficult speech comprehension and speech production: Two Activation Likelihood Estimation (ALE) meta-analyses. Brain Lang. 122:42–54.

Adank P, Nuttall HE, Kennedy-Higgins D. 2017. Transcranial magnetic stimulation and motor evoked potentials in speech perception research. Lang Cogn Neurosci. 32:900–909.

Alain C, Zendel BR, Hutka S, Bidelman GM. 2014. Turning down the noise: The benefit of musical training on the aging auditory brain. Hear Res, Music: A window into the hearing brain. 308:162–173.

Bartoli E, D'Ausilio A, Berry J, Badino L, Bever T, Fadiga L. 2015. Listener–Speaker Perceived Distance Predicts the Degree of Motor Contribution to Speech Perception. Cereb Cortex. 25:281–288.

Callan D, Callan A, Gamez M, Sato M, Kawato M. 2010. Premotor cortex mediates perceptual performance. NeuroImage. 51:844–858.

Cardin V. 2016. Effects of Aging and Adult-Onset Hearing Loss on Cortical Auditory Regions. Audit Cogn Neurosci. 199.

D'Ausilio A, Pulvermüller F, Salmas P, Bufalari I, Begliomini C, Fadiga L. 2009. The Motor Somatotopy of Speech Perception. Curr Biol. 19:381–385.

Davis MH, Ford MA, Kherif F, Johnsrude IS. 2011. Does Semantic Context Benefit Speech Understanding through "Top–Down" Processes? Evidence from Time-resolved Sparse fMRI. J Cogn Neurosci. 23:3914–3932.

Du Y, Buchsbaum BR, Grady CL, Alain C. 2014. Noise differentially impacts phoneme representations in the auditory and speech motor systems. Proc Natl Acad Sci. 111:7126–7131.

Du Y, Buchsbaum BR, Grady CL, Alain C. 2016. Increased activity in frontal motor cortex compensates impaired speech perception in older adults. Nat Commun. 7:12241.

Dubno JR, Dirks DD, Morgan DE. 1984. Effects of age and mild hearing loss on speech recognition in noise. J Acoust Soc Am. 76:87–96.

Eckert MA, Cute SL, Vaden KI, Kuchinsky SE, Dubno JR. 2012. Auditory cortex signs of age-related hearing loss. J Assoc Res Otolaryngol JARO. 13:703–713.

Eckert MA, Walczak A, Ahlstrom J, Denslow S, Horwitz A, Dubno JR. 2008. Age-related Effects on Word Recognition: Reliance on Cognitive Control Systems with Structural Declines in Speech-responsive Cortex. J Assoc Res Otolaryngol. 9:252–259.

Erb J, Obleser J. 2013. Upregulation of cognitive control networks in older adults' speech comprehension. Front Syst Neurosci. 7:116.

Fadiga L, Craighero L, Buccino G, Rizzolatti G. 2002. Speech listening specifically modulates the excitability of tongue muscles: a TMS study. Eur J Neurosci. 15:399–402.

Foster JL, Shipstead Z, Harrison TL, Hicks KL, Redick TS, Engle RW. 2015. Shortened complex span tasks can reliably measure working memory capacity. Mem Cognit. 43:226–236.

Frisina DR, Frisina RD. 1997. Speech recognition in noise and presbycusis: relations to possible neural mechanisms. Hear Res. 106:95–104.

Füllgrabe C, Moore BCJ, Stone MA. 2015. Age-group differences in speech identification despite matched audiometrically normal hearing: contributions from auditory temporal processing and cognition. Front Aging Neurosci. 6:347.

Goossens T, Vercammen C, Wouters J, van Wieringen A. 2017. Masked speech perception across the adult lifespan: Impact of age and hearing impairment. Hear Res. 344:109–124.

Harris KC, Dubno JR, Keren NI, Ahlstrom JB, Eckert MA. 2009. Speech Recognition in Younger and Older Adults: A Dependency on Low-Level Auditory Cortex. J Neurosci. 29:6078–6087.

Hervais-Adelman AG, Carlyon RP, Johnsrude IS, Davis MH. 2012. Brain regions recruited for the effortful comprehension of noise-vocoded words. Lang Cogn Process. 27:1145–1166.

Hickok G, Poeppel D. 2007. The cortical organization of speech processing. Nat Rev Neurosci. 8:393–402.

Humes LE, Dubno JR. 2010. Factors Affecting Speech Understanding in Older Adults. In: The Aging Auditory System. Springer Handbook of Auditory Research. Springer, New York, NY. p. 211–257.

Husain FT, Medina RE, Davis CW, Szymko-Bennett Y, Simonyan K, Pajor NM, Horwitz B. 2011. Neuroanatomical changes due to hearing loss and chronic tinnitus: A combined VBM and DTI study. Brain Res. 1369:74–88.

Hwang J-H, Li C-W, Wu C-W, Chen J-H, Liu T-C. 2007. Aging Effects on the Activation of the Auditory Cortex during Binaural Speech Listening in White Noise: An fMRI Study. Audiol Neurotol. 12:285–294.

Jin S-H, Liu C, Sladen DP. 2014. The effects of aging on speech perception in noise: comparison between normal-hearing and cochlear-implant listeners. J Am Acad Audiol. 25:656–665.

Killion MC, Niquette PA, Gudmundsen GI, Revit LJ, Banerjee S. 2004. Development of a quick speech-in-noise test for measuring signal-to-noise ratio loss in normal-hearing and hearing-impaired listeners. J Acoust Soc Am. 116:2395–2405.

Lin FR. 2011. Hearing Loss and Cognition Among Older Adults in the United States. J Gerontol Ser A. 66A:1131–1136.

Lin FR, Ferrucci L, An Y, Goh JO, Doshi J, Metter EJ, Davatzikos C, Kraut MA, Resnick SM. 2014. Association of hearing impairment with brain volume changes in older adults. NeuroImage. 90:84–92.

Lin FR, Ferrucci L, Metter EJ, An Y, Zonderman AB, Resnick SM. 2011. Hearing loss and cognition in the Baltimore Longitudinal Study of Aging. Neuropsychology. 25:763–770.

Lin FR, Yaffe K, Xia J, Xue Q-L, Harris TB, Purchase-Helzner E, Satterfield S, Ayonayon HN, Ferrucci L, Simonsick EM, Group for the HAS. 2013. Hearing Loss and Cognitive Decline in Older Adults. JAMA Intern Med. 173:293–299.

Londei A, D'Ausilio A, Basso D, Sestieri C, Gratta CD, Romani G-L, Belardinelli MO. 2010. Sensory-motor brain network connectivity for speech comprehension. Hum Brain Mapp. 31:567–580.

Meister IG, Wilson SM, Deblieck C, Wu AD, Iacoboni M. 2007. The Essential Role of Premotor Cortex in Speech Perception. Curr Biol. 17:1692–1696.

Möttönen R, Watkins KE. 2009. Motor Representations of Articulators Contribute to Categorical Perception of Speech Sounds. J Neurosci. 29:9819–9825.

Möttönen R, Watkins KE. 2012. Using TMS to study the role of the articulatory motor system in speech perception. Aphasiology. 26:1103–1118.

Müllensiefen D, Gingras B, Musil J, Stewart L. 2014. The musicality of non-musicians: an index for assessing musical sophistication in the general population. PloS One. 9:e89642.

Murakami T, Kell CA, Restle J, Ugawa Y, Ziemann U. 2015. Left Dorsal Speech Stream Components and Their Contribution to Phonological Processing. J Neurosci. 35:1411–1422.

Murakami T, Restle J, Ziemann U. 2011. Observation-execution matching and action inhibition in human primary motor cortex during viewing of speech-related lip movements or listening to speech. Neuropsychologia. 49:2045–2054.

Murakami T, Ugawa Y, Ziemann U. 2013. Utility of TMS to understand the neurobiology of speech. Cogn Sci. 4:446.

Nuttall HE, Kennedy-Higgins D, Devlin JT, Adank P. 2017. The role of hearing ability and speech distortion in the facilitation of articulatory motor cortex. Neuropsychologia. 94:13–22.

Nuttall HE, Kennedy-Higgins D, Hogan J, Devlin JT, Adank P. 2016. The effect of speech distortion on the excitability of articulatory motor cortex. NeuroImage. 128:218–226.

Osnes B, Hugdahl K, Specht K. 2011. Effective connectivity analysis demonstrates involvement of premotor cortex during speech perception. NeuroImage. 54:2437–2445.

Oswald FL, McAbee ST, Redick TS, Hambrick DZ. 2015. The development of a short domain-general measure of working memory capacity. Behav Res Methods. 47:1343–1355.

Panouillères MT, Boyles R, Chesters J, Watkins KE, Mottonen R. 2017. Facilitation of motor excitability during listening to spoken sentences is not modulated by noise or semantic coherence. bioRxiv. 168864.

Peelle JE, Troiani V, Grossman M, Wingfield A. 2011. Hearing Loss in Older Adults Affects Neural Systems Supporting Speech Comprehension. J Neurosci. 31:12638–12643.

Peelle JE, Troiani V, Wingfield A, Grossman M. 2010. Neural Processing during Older Adults' Comprehension of Spoken Sentences: Age Differences in Resource Allocation and Connectivity. Cereb Cortex. 20:773–782.

Peelle JE, Wingfield A. 2016. The Neural Consequences of Age-Related Hearing Loss. Trends Neurosci. 39:486–497.

Profant O, Škoch A, Balogová Z, Tintěra J, Hlinka J, Syka J. 2014. Diffusion tensor imaging and MR morphometry of the central auditory pathway and auditory cortex in aging. Neuroscience. 260:87–97.

Pulvermüller F, Huss M, Kherif F, Martin FM del P, Hauk O, Shtyrov Y. 2006. Motor cortex maps articulatory features of speech sounds. Proc Natl Acad Sci. 103:7865–7870.

Rajan R, Cainer KE. 2008. Ageing without hearing loss or cognitive impairment causes a decrease in speech intelligibility only in informational maskers. Neuroscience. 154:784–795.

Rauschecker JP, Scott SK. 2009. Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing. Nat Neurosci. 12:718–724.

Ries PW. 1994. Prevalence and characteristics of persons with hearing trouble: United States, 1990-91. Vital Health Stat 10. 1–75.

Rodd JM, Davis MH, Johnsrude IS. 2005. The Neural Mechanisms of Speech Comprehension: fMRI studies of Semantic Ambiguity. Cereb Cortex. 15:1261–1269.

Rogers JC, Möttönen R, Boyles R, Watkins KE. 2014. Discrimination of speech and non-speech sounds following theta-burst stimulation of the motor cortex. Lang Sci. 5:754.

Schneider BA, Daneman M, Pichora-Fuller MK. 2002. Listening in aging adults: from discourse comprehension to psychoacoustics. Can J Exp Psychol Rev Can Psychol Exp. 56:139–152.

Schomers MR, Kirilina E, Weigand A, Bajbouj M, Pulvermüller F. 2015. Causal Influence of Articulatory Motor Cortex on Comprehending Single Spoken Words: TMS Evidence. Cereb Cortex. 25:3894–3902.

Schomers MR, Pulvermüller F. 2016. Is the Sensorimotor Cortex Relevant for Speech Perception and Understanding? An Integrative Review. Front Hum Neurosci. 10.

Schoof T, Rosen S. 2014. The role of auditory and cognitive factors in understanding speech in noise by normal-hearing older listeners. Front Aging Neurosci. 6:307.

Scott SK, Johnsrude IS. 2003. The neuroanatomical and functional organization of speech perception. Trends Neurosci. 26:100–107.

Skipper JI, Devlin JT, Lametti DR. 2017. The hearing ear is always found close to the speaking tongue: Review of the role of the motor system in speech perception. Brain Lang. 164:77–105.

Skipper JI, Nusbaum HC, Small SL. 2005. Listening to talking faces: motor cortical activation during speech perception. NeuroImage. 25:76–89.

Smalle EHM, Rogers J, Möttönen R. 2015. Dissociating Contributions of the Motor Cortex to Speech Perception and Response Bias by Using Transcranial Magnetic Stimulation. Cereb Cortex. 25:3690–3698.

Stewart R, Wingfield A. 2009. Hearing Loss and Cognitive Effort in Older Adults' Report Accuracy for Verbal Materials. J Am Acad Audiol. 20:147–154.

Swaminathan S, MacSweeney M, Boyles R, Waters D, Watkins KE, Möttönen R. 2013. Motor excitability during visual perception of known and unknown spoken languages. Brain Lang. 126:1–7.

Szenkovits G, Peelle JE, Norris D, Davis MH. 2012. Individual differences in premotor and motor recruitment during speech perception. Neuropsychologia. 50:1380–1392.

Tay T, Wang JJ, Kifley A, Lindley R, Newall P, Mitchell P. 2006. Sensory and Cognitive Association in Older Persons: Findings from an Older Australian Population. Gerontology. 52:386–394.

Tun PA, Benichov J, Wingfield A. 2010. Response latencies in auditory sentence comprehension: effects of linguistic versus perceptual challenge. Psychol Aging. 25:730–735.

Tyler LK, Shafto MA, Randall B, Wright P, Marslen-Wilson WD, Stamatakis EA. 2010. Preserving syntactic processing across the adult life span: the modulation of the frontotemporal language system in the context of age-related atrophy. Cereb Cortex N Y N 1991. 20:352–364.

Watkins KE, Strafella AP, Paus T. 2003. Seeing and hearing speech excites the motor system involved in speech production. Neuropsychologia. 41:989–994.

Wilson SM, Saygin AP, Sereno MI, Iacoboni M. 2004. Listening to speech activates motor areas involved in speech production. Nat Neurosci. 7:701–702.

Wingfield A, McCoy SL, Peelle JE, Tun PA, Cox LC. 2006. Effects of adult aging and hearing loss on comprehension of rapid speech varying in syntactic complexity. J Am Acad Audiol. 17:487–497.

Wong PCM, Ettlinger M, Sheppard JP, Gunasekera GM, Dhar S. 2010. Neuroanatomical Characteristics and Speech Perception in Noise in Older Adults. Ear Hear. 31:471–479.

Wong PCM, Jin JX, Gunasekera GM, Abel R, Lee ER, Dhar S. 2009. Aging and cortical mechanisms of speech perception in noise. Neuropsychologia. 47:693–703.

Yang M, Chen H-J, Liu B, Huang Z-C, Feng Y, Li J, Chen J-Y, Zhang L-L, Ji H, Feng X, Zhu X, Teng G-J. 2014. Brain structural and functional alterations in patients with unilateral hearing loss. Hear Res. 316:37–43.

Table

Table 1: Participants characteristics

	Age (years)	Years of education	Musical training	MOCA	BDI-II	WM score (%)
Young	21.9 ±0.7	16.8 ±0.4	20.7 ±3.5	28.8 ±0.3	2.6 ±0.9	66.7 ± 5.7
Older NH	68.0 ±1.2	16.1 ±0.9	7.5 ±1.7	28.4± 0.3	3.8 ±1.8	50.0 ±6.6
Older HL	69.4 ±0.7	15.2 ±1.1	9.8 ±3.5	27.6 ±0.3	2.9 ±1.5	47.0 ±10.7

MOCA: Montreal Cognitive Assessment; BDI-II: Beck Depression Inventory II; WM: Working-Memory.

Errors are standard-error of the mean.

Figures legends

Figure 1: Hearing and speech perception abilities

(A) Pure tone audiometry results. The hearing thresholds are represented averaged for both ears. (B) Pure tone averages (in dB) across the frequencies 500Hz to 4 KHz C QuickSIN results presented as Signal-to-Noise Ratio (SNR) loss. (D) Proportion of correctly reported words in the speech report task performances. Data are presented in black for the young adults, in light grey for the older adults with NH and in dark grey for the older adults with HL. HL: Hearing Level. Error-bars are standard-error of the mean.

Figure 2: MEP z-scores during speech perception. The MEPs elicited during the perception of clear speech, speech in noise and Speech-correlated noise (SCN) are represented as z-scores normalised to WN for the tongue (A) and hand (B) conditions. Error bars are standard error of the mean.

Correlations between the averaged tongue MEP z-scores for the clear speech and speech in noise condition and pure tone averages (PTA) are represented for the young participants (C) and the older participants (D). Correlations are represented with the confidence interval.

Figures

Figure 1

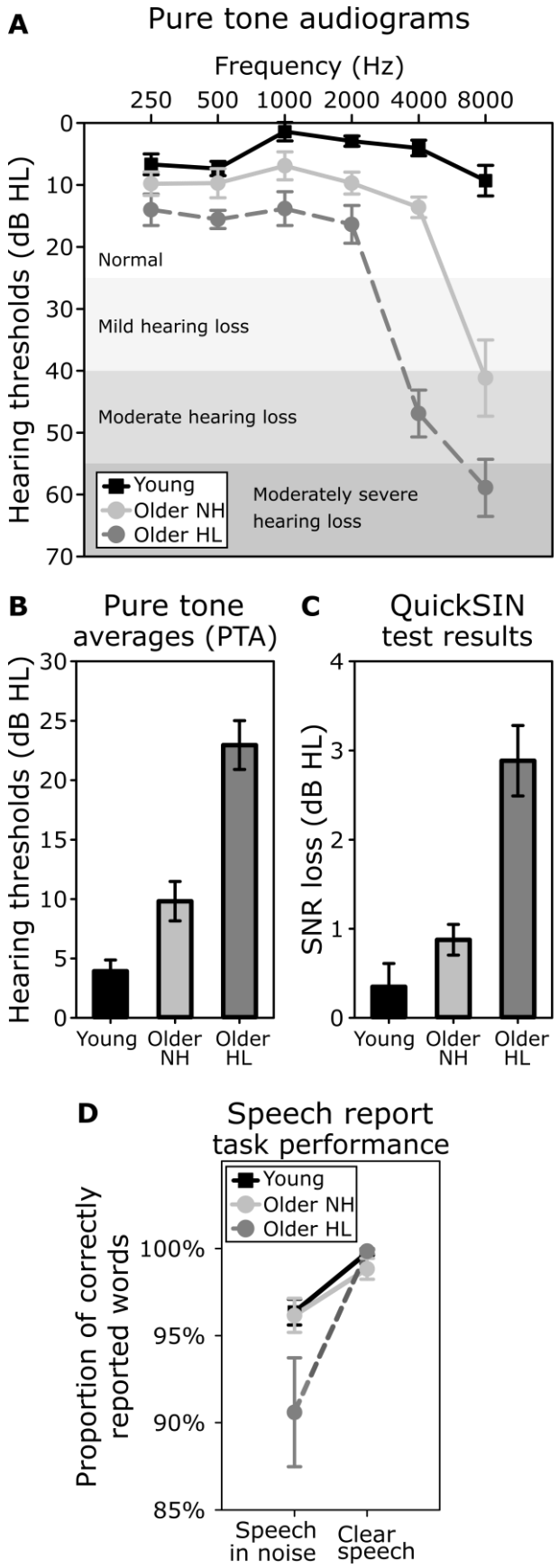
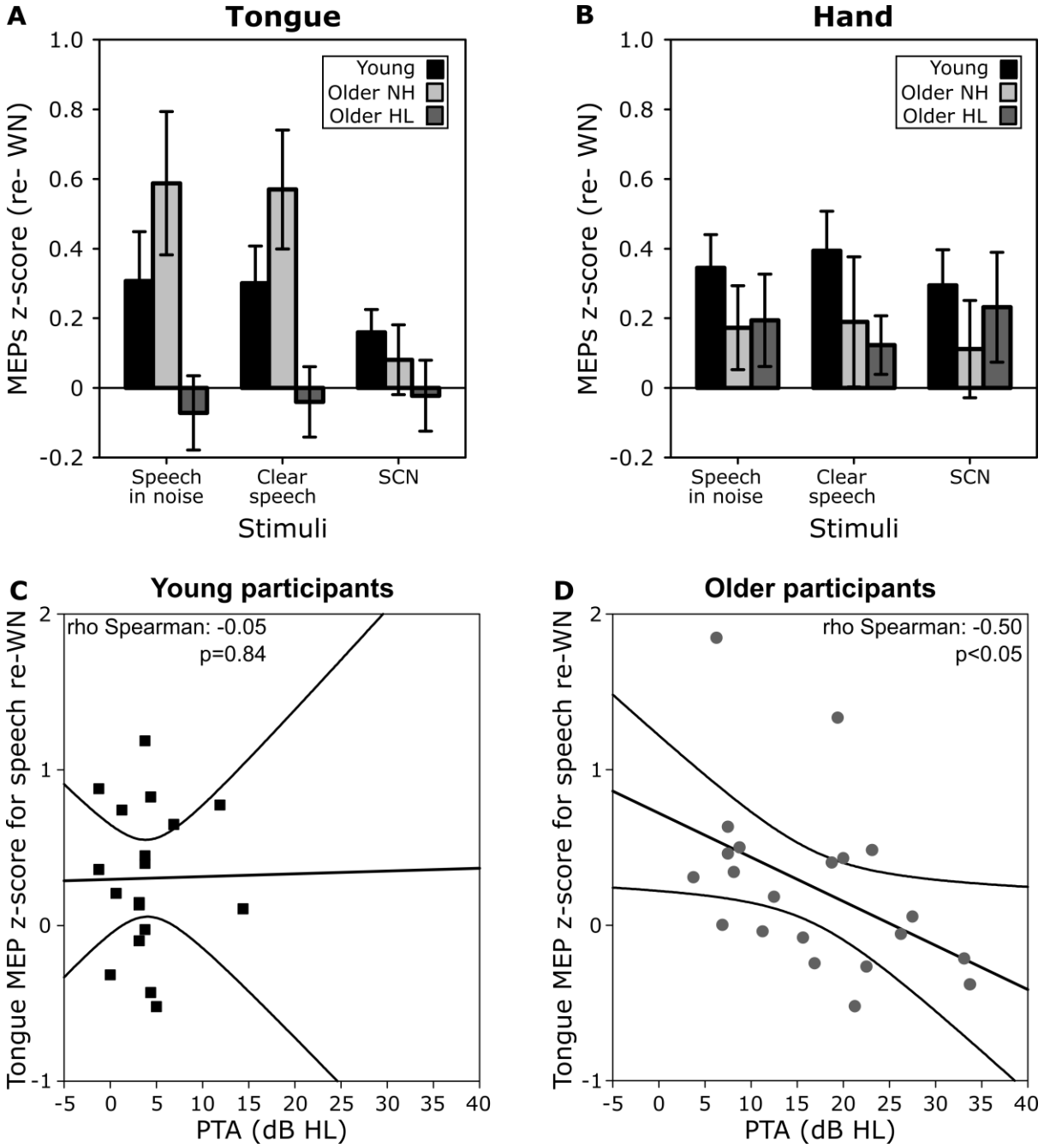

A
Pure tone audiograms
Frequency (Hz)
250 500 1000 2000 4000 8000
Hearing thresholds (dB HL)
0
10
20
30
40
50
60
70
Normal
Mild hearing loss
Moderate hearing loss
Moderately severe hearing loss
Young
Older NH
Older HL
B
Pure tone averages (PTA)
Hearing thresholds (dB HL)
0
5
10
15
20
25
30
Young
Older NH
Older HL
C
QuickSIN test results
SNR loss (dB HL)
0
1
2
3
4
Young
Older NH
Older HL
D
Speech report task performance
Proportion of correctly reported words
85%
90%
95%
100%
Young
Older NH
Older HL
Speech in noise
Clear speech

Figure 2


A
Tongue
B
Hand
Young
Older NH
Older HL
MEPs z-score (re- WN)
1.0
0.8
0.6
0.4
0.2
0
-0.2
Speech in noise
Clear speech
SCN
Stimuli
C
Young participants
rho Spearman: -0.05
p=0.84
D
Older participants
rho Spearman: -0.50
p<0.05
Tongue MEP z-score for speech re-WN
2
1
0
-1
-5
0
5
10
15
20
25
30
35
40
PTA (dB HL)