Neurobiology of Aging 35 (2014) 633–644

Contents lists available at ScienceDirect

Neurobiology of Aging

journal homepage: www.elsevier.com/locate/neuaging

Age-related deterioration of the representation of space in human auditory cortex

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ARTICLE INFO

Article history:
Received 18 July 2013
Received in revised form 23 August 2013
Accepted 28 August 2013
Available online 1 October 2013

Keywords:
Computational modeling
Electro-encephalography (EEG)
Older adults
Presbycusis
Psychophysics
Sound localization
Spatial acuity

ABSTRACT

One of the principal auditory disabilities associated with older age is difficulty in locating and tracking sources of sound. This study investigated whether these difficulties are associated with deterioration in the representation of space in the auditory cortex. In psychophysical tests, half of a group of older (>60 years) adults displayed spatial acuity similar to that of young adults throughout the frontal horizontal plane. The remaining half had considerably poorer spatial acuity at the more peripheral regions of frontal space. Computational modeling of electroencephalographic responses to abrupt location shifts demonstrated marked differences in the spatial tuning of populations of cortical neurons between the older adults with poor spatial acuity on the one hand, and those with good spatial acuity, as well as young adults, on the other hand. In those with poor spatial acuity, cortical responses contained little information with which to distinguish peripheral locations. We demonstrate a clear link between neural responses and spatial acuity measured behaviorally, and provide evidence for age-related changes in the coding of horizontal space.

1. Introduction

The ability to localize sources of sound—that is, to determine their direction and distance—is of fundamental importance to human beings and to animals. It helps listeners to know where to direct visual attention, where to venture to seek rewards, and where to retreat to avoid hazards (Moore, 2013). Compared with young human adults, older adults typically localize sources less accurately (Abel and Hay, 1996; Abel et al., 2000; Dobreva et al., 2011; Otte et al., 2013; Rakerd et al., 1998). Problems with localization have significant consequences. Self-reported difficulties in judging the location and movement of sources of sound are among the auditory disabilities that are most strongly associated with the experience of handicap, that is, with restricted social participation and reduced emotional well-being (Gatehouse and Noble, 2004; Strawbridge et al., 2000). For that reason, we have sought to understand the differences between younger and older adult listeners in the cortical processes that underpin sound localization.

The spatial location of a sound source is signaled by interaural (between-the-ears) and monaural (single-ear) cues (Grantham, 1995; Middlebrooks and Green, 1991). The interaural cues are differences in the time-of-arrival of a sound at the 2 ears, termed "interaural time differences" (ITDs), and differences in the intensity of a sound at the 2 ears, termed "interaural level differences" (ILDs). For example, if a sound source is located 90° to the right of a listener, the sound wave will reach, and, due to attenuation by the head, be more intense, at the right ear than the left ear. ITD and ILD cues are critical for localizing low- and high-frequency components of sounds, respectively, in the horizontal ("azimuthal") plane. The monaural cues are the peaks and troughs in the high end of the frequency spectrum of a sound, introduced by interactions between the sound wave and the corrugations of the outer ear. In broadband sounds, in which all cues are present, azimuthal localization is dominated by ITD cues (Macpherson and Middlebrooks, 2002; Wightman and Kistler, 1992;). Monaural cues help listeners to localize sounds in elevation and to reduce front/back confusions.

Aging is associated with a progressive bilateral loss of sensitivity to sound ("presbycusis"; Gates and Mills, 2005), which is more pronounced at higher acoustic frequencies. Thus, the loss would be expected to affect ILD cues to azimuthal location and monaural cues to elevation and front/back discrimination disproportionately. Aging is also associated with impairments in the processing of the temporal structure of sounds (Fitzgibbons and Gordon-Salant, 1996; Hopkins and Moore, 2011; Strouse et al., 1998); these temporal impairments may distort ITD cues to azimuthal location. There is good evidence that aging impairs performance on localization tasks involving monaural cues (Abel and Hay, 1996; Abel et al., 2000; Otte et al., 2013; Rakerd et al., 1998). However, the evidence that aging impairs performance on tasks involving interaural cues—for example, tasks involving localization in the frontal,

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0197-4580/$ – see front matter © 2014 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neurobiolaging.2013.08.033

azimuthal plane (a common feature of everyday listening)—is mixed (Dobreva et al., 2011; Otte et al., 2013). Interestingly, more complex tasks, such as those requiring listeners to report what 1 talker is saying amidst a background of other talkers, often show age-related differences in the ability of participants to benefit from horizontal spatial separation between sound sources (for a review, see Glyde et al., 2011). The greater consistency of these latter findings may mean that difficulties in spatial listening among older adults primarily result from the deterioration of higher-level executive functions such as attention and working memory. Such processes are known to be affected by aging (Braver and West, 2008; Kramer and Madden, 2008).

Alternatively, there may be genuine differences in the fidelity with which the auditory systems of individual older adults represent azimuthal space. We have developed a technique (Briley et al., 2013) that can test that idea. The technique quantifies the representation of azimuthal space in human auditory cortex using electroencephalography (EEG). It involves passive listening and so can probe spatial representation independent of attentional processes or other task requirements. The participant sits at the center of an array of loudspeakers (Fig. 1A) and a noise stimulus is presented that changes location every 1.5 seconds. Each shift in location elicits a transient neural response the size of which depends on the positions of the pre- and post-shift loudspeakers. The pattern of response sizes can be reproduced by a computational opponent-channel model that codes azimuthal location by the balance of activity in 2 spatial channels, 1 tuned to left, and 1 to right, auditory space (Fig. 1B). Opponent-channel coding of azimuthal location has received extensive support from studies of humans (Briley et al., 2013; Magezi and Krumbholz, 2010; Salminen et al., 2009, 2010) and other mammals (McAlpine et al., 2001; Stecker et al., 2005; Werner-Reiss and Groh, 2008).

In the current study, we used our technique with a group of older adults (>60 years), and compared the findings with those from young adults, to examine age-related changes in the representation of azimuthal space in auditory cortex. In addition, we obtained psychophysical measures of auditory spatial acuity so that we could distinguish older adults with impaired localization ability from those with good localization ability.

2. Methods

2.1. Young adult participants

Six participants undertook the psychophysical measurements (mean ± SD, 22.9 ± 2.8 years; 4 females and 2 males). EEG data for 11 young adults (23.3 ± 5.9 years; 10 females and 1 male) were taken from Briley et al. (2013). Both sets of participants had hearing thresholds equal to or greater than 20 dB HL at octave frequencies between 250 and 8000 Hz, inclusive.

2.2. Older adult participants

Eleven older adults (>60 years; 4 females and 7 males), with no history of neurological disease, undertook both the EEG and psychophysical parts of the study. None reported an adverse otological history, and none wore, or had been advised to wear, a hearing aid. As described in Results, the group was subdivided on the basis of measures of spatial acuity, forming the "younger-old" and "older-old" sub-groups. The 6 participants in the younger-old group were between 61 and 72 years of age (61.1, 62.1, 63.3, 65.1, 67.6, and 71.6 years; mean 65.1 years), whereas the 5 participants in the older-old group were between 73 and 81 years of age (73.1, 75.9, 76.6, 77.4, and 80.9 years; mean 76.8 years).

Both groups showed a presbycusic pattern of sloping, high-frequency hearing loss (Fig. 2D). Four-frequency average hearing levels, calculated as the mean hearing level at 500, 1000, 2000, and 4000 Hz in the better hearing ear, were better in the younger-old group (mean = 14.8 dB) than the older-old group (mean = 21.3 dB), a difference that approached significance (between-subjects t test; $t_9 = 2.221$, $p = 0.054$). The mean absolute interaural asymmetries across the same 4 frequencies were 2.3 dB and 4.3 dB for the younger- and older-old groups, respectively, and did not differ significantly. No participant met Noble and Gatehouse's (2004) criterion for classification as having a significant asymmetry (4-frequency average asymmetry >10 dB). The mean (±SD) sensation level of the pink-noise stimulus used in the EEG session was 50.3 (±4.9), 48.7 (±7.7), and 44.6 (±2.4) dB for the young, younger-old and older-old adults, respectively; the difference between the young and older-old groups was significant ($t_{13} = 2.391$, $p = 0.033$), but the remaining differences were not (younger-old vs. older-old: $t_9 = 1.116$, $p = 0.293$; young vs. younger-old: $t_{14} = 0.516$, $p = 0.614$). The minimum sensation levels in each group, across participants, were quite similar, with values of 41.1, 41.4, and 40.6 dB.

This study was approved by the Research Ethics Committee of the Department of Psychology of the University of York. Participants gave written consent.

2.3. EEG session procedures

EEG measurements were made in a single-walled IAC test room, located in a larger sound-treated enclosure. Participants sat at the

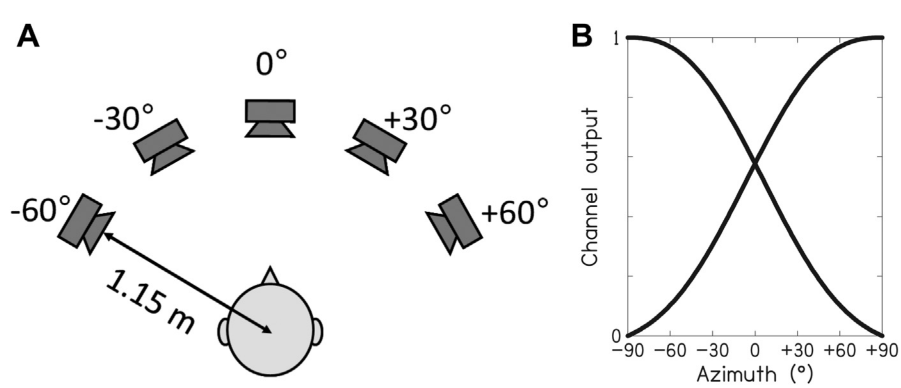

Fig. 1. (A) Schematic representation of the experimental setup for the EEG sessions. Participants faced a screen directly below the central loudspeaker (0°). Loudspeakers were positioned at approximately head height. (B) Schematic spatial tuning curves for the opponent-channel model. In this model, sound source location is computed from the balance of activity in the outputs of the 2 channels.