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Adaptation to shifted interaural time differences changes encoding of sound location in human auditory cortex☆

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ABSTRACT

The auditory system infers the location of sound sources from the processing of different acoustic cues. These cues change during development and when assistive hearing devices are worn. Previous studies have found behavioral recalibration to modified localization cues in human adults, but very little is known about the neural correlates and mechanisms of this plasticity. We equipped participants with digital devices, worn in the ear canal that allowed us to delay sound input to one ear, and thus modify interaural time differences, a major cue for horizontal sound localization. Participants wore the digital earplugs continuously for nine days while engaged in day-to-day activities. Daily psychoacoustical testing showed rapid recalibration to the manipulation and confirmed that adults can adapt to shifted interaural time differences in their daily multisensory environment. High-resolution functional MRI scans performed before and after recalibration showed that recalibration was accompanied by changes in hemispheric lateralization of auditory cortex activity. These changes corresponded to a shift in spatial coding of sound direction comparable to the observed behavioral recalibration. Fitting the imaging results with a model of auditory spatial processing also revealed small shifts in voxel-wise spatial tuning within each hemisphere.

Introduction

Spatial hearing is an important function of the human auditory system. It guides attention (Broadbent, 1954; Scharf, 1998) and improves the detection, segregation, and recognition of sounds (Bregman, 1994; Dirks and Wilson, 1969; Roman et al., 2001). Sound directions are not represented on the auditory epithelium, but must be computed from monaural and binaural acoustic cues (Blauert, 1997; Middlebrooks and Green, 1991). The association between acoustic cues and the perceived location of a sound source depends on the shape of the listener's ears and head (Carlile et al., 2005; Langendijk and Bronkhorst, 2002; Middlebrooks, 1999). In order to conserve accurate sound localization when the shape of head and ears change during development, the auditory system must be able to modify the processing of acoustic cues or their association with sound locations (Clifton et al., 1988; Hartley and King, 2010). The general ability to recalibrate spatial hearing is also crucial to people with hearing aids or cochlear implants (Byrne and Noble, 1998; Carlile, 2014; Mendonca, 2014). These findings indicate that some natural capacity for adapting to changes in auditory spatial coding must exist.

Plasticity in spatial hearing has been demonstrated during adulthood in animals (King et al., 2011; Knudsen, 2002) and humans (Wright and Zhang, 2006). Vertical sound localization can be regained within weeks after altering spectral cues (Carlile and Blackman, 2014; Hofman et al., 1998; Van Wanrooij and Van Opstal, 2005). Horizontal sound localization based on interaural level differences can be regained within a few days after plugging one ear (Bauer et al., 1966; Kumpik et al., 2010; McPartland et al., 1997). Only one study (Javer and Schwarz, 1995) manipulated interaural time differences (ITDs) and demonstrated that humans can adapt to shifted ITDs, but the mechanism remains unclear. To elucidate it, we shifted ITDs in relation to other auditory cues and vision in adult humans with programmable earplugs, and monitored participants with behavioral tests and fMRI while they regained normal sound localization.

Potential mechanisms can be derived from the known mechanisms of sound localization in the mammalian auditory system. Studies suggest that horizontal sound direction is represented by a population rate code. In the brainstem of small mammals, ITD tuning curves are wide, span both hemifields, have maxima outside of the physiological ITD range, and are steepest around the midline (Brand et al., 2002; Lesica et al., 2010; McAlpine et al., 2001; Siveke et al., 2006). Data from cats (Middlebrooks et al., 1998; Stecker et al., 2005) and monkeys

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(Werner-Reiss and Groh, 2008) also support a population rate code. Studies in humans (Magezi and Krumbholz, 2010; Salminen et al., 2009, 2010) also suggest a rate code of two neural populations, tuned to each hemifield (hemifield code: Salminen et al., 2012). These findings are in line with previous studies showing that human auditory cortex is involved in the processing of auditory space (Brunetti et al., 2005; Deouell et al., 2007; Krumbholz et al., 2005b; Zatorre et al., 2002), and are also in line with results suggesting that a majority of auditory cortical neurons are tuned to sounds from the contralateral acoustic hemifield (Krumbholz et al., 2005a; Palomäki et al., 2005; Pavani et al., 2002; Woods et al., 2009). Ferret studies showed that the auditory cortex also plays a role in experience-dependent recalibration of spatial hearing (Bajo et al., 2009; Nodal et al., 2010).

Based on previous findings on recalibration of spatial hearing with modified spatial cues, we hypothesized that manipulating ITDs would shift auditory spatial perception of our participants on the horizontal plane, and that this perceptual shift would progressively diminish as participants adapt. During such an adaptation, the perceived direction of sound sources must change. To quantify changes in sound direction perception, participants performed regular behavioral sound localization tests during the adaptation period. Based on the hemifield code and the previously observed preference for contralateral sounds, we hypothesized that behavioral adaptation would be accompanied by changes in the activation balance of the left and right auditory cortex. To test for such changes in hemispheric lateralization, we measured the amplitude and extent of fMRI responses in the left and right auditory cortex. We also aimed to determine whether adaptation was accompanied by detectable changes in directional tuning in the human auditory cortex. To characterize such changes in tuning, we computed high-resolution voxel-wise directional tuning curves before and after adaptation and fitted a computational model of sound direction coding to these curves.

Materials and methods

Participants

Twenty volunteers took part in the behavioral experiment after having provided informed consent. Six of them did not complete the experiment due to various reasons: three participants' earplugs stopped working during the experiment; two participants preferred to drop out of the experiment before the end; finally, during the scanning of one participant, the DSP device used for stimulus presentation blew a fuse. The 14 remaining participants (eight males, aged between 22 and 32 years) were right-handed (self-reported), had no history of hearing disorder or neurological disease, and had normal or corrected-to-normal vision. None of the participants had past or current psychiatric diseases, 7 out of 14 played an instrument (5/10 of the fMRI participants), but none was a professional musician. Participants had hearing thresholds of 15 dB HL or lower, for octave frequencies between 0.125 and 8 kHz. They had unblocked ear canals, as determined by a non-diagnostic otoscopy. Two participants experienced consistent front-back confusion when wearing the earplugs. We could not obtain sound localization measurements from these participants and thus excluded them from further analysis. Ten of the remaining 12 participants also took part in neuroimaging sessions. The experimental procedures conformed to the World Medical Association's Declaration of Helsinki and were approved by the local ethics committee.

Digital earplugs

We used programmable earplugs (Schönwiesner et al., 2009), based on an in-ear technology platform (Sonomax, Montreal, QC, Canada). Silicon plugs were custom-modeled to each participant's ear canals, bilaterally. We measured the attenuation provided by the earplugs with a dual-microphone set-up, one inside the ear canal, one outside (Voix and Laville, 2009). We then equipped each earplug with a miniaturized microphone, transducer, and digital signal processor (Voyager, Sound Design Technologies, Burlington, ON, Canada) featuring one audio input (32 kHz, 20 bit ADC), one amplified audio output (16 kHz, 20 bit DAC) and a specialized audio processing unit with a 2.048 MHz clock rate. The processing lag of each electronic insert was around 600 μs. Such a delay, when applied simultaneously to both ears, is too short to create perceivable audio-visual disparities (Lewald and Guski, 2003). When turned off, the earplugs provided an attenuation between ~25 dB at and below 1 kHz and ~45 dB at 8 kHz. The overall gain, transfer function, and delay of each earplug, were controlled by a custom-made software and checked with a KEMAR manikin. The gain of the earplugs was adjusted to achieve normal loudness levels and a digital filter was used to flatten the transducer's frequency transfer function. Fig. 1 shows an example of the delay and attenuation that the earplugs provided.

Overall procedure

Participants wore the earplugs initially for two days without any modification of interaural time differences (day −2 to day 0, Fig. 2). During this time, participants habituated to the earplugs, and we verified that the earplugs themselves (without delay) did not affect horizontal localization performance. A time delay of 625 μs was then added to the signal processing chain of the left earplug for the next seven days (days 0 to day 7, Fig. 2). Participants were informed that the earplugs would "slightly modify their sound perception", but they did not know the nature nor the effects of this modification. Participants were asked to wear the earplugs during all waking hours, but to remove them when sleeping or when they might be exposed to water. We tested participants' free-field sound localization performance each day; starting with an initial session before they were equipped with earplugs (day −2, Fig. 2), and finishing with a session immediately after the earplugs were removed at the end of the experiment (day 7, Fig. 2).

A subset of 10 participants underwent two identical sessions of fMRI scanning; the first session before the earplugs were worn (day −3, Fig. 2), and the second session one day before removing the earplugs (day 6, Fig. 2). To ensure that a shift in spatial hearing can be observed with the stimuli presented in the MRI scanner (see below), six of those participants performed an additional closed-field sound localization task that determined their perceived midline of the stimuli, one day before each fMRI session (day −4 and day 5, Fig. 2).

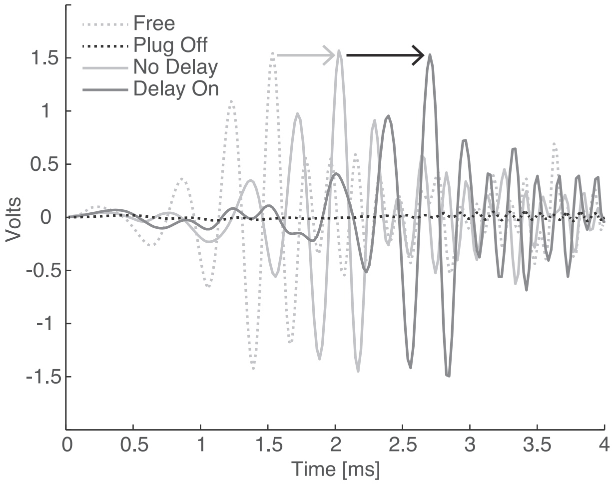

Fig. 1. Earplugs delay and attenuation. Example of recordings from one ear of a KEMAR mannequin of a 4 ms chirp stimulus presented from a loudspeaker placed in front of the mannequin's head. The same stimulus was recorded when the ear was unobstructed ("free"); with an earplug fitted to one ear of the KEMAR mannequin, inserted but switched off (i.e. full attenuation, "plug off"); with the earplug switched on, but no delay added ("no delay"), the constant AD-DA delay of the DSP is visible (grey arrow); with the earplug switched on and time delay of 625 μs added (black arrow, "delay on").