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Research paper

Human cortical sensitivity to interaural time difference in high-frequency sounds

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ABSTRACT

Human sound source localization relies on various acoustical cues one of the most important being the interaural time difference (ITD). ITD is best detected in the fine structure of low-frequency sounds but it may also contribute to spatial hearing at higher frequencies if extracted from the sound envelope. The human brain mechanisms related to this envelope ITD cue remain unexplored. Here, we tested the sensitivity of the human auditory cortex to envelope ITD in magnetoencephalography (MEG) recordings. We found two types of sensitivity to envelope ITD. First, the amplitude of the auditory cortical N1m response was smaller for zero envelope ITD than for long envelope ITDs corresponding to the sound being in opposite phase in the two ears. Second, the N1m response amplitude showed ITD-specific adaptation for both fine-structure and for envelope ITD. The auditory cortical sensitivity was weaker for envelope ITD in high-frequency sounds than for fine-structure ITD in low-frequency sounds but occurred within a range of ITDs that are encountered in natural conditions. Finally, the participants were briefly tested for their behavioral ability to detect envelope ITD. Interestingly, we found a correlation between the behavioral performance and the neural sensitivity to envelope ITD. In conclusion, our findings show that the human auditory cortex is sensitive to ITD in the envelope of high-frequency sounds and this sensitivity may have behavioral relevance.

1. Introduction

Sound source localization relies on various acoustical cues that are imposed on the sound on its way from the source to the eardrums of the listener. For humans, one of the major cues is the interaural time difference (ITD) that is best detected from the fine structure of low-frequency sounds (Middlebroks and Green, 1991; Wightman and Kistler, 1992; Macpherson and Middlebrooks, 2002). However, ITD can also be perceived in higher frequencies, provided that the sound is modulated in amplitude (Klumpp and Eady, 1956; David et al., 1959; Henning, 1974; McFadden and Pasanen, 1976; Nuetzel and Hafter, 1976, 1981). In this case, ITD is extracted from the envelope rather than the fine structure (Fig. 1). This envelope ITD cue is perceived by human listeners with a precision relevant for localizing real sound sources (Nuetzel and Hafter, 1976; Bernstein and Trahiotis, 2002; Dreyer and Oxenham, 2008; Klein-Hennig et al., 2011; Dietz et al., 2013a) but the human brain mechanisms underlying its utilization are unclear.

So far, the neural bases of the detection of envelope ITD have been studied only in non-human species (cat: Yin et al., 1984; Joris and Yin, 1995; Joris, 2003; Devore and Delgutte, 2010; rabbit: Batra et al., 1989, 1993, 1997; Wang et al., 2014; guinea pig: Griffin et al., 2005). Single units selectively tuned to envelope ITD have been found in the inferior colliculus (IC; Yin et al., 1984; Batra et al., 1989, 1993; Joris, 2003; Griffin et al., 2005; Devore and Delgutte, 2010; Wang et al., 2014) and the medial and lateral divisions of the superior olive (MSO and LSO, respectively; Joris and Yin, 1995; Batra et al., 1997). The subcortical processing of envelope ITD in

Abbreviations: ANOVA, analysis of variance; EOG, electro-oculogram; ERF, event-related field; IC, inferior colliculus; ILD, interaural level difference; IPD, interaural phase difference; ISI, inter-stimulus interval; ITD, interaural time difference; JND, just-noticeable difference; LSO, lateral superior olive; MEG, magnetoencephalography; MSO, medial superior olive; SPL, sound pressure level

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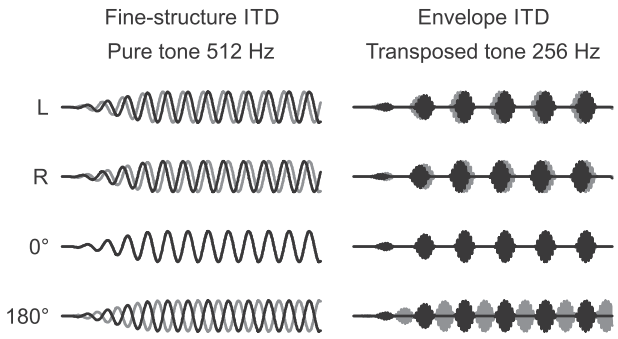

Fig. 1. Pure and transposed tones used in evaluating auditory cortical sensitivity to fine-structure and envelope ITD. The ITDs used in the MEG experiment were left-leading (L, −0.5 ms), right-leading (R, +0.5 ms), in phase (0° IPD), and opposite phase (180° IPD). Left ear signal gray, right ear signal black.

experimental animals coincides with human perception in some aspects. First, sensitivity to envelope ITD is at its strongest both in psychoacoustics (Nuetzel and Hafter, 1981; Bernstein et al., 1994; Bernstein and Trahiotis, 2002) and in single neurons (Joris and Yin, 1995; Batra et al., 1989; Griffin et al., 2005) for sounds with modulation frequencies between about 100 and 300 Hz. Second, both perceptual and neural sensitivity to ITD depend on the shape of the envelope: sensitivity to envelope ITD is stronger for a stimulus class called transposed tones than for sinusoidally amplitude modulated tones (Bernstein and Trahiotis, 2002; Griffin et al., 2005), presumably because the transposed tones induce stronger phase locking in the auditory periphery (Dreyer and Delgutte, 2006). However, generalizing results from animal studies to human brain function is not straightforward, especially in the processing of ITD. The best strategy for representing ITD may depend on factors such as hearing range and head width that determines the range of ITDs occurring in free field (Harper and McAlpine, 2004). Therefore, obtaining data specifically on human brain activity is essential for understanding the neural mechanisms of envelope ITD detection.

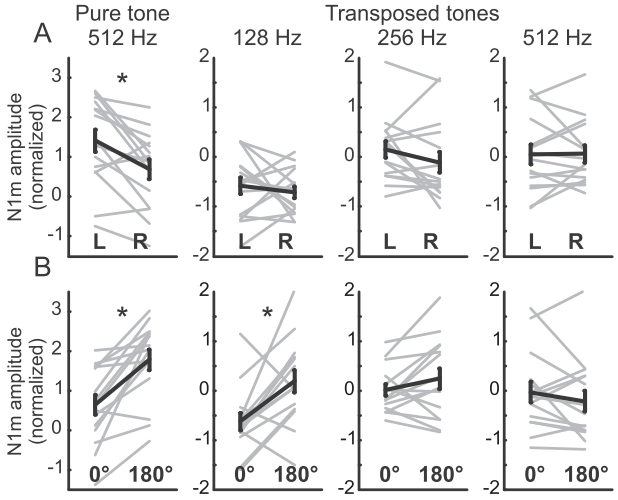

Fig. 2. Right-hemispheric N1m amplitudes averaged over 15 participants (± standard error of the mean). Gray lines depict individual subjects. (*A*) Larger right-hemispheric N1m responses were found for the left- (L) than the right-leading (R) fine-structure ITD for the pure tone stimulus. For the transposed tones, N1m amplitude did not differ between these two ITDs. (*B*) The N1m amplitude was larger for the opposite-phase (180°) than for the in-phase (0°) stimulus for the pure tone and for the transposed tone modulated at 128 Hz. For transposed tones of 256 and 512 Hz no differences were found. Significant effects marked with an asterisk.

While the human brain mechanisms related to envelope ITD remain unexplored, sensitivity to fine-structure ITD has been studied extensively (Halliday and Callaway, 1978; McEvoy et al., 1993; Sams et al., 1993; Krumbholz et al., 2005; Palomäki et al., 2005; Zimmer and Macaluso, 2005; Magezi and Krumbholz, 2010; Salminen et al., 2010; Dietz et al., 2013b). The human auditory cortex shows contralateral preference for fine-structure ITD: response amplitudes are larger for stimuli in which the signal in the contralateral ear is leading than for stimuli in which the leading signal is in the ipsilateral ear (Krumbholz et al., 2005; Palomäki et al., 2005). This shows, for instance, in MEG recordings of the N1m (McEvoy et al., 1993; Palomäki et al., 2005), a response peak occurring at around 100 ms after sound onset and originating from secondary auditory areas (Liégeois-Chauvel et al., 1994; Jääskeläinen et al., 2004). However, most measures of brain activity available in humans, the N1m included, are population-level responses: they reflect the compound activity of neurons with various tuning properties. To tease apart the contributions of neural populations with different ITD tuning properties, previous studies have capitalized on the sensitivity of the auditory cortical responses to stimulation history (Halliday and Callaway, 1978; McEvoy et al., 1993; Magezi and Krumbholz, 2010; Salminen et al., 2010; Dietz et al., 2013b). For instance, the N1m amplitude is larger for probe sounds preceded by adaptors with differing fine-structure ITD than for those preceded by adaptors with the same ITD (McEvoy et al., 1993; Salminen et al., 2010). This is presumably due to selective tuning to fine-structure ITD in auditory cortical neurons. When the ITDs are the same, the probe and the adaptor activate the same neurons and adaptation is strong. However, when the probe and the adaptor differ in ITD, neurons selectively tuned to the probe ITD are not activated by the adaptor and thereby their activity is attenuated less. At the population level, this results in larger N1m response amplitudes.

Here, we conducted an MEG study aimed at recording sensitivity to envelope ITD in the human auditory cortex. The stimuli were transposed tones with envelope ITDs and, for comparison, a low-frequency pure tone with fine-structure ITD. We recorded N1m responses to two pairs of ITD values (Fig. 1). First, ITDs of −0.5 and +0.5 ms were used in order to test contralateral preference and selective adaptation to envelope ITD. These ITDs correspond to spatial locations about 60° from the midline to the left and to the right (Middlebrooks and Green, 1990) and are therefore well within the physiologically plausible range of ITDs. Second, we used an ITD corresponding to an interaural phase difference (IPD) of 180° and compared this to an ITD of 0 ms. In the former case, the ear signals have opposite phase, whereas in the latter case they are in phase. At low frequencies, the opposite phase stimulus corresponds to a very long ITD that does not occur in free field. Nevertheless, this condition was included due to previous animal studies showing preference for such long ITDs in the LSO and IC (Joris and Yin, 1995; Batra et al., 1997; Griffin et al., 2005). Finally, to test whether the auditory cortical activity is related to behavioral performance and also to confirm that our untrained participants were able to detect envelope ITD, we conducted a brief psychoacoustical test and compared the results to the N1m amplitudes at the individual level.

2. Materials and methods

2.1. Participants

Fifteen subjects (age 21–33, mean 25, standard deviation 4 years, 3 female) took part in the MEG recordings with written informed consent and the approval of the Ethical Committee of Aalto University. Nine of the subjects also participated in the psychoacoustical experiment. All participants in the psychoacoustical