



## Research paper

## Integrated processing of spatial cues in human auditory cortex



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## ABSTRACT

Human sound source localization relies on acoustical cues, most importantly, the interaural differences in time and level (ITD and ILD). For reaching a unified representation of auditory space the auditory nervous system needs to combine the information provided by these two cues. In search for such a unified representation, we conducted a magnetoencephalography (MEG) experiment that took advantage of the location-specific adaptation of the auditory cortical N1 response. In general, the attenuation caused by a preceding adaptor sound to the response elicited by a probe depends on their spatial arrangement: if the two sounds coincide, adaptation is stronger than when the locations differ. Here, we presented adaptor–probe pairs that contained different localization cues, for instance, adaptors with ITD and probes with ILD. We found that the adaptation of the N1 amplitude was location-specific across localization cues. This result can be explained by the existence of auditory cortical neurons that are sensitive to sound source location independent on which cue, ITD or ILD, provides the location information. Such neurons would form a cue-independent, unified representation of auditory space in human auditory cortex.

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## 1. Introduction

The human ability to localize sound sources relies on various acoustical cues of which the most important are the interaural time and level difference (ITD and ILD, respectively; Middlebrooks and Green, 1991). Both of these cues are informative about the location of a sound source in the horizontal plane, that is, about the laterality of the sound source. Initially, ITD and ILD are extracted separately by specialized brainstem nuclei (Grothe et al., 2010) but for reaching a coherent representation of auditory space, the nervous system needs to combine the information in these two cues.

Here, we conducted magnetoencephalography (MEG) recordings in search for such an integrated representation of ITD and ILD in the human auditory cortex.

The auditory system appears to weight the ITD and ILD information differently, depending on the frequency content, when combining location information. At low frequencies, horizontal sound source localization is dominated by ITD, whereas it relies primarily on ILD at higher frequencies (Middlebrooks and Green, 1991; Wightman and Kistler, 1992; Macpherson and Middlebrooks, 2002). For broadband sounds, perceived location is influenced by both. Previous human electrophysiological studies on cue integration have, however, used low-frequency stimuli (Johnson and Hautus, 2010; Altmann et al., 2014; Edmonds and Krumbholz, 2014) or applied a constant ILD to a broadband sound (Schröger, 1996; Urgan et al., 2001; Tardif et al., 2006). Though ILD can be detected in low-frequency sounds (Hafer et al., 1977; Yost and Dye, 1988) and also the human auditory cortex is sensitive to it (Salminen, 2015), large low-frequency ILDs occur in free-field conditions only when the sound sources are within about 50 cm from the center of the head (Brungart and Rabinowitz, 1999). Therefore, a low-frequency sound might not capture the aspects of

*Abbreviations:* ANOVA, analysis of variance; BIC, the nucleus of the brachium of IC; EEG, electroencephalography; EOG, electro-oculogram; ERF, event-related field; ERP, event-related potential; GUI, graphical user interface; HRTF, head-related transfer function; IC, inferior colliculus; ICC, central nucleus of IC; ILD, interaural level difference; ISI, inter-stimulus interval; ITD, interaural time difference; LSO, lateral superior olive; MEG, magnetoencephalography; MSO, medial superior olive; SPL, sound pressure level

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ILD processing most relevant in natural conditions. One attempt has also been made at finding cue integration for a high-frequency sound in which a prominent ILD would occur in natural conditions (Altmann et al., 2014). However, for this sound, no sensitivity to ITD alone was shown. ITD can be detected in a high-frequency sound if suitable amplitude modulation is present (Nuetzel and Hafter, 1976; Bernstein and Trahiotis, 2002) and also human cortical sensitivity to high-frequency ITD has been shown in a previous study assessing ITD processing specifically (Salminen et al., 2015). Yet, both neural and perceptual sensitivity to ITD in high-frequency sound is less robust than at lower frequencies and may rely on separate mechanisms. Therefore, a broadband stimulus is needed to assess cue integration so that both ITD and ILD processing mechanisms are fully involved.

Previous human electrophysiological studies have provided evidence for cue integration in terms of subadditivity of event-related potentials (ERPs): an abrupt appearance of ITD and ILD concurrently in a continuous sound or in a stream of sound bursts results in a response of smaller amplitude than the sum of the responses to each cue in isolation (Schröger, 1996; Altmann et al., 2014; Edmonds and Krumbholz, 2014). This subadditivity has been interpreted as evidence for an overlap between the cortical generators of ITD and ILD sensitive responses. However, such overlap does not necessarily imply location-sensitive mechanisms. A recent study found that the response amplitudes to concurrent changes in ITD and ILD did not depend on whether the ITD and ILD cues corresponded to the same side of the auditory space or not (Altmann et al., 2014). As a result, subadditivity occurred independent of location-consistency across the two cues. Therefore, the overlap between ITD and ILD sensitive mechanisms suggested by subadditive effects might not be sensitive to location. A mechanism not sensitive to the consistency of location information across the two cues would not promote an integrated representation of spatial location. Integration and segregation in the processing of spatial cues has also been assessed by comparing the activity elicited by ITD and ILD stimuli in terms of, for instance, amplitude or source location of cortical activity (Ungan et al., 2001; Tardif et al., 2006; Johnson and Hautus, 2010). In such a design, integrated processing would be manifested as similarity between the activity patterns elicited by the two cues. However, the absence of differences is a negative finding and may also result from the insensitivity of the recording method to potential underlying differences.

Here, we conducted an MEG experiment aimed at revealing integrated processing of ITD and ILD in human auditory cortex. To this end, we used broadband sound stimuli and developed an experimental design that relies on the location-dependent adaptation of the N1 response. The N1 is an auditory cortical response peak occurring in ERPs and event-related fields (ERFs) approximately 100 ms after the sound onset (Picton, 2011). In general, the amplitude of the N1 to a probe sound depends on the location of a preceding adaptor sound: when the adaptor is presented at the same location as the probe, N1 amplitude is smaller than when the adaptor and probe locations differ (Fig. 1A; Butler, 1972; McEvoy et al., 1993; Ahveninen et al., 2006; Salminen et al., 2009). This has been interpreted to reflect spatial selectivity in auditory cortical neurons. When the probe and adaptor are presented from the same location, they activate the same neurons and adaptation is strong. In contrast, when the probe and adaptor locations differ, the two sounds activate separate populations of spatially selective neurons and therefore adaptation is weaker. Here, we used probe and adaptor sounds in which ITD and ILD were manipulated independently (Fig. 1B). For instance, we presented probe sounds with ILD corresponding to a location in the left and adaptors containing ITD corresponding to the same location or to a location on the opposite side of the midline. In this case, adaptation would be location-

specific only if there are neurons that are sensitive to both cues. Such neurons would detect the coinciding spatial cues in the adaptor and the probe resulting in location-specific adaptation (Fig. 1B, top). However, if such neurons do not exist and the cues are instead represented by separate populations, ILD-sensitive neurons would be activated and thereby adapted similarly by the ITD adaptors in the left and right side and adaptation would not be location-specific (Fig. 1B, bottom). Similarly, ITD-sensitive neurons would be unaffected by the location information in the ILD. Therefore, any location-specific adaptation in such a scenario would indicate that neurons consistently sensitive to both cues do indeed exist.

## 2. Materials and methods

### 2.1. Subjects

Nineteen healthy volunteers took part in the experiment (mean age 26, std 4, 7 female) with written informed consent and the approval of the Ethical Committee of Aalto University. The MEG data of two subjects was discarded due to a poor signal to noise ratio. Seventeen of the participants took part in the psychoacoustical experiment, which also contained two additional healthy volunteers.

### 2.2. Stimulus generation

The stimuli were bursts of broadband noise in which ITD and ILD were independently manipulated. A broadband sound was used because the relative weights of the two cues depend on sound frequency (Middlebrooks and Green, 1991; Wightman and Kistler, 1992; Macpherson and Middlebrooks, 2002) and both ITD and ILD are prominently present in wideband stimuli. The ITD and ILD values imposed on the stimuli were determined from head-related transfer functions (HRTFs) that were individually recorded for each participant. The cues were imposed on the stimuli independently so that one of the cues corresponded to a location on the left or right side of the midline while the other cue remained at zero. This HRTF-based procedure was adopted for two reasons. First, ILD values depend strongly on frequency (Shaw, 1974) and this frequency-dependency is encoded in the HRTFs. Second, this procedure ensures that the ITD and ILD values correspond to actual locations in the external space.

The use of HRTF-based ITD and ILD values deviates from previous studies that have used either somewhat arbitrarily selected values (Schröger, 1996; Ungan et al., 2001; Tardif et al., 2006) or values that resulted in an equal lateralization across cues in a psychoacoustical experiment (Johnson and Hautus, 2010; Edmonds and Krumbholz, 2014; Altmann et al., 2014). However, the psychoacoustical matching of ITD and ILD has so far led to cues that do not necessarily correspond to the same location in the external space and to ILDs that are too large to occur under natural conditions in the low-frequency stimuli employed. Hence, we decided to avoid the problem of matching the ILD and ITD values in terms of both perceived laterality and the external sound source location by imposing physically matching ITD and ILD cues and assessing the perceived laterality in a psychoacoustical experiment.

HRTFs were measured for each participant in an anechoic chamber with the microphone (Knowles FG-233329-P07) positioned at the blocked ear canal entrance point (see, e.g. Møller et al., 1995). The loudspeakers were placed at the height of the ears at nine lateral angles ( $0^\circ, \pm 15^\circ, \pm 30^\circ, \pm 45^\circ, \text{ and } \pm 90^\circ$ ) in the horizontal plane. Subjects were seated in a chair at the center of the anechoic chamber, and were asked to keep the head still facing the loudspeaker positioned at  $0^\circ$  while the transfer functions were

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