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Research Report

Spatial processing in human auditory cortex: The effects of 3D, ITD, and ILD stimulation techniques

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Abstract

Here, the perception of auditory spatial information as indexed by behavioral measures is linked to brain dynamics as reflected by the N1m response recorded with whole-head magnetoencephalography (MEG). Broadband noise stimuli with realistic spatial cues corresponding to eight direction angles in the horizontal plane were constructed via custom-made, individualized binaural recordings (BAR) and generic head-related transfer functions (HRTF). For comparison purposes, stimuli with impoverished acoustical cues were created via interaural time and level differences (ITDs and ILDs) and their combinations. MEG recordings in ten subjects revealed that the amplitude and the latency of the N1m exhibits directional tuning to sound location, with the amplitude of the right-hemispheric N1m being particularly sensitive to the amount of spatial cues in the stimuli. The BAR, HRTF, and combined ITD + ILD stimuli resulted both in a larger dynamic range and in a more systematic distribution of the N1m amplitude across stimulus angle than did the ITD or ILD stimuli alone. Further, the right-hemispheric source loci of the N1m responses for the BAR and HRTF stimuli were anterior to those for the ITD and ILD stimuli. In behavioral tests, we measured the ability of the subjects to localize BAR and HRTF stimuli in terms of azimuthal error and front–back confusions. We found that behavioral performance correlated positively with the amplitude of the N1m. Thus, the activity taking place already in the auditory cortex predicts behavioral sound detection of spatial stimuli, and the amount of spatial cues embedded in the signal are reflected in the activity of this brain area.

Theme: Sensory systems

Topic: Auditory systems: central physiology

Keywords: Magnetoencephalography (MEG); N1m; Auditory; Spatial; Localization cue

1. Introduction

Localizing sound sources is particularly important for directing attention towards events in the auditory environment, and the detection of sound source direction is crucial for survival in many species. The human auditory system exploits sound localization cues embedded in auditory signals (for reviews, see [2,12]). The primary cues for azimuthal sound source localization are the interaural time and level differences (ITD and ILD, respectively), which are caused by a differential distance between the sound source and the ears and the acoustical shadowing effects of the head. Elevation is resolved through utilizing the spectral cues arising from the filtering effects of the pinna, the head, and the body. The physiological basis of spatial localization has been extensively studied using animal models (for reviews, see [7,24]) where sites sensitive to ITD, ILD, and spectral cues [39] and topographical mappings of auditory space [7,22] have been found in the midbrain. In the primary auditory cortex, certain

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neurons have spatial receptive fields [3], and are organized in clusters of similar directional tuning [7].

With the introduction of non-invasive brain imaging techniques measuring the blood flow as well as the electric and magnetic activity of the human brain, research on the neural underpinnings of sound localization in humans has gained momentum. While functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) provide for good accuracy in identifying activated brain areas, the temporal dynamics of sound source localization can be more precisely tackled with the study of rapid changes in neuronal currents. These are reflected in electro- and magnetoencephalography (EEG and MEG, respectively) [10,15] where cortical responses to sensory stimulation can be measured with an excellent temporal accuracy in terms of the event-related potential (ERP) and magnetic field (ERF). In the auditory domain, the N1m deflection and its derivative mismatch negativity (MMN) are commonly used to index activation of auditory cortex [19,26,27,31].

The MEG is sensitive to magnetic interference caused by loudspeakers and any other electro-acoustic transducer placed near the measurement device. Therefore, an acoustic tube sound system with compromised audio quality, delivering a two-channel mock description of the auditory environment, is typically used for transmitting auditory stimuli directly to the left and right ear of the subject. This, however, is already sufficient for studying the processing of ITD and ILD modulations in spatial stimuli. Importantly, MEG research [11,32,33] has benefited from the recent development of headphone-based 3D-sound technology such as head-related transfer functions (HRTF), which provide for an accurate (re-)presentation of a realistic 3D sound field using binaural stimulus presentation through MEG-compatible earphones. Contrasting ITD and ILD modifications, whereby the subject experiences the sound as originating *inside* the head, 3D sounds are perceived to occur in specific locations *outside* the head. Thus, 3D sound technology provides for a marked improvement in the experienced three-dimensional aspect of stimulation which, consequently, widens the scope of investigations concerning the cortical processing of auditory space.

Previous MEG and EEG studies have revealed that activation in the auditory cortices of both hemispheres is stronger for contralateral auditory stimulation [11,32–35,37,51,52]. These findings are further corroborated by results obtained in animal models [14,18]. However, unlike in animal models [53], the dominant role of the right-hemispheric auditory areas in sound localization in humans has been highlighted in measurements of the human brain [17,21,32,33,54], and in studies on patients with right-hemispheric lesions [8,9,53]. Previously, using non-individualized HRTF stimuli presented in the azimuthal plane, we found that the auditory N1m is more prominent for stimuli presented in the contralateral hemifield, and, importantly, that the amplitude of the N1m elicited by spatial stimuli exhibits almost twice as large a dynamic range in the right auditory cortex than in the left [32,33]. We also found that right-hemispheric preponderance holds across different types of stimulation, with speech stimuli increasing the N1m amplitude by nearly a factor of two compared to non-speech stimuli [33]. However, differences in the hemispheric dominance across individuals has also been reported [11]. Interestingly, behavioral studies have found that, in binaural listening, subjects localize more accurately stimuli in the left hemifield [4], and in monaural listening conditions, subjects localize more accurately with their left ear [6], which indicates a right-hemispheric dominance in auditory localization.

The cortical processing of spatially impoverished (e.g., ITD and ILD) and binaural vs. spectral cues have been investigated in separate studies. Ungan et al. [46] found that ERP responses to ITD- and ILD-modulated stimuli had significantly different scalp topographies. Schröger [40] found that combined ITD/ILD deviants elicited a larger-amplitude MMN than deviants containing ITD or ILD cues alone. Both of these EEG studies suggested that ITD and ILD cues are processed by different cortical mechanisms. Moreover, in MEG measurements exploiting individual HRTF-based stimulation only, Fujiki et al. [11] found that azimuthal (mainly binaural) cues are processed earlier than elevation (spectral) cues, which led the authors to suggest that auditory cortex may treat spectral cues differently from binaural ones. Related conclusions were made by Kaiser et al. [20], who suggested that the ITD cues were processed earlier (100–140 ms) than the spectral variation in the stimuli (around 180 ms).

Hemodynamic measures [5,13,25,48,54] appear to have found areas in the brain which are specifically activated by spatial sound stimulation. In general, on the basis of these findings, it seems that parietal brain areas have a special role in the processing of spatial content in auditory stimulation. For example, Bushara et al. [5], using PET, discovered areas specific to auditory (as opposed to visual) spatial localization in the superior parietal and prefrontal cortices indicating that auditory spatial processing extends well beyond the temporal auditory areas. Further, Zatorre et al. [54] found that spatial stimuli presented simultaneously from different locations elicit activity in posterior auditory cortex indicating that this area is involved in disambiguating overlapping auditory sources. Moreover, they found that inferior parietal cortex is specifically activated during a spatial localization task with the strength of this activation correlating with localization accuracy in terms of absolute error.

Based on the abovementioned data, several issues remain to be clarified. Firstly, there exist very little data on the possible differences between cortical activity elicited by spatial stimuli containing prominent spatial cues vs. impoverished spatial stimuli containing only ITD and ILD cues. In our understanding, no MEG study specifically comparing the effects of spatially enriched 3D and impoverished ITD and ILD stimuli on brain dynamics has