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Research Report

Asymmetrical representation of auditory space in human cortex

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ABSTRACT

Recent single-neuron recordings in monkeys and magnetoencephalography (MEG) data on humans suggest that auditory space is represented in cortex as a population rate code whereby spatial receptive fields are wide and centered at locations to the far left or right of the subject. To explore the details of this code in the human brain, we conducted an MEG study utilizing realistic spatial sound stimuli presented in a stimulus-specific adaptation paradigm. In this paradigm, the spatial selectivity of cortical neurons is measured as the effect the location of a preceding adaptor has on the response to a subsequent probe sound. Two types of stimuli were used: a wideband noise sound and a speech sound. The cortical hemispheres differed in the effects the adaptors had on the response to a probe sound presented in front of the subject. The right-hemispheric responses were attenuated more by an adaptor to the left than by an adaptor to the right of the subject. In contrast, the left-hemispheric responses were similarly affected by adaptors in these two locations. When interpreted in terms of single-neuron spatial receptive fields, these results support a population rate code model where neurons in the right hemisphere are more often tuned to the left than to the right of the perceiver while in the left hemisphere these two neuronal populations are of equal size.

1. Introduction

Auditory localization has a unique role in orienting in the environment. While vision is limited to locations in front of the perceiver, audition allows the detection of objects in all directions and even when they are obscured by visual obstacles. Consequently, the auditory system provides crucial spatial information for directing other senses towards interesting objects and events. Recent studies suggest that sound source location in the horizontal plane is represented in the cortex by a population rate code. According to this model, auditory spatial receptive fields are centered either to the left or right of the subject and span the whole hemifield. This neural code has been studied in detail in the monkey with single-neuron recordings (Woods et al., 2006; Werner-Reiss and Groh, 2008). Human psychophysical (Boehnke and Phillips, 1999) and neuroimaging (Salminen et al., in press) results are also consistent with the population rate code but very little is

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still known about the details of its neuronal implementation. Here, we conducted magnetoencephalography (MEG) measurements to study the differences between the representations of auditory space in the two cortical hemispheres.

Single-unit recordings in the monkey show that the implementation of the population rate code is asymmetrical in the two cortical hemispheres (Benson et al., 1981; Ahissar et al., 1992; Woods et al., 2006). Neurons are more often tuned to the hemifield contralateral to the measurement site than to the ipsilateral side. Indications of contralateral preference have also been found in the human cortex. Stronger activity is often found in the hemisphere contralateral to the sound source location (Ungan et al., 2001; Palomäki et al., 2005; Krumbholz et al., 2005, 2007) and this could potentially reflect a larger number of neurons being tuned to the contralateral than to the ipsilateral hemifield. The right and the left hemisphere seem to differ in the magnitude of the contralateral preference although this issue is not entirely clear: some studies show a stronger contralateral preference in the right than in the left hemisphere (Palomäki et al., 2002, 2005; Tiitinen et al., 2006) while others suggest that the asymmetry is larger in the left hemisphere (Ungan et al., 2001; Krumbholz et al., 2005, 2007). Thus, it remains unresolved what the relative sizes of the contralaterally and ipsilaterally tuned populations are in the human cortex.

Psychophysical studies have revealed several sources of location information embedded in sound (Middlebrooks and Green, 1991). At low sound frequencies, the most prominent cue is the interaural time difference (ITD) that results from the sound reaching one ear before the other and occurs both at the onset and along the whole duration of the sound. At higher frequencies, the head of the listener casts a shadow on the sound and thus creates an interaural level difference (ILD). Also, at higher frequencies, the pinnae, the head, and the body of the listener alter the frequency spectrum of the sound in a direction-specific manner. These cues do not occur as independent entities in the sound waveform. Instead, they are imposed on sound signals that already have complex spectro-temporal structure and, consequently, the availability and usefulness of different types of localization cues diverges from one sound source to another. For instance, while a wide-band noise sound includes all of the localization cues, a speech sound has less energy in the high frequencies and, thus, carries less of the spectral cues and has a smaller ILD. How this is reflected in the cortical representations of sound source location is not known.

The N1m response, occurring in the event-related field at around 100 ms after sound onset, and its electrical counterpart N1 have proven to be useful measures of spatial sensitivity in the human auditory cortex. The N1m is generated in multiple secondary (belt and parabelt) areas of auditory cortex (for a review, see May and Tiitinen, in press) and it varies in amplitude according to sound source location. It is maximal for sources contralateral to the hemisphere from which it is measured and minimal for ipsilateral sources (Palomäki et al., 2005). The N1 and N1m responses, when obtained in a stimulus-specific adaptation paradigm, can provide information on the spatial selectivity of auditory cortical neurons (Butler, 1972; Salminen et al., in press). In this paradigm, sounds are presented in adaptor-probe pairs and the effect of the preceding adaptor on the response to the following probe is measured (Fig. 1). When the adaptor is presented at the same location as the probe, the two sounds activate the same population of spatially selective neurons and, consequently, the attenuation of the amplitude of the N1m response is maximal. However, when the adaptor is presented from a different location than the probe, the neurons activated by the probe but not by the adaptor are presumably not influenced by the preceding adaptor presentation and, thus, respond to the probe strongly. This selectivity, then, leads to an increase in the amplitude of the N1m response.

The aim of the present study was to compare the spatial selectivity between the cortical hemispheres and to estimate the relative sizes of the contralaterally and ipsilaterally tuned neuronal populations in each hemisphere. To this end, we presented spatial sound stimuli, individually prepared for each subject, in a stimulus-specific adaptation paradigm and measured the attenuation of the N1m response. To facilitate comparisons between the hemispheres, the sound sources were situated symmetrically with respect to the midline. The probe sound was always directly in front of the subject and adaptors were presented in the left and right hemifields. The

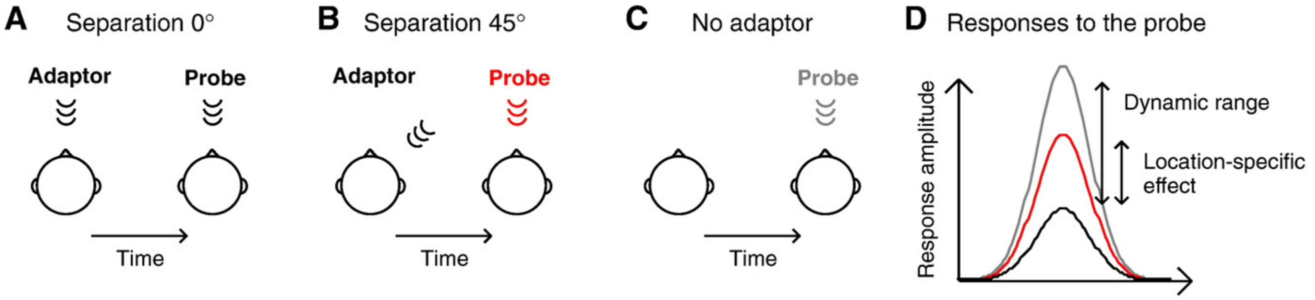

Fig. 1 – Illustration of the stimulus-specific adaptation paradigm. (A) Two sounds, an adaptor and a probe are sequentially presented and the brain responses to the probe are measured. When the adaptor and the probe are presented from the same location directly in front of the subject, adaptation is maximal and responses are small. (B) The adaptor is then presented from a location 45° to the right from the probe. Assuming that the neuronal population giving rise to the response is selective to sound source location, this leads to a less attenuated response to the probe. (C) The largest responses occur when no adaptor sound is presented. (D) The difference between the response amplitudes measured in these conditions can be used as a measure of neuronal selectivity to sound source location.