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Behavioral Detection of Spatial Stimuli Is Reflected in Auditory Cortical Dynamics

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ABSTRACT

We studied the cortical processing of spatial stimuli by magnetoencephalographic (MEG) measurements using broadband noise bursts presented from eight sound source directions in the horizontal plane. The stimuli were individually created for each subject by using three-dimensional (3D) sound techniques. The subjects carried out a behavioral task where their accuracy for localizing the 3D stimuli was established. We found that the auditory N100m response was sensitive to the sound source direction, exhibiting contralaterally more preponderant responses in both the left and the right hemisphere. Generally, responses were more prominent in the right hemisphere. The behavioral performance of the subjects correlated positively with N100m amplitude organization, showing that the dynamics of auditory cortex predict behavioral sound detection.

KEY WORDS

Auditory cortex, Spatial sound localization, Magnetoencephalography, MEG, N100m.

INTRODUCTION

The human auditory system exploits binaural localization cues, the interaural time and level differences (ITD & ILD respectively) and spectral cues produced by the filtering effects of the pinna, the head and the body [Blauert, 1997]. Previous brain research has addressed auditory spatial processing in headphone listening by employing ITD and ILD modifications whereby the sounds are experienced as originating inside the head. Recent developments in 3D-sound technology, however, have opened up the possibility of presenting spectrotemporally rich stimulation through headphones, resulting in the stimuli being perceived as originating in genuine 3D-space.

Studies of auditory spatial processing in the human brain have rapidly gained momentum [Fujiki, 2002] [Pantev, 1998] [Teder-Sälejärvi, 1998] and it has been established that right-hemispheric auditory areas are specialized in the processing of spatial information [Kaiser, 2000] [Palomäki, 2000] [Palomäki, 2002] [Zatorre, 2002]. Further insight into spatial processing could be gained by linking brain processes to psychophysical measures. For this purpose, we presented individualized 3D stimuli to subjects in MEG measurements and in separate behavioral measurements where the subject indicated the perceived direction of the sound source. We then determined how well the N100m response predicted behavioral performance.

METHODS

Ten subjects participated in the experiment with informed consent. For creating individualized 3D stimuli, microphones were attached to the entrance of the subject's ear canals and recordings were made using a 50-ms, 10-kHz noise burst presented through loudspeakers at eight locations in the horizontal plane (0°, 45°, 90°, 135°, 180°, -135°, -90° and -45°, where 0°/180° = front/back & –90°/90° = left/right, respectively). In MEG recordings, the stimuli were delivered to the subject's ears with a tubephone sound system (100 Hz – 10 kHz, ±7.5 dB) using an interstimulus interval of 750 ms. The binaural loudness of the stimuli was balanced to 10 sones using a loudness model [Moore, 1996]. The audio system was calibrated to 74 dB sound pressure level (SPL, A-weighted) measured for the 0° stimulus at the earpiece of the tubephone system using a custom-made model of the ear canal and a TES 1351 type 2 SPL meter. Thus, approximately the same binaural loudness was used across the different experimental conditions and subjects.

Brain activity was recorded (passband 0.03-200 Hz, sampling rate 600 Hz) with a 306-channel whole-head magnetometer (Vectorview, Elekta Oy, Finland). The subject sat in a reclining chair under instruction not to pay attention to the auditory stimuli and to concentrate on watching a self-selected silent film. Over 100 instances of each direction angle were presented to each subject in a random order. The responses were averaged and baseline-corrected with respect to a 100-ms pre-stimulus period and bandpass filtered at 2-30 Hz. The N100m amplitude was analyzed from the gradiometer sensor pairs displaying maximum responses and its source location was estimated using unrestricted equivalent current dipoles (ECDs), separately above the left and right hemisphere.

The subjects performed a behavioral localization task where responses to 480 random-order stimulus presentations were collected utilizing a computerized test program where the subject used a mouse to indicate the horizontal direction of the stimuli. Localization accuracy was measured in terms of the mean angular error, front-back confusions, and the number of misses. Front-back confusions, that is, where a stimulus arriving from the front (0°, 45°, -45°) was perceived as arriving from behind (135°, 180°, -135°) or *vice versa*, were counted and corrected. We hypothesized that the amplitude of the right-hemispheric N100m reflects behavioral sound localization by being an increasing monotonic function of the horizontal angle, varying from an ipsilateral minimum to a contralateral maximum. This leads to a hypothetical amplitude order of 90°, 45°/135°, 0°/180°, -45°/-135°, and -90°. For testing this hypothesis we developed an Angular Organization Test (AOT) which ranks the individual subject’s N100m amplitudes in terms of a

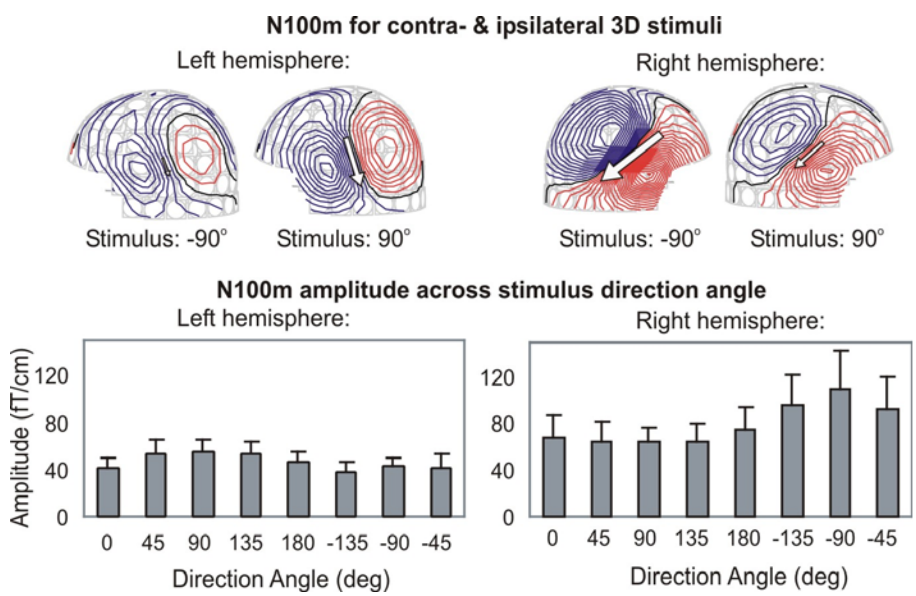

Figure 1. *Top:* grand-averaged N100m responses for contra- and ipsilateral stimulation. *Bottom:* the N100m amplitude behavior for 3D stimuli from eight direction angles. The right-hemispheric N100m is more prominent and displays a larger dynamic range.

distance measure: In the test, the N100m responses for the different angles are ordered according to amplitude. If this order exactly corresponds to the hypothesis, the distance equals zero. If the order differs from the hypothesis, the ordinal distances between the hypothesized and observed positions are summed. This procedure yields a ranking-order scale ranging from 0 to 8, reflecting how well the amplitude of the N100m corresponds to the hypothesis.

RESULTS

Stimulus direction angle had a significant effect on the amplitude of both the left- ($F[7,63] = 4.21$, $P < 0.001$) and right-hemispheric ($F[7,63] = 5.73$, $P < 0.001$) N100m responses and, in both hemispheres, the N100m elicited by contralateral stimulation was larger than that elicited by ipsilateral stimulation (Fig. 1). Overall, the response amplitudes were larger in the right than left hemisphere, the difference approaching statistical significance in both gradiometer analysis (79 vs. 47 fT/cm; ($F[1,9] = 4.35$, P = 0.067) and ECD modeling (19.7 vs. 14.4 nAm; $F[1,9] = 3.17$, P = 0.11). Moreover, the interaction between hemisphere and direction angle was statistically significant ($F[1,63] = 2.89$, $P < 0.05$) presumably due to the larger dynamic range of the N100m amplitude in the right hemisphere. Stimulus direction angle also had a significant effect on the latency of the N100m in the right hemisphere ($F[7,63] = 2.19$, $P < 0.05$) with left-hemifield stimulation resulting in shorter response latencies (123 ms) than right-hemifield stimulation (129 ms). No significant effects on the N100m latency were observed in the left hemisphere (*P* = n.s.). Direction angle did not have significant effects in the ECD source locations of the N100m (*P* = n.s.). The AOT-measure, reflecting how well the N100m amplitude was organized according to stimulus direction angle, yielded an average index of 2.90.

Figure 2 shows the perceived direction angle as a function of the actual stimulus direction. The subjects were able to localize the stimuli correctly, as indicated by the linear relationship between stimulus direction angle and behaviorally reported angle ($F[7,63] = 474.24$; $P < 0.001$, misses = 1.22%, front-back confusions = 24.5%). On the average, the mean angular error was 12.5° ($F[7,63] = 3.92$; $P < 0.01$). The angular errors for stimuli presented from the front-back (9.0°) and left-right directions (8.5°)

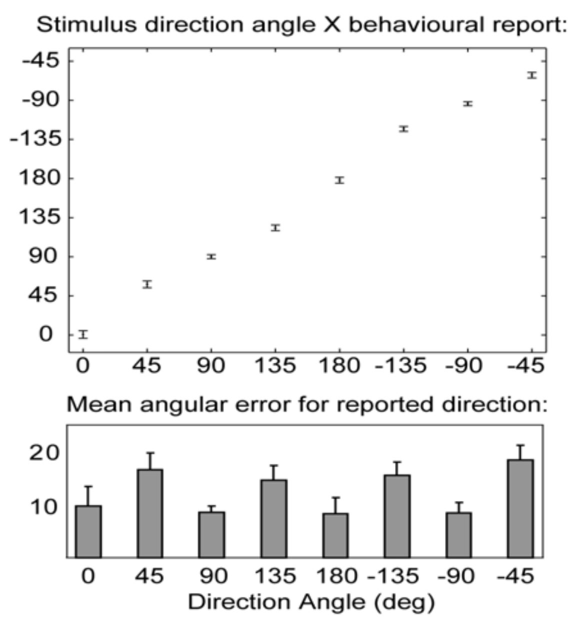

Figure 2. *Top:* the perceived direction angle as a function of actual stimulus direction (bars indicate standard error of the mean). *Bottom:* mean angular error of behavioral responses (degrees). Note the linear relationship between the actual and perceived direction angle and differences between front/back and left/right vs. oblique directions.

were smaller than those for the stimuli presented from oblique angles (16.3°). The correlation coefficient between the angular error averaged over stimulus direction angle and the AOT test was r = 0.80 (P < 0.01), indicating that the behavioral localization ability of the subjects is reflected in the organization of N100m amplitude according to the hypothesized pattern.

DISCUSSION

Corroborating the results of previous research [Kaiser, 2000] [Palomäki, 2000] [Palomäki, 2002], we found that the right hemisphere of the human brain appears to have a dominant role in spatial processing. Firstly, the variation of the N100m amplitude across stimulus direction angle was larger in the right hemisphere. Presumably, a larger dynamic range of the N100m amplitude allows for better behavioral discrimination. Secondly, we found that the latency of the right-hemispheric N100m exhibits directional tuning to sound location. Finally, the statistically non-significant source location shifts in ECDs for the N100m responses elicited by 3D stimuli do not support the idea that auditory cortex uses a location code to represent 3D information. Thus, it appears the processing of spatial information in auditory stimuli is reflected both in the amplitude and latency behavior of the N100m response.

In assessing how brain dynamics are reflected in overt behavior, the AOT result revealed that 3D stimuli elicited right-hemispheric N100m responses with amplitudes consistently organized according to stimulus direction angle. The AOT result was further validated by the correlation between the AOT results and the behavioral results on mean angular error. This correlation suggests that the amplitude organization of the N100m predicts behavioral localization performance for stimuli containing spatial cues.

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