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Automatic cortical responses to sound movement: A magnetoencephalography study

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ABSTRACT

The aim of the present study was to clarify what change detection process leads to the elicitation of the auditory change-sensitive N1ms using magnetoencephalography (MEG). We brought our attention to whether these N1ms would be elicited if physical changes to the stimulus are eliminated. For this purpose, sound movement (SM), which entails a very subtle change only to the manner of stimuli presentation, was used in the present study. SM presentation was achieved by inserting an interaural time difference to one ear. The results indicate that both SM and the onset of the control stimulus (ON) elicited MEG responses at the superior temporal gyrus (STG) of both hemispheres. ON-N1m peak latencies were significantly shorter than those of SM-N1m as well. Interestingly, the pre-event (ON or SM) length (PreEL) was a significant factor determining the amplitude of the STG activity. Due to these findings, we hypothesize that both ON and SM activate similar groups of neurons or even an identical group of neurons. In addition, since correlations between PreEL and ON/SM-N1m amplitude exist, it is suggestible that N1m is not merely a nonspecific automatic response to physical change, but rather a much more sophisticated change-sensitive response employing a memory mechanism.

Lately, unimodal and multimodal cortical areas that detect changes in human somatosensory, auditory, and visual systems had been identified [7,27]. Our previous investigation on the auditory system using magnetoencephalography (MEG) has indicated that the onset (ON) and offset (OFF) of sound stimuli with various interstimulus intervals (ISIs) elicit a magnetic component approximately 100 ms after the presentation of the stimulus (N1m) [30]. All estimated dipoles of these N1ms were located in the vicinity of the superior temporal gyrus (STG) of both hemispheres [30]. In addition, interestingly, OFF-N1m's amplitude varied depending on the ISI, suggesting that a memory mechanism may be controlling the amplitude of N1m by comparing the pre-stimulus and post-stimulus conditions. Moreover, in our recent study, a frequency change of a pure tone (CHANGE) elicited change-sensitive N1ms with source localized also in STG, in which the amplitudes were ISI dependent [31].

In line with our previous findings, electroencephalography and MEG studies of others have also reported the ISI dependency of auditory N1m amplitude [12,26]. Furthermore, STG activity dependency on ISI has been specifically reported [14,27]. Based on our findings on N1m characteristics under auditory ON, OFF, and CHANGE conditions [27,30,31], along with others' findings on N1ms following abrupt auditory changes [13,19,22,23], we hypothesize that N1m is sensitive to auditory change. However, it still remains unclear exactly how this change-sensitive N1m is elicited.

Sound localization, the binaural hearing ability to detect sound sources, is another field of interest for investigating the change-sensitive N1m and its elicitation mechanism. Sound movement (SM), an auditory perception of sound source moving laterally due to insertion of an interaural time difference (ITD) to one ear, has been utilized in various studies exploring sound localization. ITD, along with interaural intensity difference (IID) and spectral cues, is a primary binaural acoustic cue relied on when localizing sound. Halliday and Callaway [9] first reported that such SM presentations elicit late auditory evoked potentials within latencies of 100–300 ms. Though human brain responses, including N1ms, to sound localization by, for example, altering ITDs and/or IIDs have been studied extensively [e.g. 17,28,29], very few studies have investigated the effects of altering the acoustics prior to SM presentation on SM related brain responses [18,20].

Since our main interest lies in understanding the change detection process leading to the elicitation of change-sensitive N1ms, we brought our attention to whether change-sensitive N1ms would be elicited if physical changes to the auditory stimulus were elim-

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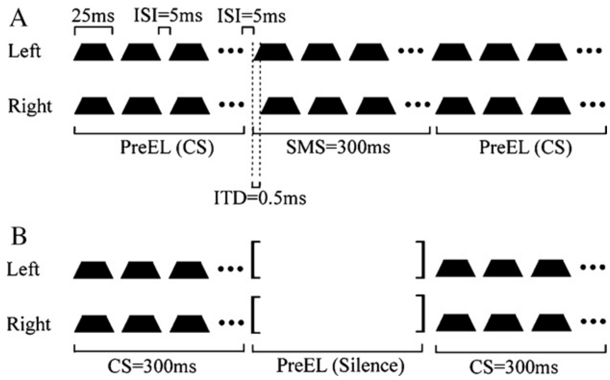

Fig. 1. Experimental designs. (A) In Experiment 1, effects of the CSL on SM were examined. The PreEL, consisting of CS presented coherently to both ears, was followed by a 5 ms ISI and the SMS, which was always 300 ms in duration and included an ITD of 0.5 ms to the right ear creating SM. The four PreEL conditions were 500, 1500, 3000, and 6000 ms. (B) In Experiment 2, effects of the length of the preceding silence on N1m of ON of the CS were examined. Repeats of the 300 ms long CS was separated by a 5 ms ISI followed by the PreEL consisting of silence. The same four PreEL conditions from Experiment 1 were used.

inated. For this purpose, SM, which entails a very subtle change only to the manner of stimuli presentation, was used in the present study. Considering the fact that the sound stimulus itself would not be physically altered, the SM stimulus (SMS) was expected not to evoke a change-sensitive response when presented monaurally. Furthermore, for comparison of SM-N1ms to other types of change-sensitive N1ms, we also recorded ON-N1ms elicited by ON stimulus preceded by various lengths of silence. We hypothesize that the sound source change is detected through an automatic comparison of the sound sources of the stimuli with and without SM by using a short-term memory mechanism, and thus elicits the automatic change-sensitive N1ms.

The study was performed on eight (one female and seven males) healthy right-handed volunteers of ages 25–45 (mean age: 31.1) who had no history of hearing impairment. The study was in accordance with the Declaration of Helsinki and was approved in advance by the Ethics Committee of the National Institute for Physiological Sciences, Okazaki, Japan. Furthermore, written consents were obtained from all subjects beforehand.

Sound stimuli were presented to each subject through ear pieces (E-A-Rtone 3A, Aero Company, Indianapolis, IN). Subjects sat relaxed and watched a self-selected silent movie throughout the experiment. Subjects were instructed to simply watch the movie without attending to the sound stimuli. This study was comprised two experiments (Fig. 1). The two experiments used the same fundamental sound stimulus and only differed in how the stimuli were presented to the subjects' ears. The fundamental sound stimuli, rephrased as control stimulus (CS), consisted of a repeated 25 ms 800 Hz pure tone (includes 5 ms rise and 5 ms fall) with a silent 5 ms ISI, and was coherently presented to both ears.

In Experiment 1, effects of the CS length (CSL) on SM were examined (Fig. 1A). A sequence of the CS with a length of 500, 1500, 3000, or 6000 ms followed by a 5 ms ISI and the SMS of 300 ms were presented repeatedly. The SMS was the CS modified with an ITD of 0.5 ms to the right ear. Thus, the ISI immediately preceding the SMS perceived by the right ear was lengthened by 0.5 ms to be 5.5 ms instead of the standard 5 ms ISI separating each CS. Each CSL condition was performed separately and the order of the conditions was randomized among subjects. In addition to the four CSL conditions, a control condition was conducted in order to examine the effects of the SMS when presented monaurally. Each left and right sounds of the 3 s-CS-SMS condition were presented monaurally, in the order of the left ear, then the right ear.

In Experiment 2, effects of the length of the preceding silence on N1m of ON of the CS were examined (Fig. 1B). The 300 ms long CS was presented repeatedly at a trial–trial interval of either 500, 1500, 3000 or 6000 s. That is, effects of the length of the silent period on N1m of ON of CS were examined in a similar manner to Experiment 1's effects of CSLs on N1m of SMS. To simplify, the length prior to an event (ON or SM) will be referred as the pre-event length (PreEL).

The experiments were carried out in a magnetically shielded room. Subjects were instructed to watch a silent movie throughout the experiment. Auditory evoked magnetic fields (AEFs) were recorded with a helmet-shaped 306-channel MEG system (Vector-view. ELEKTA Neuromag. Helsinki, Finland), comprised102 identical triple sensor elements. Each sensor element consisted of two orthogonal planar gradiometers and one magnetometer coupled to a multi-superconducting quantum interference device (SQUID) and thus provided 3 independent measurements of the magnetic fields. In this study, we analyzed MEG signals recorded from 204 planar-type gradiometers. These planar gradiometers are powerful enough to detect the largest signal just over local cerebral sources. The signals were recorded with a bandpass of 0.1–200 Hz and digitized at 1000 Hz. For each condition, 100 artifact-free trials were recorded.

All MEG data display and analyses were carried out using Neuromag softwares. To identify sources of the evoked activities, the equivalent current dipole (ECD), which best explains the measured data, was computed using a least-squares search. A subset of 14–20 channels including the local signal maxima was used for the estimation of ECDs. These calculations gave the three-dimensional (3D) location, orientation, and strength of the ECD in a spherical conductor model, which was based on the each subject's magnetic resonance imaging (MRI) to show the source location. The goodness-of-fit value of the ECD was calculated to indicate in percentage terms how much the dipole accounts for the measured field variance. Model adequacy was assessed by examining percentage variance [11]. Only ECDs explaining more than 80% of the field variance at selected periods of time were used for further analysis. The data acquisition and analysis followed [10]. MRI scans were obtained from all subjects with a 3.0-T MRI scanner (Allegra, Siemens, Erlangen, Germany). T1-weighted coronal, axial and sagittal image slices obtained every 1.5 mm were used for rendering the 3D reconstruction of the brain's surface.

Since the source location of the main magnetic component at around 100 ms did not differ significantly among conditions, which will be elaborated below, the amplitude and latency were compared among conditions using magnetic responses of a single sensor with the largest amplitude in each hemisphere. The peak latency and amplitude of each cortical source activity were submitted to a three-way repeated measure ANOVA (hemisphere × event × PreEL). The statistical significance of the source location was assessed by a discriminant analysis using x, y, and z coordinates as variables for each condition.

It must be noted that there are possible limitations associated with our results due to the relatively small sample size of our study ($n = 8$). In Experiment 1, all subjects reported that the left and right stimuli were identical when SMS was presented monaurally, confirming that SM is mediated by binaural interaction. When the SMS was presented binaurally, all subjects perceived the sound source shift from the center of the head to the vicinity of the left ear.

Both the SMS in Experiment 1 and ON of CS (abbreviated as ON from now on) in Experiment 2 elicited clear MEG responses at the temporal areas of both hemispheres (Fig. 2B). However, no identifiable SM evoked activity was present when the SMS was presented monaurally in Experiment 1. ECD analyses indicated activation of STG in both hemispheres. When ON- and SMS-N1m ECD locations were compared for each PreEL condition unihemispherically, the ECD locations did not differ significantly (Wilks' Lambda Test: p