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Differential offset and onset responses to interruptions and resumptions of verbal streams in the human auditory cortex

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Abstract. We used neuromagnetic measurements while nine subjects listened to (i) a series of spoken sentences and (ii) white noise whose amplitude was modulated by the envelope of the spoken sentences as control stimuli, both included sudden and brief interruptions. Auditory evoked magnetic fields corresponding to the interruption and resumption of the speech were measured. Statistically significant enhancement was observed only in the N1m component of the auditory evoked offset response ($N1m_{off}$) to the interruptions of the verbal stream compared to the onset response ($N1m_{on}$) to the resumptions of the stream. This enhancement in the offset auditory response was not observed in the responses to the interruptions and resumptions in the noisy control. These results indicate the different neural substrates underlying the generation of offset and onset auditory responses to the interruptions and resumptions of verbal streams.

Keywords: verbally presented natural language, N1m, offset response, auditory cortex, magnetoencephalography (MEG)

1. Introduction

Recent neuroimaging studies have suggested that the human auditory area in the temporal cortex plays an important role in the language specific processing of verbally-presented language streams [Binder et al., 1996; Dhankhar et al., 1997; Vouloumanos et al., 2001]. In these studies, neural activities in the auditory cortex were assessed in terms of hemodynamic or metabolic changes. On the other hand, relatively simple stimuli, such as phoneme or consonant-vowel-consonant combinations, were widely used in previous studies of early auditory language processing in the auditory cortex using EEG and MEG [Näätänen et al., 1997; Numminen et al., 1999; Tervaniemi et al., 1999], largely due to the difficulty in controlling precisely the onset and duration of natural auditory language stimuli. Motivated by an interest in how our spoken language processing is affected by brief interruptions of verbal streams in realistic situations, which sometimes occur during cellular phone communication [Enderes et al., 2000], we used neuromagnetic measurements (magnetoencephalography: MEG) to assess brain responses to brief interruptions and resumptions embedded in spoken natural language stream to investigate characteristics of the auditory language processing in the human auditory cortex with precise control on temporal changes in stimulus amplitude. Sudden interruptions and resumptions in the auditory stream evoke prominent components of event-related potentials $N1_{off}$ and $N1_{on}$, respectively, and their magnetic counterparts $N1m_{off}$ and $N1m_{on}$ around a latency of 100 ms [Hari et al., 1987; Pantev et al., 1996]. These components are thought to be generated from almost the same or overlapping regions in the primary auditory cortex [Hari et al., 1987; Pantev et al., 1996]. $N1_{on}$ and $N1_{off}$ components reflect the early stage of auditory language processing in the human auditory cortex in the superior temporal cortices, and their amplitudes, latencies, and lateralization are known to be affected in developmental language disabilities such as dyslexia [Leppänen and Lyytinen, 1997][Shaul, 2007], which indicate the clinical significance of these components in diagnosing developmental language impairments. Measuring the $N1m_{off}$ and $N1m_{on}$ components using a whole-cortex-type MEG

system, we evaluated the neural activity in the human auditory cortex evoked by sudden interruptions and resumptions of spoken language.

2. Material and Methods

Nine healthy subjects aged 22-47 years (one female) participated in the experiment as volunteers. All were right-handed, with normal hearing, with no history of neurological disorders, and were all native Japanese speakers. Written informed consent was obtained from each subject prior to the experiment complying with the human research policies of the internal review board of the National Institute of Advanced Industrial Science and Technology.

The auditory stimuli consisted of (i) six different TV news broadcasts read by a male newscaster in Japanese (NEWS), and (ii) six different noisy sounds (NOISE) delivered to each subjects' right or left ear. Each news sentence was one minute long with ten randomly inserted interruptions, each of which lasted 500 ms (Figure 1). Each noisy sound was similarly one minute long, created as the product of white noise and the same envelope as the news sentence with ten interruptions, so that the sound pressure levels just before the interruptions and after the resumptions were exactly the same as those in the corresponding target (NEWS) stimuli. Thus a twelve minute sound as the auditory stimulus was generated by combining six news and six noisy sounds randomly in order to counterbalance the presentation order of NEWS and NOISE conditions. The stimuli were controlled by PsyScope software (Cohen et al., 1993) on a Macintosh computer (PowerMac G3 DT/233, Apple Computer Inc., Cupertino, CA). The sound stimuli were generated by a small speaker (Eartone, Aearo Co., Indianapolis, IN) and were delivered with plastic tubes 0.8 m long terminating in ear inserts. The maximum sound intensity was adjusted to be comfortable to each subject (60 – 75 dB SPL; mean, 65 dB SPL). The subjects were instructed to fixate on a small visual target in front of them and to passively listen to the continuous auditory stimuli.

MEG signals were measured with a whole-cortex-type 122-channel DC-SQUID (Superconducting Quantum Interference Device) system (Neuromag 122, Elekta-Neuromag, Helsinki, Finland), which was located in a magnetically shielded, air-conditioned room. The sensor array covered the whole scalp and contained 61 pairs of orthogonal planar gradiometers; each of these sensor pairs measured two independent tangential derivatives of the magnetic field component normal to the helmet-shaped surface approximating the shape of the scalp (Hämäläinen et al., 1993). With this planar gradiometer configuration, the largest MEG signal occurs just above a dipolar neural source.

MEG signals were measured while the subjects listened to the NEWS and NOISE sounds. The interruption-related epochs of 2,500 ms, including a 500 ms pre-interruption baseline, were recorded with a pass-band of 0.03 – 100 Hz and a sampling rate of 500 Hz. More than 60 epochs were averaged for each NEWS and NOISE condition. The epochs with an MEG signal change exceeding 1,500 fT/cm were rejected from the signal averaging to exclude signal contamination by large external noise.

The averaged data were filtered with a digital low-pass filter with a cutoff frequency of 30 Hz. The averaged and filtered data were used to compute the root-mean-square (RMS) amplitudes of the field strength across the 26 pairs of MEG sensor channels covering the subjects' left and right temporal areas around the auditory $N1m_{off}$ and $N1m_{on}$ field extrema. RMS values were calculated in the time range between 50 and 200 ms after the interruptions and the resumptions of auditory stream at the intervals of

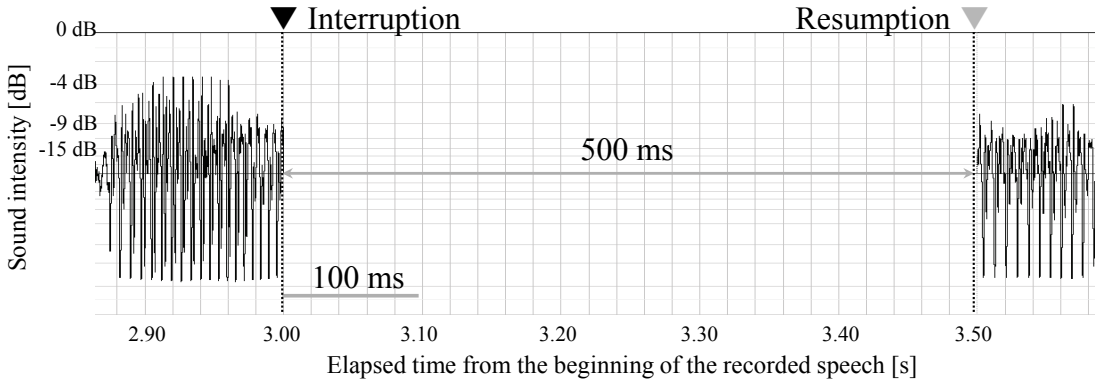

Figure 1. *Typical acoustic waveforms of the sudden interruptions with 500 ms duration embeded in the natural spoken language stream.*

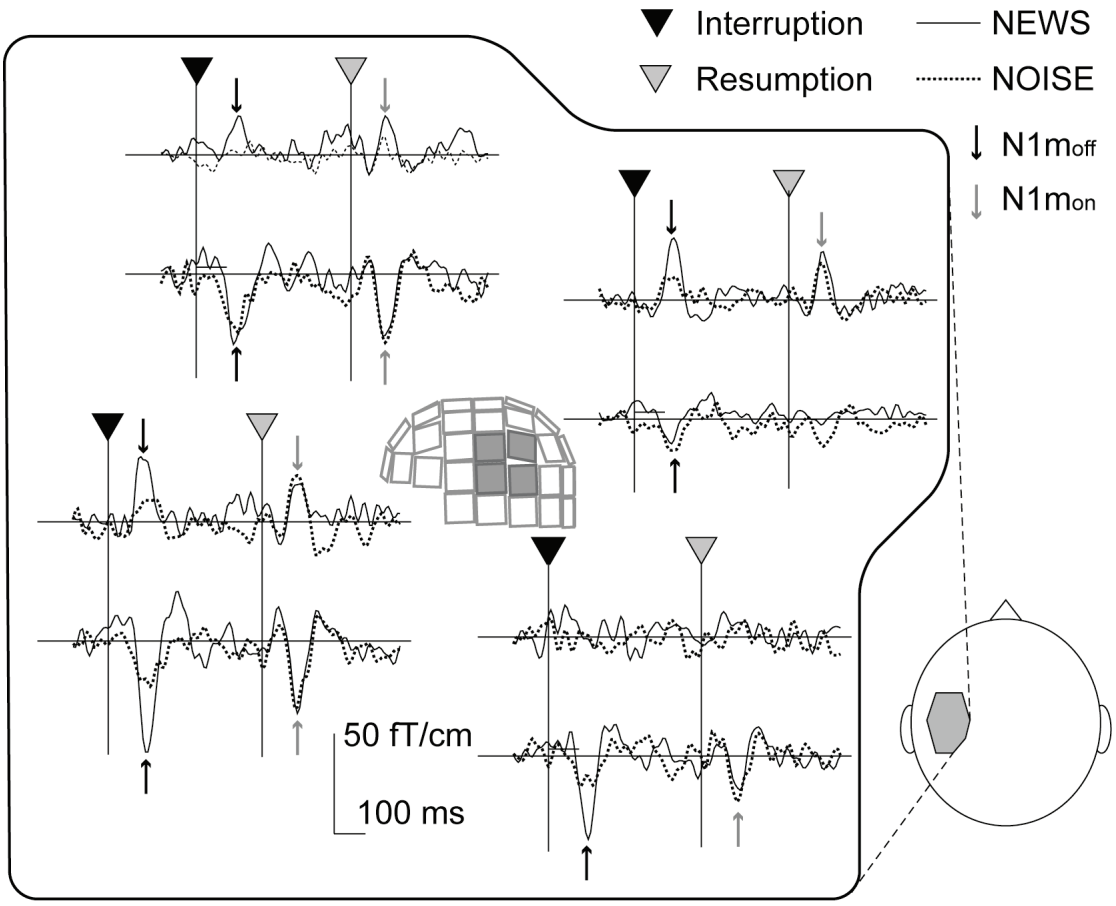

Figure 2. *Typical waveforms of the neuromagnetic responses to the sudden interruptions and resumptions of auditory streams in the NEWS (solid lines) and NOISE (dotted lines) conditions, which were delivered to each subject's right ear. $N1m_{off}$ (black arraws) and NIm_{on} (gray arrows) waveforms in both conditions measured at 4 pairs of orthogonal planar gradiometric sensors (Hämäläinen et al., 1993) covering the left auditory cortex are depicted. Each pair of waveforms shows two independent tangential derivatives along the longitudes (upper plots) and the latitudes (lower plots) of the brain magnetic field normal to the helmet-shaped sensor surface measured by the planar gradiometric system.*

2 ms. $N1m_{off}$ and $N1m_{on}$ peak amplitudes were defined as the peak amplitude of RMS values around 100 ms after the interruption (black triangles in Fig. 2) and resumption (gray triangles in Fig. 2) detected by visual inspection. RMS amplitudes for $N1m_{off}$ and $N1m_{on}$ were averaged over all subjects and differences between conditions were evaluated using an analysis of variance (ANOVA) with Tukey's post-hoc test.

3. Results

Figure 2 shows typical waveforms of the neuromagnetic responses to the sudden interruptions of auditory streams in the NEWS and NOISE conditions, which were delivered to each subject's right ear. The waveforms were event-related MEG responses to the interruption (black triangles) and resumptions (gray triangles) embedded either in the spoken sentences (NEWS) or amplitude modulated white noise (NOISE) measured at the MEG sensors covering left auditory cortex. In all subjects, $N1m_{off}$ components and N1mon components were observed in both conditions at the latencies around 100 ms after the interruption and the resumption, respectively. Significant enhancement of the $N1m_{off}$ MEG

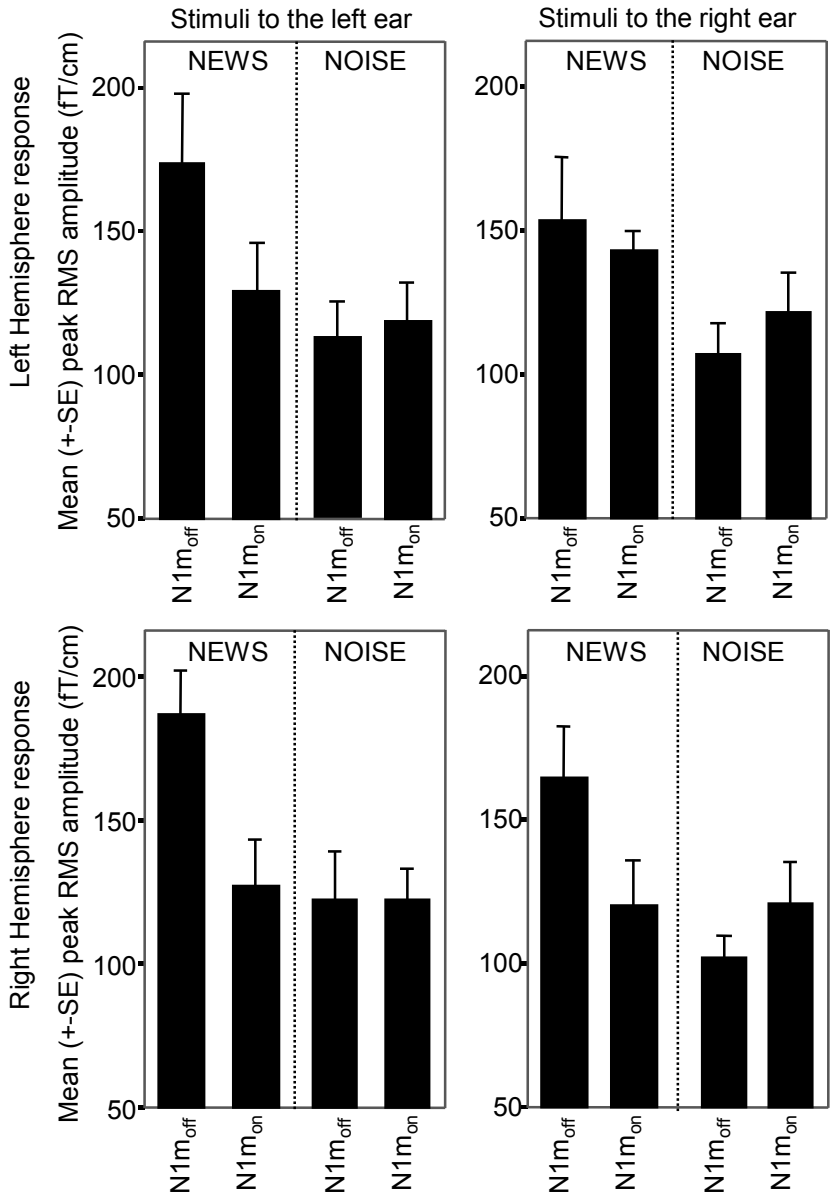

Figure 3. *Mean and standard error of the $N1m_{off}$ and $N1m_{on}$ peak amplitudes in the NEWS and NOISE conditions.*

component in the NEWS condition compared to the NOISE condition was observed in the temporal MEG channels covering the subject's auditory cortex.

The mean $N1m_{off}$ and $N1m_{on}$ peak amplitudes in the two conditions are presented in Fig. 3. The $N1m_{on}$ peak amplitudes measured in the left hemisphere in the NEWS condition were larger than those in the NOISE condition but were not statistically significant. $N1m_{on}$ peak amplitudes in the right hemisphere did not show any difference between the conditions. In contrast, the peak amplitudes of the $N1m_{off}$ component in the NEWS condition were significantly greater than those in the NOISE condition in all stimulus-response combinations, where statistical significance (p-values) of the differences were (a) $p = 0.0007$ for the left auditory cortex responses to the left ear stimuli, (b) $p = 0.0007$, for the left auditory cortex responses to the right ear stimuli, (c) $p = 0.009$ for the left auditory cortex responses to the right ear stimuli, and (d) $p<0.0001$ for the right auditory cortex responses to the right ear stimuli.

4. Discussion

Using sudden interruptions and resumptions of spoken sentences, we controlled the offset and onset times of natural language stimuli precisely so that we could measure the offset and onset event-related responses from the auditory cortex ($N1m_{off}$ and $N1m_{on}$). The results show that sudden interruptions of spoken sentences evoked significant enhancement of $N1m_{off}$ response in the NEWS condition compared to that in the NOISE condition in both hemispheres. $N1m_{on}$ responses in the left hemisphere showed slight increase in the NEWS condition compared to the NOISE condition, which might be explained by the harmonic contents only exist in the NEWS condition, but were not statistically significant.

These results suggest that the enhancement of the $N1m_{off}$ component in the NEWS condition was not merely due to differences in the acoustic properties between the two stimulus conditions used in this study, since the $N1m_{off}$ and $N1m_{on}$ components are considered to share the same neural mechanism [Hari et al., 1987; Pantev et al., 1996] and differences in the acoustic properties, such as harmonic structures, between the two conditions would modify the amplitudes of both the $N1m_{off}$ and $N1m_{on}$ components in the same manner. Increased attention or arousal during the NEWS condition compared to the NOISE condition might be another possibility to explain the increase in $N1m_{off}$ amplitudes in the NEWS condition, however, the fact that there was no significant difference between the amplitudes of the $N1m_{on}$ components between the NEWS and the NOISE conditions indicates that the subjects' attention to the auditory stimuli, which would significantly affect the amplitudes of both the $N1m_{off}$ and $N1m_{on}$ components [Näätänen 1990 for review], were equally allocated among both conditions.

$N1m_{on}$ peak amplitude in the NEWS condition is larger than that in the NOISE condition only in the left hemisphere, which might reflect the left hemisphere dominance for auditory language processing in the human auditory cortex [Näätänen et al., 1997].

The current results suggest that the human auditory cortex plays an important role in perceiving interruptions of verbal streams. If a verbally presented sentence is suddenly and briefly interrupted, it elicits an interruption not only of the acoustic power, but also of its semantic flow. Top down regulation to the primary auditory processing while listening to the language stream might enhance the $N1m_{off}$ response to the interruption of the verbal stream but not the $N1m_{on}$ response to the resumption of the stream which shares the same acoustic features.

5. Conclusions

We investigated whether neural activities in the auditory cortex are modulated by language-specific processing. Using auditory natural language stimuli with sudden and brief interruptions, we observed enhanced offset auditory responses to the interruptions embedded in the spoken sentences compared to the onset responses to the resumptions of the stream. This enhancement was not observed in the auditory responses corresponding to the interruptions and resumptions in the noisy control stimuli. The current results suggest language specific modulation of the neural activity in the human auditory cortex during the processing of verbal streams.

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