Persistent Responsiveness of Long-Latency Auditory Cortical Activities in Response to Repeated Stimuli of Musical Timbre and Vowel Sounds

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Long-latency auditory-evoked magnetic field and potential show strong attenuation of N1m/N1 responses when an identical stimulus is presented repeatedly due to adaptation of auditory cortical neurons. This adaptation is weak in subsequently occurring P2m/P2 responses, being weaker for piano chords than single piano notes. The adaptation of P2m is more suppressed in musicians having long-term musical training than in nonmusicians, whereas the amplitude of P2 is enhanced preferentially in musicians as the spectral complexity of musical tones increases. To address the key issues of whether such high responsiveness of P2m/P2 responses to complex sounds is intrinsic and common to nonmusical sounds, we conducted a magnetoencephalographic study on participants who had no experience of musical training, using consecutive trains of piano and vowel sounds. The dipole moment of the P2m sources located in the auditory cortex indicated significantly suppressed adaptation in the right hemisphere both to piano and vowel sounds. Thus, the persistent responsiveness of the P2m activity may be inherent, not induced by intensive training, and common to spectrally complex sounds. The right hemisphere dominance of the responsiveness to musical and speech sounds suggests analysis of acoustic features of object sounds to be a significant function of P2m activity.

Keywords: adaptation, auditory cortex, auditory-evoked response, P2m, magnetoencephalography

Introduction

The long-latency auditory-evoked potential of N1 (Ritter et al. 1968; Budd et al. 1998) and magnetic field of N1m (Hari et al., 1982; Tiitinen et al., 1993) show strong attenuation of the response when auditory stimuli are presented repeatedly due to adaptation of auditory cortical neurons. The N1m response reflects neural activities having multiple recovery times, of the order of seconds, to the change in repetition period (Sams et al. 1993; Loveless et al. 1996). Occurring at a longer latency subsequent to N1m, the magnetic P2m response shows different behaviors to repeated auditory stimuli. The attenuation of the dipole moment of the P2m response is smaller for repetition of chords than single tones of piano timbre (Kuriki et al. 2006), in contrast to the dipole moment of the N1m response, which is strongly adapted equally to chord and single piano tones. As a result, notable P2m peaks are present in the responses to a sequence of consecutive chords. Adaptation of the P2m activity is more suppressed in individuals with long-term musical training than in individuals without musical experience.

The amplitude of the potential P2 response is enhanced by training in acoustic discrimination with complex sounds (Tremblay et al. 2001; Atienza et al. 2002; Reinke et al. 2003). The potential P2 (Shahin et al. 2003) and magnetic P2m (Kuriki et al. 2006) responses elicited by musical timbre are also augmented in musically well-experienced people. When an acoustic feature is manipulated, the spectral complexity of piano sounds increases the amplitude of the P2 response, but not N1, preferentially in musically experienced people (Shahin et al. 2005). These observations of the response amplitude suggest high susceptibility to modification of auditory cortical neurons of the P2/P2m responses by acoustic/musical training. Slow development of long-latency auditory responses in humans (Paetau et al. 1995; Ponton et al. 2000) and plasticity of the neurons in the auditory cortex revealed in animal studies on learning effects (Edeline 1999; Weinberger 2004) may be the basis of the training effects of P2/P2m responses.

The robustness of P2m activity to repetitive stimuli might be related to object analysis in the “what” pathway of auditory information, which contrasts with spatial analysis in the “where” pathway (Romanski et al. 1999; Rauschecker and Tian 2000). For N1/N1m activities, strong adaptation of feature-specific neurons in the posterior auditory cortex has been suggested to serve as a novelty detection mechanism in the “where” pathway, filtering out monotonous sounds in the environment but being recovered quickly by a novel (deviant) sound to allocate attention to the source (May et al. 1999; Jääskeläinen et al. 2004). Assuming that the P2m neurons with robust activity are involved in the “what” pathway of object analysis, we expect that high responsiveness of P2m is observed commonly in ecologically relevant sounds, such as vowel speech, and is not caused by intensive or long-term training but is intrinsic.

The results of various imaging studies indicate the existence of a hemispheric difference in auditory responses to speech and speech-like sounds. Left hemisphere dominance of cortical activity appears when phonetic cues characterized by rapid frequency change, that is, voice onset in consonant-vowels, are processed (Poeppe et al. 1996; Belin et al. 1998; Kayser et al. 2001; Zatorre and Belin 2001; Jäncke et al. 2002). This hemispheric specialization is supported by the anatomical asymmetry of the auditory cortical structure, which facilitates fast temporal processing in the left hemisphere (Penhune et al. 1996; Zatorre et al. 2002). However, for vowels with no rapid spectral or temporal change, diverse results for N1m responses that do not converge with respect to the hemispheric effect have been reported in magnetoencephalographic (MEG) studies (Gootjes et al. 1999; Mäkelä et al. 2003; Shestakova et al. 2004; Tiitinen et al. 2005). Little is known about the hemispheric laterality of the P2m response to the acoustic or phonetic feature of speech sounds.

Here, we report the results of a study on the responsiveness of N1m and P2m activities to repetitive stimulation of piano tones and vowel sounds. Pure tones were used as control stimuli. We employed a dichotic listening scheme to detect the...
N1m and P2m responses from the auditory cortex exclusively of one hemisphere based on contralateral pathway dominance (Kimura 1961, 1967). None of the participants in the study had received musical training. We examined whether P2m responses exhibit weak adaptation and/or high sensitivity to vowel sounds as well as musical sounds, in comparison with the responses to pure tones that have a single frequency component, and whether specific responsiveness of the P2m response to a musical sound is observed in musically nonexperienced subjects. Different responsiveness is expected for the N1m response to these complex sounds. We also examined hemispheric effects on the N1m and P2m responses, focusing on the issue of whether any difference in the responsiveness to the complex sounds and pure tones depends on the hemisphere.

Materials and Methods

Subjects

Five male subjects (mean age ± standard deviation [SD] of 24.2 ± 2.4 years) and 5 female subjects (22.2 ± 2.7 years) participated in the experiment. The subjects were all right handed as evaluated with Edinburgh test. They had never played an instrument and had never received formal musical education except for music courses in elementary school and junior high school. All the subjects gave written informed consent to participate in the study after receiving a thorough explanation of the MEG recording. The study was approved by the Ethics Committee of the School of Medicine, Hokkaido University.

Stimuli and Presentation

Measurements were made in 2 separate sessions using variants of a piano tone and vowel speech. In the piano session, an A3 piano tone (fundamental frequency of 220 Hz) and pure tones of its harmonics (440 and 880 Hz) were used. In the vowel session, a vowel sound /a/ pronounced by a male broadcast announcer and pure tones of 2 peak frequencies (238 and 365 Hz), which are included in the F1 formant of the vowel, were used. The contours of the pure tones used in the piano and vowel sessions were shaped to follow the envelope of the piano tone and the vowel speech, respectively. The stimuli consisted of repetition of 3 identical tones or speech of 312.5 ms in duration and a silence period of the same length. Figure 1 shows the waveforms and frequency spectra of stimulus sounds. An oddball sound of white noise was inserted in a stimulus sequence, replacing 1 of the 3 sounds in the sequence. In each of the piano or vowel sessions, sequences of piano tones or vowel sounds were mixed with pure-tone sequences of 2 frequencies in random order. The interstimulus intervals between the sequences were 1000-1050 ms. Sequences that included the oddball sound were also mixed with the normal stimuli sequences to about 10% probability.

MEG Recording

The stimuli were delivered monaurally to subjects at a level of sound pressure of 40 dB above the hearing threshold with magnetic-free earpieces and ear tubes. A 1/f pink noise of 75 dB in sound pressure level was applied to the ear contralateral to the stimulation side. Prior to MEG recording, the hearing threshold had been measured for each stimulus sequence for the right ear and left ear stimulation of each subject. The frequency characteristic of the sound delivery system, including an amplifier and a transducer, was adjusted to within 2 dB from 20 Hz to 4 kHz by means of an equalizer. MEG measurements were made using a custom-made helmet-shaped SQUID system (Elekta-Neuromag, Helsinki), which has 76- and 19-channel magnetometers arranged on a lower layer and upper layer, respectively, and 6 reference channels for noise cancellation. The 2 sensor layers formed concentric spherical surfaces separated by 4 cm. The lower layer of 76 channels, separated from each other by 2.5 cm, was used in this study. Subjects were instructed to respond to oddballs by movement of the right or left index finger, which was detected by a laser-light switch. A single session of recordings lasted for about 30 min with short intermissions. The piano and vowel sessions were repeated for right ear and left ear stimulation in each subject. The order of recordings of piano/vowel sessions and right/left ear stimulation was randomized across the subjects.

Data Analysis

MEG responses to oddball sequences and those exceeding 3 pT in amplitude were excluded. More than 200 epochs of 2075 ms in duration, which included a 200-ms prestimulus period for the baseline, were averaged. The averaged responses were filtered to 1-20 Hz.

Figure 1. Waveforms and frequency spectra of stimulus sounds. In the piano session of measurement, the A3 piano tone and pure tones of 440 and 880 Hz harmonics were used, whereas the vowel /a/ and pure tones of 238 and 365 Hz of the first Formant were used in the vowel session.
The cutoff frequencies of 1 and 20 Hz were used to reduce the low-frequency and power line (50 Hz) noises in environment, respectively, which existed at high amplitudes in the signals detected by the magnetometer-type sensors. Effects of these narrow bandwidth were examined by widening the cutoff frequencies of the filter to a passband of 0.3–40 Hz. The waveforms of N1m and P2m responses were unchanged after this process, except a slight rounding of the peaks (see Fig. 2b). An increase of the power line noise and a small shift of the baseline appeared. These results may assure the selected bandwidth in the analysis of measured signals.

To represent the waveform of response, the magnetic fields of 12 adjacent channels at the field maximum in the posterior temporal region were used to calculate the root-mean-squared (RMS) amplitude of $B_{\text{RMS}}=(\sum B^2_i/12)^{1/2}$. Single equivalent current dipoles (ECDs) were localized at the peaks of N1m and P2m responses using the field data in the right and left hemispheres contralateral to the stimulated ear. ECDs having more than 80% of the goodness-of-fit value were selected. The grand mean of the coordinates of ECDs across subjects was obtained for N1m and P2m responses from the selected ECDs of 8–9 subjects for each condition of stimuli and hemispheres. Then, the waveform of the dipole moment of N1m and P2m responses was obtained by taking an inner product of the measured fields in a single hemisphere and the template dipole fields that were calculated from the grand mean ECD (Kuriki et al. 2006). Different sources of the grand mean N1m and P2m obtained from the 8–9 subjects were used in the calculation of the template dipole fields. The values of correlation between the measured and template fields in the calculation of this subspace projection were more than 85%, mostly above 90% in the responses to the first-stimulus sound. The general principle of the subspace projection was described by Hamalainen (1995) and Tesche et al. (1995). This method enables quantitative evaluation of the dipole moment in the absence of any subjective steps (Hertrich et al. 2004). The magnitudes of the N1m and P2m components were determined as the peak values in the time series of the dipole moment of each component.

To examine the effects of stimulus sound, analysis of variance (ANOVA) and post hoc Scheffe’s tests were conducted for the dipole moments of N1m and P2m responses. Because MEG measurements were repeated for the right ear and left ear stimulations in piano and vowel sessions, a quantitative comparison was made between the responses to piano/vowel sounds and pure tones, across which the stimulation level was equated above the hearing threshold at each ear. Thus, an ANOVA test within each hemisphere was carried out with the factors of stimulus and stimulus order. To examine the attenuation of the dipole moment by stimulus repetition, the dipole moments of the second and third stimuli were normalized by the moment of the first stimulus in individual subjects. The mean of the normalized moments of the second and third stimuli was analyzed by ANOVA and Scheffe’s tests with stimulus as the factor.

**Results**

**Behavioral Performance**

The mean (and SD) accuracy of the detection of oddball stimuli was 97.8% (4.18%), indicating that subjects listened attentively to the stimuli during MEG recording. The stimulus sound pressure levels presented to the subjects at 40 dB above the hearing threshold, averaged across 2 ears, were 78.1 (1.10), 72.1 (0.93), 69.9 (0.62), and 63.3 (0.64) dB for pure tones of 238, 365, 440, and 880 Hz, respectively, in the piano and vowel sessions. The frequency dependence of these sound pressures qualitatively agrees with the equal-loudness contour (ISO226) of the human auditory system, which has a minimum threshold at about 1 kHz and increases as the frequency decreases to be 10 dB higher at 250 Hz. The stimulus sound pressures of piano tone and vowel speech were 67.8 (0.85) and 66.3 (1.0) dB, respectively. These values correspond to the levels of pure-tone stimuli at 500–600 Hz, which are within the range of main spectral peaks of the A3 tone (220–880 Hz) and vowel (120–1200 Hz).

**Activities of N1m and P2m Responses**

Figure 2 shows examples of the measured fields for successive piano tones and the calculated dipole moment in the right hemisphere of one subject. The superposed responses of 41 channels in (a) show clear N1m and P2m peaks, which were reduced in amplitude to nearly constant levels for the second and third stimuli. The time course of dipole moment in (b) was obtained by projecting the measured fields in (a) on the fields of the grand mean of N1m dipoles. Stable moments for the second and third stimuli suggest invariable location and direction of current of the N1m source. In addition, appreciable negative peaks were obtained for P2m, but the P2m moment was evaluated from the projection of the measured fields on the fields of the mean P2m dipole. There was no significant difference in the mean locations of N1m and P2m dipoles between piano tone and vowel speech. They were located in the auditory cortex at about Heschl’s gyrus in the superior temporal plane. The grand mean dipoles for N1m source averaged over all the stimulus sounds indicated that the P2m source was anterior and medial to the N1m source (Fig. 3). The anteriority of the P2m source to the N1m was observed in the left hemisphere of 15 of the 18 subjects and in the right hemisphere of 11 of the 14 subjects, in whom the dipoles were localized across control and main sessions.

Figure 4 shows the grand mean amplitude of RMS fields across subjects of the right hemisphere obtained in the piano and vowel sessions. The reduction in the peak amplitude of the N1m...
Scheffé’s test revealed that the moments of piano tones were significantly larger than the moments of pure tones of 440 Hz (\(P < 0.002\)) and 880 Hz (\(P < 0.029\)) in the right hemisphere and of 880 Hz (\(P < 0.031\)) in the left hemisphere. Similarly, main effects of stimulus on P2m were found in the right hemisphere (\(F_{2,18} = 10.9, P < 0.001\)) and left hemisphere (\(F_{2,18} = 15.5, P < 0.001\)), indicating that the moments of piano tones were larger than the moments of pure tones of 880 Hz (\(P < 0.001\)) in the right hemisphere and of 440 Hz (\(P < 0.002\)) and 880 Hz (\(P < 0.001\)) in the left hemisphere. In the vowel session, there were no significant effects of stimulus on N1m in both hemispheres. Effects of stimulus on P2m were also nonsignificant in most cases, except in the left hemisphere (\(F_{2,18} = 7.65, P < 0.004\)) for the moment of the vowel larger than that of 238-Hz tone (\(P < 0.004\)). Effects of stimulus order on N1m and P2m were evident in both hemispheres in the piano and vowel sessions (\(F_{2,18} > 17.8, P < 0.001\) for all conditions), the moment of the first stimulus being larger that the moments of the second and third stimuli. However, there were no significant differences in the moments of the second and third stimuli, suggesting that the attenuation of both N1m and P2m responses by the repetition of stimuli was saturated from the second stimulus.

**Normalized Dipole Moments**

We examined the attenuation of the dipole moment by stimulus repetition in terms of the normalized dipole moment. The moments of the second and third stimuli were normalized by the moment of the first stimulus and averaged. Responses to the piano tone, 440-Hz tone, vowel, and 365-Hz tone in single subjects for each were omitted from the analysis because of the extremely small amplitudes of N1m or P2m. The grand mean values of the obtained normalized moments are summarized in Table 1. It is noted that the normalized moment is 1.0 when there is no attenuation, being smaller for larger attenuation of the moment by stimulus repetition. As indicated in Table 1, significant effects of stimulus were found on P2m in the right hemisphere for the piano (\(F_{2,16} = 11.9, P < 0.001\)) and vowel (\(F_{2,16} = 5.13, P < 0.019\)) sessions, the normalized P2m moments being larger for the piano tone (A3) than for the pure tones of 440 (\(P < 0.004\)) and 880 Hz (\(P < 0.001\)). Furthermore, the normalized P2m moments were larger for the vowel /a/ than the 238-Hz tone (\(P < 0.020\)). The difference between the vowel and 365-Hz tone was not significant, but a paired t-test (2 tailed) showed a marginal difference (\(P < 0.090\)) with the vowel being larger than 365 Hz. No significant differences were found in the normalized moments of P2m for the piano and vowel sessions in the left hemisphere or the normalized moments of N1m in either hemisphere or session.

**Discussion**

We used a dichotic listening scheme in stimulus presentation and conducted separate MEG measurements to analyze the right hemisphere and left hemisphere responses. In the responses of the analysis side, interference from the auditory cortex of the other side may be minimal because of the contralateral pathway dominance in dichotic listening (Kimura 1961, 1967). We made quantitative comparison of the responses elicited by piano/vowel sounds and pure tones for N1m and P2m in each hemisphere. The intrahemispheric analysis may not be influenced by the existence of difference in the suppression of the ipsilateral pathway of the right and left hemispheres.
When the hemispheric effect was analyzed, we examined the dependence of the difference in the dipole moment or normalized moment of the responses on the hemisphere side.

### Persistent Responsiveness

The normalized moments of the P2m response were significantly larger for both piano and vowel sounds than for pure tones with the intensity equated in hearing level, which was found in the right hemisphere but not in the left hemisphere. This result suggests that the adaptation by stimulus repetition of the neural activity of P2m is reduced for spectrally complex sounds, irrespective of musical or nonmusical timbres. The right-sided laterality suggests acoustic processing of the relevant function of P2m activity. Furthermore, weak adaptation to piano tones was observed in musically nonexperienced subjects, suggesting that persistent responsiveness of P2m activity may be innately present in auditory cortical neurons but not induced by training effects. It can be strengthened by practice, however, because adaptation of the P2m response to piano tones is more suppressed in musical subjects than in nonmusical subjects (Kuriki et al. 2006). In clear contrast to P2m, there was no significant difference in the normalized moments of the N1m responses to piano/vowel sounds and pure tones in the right and left hemispheres. These observations regarding the adaptation of N1m and P2m activities are in general agreement with the results of recent MEG studies showing distinct sensitivities of N1m and P2m responses to piano-timbre tones (Shahin et al. 2005; Kuriki et al. 2006).

Within the auditory cortex of primates and humans, the caudomedial and rostrolateral portions in the parabelt area that surrounds the primary auditory cortex contribute to the spatial and object streams, respectively (Rauschecker and Tian 2000). In this anatomical relationship, the dipole source of P2m is estimated to be in the parabelt area at a site anterior to Heschl's gyrus of the primary auditory cortex (Godey et al. 2001). Anterior location of the P2m source to that of the N1m has also been confirmed (Hari et al. 1987; Papanicolaou et al. 1990; Lütkenhöner and Steinstrater 1998; Kuriki et al. 2006). Though not statistically significant, the P2m sources were located anteriorly to the N1m sources in the right and left hemispheres in this study. The N1m response is generated by 2 auditory cortical sources of an early posterior and a late anterior subcomponent dominating the ascending and descending aspects of the response, respectively (Sams et al. 1993; Loveless et al. 1996). The anterior subcomponent of N1m shows weak adaptation to repetitive stimuli with decrease in the frequency interval of successive stimuli, in contrast to the strong adaptation of the posterior N1m (Ja¨a¨skeläinen et al. 2004). Thus, the anterior N1m has been suggested to be involved in attentional analysis of object features in the "what" processing pathway. The weakness of adaptation, its right hemisphere dominance, and the anteriority of the dipole source give strong support to the notion that P2m neurons are involved in the "what" pathway of acoustic feature analysis.

### Table 1

<table>
<thead>
<tr>
<th></th>
<th>Left hemisphere N1m (SE)</th>
<th>Left hemisphere P2m (SE)</th>
<th>Right hemisphere N1m (SE)</th>
<th>Right hemisphere P2m (SE)</th>
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<tr>
<td><strong>Piano session</strong></td>
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<tr>
<td>A3</td>
<td>0.46 (0.05)</td>
<td>0.63 (0.08)</td>
<td>0.57 (0.05)</td>
<td>0.85 (0.08)**</td>
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<td>440 Hz</td>
<td>0.52 (0.05)</td>
<td>0.63 (0.05)</td>
<td>0.52 (0.06)</td>
<td>0.58 (0.06)**</td>
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<tr>
<td>880 Hz</td>
<td>0.63 (0.08)</td>
<td>0.53 (0.05)</td>
<td>0.53 (0.05)</td>
<td>0.58 (0.04)*</td>
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<tr>
<td><strong>Vowel session</strong></td>
<td></td>
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<tr>
<td>/a/</td>
<td>0.53 (0.06)</td>
<td>0.59 (0.11)</td>
<td>0.53 (0.03)</td>
<td>0.90 (0.13)**</td>
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<tr>
<td>238 Hz</td>
<td>0.51 (0.05)</td>
<td>0.42 (0.05)</td>
<td>0.60 (0.04)</td>
<td>0.48 (0.06)**</td>
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<tr>
<td>365 Hz</td>
<td>0.57 (0.06)</td>
<td>0.53 (0.10)</td>
<td>0.55 (0.07)</td>
<td>0.61 (0.10)</td>
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Note: SE, standard error. Statistical significance was found for the pairs designated by "*". 

*P < 0.001; **P < 0.004; ***P < 0.02.

(Fujiki et al. 2002). When the hemispheric effect was analyzed, we examined the dependence of the difference in the dipole moment or normalized moment of the responses on the hemisphere side.

### Persistent Responsiveness

The normalized moments of the P2m response were significantly larger for both piano and vowel sounds than for pure tones with the intensity equated in hearing level, which was found in the right hemisphere but not in the left hemisphere. This result suggests that the adaptation by stimulus repetition of the neural activity of P2m is reduced for spectrally complex sounds, irrespective of musical or nonmusical timbres. The right-sided laterality suggests acoustic processing of the relevant function of P2m activity. Furthermore, weak adaptation to piano tones was observed in musically nonexperienced subjects, suggesting that persistent responsiveness of P2m activity may be innately present in auditory cortical neurons but not induced by training effects. It can be strengthened by practice, however, because adaptation of the P2m response to piano tones is more suppressed in musical subjects than in nonmusical subjects (Kuriki et al. 2006). In clear contrast to P2m, there was no significant difference in the normalized moments of the N1m responses to piano/vowel sounds and pure tones in the right and left hemispheres. These observations regarding the adaptation of N1m and P2m activities are in general agreement with the results of recent MEG studies showing distinct sensitivities of N1m and P2m responses to piano-timbre tones (Shahin et al. 2005; Kuriki et al. 2006).

Within the auditory cortex of primates and humans, the caudomedial and rostrolateral portions in the parabelt area that surrounds the primary auditory cortex contribute to the spatial and object streams, respectively (Rauschecker and Tian 2000). In this anatomical relationship, the dipole source of P2m is estimated to be in the parabelt area at a site anterior to Heschl's gyrus of the primary auditory cortex (Godey et al. 2001). Anterior location of the P2m source to that of the N1m has also been confirmed (Hari et al. 1987; Papanicolaou et al. 1990; Lütkenhöner and Steinstrater 1998; Kuriki et al. 2006). Though not statistically significant, the P2m sources were located anteriorly to the N1m sources in the right and left hemispheres in this study. The N1m response is generated by 2 auditory cortical sources of an early posterior and a late anterior subcomponent dominating the ascending and descending aspects of the response, respectively (Sams et al. 1993; Loveless et al. 1996). The anterior subcomponent of N1m shows weak adaptation to repetitive stimuli with decrease in the frequency interval of successive stimuli, in contrast to the strong adaptation of the posterior N1m (Ja¨a¨skeläinen et al. 2004). Thus, the anterior N1m has been suggested to be involved in attentional analysis of object features in the "what" processing pathway. The weakness of adaptation, its right hemisphere dominance, and the anteriority of the dipole source give strong support to the notion that P2m neurons are involved in the "what" pathway of acoustic feature analysis. In an extension of the previous suggestion of frequency and/or temporal processing of complex sounds (Kuriki et al. 2006), we speculate that the analyses of multiplicity of spectral components and regularity of the temporal waveform might be specifically involved in the function of P2m activity.
In an MEG study using successive vowels and envelope-matched tones presented at a short interstimulus interval, Teismann et al. (2004) showed that the relative amplitude of N1m of the fourth-stimulus response to that of the first-stimulus response is significantly larger in the left hemisphere than in the right hemisphere for the vowel /a/ but not for a pure tone of single frequency. They suggested that the persistent responsiveness of the N1m response to vowels represents the left dominant auditory speech processing, but they did not describe the P2m response. Because their measurements were conducted separately for the right and left hemispheres as in this study, comparison of the results (Fig. 3 in Teismann et al. 2004) between the vowel and pure tone within each hemisphere would give more accurate evaluation than interhemispheric comparison. Visual inspection of their data suggests that the relative amplitude of N1m is lower for the vowel than the pure tone in the right hemisphere. Here, the N1m response may substantially include the contribution of the posterior subcomponent of N1m due to a long intertrain interval of stimulation of 4-5 s (Teismann et al. 2004). Their results therefore suggest that the posterior N1m activity in the right hemisphere is more adapted to vowel sounds than pure tones, which may subserve the detection of ecologically irrelevant unexpected sounds (May et al. 1999; Jääskeläinen et al. 2004). In contrast, observations in the present study did not show significant difference in the normalized moment of N1m between the vowel and pure tones, either in the right or left hemisphere. Such behaviors may be ascribed to the short intertrain interval of 1 s in this study, which may have reduced the contribution of the posterior subcomponent to the observed N1m response. In addition to this, the attention to stimuli in the discrimination task in this study, in contrast to nonattentive listening while video watching (Teismann et al. 2004), may alter the stimulus dependence of adaptation of the posterior component of N1m activity. Modification by attention of the auditory-evoked responses at N1m latency have been widely reported (Rif et al. 1991; Woldorff et al. 1993; Petkov et al. 2004; Obleser et al. 2004).

Magnitude of Activities

The results of the vowel session showed no significant differences in the dipole moments of N1m or P2m between the vowel /a/ and pure tones of 238/365 Hz. This tendency was observed in the 2 hemispheres, except for the P2m moment of the vowel being larger than that of the pure tone of 238 Hz in the left hemisphere. Considering that the normalized moment of P2m was larger for the vowel than pure tones in the right hemisphere, weak adaptation may be an important factor, compared with the magnitude of activity, in the neural function of P2m. Contrary to this, the dipole moments of N1m and P2m were significantly larger for the piano tone A3 than pure tones of 440/880 Hz in both hemispheres. This point will be discussed later.

As for the hemisphere effect, diverse results for vowel-evoked MEG responses under various recording conditions have been obtained. The amplitude of N1m is larger for vowels than piano and pure tones in the left hemisphere with binaural stimulation under the condition of a target detection task (Gootjes et al. 1999), and the N1m amplitude is larger for vowels synthesized from a natural periodic wave than for simulated vowels made of tonal and noise waves in both hemispheres with binaural stimulation in passive recording (Ttitinen et al. 2005). A laterality index of N1m given by LI = (L - R)/(L + R) shows left hemisphere dominance of LI > 0 in strongly right-handed subjects measured with binaural stimulation under a matching task, where L and R refer to the ratio of the N1m strength to the vowel and tone responses over the left and right hemispheres, respectively (Kirveskari et al. 2006). This index is relevant to the data in this study because the value of L and R can be obtained from the N1m moments of the vowel and tone responses within the hemisphere. The calculated results showed that the LI was positive only in 3 of 9 right-handed subjects. The mean value of LI across subjects was close to zero but not positive to be left-side dominant.

We infer that binaural interaction and attention effects may have contributed to the diversity of the above results on the hemisphere effect of N1m. Our observations suggest no clear hemispheric difference in the magnitude or the ratio of N1m of vowel and pure-tone responses under the conditions of the dichotic listening that excludes binaural interaction and a sound detection task that requires acoustic processing. In the sustained field that occurs after P2m latency, the dipole moment is larger for vowels than pure tones, being more pronounced in the left hemisphere than in the right hemisphere with monaural stimulation under the condition of a target detection task (Eulitz et al. 1995). We did not observe the component of sustained field for vowel stimulus in this study. This may be the result of short intervals (1.0-1.05 s) between the sequential stimuli that lasted for a long period (1.9 s), whereas long interstimulus intervals (1.8-2.3 s) compared with stimulus periods (0.49-0.6 s) were used in the previous MEG studies reporting prominent sustained fields (Hari et al. 1989; Eulitz et al. 1995).

Shahin et al. (2005) observed significantly larger amplitude of P2m, but not N1m, for piano than pure tones in both musically experienced and nonexperienced subjects, but hemispheric difference was not examined. In their experiment, the sound intensity was adjusted above the hearing threshold measured for each stimulus, and the envelope of the stimulus sounds was matched. In a recent study, Lütkenhöner et al. (2006) found larger amplitude (and dipole moment) of N1m for piano tones than for envelope-matched pure tones in both musicians and nonmusicians in the left hemisphere. They adjusted the stimulus intensity above the pure-tone threshold. It seems that adjustment of the stimulus intensity and fine matching of the stimulus envelope have strong effects on the amplitude of piano-tone responses.

In the present study, the piano tones elicited significantly larger N1m and P2m moments than did pure tones in both hemispheres. Visual inspection of the stimulus waveforms indicated a bump structure at the beginning of the piano tone, which may correspond to "attack" of key (see the waveform of A3 in Fig. 1). This bump structure was not simulated in the envelope of the waveform of pure tones. Because the N1m response is sensitive to the onset parameters of stimulus (Hari et al. 1987; Hari 1990; Biermann and Heil 2000), the amplitude of N1m and P2m responses may reflect the maximum slope in the initial envelope, whereas the hearing threshold may be given by the average amplitude during the length of the sound. We computed the ratio of the maximum sound pressure in the initial 100 ms to the average sound pressure of the whole envelope. The results showed that the maximum-to-average pressure ratios were 2.0 for piano tones and 1.8 for 440 and 880 Hz in the piano session and 1.1 for /a/ and 1.2 for 238 and...
368 Hz in the vowel session. Thus, the initial envelope of the stimulus waveform may be responsible for the enhanced N1m and P2m moments for piano tones.

Notes

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References


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