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Neurophysiological Correlate of Binaural Auditory Filter Bandwidth and Localization Performance Studied by Auditory Evoked Fields

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1. Introduction

Binaural hearing is specifically useful for our ability to separate a speech from a background noise and localize sounds. Binaural hearing performances are influenced by binaural auditory filter, interaural time delay (ITD), interaural correlation (IAC), and so on. Some psychological experiments have clarified binaural auditory filter bandwidths (Kollmeier & Holube, 1989; Holube et al., 1998) and performance of sound localization related to ITD and IAC (Mills, 1958; Jeffress et al., 1962). However, little is known about the neural correlates, which makes an important contribution to our understanding of the auditory system. Therefore, we tried to estimate binaural auditory filter bandwidth and localization performance by the response in human auditory cortex.

Frequency selectivity has an important role in many aspects of auditory perception. For example, one sound may be obscured or rendered inaudible in the presence of other sounds. Frequency selectivity represents the ability of the auditory system to separate out or resolve the frequency components of a complex sound and can be characterized by the auditory filter bandwidths. Auditory filter bandwidths have been used to identify a fundamental perceptual unit that defines the frequency resolution of the auditory system – the critical bandwidth (CBW). The critical band (CB) concept has been used to explain a wide range of perceptual phenomena involving complex sounds.

Physiological correlates of the CBW have been described in several studies examining the auditory evoked potential (AEP) or auditory evoked field (AEF) in humans. Zerlin (1986) reported an abrupt increase in the amplitude of wave V of the brainstem AEP responses when the bandwidth of a two-tone complex approximated the CBW. Burrows & Barry (1990) reported that the amplitude of Na of the AEP rapidly increased when the frequency separation of a two-tone complex increased beyond the CBW. Soeta et al. (2005) and Soeta & Nakagawa (2006a) found that the amplitude of the N1m of AEFs increased with increasing the bandwidth of a bandpass noise or the frequency separation of a two-tone complex increased beyond the CBW. These studies have focused on physiological correlates of the monaural auditory filter in human auditory cortex; however, relatively little is known about the physiological correlates of the binaural auditory filter in the human auditory cortex. In natural listening environments, both the monaural and binaural auditory filters contribute

to the performance of the auditory system in separating desired a speech from an undesired background noise (Kollmeier & Holube, 1989). Therefore, the physiological correlates of the binaural auditory filter in human auditory cortex merit investigation.

Performance of sound localization is also important in natural listening environments. There are two possible cues as to the sound localization: an ITD and an interaural level difference (ILD). Consider a sinusoidal sound source located to one side of the head in the horizontal plane with an azimuth of 45° and an elevation of 0° . The sound reaching the farther ear is delayed in time and is less intense than that reaching the nearer ear. Owing to the physical nature of sounds, ITDs and ILDs are not equally effective at all frequencies (Moore, 2003). For low-frequency tones, ITDs provide effective and unambiguous information about the location of the sounds. However, for higher-frequency sounds, ITDs provide ambiguous cues. For sinusoids, the physical cues of ILDs should be most useful at high frequencies, while the cues of ITDs should be most useful at low frequencies. The idea that sound localization is based on ILDs at high frequencies and ITDs at low frequencies has been called the "duplex theory." The minimum audible angle (MAA) for sinusoidal signals presented in the horizontal plane as a function of frequency has been investigated previously (Mills, 1958). The resolution of auditory space is measured in terms of the MAA, which is defined as the smallest detectable difference between the azimuths of two identical sources of sound. Performance worsens around 1500-1800 Hz. This is consistent with the duplex theory, which states that ITD differences above 1500 Hz between the two ears are ambiguous cues for localization, while ILDs up to 1800 Hz are small and do not change much with azimuth (Moore, 2003). Physiological correlates of the localization performance related to ITDs is still unclear.

ITDs can be measured by the interaural cross-correlation function (IACF) between two sound signals received at both the left and right ears. Whether there exist physiological processes that correspond to IACF processes is an important question, and answers have generally been sought in utilizing the so-called coincidence, or cross-correlation model for the evaluation of ITD first proposed by Jeffress (1948). Numerous theories of the binaural system rely on a coincidence detector or cross-correlator to act as a comparator element for signals arriving at both ears (e.g., Webster, 1951; Sayers & Cherry, 1957; Jeffress et al., 1962; Osman, 1971; Colburn, 1977; Lindemann, 1986; Joris et al., 1998). IAC can also be measured by the IACF. The width of the sound image changes according to the IAC (Licklider, 1948; Kurozumi & Ohgushi, 1983; Ando & Kurihara, 1986; Blauert & Lindemann, 1986). When sounds are delivered dichotically, the sound image varies with the IAC of the sound. If the IAC is high, the sound image is fused and occupies a narrow region. As the IAC decreases, the sound becomes more diffuse. Localization performance has been previously measured as a function of the degree of IAC (Jeffress et al., 1962; McEvoy et al., 1991; Zimmer & Macaluso, 2005), and the results showed that localization performance decreases slowly as the IAC is reduced especially below $IAC \approx 0.2$.

Stimuli with ITDs have frequently been used in AEP and AEF studies of sound localization, and the processes underlying sound source localization have been analyzed (Ungan et al., 1989; McEvoy et al., 1990; Sams et al., 1993; McEvoy et al., 1993; 1994). The amplitude of N1m has been found to decrease with decreasing contralaterally-leading ITD (McEvoy et al., 1993; Sams et al., 1993). Magnetoencephalographic (MEG) research has benefited from the recent development of headphone-based 3D-sound technology, including head-related transfer functions, which are digital filters capable of reproducing the filtering effects of the pinna, head, and body (Palomäki et al., 2000; Fujiki et al., 2002; Palomäki et al., 2002; 2005). This research has found that the amplitude and latency of the N1m exhibits directional

tuning to the sound location, with the amplitude of the right-hemisphere N1m being particularly sensitive to the amount of spatial cues in the stimuli. However, the processes underlying sound localization performance in the human auditory cortex have not been analyzed yet.

Therefore, in order to clarify the processes underlying basic binaural hearings in human auditory cortex, we investigated the physiological counterparts of binaural auditory filter bandwidth as a function of frequency and localization performance related to ITD, frequency, and IAC by AEFs.

2. Estimation of binaural auditory filter bandwidth

Some psychological experiments have examined whether monaural and binaural conditions have the same auditory filter bandwidths, and differences between the monaural and binaural conditions have been found (e.g., Kollmeier & Holube, 1989; Holube et al., 1998). However, there is little evidence of the physiological correlates of the auditory filter bandwidths under binaural listening conditions. Here, physiological counterparts to the binaural auditory filter bandwidth in the human auditory cortex were examined by AEFs. We tried to estimate the binaural auditory filter bandwidth as a function of frequency based on the amplitudes of the N1m components, which is prominent, robust, and controlled by the physical aspects of the stimulus (Näätänen & Picton, 1987).

The tone frequencies used in this experiment, f_1 and f_2 , were geometrically centered on 125, 250, 500, 1000, 2000, 4000, and 8000 Hz. Frequency separations ($f_2 - f_1$) were set at 2-160% of the center frequency. The higher frequency tone (f_2) was presented to the right ear and the lower frequency tone (f_1) was presented to the left ear. The duration of the stimuli used during the experiments was 0.5 s, including cosine rise and fall ramps of 10 ms. Participants were presented with stimuli dichotically at a sound pressure level (SPL) of 60 dB through insert earphones (Etymotic Research ER-2, Elk Grove Village, Illinois, USA) with 29-cm plastic tubes and eartips inserted into the ear canals. SPLs of all stimuli were checked with an ear simulator (Brüel & Kjaer Ear Simulator Type 4157, Naerum, Denmark).

Eight right-handed participants (22-37 years) took part in the experiment. All had normal audiological status and no history of neurological diseases. Informed consent was obtained from each participant after the nature of the study was explained. The study was approved by the Ethics Committee of the National Institute of Advanced Industrial Science and Technology (AIST).

AEFs were recorded using a 122-channel whole-head MEG system (Neuromag-122™; Neuromag Ltd., Helsinki, Finland) in a magnetically shielded room (Hämäläinen et al., 1993). Seven experimental sessions, each with a different center frequency, were carried out. In each session, stimuli were presented in a randomized order with an interstimulus interval selected at random from 1.0 to 1.5 s. To maintain a constant level of vigilance, participants were instructed not to pay attention to sounds but to concentrate on a self-selected silent movie projected on a screen in front of them. Magnetic data were sampled at 400 Hz after being band-pass-filtered between 0.03 and 100 Hz, and then averaged approximately 100 times. Responses were rejected if the magnetic field exceeded 3000 fT/cm in any channel. The averaged responses were digitally filtered between 1.0 and 30.0 Hz. The mean amplitude of the pre-stimulus period of the 0.2 s was used as the baseline level.

Source analysis based on the model of a single moving equivalent current dipole (ECD) in a spherical volume conductor was applied to the measured field distribution. Source

estimates were based on a subset of 40-44 channels in the latency range of 70-130 ms over each left and right temporal hemisphere. ECDs were found separately for the left and right hemisphere data using a least-squares search (Hämäläinen et al., 1993). The amplitudes and latencies of the dipole with the maximal goodness of fit were defined as the N1m amplitudes and latencies for further analysis. Only dipoles with a goodness of fit of more than 80% were included in further analyses. The dipole location and orientation were determined in a head-based coordinate system with the origin set to the midpoint of the medial-lateral axis (x-axis) between the entrances of the left and right ear canals. The posterior-anterior axis (y-axis) was positioned through the nasion and the origin, and the inferior-superior axis (z-axis) was positioned through the origin perpendicular to the x-y plane.

Clear N1m responses were observed in both the right and left temporal regions in all participants with all stimuli (Fig. 1). The N1m latencies were not significantly affected by frequency separation and hemisphere with all center frequencies.

When the frequency separation was less than 10-20% of the center frequency, the N1m amplitude was independent of the frequency separation. When the frequency separation was more than about 10-20% of the center frequency, the N1m amplitude increased with increasing frequency separation (Fig. 2). Thus, N1m amplitudes show CB-like behavior under dichotic conditions. Regarding the increase in N1m amplitude above the CBW of the dichotically presented two-tone frequencies, Yvert et al. (1998) showed that the N1m amplitude increased with increasing frequency separation when the frequency separation

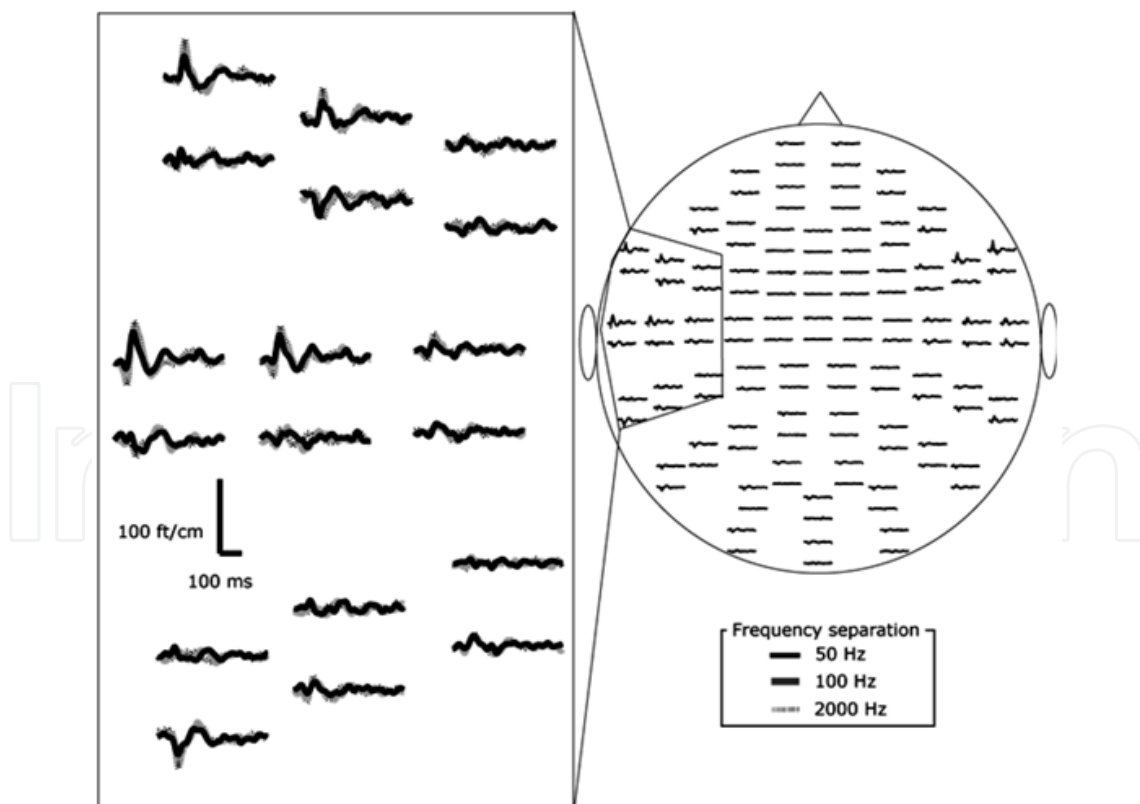


Fig. 1. Typical waveforms of AEFs in response to dichotically presented two-tones with different frequency separations from 122 channels in one subject. The center frequency was 1000 Hz. The waveforms of the AEFs have different frequency separations.

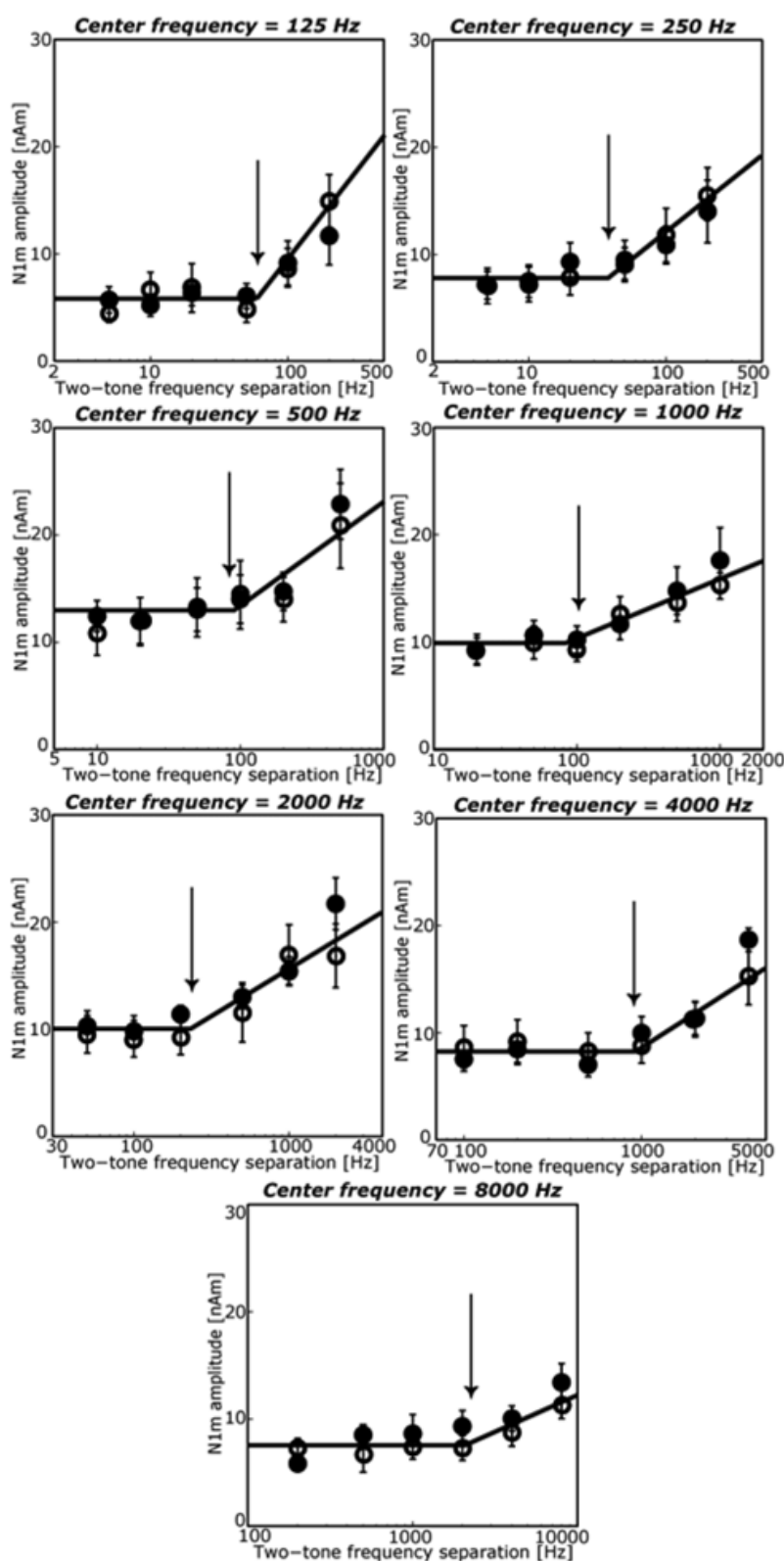


Fig. 2. Mean N1m amplitudes (\pm SEMs) from the right (\bullet) and left (\circ) hemispheres as a function of the frequency separation. The data have been fitted with the best combination of two straight lines, one of zero slope for narrow frequency separations, and one of non-zero slope, by the method of least squares. The intersection estimates the critical bandwidth.

was more than 25% of the center frequency, which is consistent with the present finding. These results indicate that each tone stimulates both left and right hemispheres, and that the overall spectrum of the binaural stimulus becomes broader as the interaural frequency difference increases. This in turn reduces the interference between ipsilateral and contralateral pathways (binaural interaction) and activates many neurons in the auditory cortex.

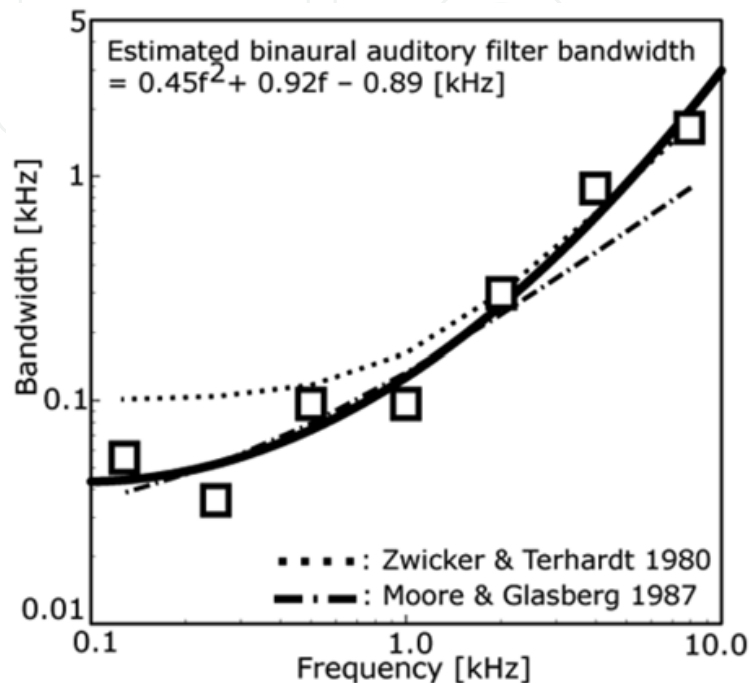


Fig. 3. The symbols (\square) indicate the estimates of the binaural auditory filter bandwidth from the N1m amplitudes at various center frequencies. The curve fitted to the data is specified by the equation in the figure. For comparison, the dotted line and dash-dot line show the the monaural CB function (Zwicker & Terhardt, 1980) and equivalent rectangular bandwidth of the auditory filter (Moore & Glasberg, 1987), respectively.

We estimated the binaural auditory filter bandwidth by fitting the N1m amplitude as a function of frequency separation with the best combination of two straight lines as shown by the arrows in Fig. 2 in each center frequency. The averaged N1m amplitude from the left and right hemispheres was used for this fitting, because the main effect of hemisphere on the N1m amplitude was not significant. The estimated binaural critical bandwidth was approximately 10-20% of the center frequency and fitted to an equation (Fig. 3). The resulting function was $0.45f^2 + 0.92f - 0.89$ (Fig. 3). For comparison, the dotted line and dash-dot line show the estimated monaural auditory filter bandwidth (Zwicker & Terhardt, 1980; Moore & Glasberg, 1987). For the diotic condition, the effects of frequency separation of a two-tone complex and a three-tone complex on the AEFs have also been examined when the center frequency was 1000 Hz (Soeta & Nakagawa, 2006a). The auditory filter bandwidth was estimated in a similar way to that used in this study; the estimated auditory filter bandwidth was 153 Hz for a two-tone complex and 236 Hz for a three-tone complex. For the monaural condition, Sams & Salmelin (1994) investigated the frequency tuning of the human auditory cortex by masking tones using continuous white-noise maskers with frequency notches at the tone frequencies. The estimated auditory filter bandwidth for 1000

and 2000 Hz tones were 247 and 602 Hz, respectively. The reasons for these differing bandwidths are unclear. One factor might be the influence of a different presentation of the stimulus; that is, dichotic, diotic and monaural presentation. Additionally, different spectra or temporal shapes of the stimulus may have contributed to the discrepancies. Finally, different participants may have contributed to the discrepancies.

All estimated ECDs were located at or near the Heschl's gyrus or planum temporale. The effects of frequency separation on the ECD locations of the N1m in each hemisphere and each center frequency were statistically analyzed by a repeated-measure ANOVA. While this analysis yielded some significant main effects of frequency separation for some of the dipole dimensions with a center frequency of 125 and 8000 Hz, none of these significant effects was replicated among center frequencies. It has been suggested that there is a hierarchy of pitch processing in which the center of activity moves away from the primary auditory cortex as the processing of music and speech proceeds, and the early stage of processing depends on core areas bilaterally; that is, pitch processing is largely symmetric in the hierarchy up to and including lateral Heschl's gyrus (Patterson et al., 2002; Zatorre et al., 2002; Hickok & Poeppel, 2004). In the present study, hemispheric differences in the latency and amplitude of the N1m were not observed. This might indicate that binaural frequency selectivity is symmetric up to the primary auditory cortex, including core areas of the auditory cortex such as Heschl's gyrus and planum temporale.

3. Estimation of localization performance related to ITD and frequency

For low-frequency tones, ITD provide effective and unambiguous cue for sound localization. For higher frequency sounds, however, ITD provide ambiguous cues. For pure tones, ITDs are only helpful when localizing sounds with frequencies less than 1500 Hz (Mills, 1958). The wavelength of the sound is about twice the distance between the two ears at these frequencies. Phase cues for tones with shorter wavelengths are ambiguous since after the first cycle of the wave, it is unclear which ear is leading or lagging. The present study aimed to evaluate responses related to the localization performance of ITDs, AEFs elicited by pure tones with different ITDs and frequencies were analyzed.

The stimuli used in this study were pure tones (sinusoidal sounds) of 800 and 1600 Hz. The ITD is an effective cue for sound localization when the frequency of the pure tone is 800 Hz, though it is not an effective cue for sound localization when the frequency of the pure tone is 1600 Hz (Mills, 1958). The stimulus duration used in the experiment was 500 ms, including rise and fall ramps of 10 ms. Stimuli were presented binaurally to the left and right ears through plastic tubes and earpieces inserted into the ear canals. All signals were presented at 60 dB SPL, and the ILD was set to 0 dB.

Ten right-handed participants (22-37 years) took part in the experiment. They all had normal audiological status and no history of neurological diseases. Informed consent was obtained from each participant after the nature of the study was explained. The study has been approved by the ethics committee of the National Institute of Advanced Industrial Science and Technology (AIST).

AEFs were recorded using a 122-channel whole-head MEG system in a magnetically shielded room (Hämäläinen et al., 1993). Two experimental sessions, each with a different frequency (800 or 1600 Hz), were conducted. In each session, combinations of a reference stimulus (ITD = 0.0 ms) and left-leading test stimuli (ITD = 0.1, 0.4, 0.7 ms) were presented alternately at a constant 1.5 s interstimulus interval. Usually, ITDs range from 0 ms for a

sound at 0° azimuth (for a sound straight ahead) to about 0.7 ms for a sound at 90° azimuth (directly opposite one ear). To maintain a constant vigilance level, the participants were instructed to concentrate on a self-selected silent movie that was being projected on a screen in front of them and to ignore the stimuli. The method of MEG data analysis, that is, the latency, amplitude and ECD location of the N1m component, was the same way that we did in the previous experiment.

All the stimuli elicited prominent N1m responses in both the left and right hemispheres, with the near-dipolar field patterns, indicating sources in the vicinity of the auditory cortex of each hemisphere. The N1m latencies were not significantly affected by ITD and hemisphere in both frequencies (Fig. 4).

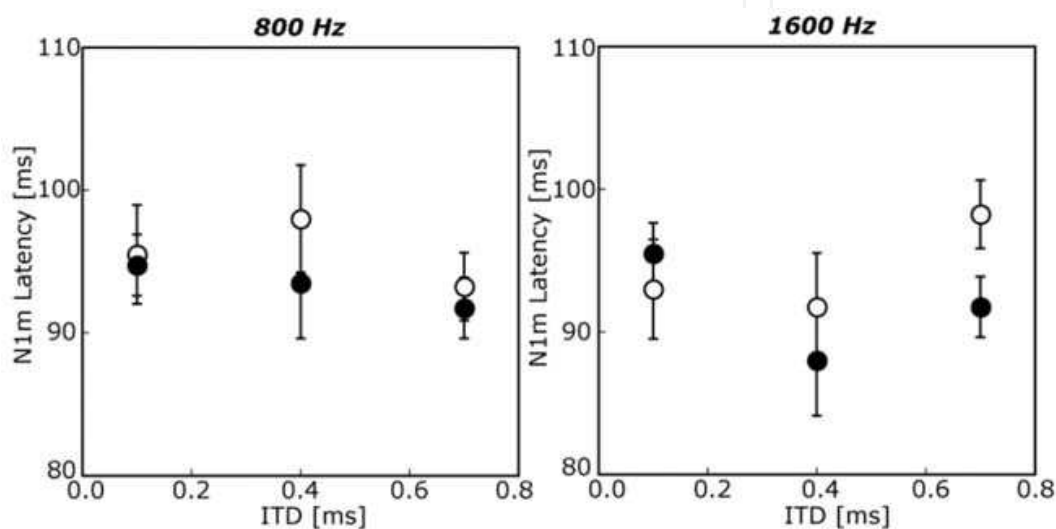


Fig. 4. Mean N1m latencies (\pm SEMs) as a function of the ITD from the right (●) and left (○) hemispheres.

Figure 5 shows the N1m amplitude as a function of ITD. When the frequency of the pure tone was 800 Hz, the N1m amplitude increased with increasing ITD. The main effect of the ITDs was significant ($P < 0.005$). This result is consistent with previous findings (McEvoy et al., 1993; Sams et al., 1993; Palomäki et al., 2005). The main effect of the hemispheres on the N1m amplitude was not significant. There were no significant interactions between the ITDs and hemispheres. When the frequency of the pure tone was 1600 Hz, the main effect of the ITDs was not significant. Humans can detect ITDs only up to 1500 Hz (Mills, 1958). When an ITD is conveyed by a narrowband signal such as a tone of appropriate frequency, humans may fail to derive the direction represented by that ITD. This is because they cannot distinguish the true ITD contained in the signal from its phase equivalents that are $ITD + nT$, where T is the period of the stimulus tone and n is an integer. This uncertainty is called phase-ambiguity.

Whether brain activity correlates with participants' localizations has been previously assessed using functional magnetic resonance imaging (fMRI) (Zimmer & Macaluso, 2005), with the results indicating that better localization performance is associated with increased activity both in Heschl's Gyrus (possibly including the primary auditory cortex) and in posterior auditory regions that are thought to process the spatial characteristics of sounds and generate the N1m components. Therefore, the present results indicate that localization performance could be reflected in N1m amplitudes.

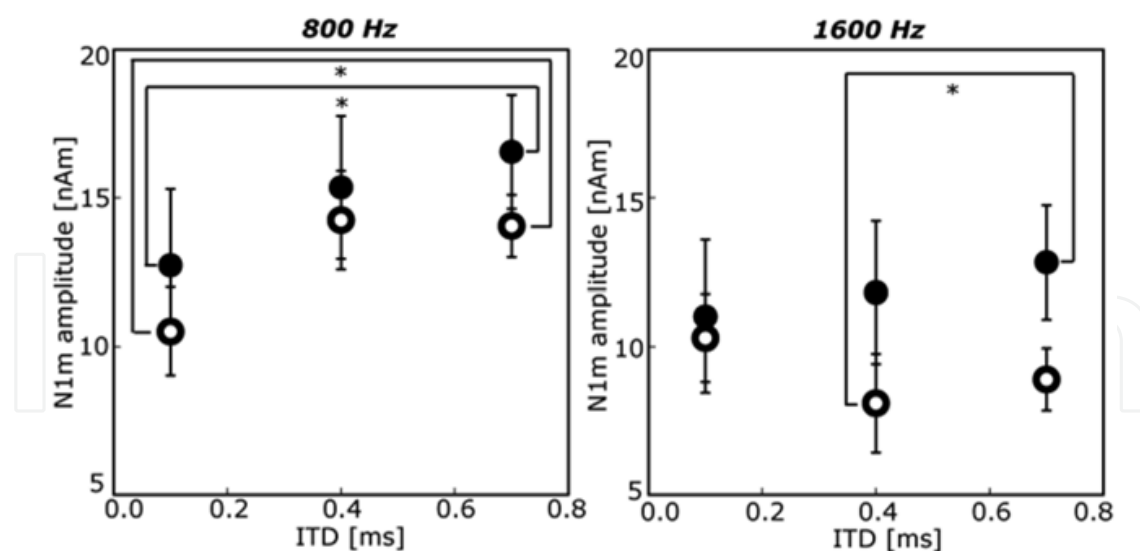


Fig. 5. Mean N1m amplitudes (\pm SEMs) as a function of the ITD from the right (●) and left (○) hemispheres. Asterisks indicate statistical significance ($*P < 0.05$; Post hoc Newman-Keuls test).

There was a tendency that the N1m amplitudes in the right hemisphere were larger than those in the left hemisphere, although a significant effect was only found when the frequency of the stimulus was 1600 Hz ($P < 0.05$). The previous studies indicated that the N1m amplitude was significantly larger for stimuli presented with contralaterally-leading ITDs than for those with ipsilaterally-leading ITDs (McEvoy et al., 1993; 1994; Palomäki et al., 2000; 2002; 2005). These agree with our findings.

It has been found that the participant does not merely use the sound signals perceived at a given moment, but also makes a comparison with stored stimulus patterns in localization of a sound source (Plenge, 1974). The spectral cues generated by the head and outer ears vary between individuals and have to be calibrated by learning, which most probably takes place at the cortical level (Rauschecker, 1999). It has been reported that auditory training might develop enhanced auditory localization by using AEP (Munte et al., 2003). Three of the ten participants had increasing N1m amplitudes clearly with increasing ITDs in the right hemisphere even when the frequency of the stimulus was 1600 Hz. This might indicate that the effects of ITDs on N1m amplitudes depend on the individual, which is related to learning, training and so on.

The location of the ECDs underlying the N1m responses did not vary as a function of ITD in agreement with the previous results (McEvoy et al., 1993; Sams et al., 2003). Stimuli presented with different ITDs may excite somewhat different neuronal populations, though the cortical source location of the N1m did not vary systematically as a function of ITD. Therefore, we may conclude that the present data do not show an orderly representation of ITDs in the human auditory cortex that could be resolved by MEG.

4. Estimation of localization performance related to ITD and IAC

The detection of ITD for sound localization depends on the similarity between the left and right ear signals, namely IAC. Human localization performance deteriorates with decreasing IACs. The psychological responses to ITDs in relation to IACs have been obtained in humans (Jeffress et al., 1962; McEvoy et al., 1991; Zimmer & Macaluso, 2005), and the

neurophysiological responses have been limited to animal studies (e.g., Yin et al., 1987; Yin & Chan, 1990; Albeck & Konishi, 1995; Keller & Takahashi, 1996; Saberi et al., 1998; D'Angelo et al., 2003; Shackleton et al., 2005). The present study aimed to evaluate the effects of ITDs of noises with different IACs on the AEF. In order to evaluate responses in the auditory cortex related to the ITDs and IACs of the sound, the AEFs elicited by noises with different ITDs and IACs were analyzed.

Bandpass noises were employed for acoustic signals. To create bandpass noises, white noises, each of 10 s duration, were digitally filtered between 200 and 3000 Hz (Chebychev bandpass: order 18). The IACF between the sound signals received at each ear $f_l(t)$ and $f_r(t)$ is defined by

$$\Phi_{lr}(\tau) = \frac{1}{2T} \int_{-T}^{+T} f_l'(t) f_r'(t + \tau) dt, \quad (1)$$

where $f_l'(t)$ and $f_r'(t)$ are obtained after passing through the A-weighted network, which approximately corresponds to ear sensitivity (Ando et al., 1987; Ando, 1998). The normalized IACF is defined by

$$\phi_{lr}(\tau) = \frac{\Phi_{lr}(\tau)}{\sqrt{\Phi_{ll}(0)\Phi_{rr}(0)}}, \quad (2)$$

where $\Phi_{ll}(0)$ and $\Phi_{rr}(0)$ are the autocorrelation functions at $\tau = 0$ for the left and right ear, respectively. The IAC is defined as the maximum of the IACF. The IAC of the stimuli was controlled by mixing in-phase diotic bandpass and dichotic independent bandpass noises in appropriate ratios (Blauert, 1983). The frequency range of these noises was always kept the same. The stimulus duration used in the experiment was 0.5 s, including rise and fall ramps of 10 ms, which were cut out of a 10 s long bandpass filtered noise with varying IAC and ITD. For stimulus localization, two cues were available to participants: envelope ITD and ongoing ITD. In this experiment, the envelope ITD was zero for all stimuli, and the ongoing ITD was varied, as shown in Fig. 6. Here, "envelope" refers to the shape of a gating function with 10-ms linear ramps at the onset and offset. Stimuli were presented binaurally to the left and right ears through plastic tubes and earpieces inserted into the ear canals. To check the frequency characteristics of the stimuli, stimuli were measured with an ear simulator. Figures 7 and 8 show examples of the power spectrum and the IACF of some of the stimuli measured. All signals were presented at 60 dB SPL, and the ILD was set to 0 dB.

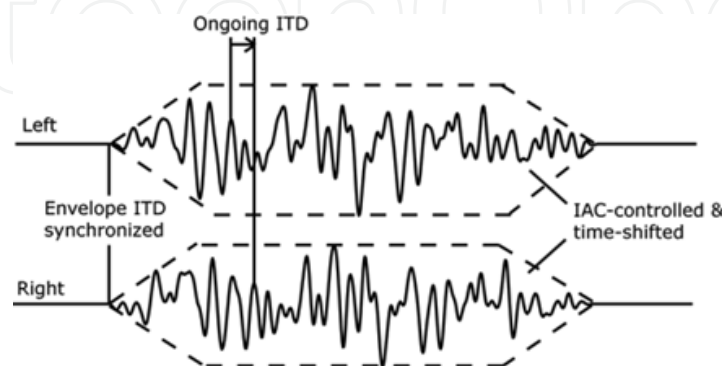


Fig. 6. Illustration of the stimuli used in the experiments. The fine structure (IAC controlled) of the stimulus was interaurally delayed, while the envelopes were synchronized between the ears.

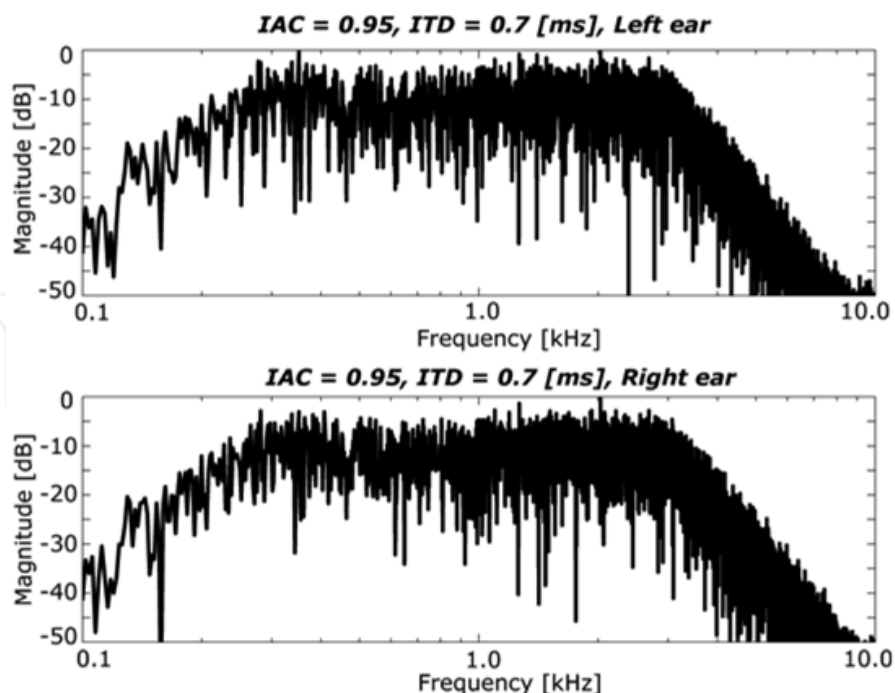


Fig. 7. Power spectrums of the stimuli used in the experiments.

Ten right-handed participants (22-35 years) took part in the experiment. They all had normal audiological status and none had a history of neurological disease. Informed consent was obtained from each participant after the nature of the study was explained. The study was approved by the Ethics Committee of the National Institute of Advanced Industrial Science and Technology (AIST).

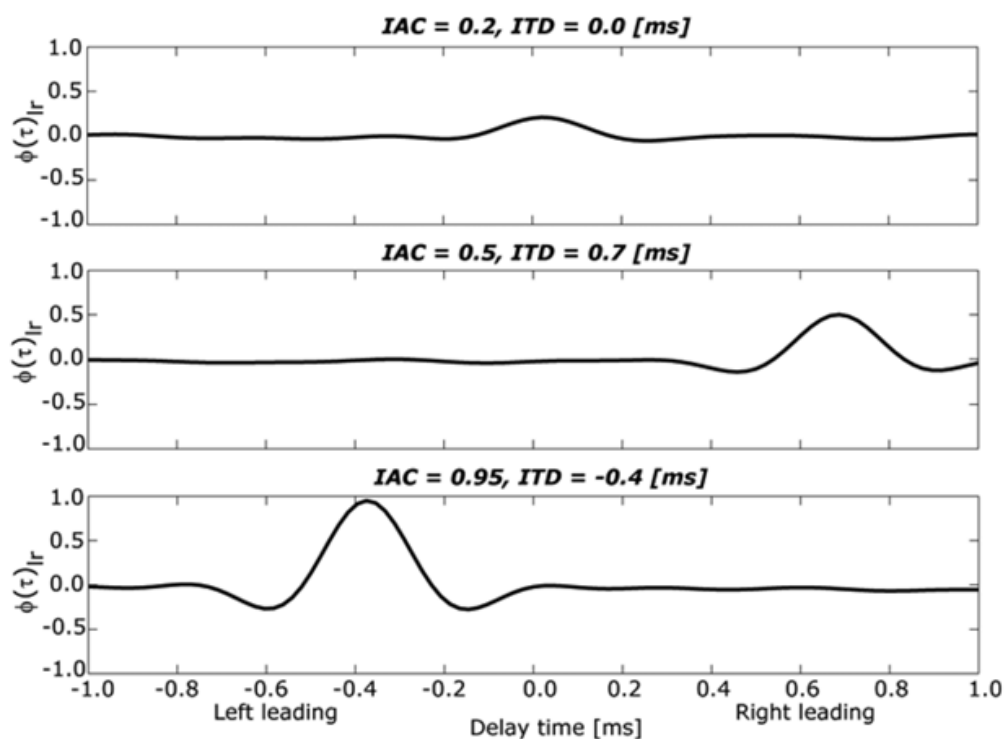


Fig. 8. IACFs of some of the stimuli used in the present study.

AEFs were recorded using a 122-channel whole-head MEG system in a magnetically shielded room (Hämäläinen et al., 1993). Combinations of a reference stimulus (IAC = 0.0) and test stimuli were presented alternately at a constant interstimulus interval of 1.5 s. Auditory evoked responses are affected by the preceding stimulus IAC (Ando et al., 1987; Chait et al., 2005). In order to reduce the effect of the IAC of the preceding stimulus, stimulus were alternated with the reference stimulus. The ITD of the test stimuli were 0, ± 0.1 , ± 0.4 , and ± 0.7 ms, which had the IAC of 0.95 or 0.5. Two experimental sessions, each had right or left leading ITDs, were carried out. In order to maintain a constant vigilance level, the participants were instructed to concentrate on a self-selected silent movie that was being projected on a screen in front of them and to ignore the stimuli. The method of MEG data analysis was the same way that we did in the previous experiment.

All the stimuli elicited prominent N1m responses in both the left and right hemispheres, with near-dipolar field patterns (Fig. 9). Figures 10 show the N1m latency as a function of ITD. The N1m latency was not influenced by the ITDs. There was a tendency that the N1m latencies in the right hemisphere were shorter than those in the left hemisphere in the case of right-leading stimuli. That is, ipsilaterally localized stimuli produced shorter latencies in the case of right-leading stimuli. This result is consistent with previous findings (McEvoy et al., 1994; Palomäki et al., 2005).

Figures 11 show the N1m amplitude as a function of ITD. When the IAC of the stimulus was 0.95, the effect of ITD on the N1m amplitude was significant. The N1m amplitude increased with increasing ITD in the right hemisphere in the case of a left-leading stimulus and in both the left and right hemispheres in the case of a right-leading stimulus. This result is consistent with previous findings (McEvoy et al., 1993; Sams et al., 1993; Palomäki et al., 2005). The N1m amplitude increased slightly with increasing ITDs in the hemisphere contralateral to the ITDs when the IAC of the stimulus was 0.5; however, the main effect of ITDs on the N1m amplitude was not significant. Localization performance worsens with decreasing IACs (Jeffress et al., 1962; McEvoy et al., 1991; Zimmer & Macaluso, 2005); therefore, the present results indicate that localization performance is reflected in N1m amplitudes. Put another way, there is a close relationship between the N1m amplitudes, ITDs, and IACs of the stimuli.

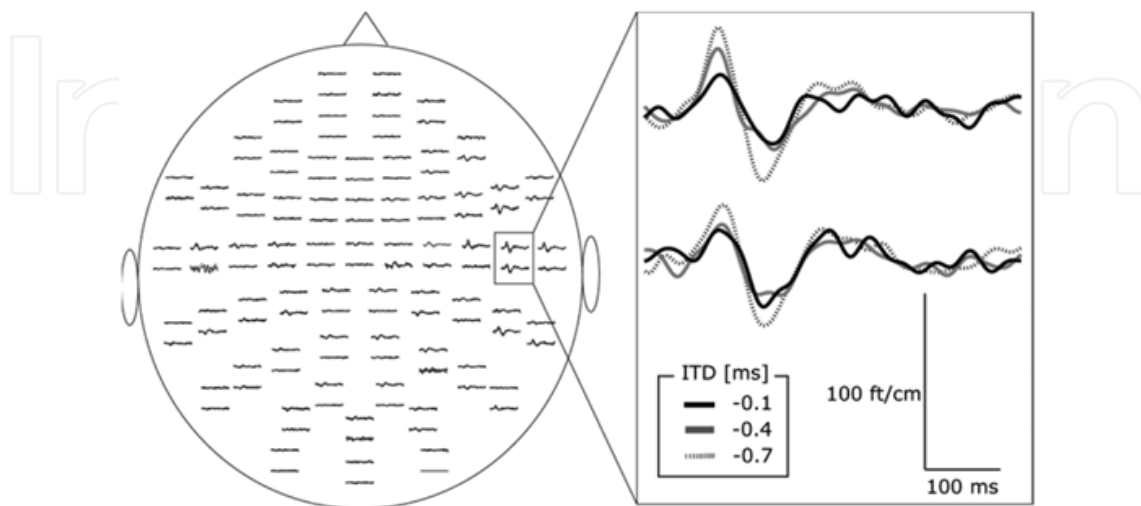


Fig. 9. Typical waveforms of AEFs from 122 channels in a subject when the IAC of the stimulus was 0.95.

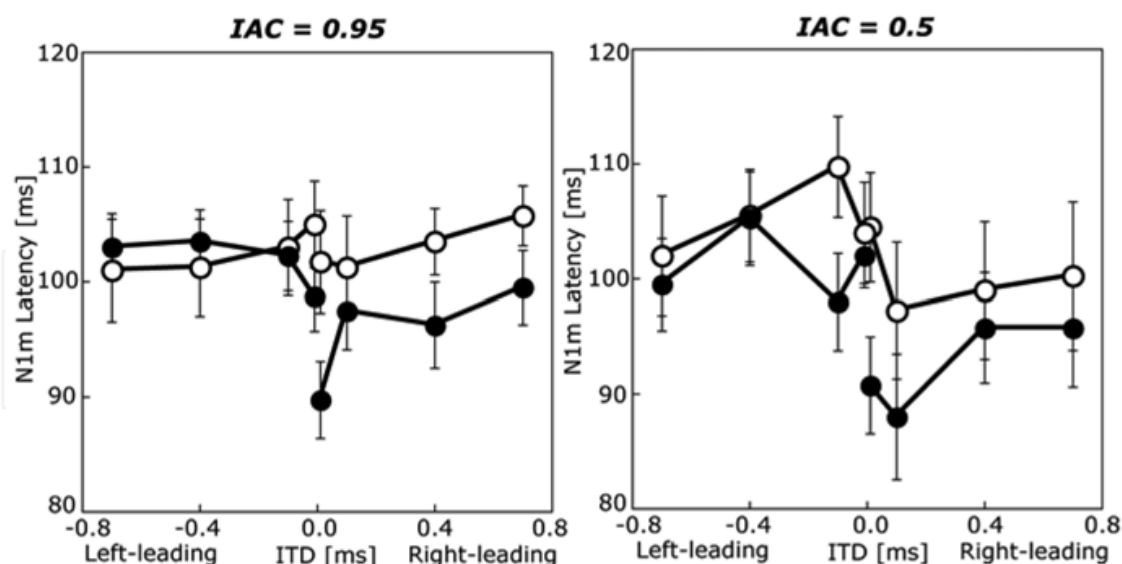


Fig. 10. Mean N1m latencies (\pm SEMs) as a function of the ITD from the right (●) and left (○) hemispheres.

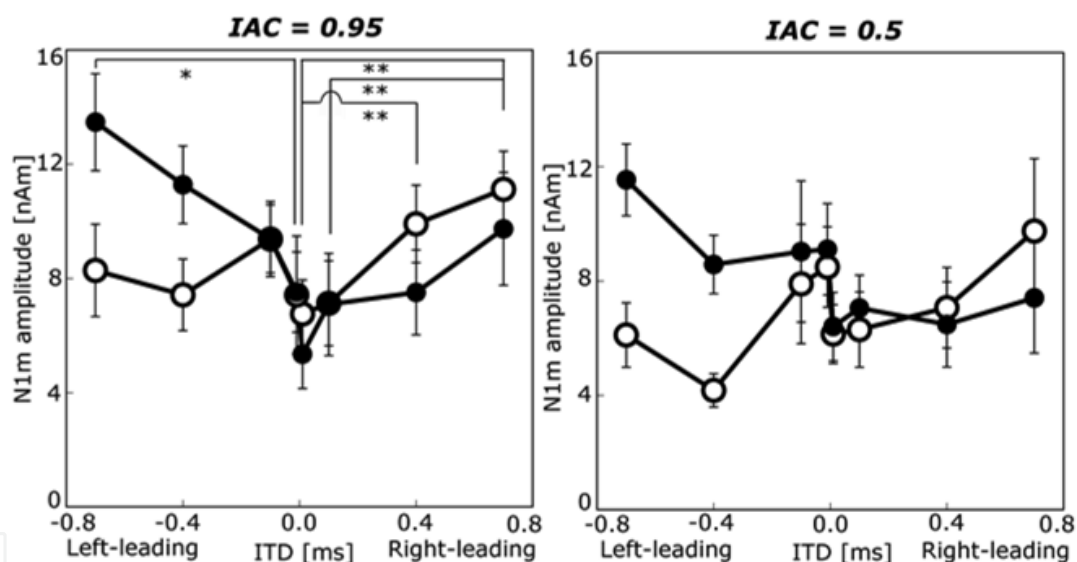


Fig. 11. Mean N1m amplitudes (\pm SEMs) as a function of the ITD from the right (●) and left (○) hemispheres. Asterisks indicate statistical significance (* $P < 0.05$, ** $P < 0.01$; Post hoc Newman-Keuls test).

The effects of ITD and IAC on brain activity have recently been investigated using fMRI (Zimmer & Macaluso, 2005). The results showed that activity in Heschl's gyrus increased with increasing IAC and activity in posterior auditory regions also increased with increasing IAC, primarily when sound localization was required and participants successfully localized sounds. It was concluded that IAC cues are processed throughout the auditory cortex and that these cues are used in posterior regions for successful auditory localization. The activity in posterior regions might affect our findings of the N1m amplitude.

The right hemisphere dominance of the human brain in spatial processing has previously been reported (Burke et al., 1994; Butler, 1994; Ito et al., 2000; Kaiser et al., 2000; Palomäki et al., 2000; 2002; 2005). When the head-related transfer functions, ITD, and ILD were varied,

the N1m amplitude in the right hemisphere was larger than that in the left hemisphere (Palomäki et al., 2002; 2005). In our study, the N1m amplitude in the right hemisphere was larger than that in the left hemisphere only in the case of a left-leading stimulus. However, the effects of ITDs on the right hemisphere were significant, with the N1m amplitude increasing with increasing ITD in the right hemisphere in the case of both left- and right-leading stimuli. These may indicate the right hemisphere dominance in spatial processing. The pattern of the right-hemisphere dominance observed in the current study is strikingly similar to that found in a previous fMRI study on the processing of sounds localized by ITDs (Krumbholz et al., 2005).

Figure 12 shows the averaged ECD locations in the left and right hemispheres. The ECD locations did not show any systematic variation across participants as a function of the ITDs or IACs. The location of the ECDs underlying the N1m responses did not vary as a function of ITD or IAC, a finding in agreement with previous MEG results (McEvoy et al., 1993; Sams et al., 1993; Soeta et al., 2004). As for fMRI, similarly, little evidence exists for segregated representations of specific ITDs or IACs in auditory cortex (Woldorff et al., 1999; Maeder et al., 2001; Budd et al., 2003; Krumbholz et al., 2005; Zimmer & Macaluso, 2005). Stimuli with different ITDs or IACs may excite somewhat different neuronal populations, although the cortical source location did not differ systematically as a function of ITD or IAC. Therefore, we conclude that the present data do not show an orderly representation of ITD or IAC in the human auditory cortex that can be resolved by MEG.

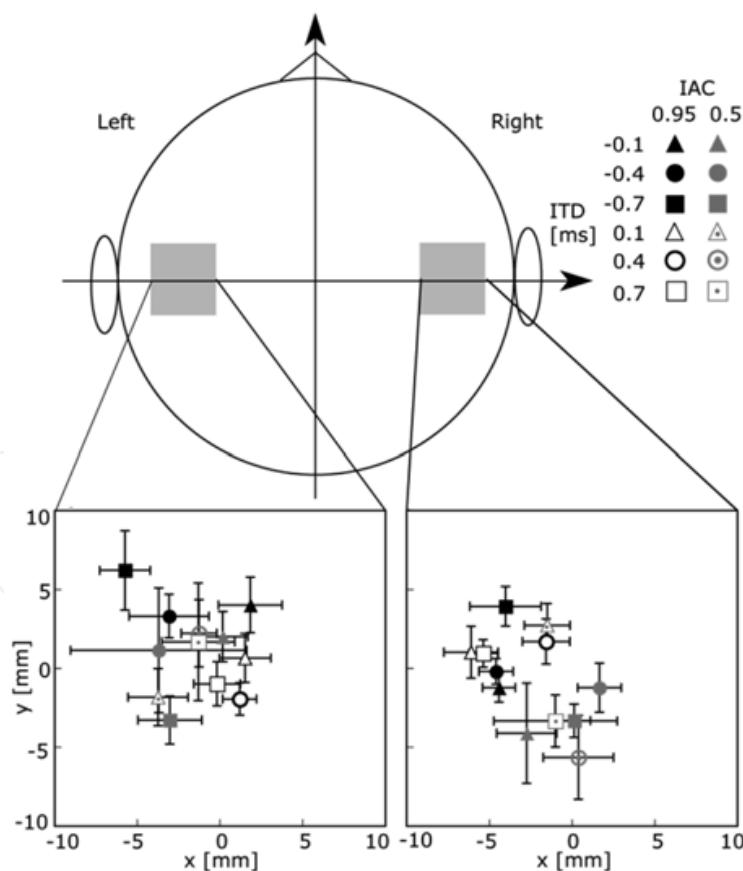


Fig. 12. Mean ECD location (\pm SEM) of all subjects in the left and right temporal planes. The ECD locations were normalized within each subject with respect to the position of ITD = 0.0 ms.

Recently it has been suggested that ITDs may be coded by the activity level in two broadly tuned hemispheric channels (McAlpine et al., 2001; Brand et al., 2002; McAlpine & Grothe, 2003; Stecker et al., 2005). The present study showed that the N1m amplitude varies with the ITD; however, the location of the ECDs underlying the N1m responses did not vary with the ITD. This could suggest that different ITDs are coded non-topographically but by response level. Thus, the current data seem to be more consistent with a two-channel model (McAlpine et al., 2001; Brand et al., 2002; McAlpine & Grothe, 2003; Stecker et al., 2005) rather than a topographic representation model (e.g., Jeffress, 1948).

5. Conclusion

We tried to estimate binaural auditory filter bandwidth as a function of frequency and localization performance related to ITD, frequency, and IAC by the response in human auditory cortex. First, in order to estimate binaural auditory filter bandwidth, two tones with different frequency separations and center frequencies, which were presented dichotically to the left and right ears, were used as the sound stimuli and AEFs were evaluated. The results indicated that the N1m amplitudes are approximately constant when the frequency separation is less than 10-20% of the center frequency; however, the N1m amplitudes increase with increasing frequency separation when the frequency separation is greater than 10-20% of the center frequency (Soeta & Nakagawa, 2007; Soeta et al., 2008). These results indicate that binaural auditory filter bandwidth is approximately 10-20% of the center frequency. The estimated binaural auditory filter bandwidth is roughly consistent with the estimated monaural auditory filter bandwidth by psychological experiment (Zwicker & Terhardt, 1980; Moore & Glasberg, 1987). Second, in order to identify the physiological correlates of the localization performance related to ITD and frequency, the AEFs in response to ITDs of pure tone with different frequency were examined. The results indicated that the N1m amplitudes increase with the ITDs when the frequency of the pure tone is 800 Hz; however, the N1m amplitudes do not vary with the ITDs when the frequency of the pure tone is 1600 Hz (Soeta & Nakagawa, 2006b). The results indicate that localization performance related to ITD and frequency is reflected in N1m amplitudes because ITDs provide effective and unambiguous information for low-frequency tones; however, ITDs provide ambiguous cues for higher-frequency tones. Finally, in order to identify the physiological correlates of the localization performance related to ITD and IAC, the AEFs in response to ITDs of bandpass noise with different IACs were examined. When the IAC is 0.95, the N1m amplitudes significantly increase with increasing ITD; however the effect of ITD on the N1m amplitudes is not significant when the IAC is 0.5 (Soeta & Nakagawa, 2006c). The results suggest that localization performance related to ITD and IAC is also reflected in the N1m amplitudes because human localization performance deteriorates with decreasing IACs. The results of two experiments related to localization performance suggest that ITDs are coded non-topographically but by response level.

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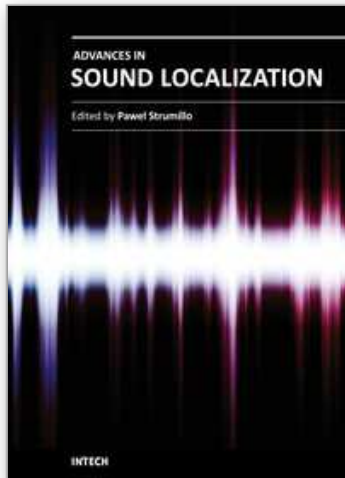
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Sound source localization is an important research field that has attracted researchers' efforts from many technical and biomedical sciences. Sound source localization (SSL) is defined as the determination of the direction from a receiver, but also includes the distance from it. Because of the wave nature of sound propagation, phenomena such as refraction, diffraction, diffusion, reflection, reverberation and interference occur. The wide spectrum of sound frequencies that range from infrasounds through acoustic sounds to ultrasounds, also introduces difficulties, as different spectrum components have different penetration properties through the medium. Consequently, SSL is a complex computation problem and development of robust sound localization techniques calls for different approaches, including multisensor schemes, null-steering beamforming and time-difference arrival techniques. The book offers a rich source of valuable material on advances on SSL techniques and their applications that should appeal to researches representing diverse engineering and scientific disciplines.

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