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Research

Auditory Hemispheric Specialization Depends on Temporal and Spectral Frequencies

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Abstract

Objective

To investigate the specialization of the auditory cortical hemispheres to process temporal and spectral auditory stimuli using steady-state auditory evoked potentials (S-AEPs) with interhemispheric coherence analysis.

Methods

Tone-burst (TB) stimuli on 500 Hz and 2000 Hz carrier frequencies were presented monaurally to elicit S-AEPs in 10 normal subjects. The modulation frequencies were varied from 15 to 90 Hz in 5 Hz steps for each carrier frequency. Nine recording electrodes were placed coronally including Cz and were referred to an electrode at the 7th cervical spinous process. A total of 100 responses of 1 sec epoch were averaged, and subjected to discrete fast Fourier transforms (FFTs) to yield the amplitude of the first harmonic (1F) component and interhemispheric coherence (Coh) value between homologous electrodes.

Results

Three amplitude peaks at around 15-20, 40-45 and 80 Hz were elicited by the modulation frequencies for both carrier frequencies. The 1F amplitude at the temporal electrode contralateral to the stimulated ear was significantly larger than that on the ipsilateral side for both tones. The interhemispheric Coh values between T3 and T4 elicited by stimulating the right ear were greater than those to left ear stimulation at around 35-45 Hz, and this difference reversed at 50 to 90 Hz for 500 Hz TB. This characteristic was not found for 2000 Hz.

Conclusion

The presence of three tuning peaks indicates the existence of subgroups of neurons specialized for emporal processing. The results indicate a difference in the processing of temporal and spectral information in the human auditory cortex.

Significance

Auditory hemispheric specialization for temporal processing depends on modulation and carrier frequencies.

Key Words

Steady-State Auditory Evoked Potentials, Tone-Burst Stimulation, Temporal and Spectral Information Processing, Interhemispheric Coherence

Introduction

The temporal and spectral properties of auditory signals are important for the perception of complex auditory stimulus patterns that include both slowly and rapidly changing acoustic events. The temporal factors include the duration of the signals and the intervals between sounds, such as speech, whereas spectral factors involve pitch processing. Cortical hemispheric asymmetries are well known to exist for the processing of speech and tonal patterns. Neuropsychological, electrophysiological, and neuroimaging studies have shown that temporal information is processed predominantly in the left auditory cortex, and spectral information is processed in the right auditory cortex [1-6].

The results of a magnetoencephalographic (MEG) [7] and perceptual [8,9] studies have shown that pitch fades as the interclick intervals increases beyond 25 ms (or 40 Hz). Lu et al. [10] have shown that temporal coding neurons are dominant for stimulus frequencies less than 40 Hz while the

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rate-coding neurons are dominant at higher than 40 Hz in the auditory cortex of marmoset monkey. Our recent study [11], using S-AEPs to 500 Hz TB stimulation with coherence (Coh) analysis, showed that 40 Hz auditory information was predominantly processed in the left auditory cortex. This finding may be related to the dominance of the left auditory cortex for rapid temporal processing. However, a recent MEG study [12] has shown the right hemispheric predominance of 40 Hz steady-state responses to 500 Hz TB stimulation. Therefore, which hemisphere is predominantly involved in auditory temporal and spectral information processing has been contradictory.

Coh analysis has been used to determine the underlying changes in cortical connectivity [1, 13-18]. Application of Coh analysis to S-AEPs has enabled us to evaluate the correlations of interhemispheric function during auditory information processing [11]. Overall, we concluded that a wider modulation of the temporal and spectral parameters was necessary to determine the hemispheric specialization for spectral and temporal processing. Therefore, the purpose of this study was to determine how the two auditory cortices are activated and interact to stimuli of different modulation and carrier frequencies.

Methods

Subjects

Ten healthy subjects (6 men and 4 women), ages 24-40 years, were studied. All subjects were right-handed and reported no clinical history of hearing loss or neurological disorders. Informed consent was obtained after the nature of the experiment had been fully explained. The experimental procedures were approved by the Ethics Committee of the Graduate School of Medical Sciences, Kyushu University. The recording of this experiment was done from 2002 to 2005.

Auditory Stimulation and AEP Recordings

An auditory stimulator (Neuropack 8, Nihon Kohden, Japan) delivered a controlled TB stimulus (4 ms plateau and 2 ms rise/fall time) to each ear by earphones. The stimulus waveform was the product of a fixed amplitude carrier signal and a modulation term that varied sinusiodally. The carrier frequency was set at 500 Hz or 2000 Hz, and the modulation frequency was varied from 15 to 90 Hz (61 Hz was used instead of 60 Hz). At all temporal frequencies, the stimulus intensity was held at 50 dBSL, which was determined when a 40-Hz TB was given in both carrier frequencies. White noise was given to the contralateral ear at an intensity of 40 dBSL. All subjects were instructed to keep their eyes closed and to remain completely relaxed while lying horizontally on a bed.

The S-AEPs were recorded using silver-silver chloride electrodes that were placed over C1, C2, C3, C4, C5, C6, T3, T4, and Cz (International 10-20 system), with the reference electrode at the 7th cervical spinous process (SC7) (Picton et al., 2003). The impedance of the electrodes was maintained below 5 Kohm. The AEP signals were analog-filtered between 0.5 and 200 Hz.

Data Analysis

The analog data were digitized at a sampling rate of 1 kHz/channel and 100 samples of 1 sec epoch were averaged by a computer (PC-MA86TMGDMEG6, GE Marquette, Tokyo). Epochs containing baseline deviations greater than 100 μV were automatically rejected. The averaged responses were then subjected to fast Fourier transforms (FFTs) which yielded the amplitude (square root of the power) and phase of the first harmonic (1F) responses for each temporal frequency.

The Coh value between any two electrodes was measured at 1F. The Coh value between two signals x and y at each frequency f was calculated as,

$$[\mathrm{Coh}\ xy\ (f)\ ]2 = [S\ xy\ (f)]\ 2/\ [Sxx\ (f)*Syy\ (f)],$$

where Sxy (f), Sxx (f) and Syy (f) are cross-spectrum and auto spectrum estimates of the x and y signals, respectively [1,19,20]. Based on the assumption that the Coh between the two electrographic signals reflects a functional correlation, the Coh value of 1F between homologous electrode pairs was measured [1,11]. The Coh values range between 0 and 1 by definition. A value of 1 indicates that the two signals are totally related linearly at each frequency, while values below a certain minimum (which is determined by the number of degrees of freedom characteristic for the computation) do not support the presence of any linear relationship. According to our previous study [1,11], we mainly analyzed the amplitudes and Coh values of the electrodes at T3 and T4.

A three-way analysis of variance (ANOVA) with repeated measures was performed to determine the effects of the electrode positions (T3 vs. T4), stimulus sides (left vs. right) and carrier frequencies (500 Hz vs. 2000 Hz) on the amplitudes of 1F at each modulation frequency. A two-way analysis of covariance (ANCOVA) was used for the Coh values between each frequency for each condition ($P < 0.05$ was considered to be statistically significant).

Results

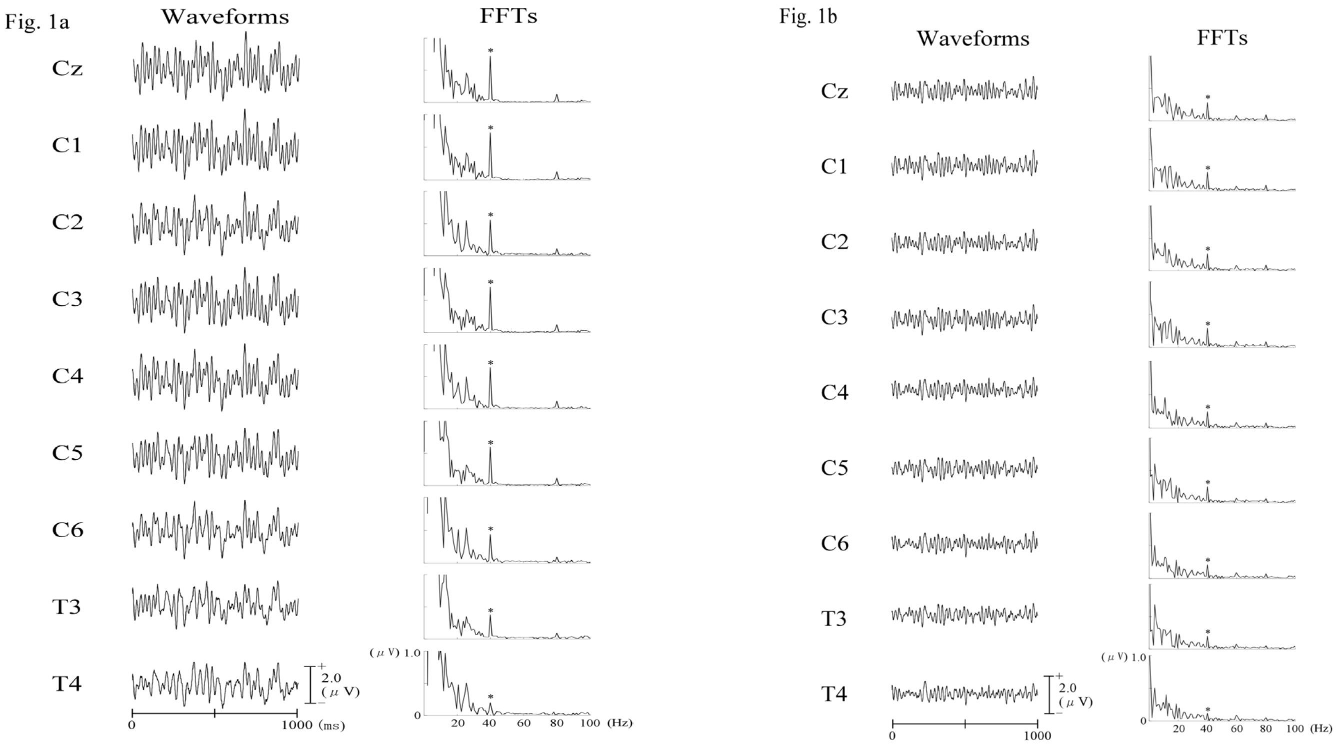

Figure 1a, b : Representative waveforms of S-AEPs at 40 Hz and their FFTs that were elicited by 500 Hz (a) and 2000 Hz (b) TB stimulations delivered to right ear from one subject are shown in Figure 1. In both carrier frequencies, the waveforms of the S-AEPs were quasi-sinusoidal that corresponded to a modulation frequency of 40 Hz (Figure 1a, b, left) at all recording electrodes. FFTs revealed that the 40-Hz component (or 1F component) was the major component in the amplitude spectrum (Figure 1a,b, right). The 1F component was larger in the left hemisphere (contralateral to the stimulus side) than in the right hemisphere.

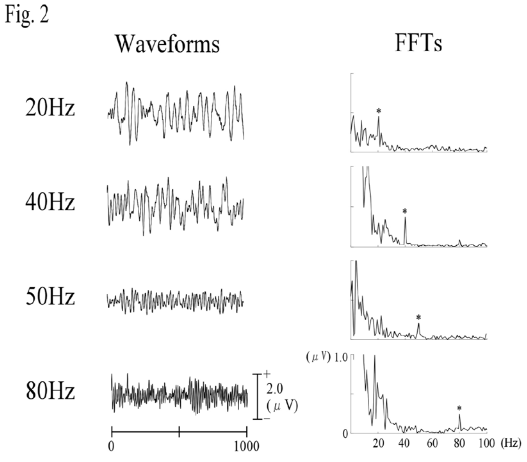

Figure 2 : Representative waveforms of the S-AEPs recorded at T3 are shown in Figure 2 (left). These responses were elicited by 20, 40, 50, and 80 Hz on a carrier frequency of 500 Hz TB delivered to the right ear. The waveforms of the S-AEPs were quasi-sinusoidal and corresponded to each modulation frequency. FFTs revealed that the 1F component was the major component of the amplitude spectrum (Figure 2, right).

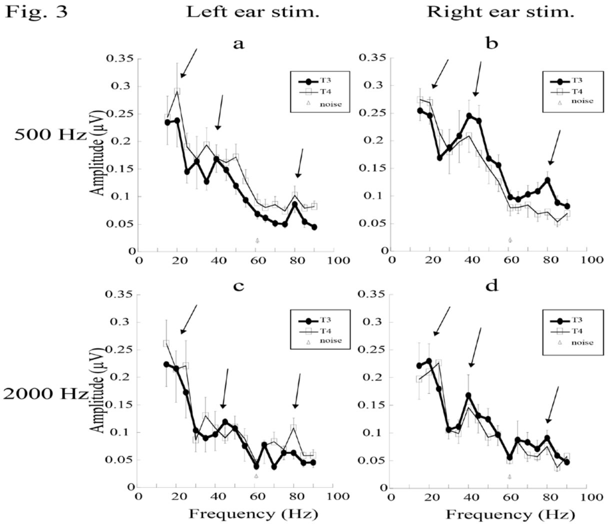

Figure.3 : The mean 1F amplitudes at the T3 and T4 electrodes in response to left (Figure 3a, c) and right ear stimulation (Fig. 3b, d) are also shown in Figure 2 for carrier frequencies of 500 (Figure 3a, b) and 2000 Hz TB (Figure 3c, d). Three peaks at around 15-20, 40-45, and 80 Hz were clearly recorded at both electrodes.

Fig. 4

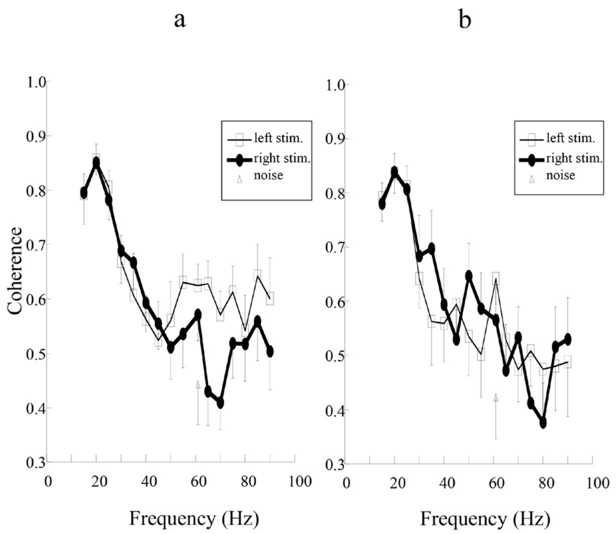

Figure4: The interhemispheric Coh values of 1F between T3 and T4 for the different modulation frequencies on carrier frequency of 500 (Figure 4a) and 2000 Hz (Figure 4b) are shown in Figure 4. The Coh values for stimulation at 15 to 30 Hz modulation frequencies were not significantly different (Figure 4a). However, the Coh values between 35 and 45 Hz for right ear stimulation tended to be larger than those to left ear stimulation and this difference reversed between 50 and 90 Hz (ANCOVA, F (1, 169) =3.80, *P* = 0.0528). This modulation frequency dependency at 500 Hz TB was less clear at 2000 Hz TB.

Discussion

Three major findings were made on the properties of the 1F amplitudes and interhemispheric Coh values. First, three amplitude peaks were observed at around 15-20, 40-45, and 80 Hz to the different modulation frequencies for both 500 and 2000 Hz carrier frequencies. Second, the interhemispheric Coh values were greater between 35 and 45 Hz in the left hemisphere than in the right hemisphere, and the opposite was true between 50 and 90 Hz at 500 Hz. And third, the reversal of the hemispheric contribution in the Coh values to each modulation frequency was observed at 500 Hz but not at 2000 Hz TB. Our finding that the amplitudes on the contralateral side of the stimulated ear were larger than those of ipsilateral is consistent with previous studies [11,21,22].

Prior to discussing the physiological implications of our major findings, we should mention the reliability of the responses at the temporal electrodes (T3, T4), the SC7 reference, and Coh analysis. An earlier AEP study using brain electric source analysis revealed two cortical sources (tangential and radial components) generated from brainstem and auditory cortices [23,24], in which the radial activity was smaller than the tangential one. The tangential activity recorded from the electrodes at around the vertex reflects the activities from both auditory cortices. Thus, the analysis of the tangential component is not suitable for the hemispheric specialization. In contrast, the radial component recorded from the temporal electrodes (T3, T4) reflects the activity mainly from the ipsilateral auditory cortex. Therefore, the use of temporal electrodes is more appropriate for the study of the hemispheric specialization [11]. However, the temporal electrodes are susceptible to noise due to the temporal muscles. The use of FFTs may increase the signal to noise ratio of 1F amplitude in the stimulated condition.

Coh measurements can only be meaningful if the reference electrode is truly inactive [25,26]. The reference electrode at SC7 did not influence the topography of AEPs, and response amplitudes were significantly larger for the reference electrode at SC7 than at the mastoid reference [27]. This finding indicated that the SC7 was not a problematic as a reference. Coh values are also affected by the amplitude differences between the two electrodes. However, no significant difference was found between the response to the left ear stimulation at T4 and to right ear stimulation at T3, and vice versa. Thus, the difference of Coh values between two ear stimulations resulted from the hemispheric functional specialization but not from the amplitude difference. Because the Coh values depend on the information of both amplitude and phase, the Coh analysis is more useful for the investigation of the hemispheric specialization than the analysis of amplitude alone. In addition, Coh analysis can reveal the functional interaction between bilateral auditory cortices [28]. Taken together, our major findings are not artifactual and worth analyzing and discussing.

Three Tuning Peaks for Temporal Processing

Three amplitude peaks were observed at approximately 15-20, 40-45, and 80 Hz for modulation frequencies for both 500 and 2000 Hz. [29] first reported that S-AEPs to 40 Hz stimulation showed a maximum amplitude that was smaller at a subharmonic rate of 20 Hz with a minimum at 25 and 55 Hz.[30,31] also showed that signal averaging and Fourier analysis provided the same amplitude/rate function as [29]. [32] demonstrated the two amplitude peaks at 45 and 90 Hz, and Ross et al. [33] further distinguished three ranges of group delays (apparent latency) at 20, 40 and 80 Hz, in a MEG study.

The temporal resonance of the sensory system plays an important role in extracting stimulus features by acting as neural filters in the temporal domain. In the visual system, there are three subsystems for temporal tuning which are at high (40-50 Hz), intermediate (about 16 Hz) and low (about 10 Hz) frequencies, and they are generated in different brain regions [34,35]. High- and intermediate- frequency responses originate from the visual cortex, whereas low-frequency responses are generated in a much wider region of the visual cortex [35]. High-frequency responses depend on the luminance of the stimulus while intermediate- frequency responses depend on the color [34,35]. Low-frequency responses pass through a tuned cortical filter centered at about 10 Hz as the alpha activity [35].

In the auditory system, the neural sources of the 40 Hz responses have been suggested to be in the primary auditory cortex [36]. Lins and Picton [37] found a significant difference in the apparent latency between the 40- and 80- Hz S-AEPs as well as a differential effect of sleep on these responses. They suggested that different steady-stimulus rates selectivity activated specific clusters of neurons in the cortex. Schoonhoven et al. [38] also concluded that the modulation frequency at both 40 and 80 Hz were originated from the auditory cortex. Ross et al. [33] distinguished three ranges of group delays (apparent latency) at 20, 40 and 80 Hz, and MEG responses were dominated by activity in the auditory cortex. Giraud et al. [39] presented some evidence for restricted cortical regions responding to low or high modulation frequencies in an fMRI study. Although the previous EEG study [23] has concluded that the 88-Hz response mainly originates from the brainstem source whereas the 39-Hz response is dominated by cortical sources, our findings indicate that the auditory system at the level of cortex has three subsystems for the temporal coding, at around 15-20, 40-45 and 80 Hz, as observed in the visual system.

Reversible Hemispheric Contribution To Temporal Processing

Larger interhemispheric Coh values were observed between 35 and 45 Hz in the left hemisphere compared to the right hemisphere at 500 Hz TB. However, this predominance was reversed between 50 to 90 Hz. Which hemisphere has a predominant contribution to the auditory temporal information processing has been contradictory. A recent study on the auditory cortex of marmoset monkey showed that the timing of relatively slowly occurring sequential acoustic events (<40 Hz) can be explicitly represented by the temporal discharge patterns of the stimulus-synchronized population while faster rates of acoustic events can be implicitly represented by the average discharge rate of neurons in the non-synchronized population [10]. Their results suggested that the temporal-coding neurons are dominant at less than 40 Hz while the rate-coding neurons are dominant at higher than 40 Hz. The former is important for discriminating each sound while the latter is crucial for the perception of rate or pitch [10]. An earlier MEG study also showed that the sustained field response fades away when the interclick intervals are shorter than 25 ms (or 40 Hz), which supports the hypothesis that this response is concerned with pitch processing [7]. These results suggest that a temporal frequency of 40 Hz is the critical frequency for the auditory temporal processing system. Therefore, the dominant hemisphere for temporal processing could be reversed at around 45-50 Hz.

A recent MEG study [33] showed the right hemispheric predominace of 40 Hz steady-state responses, which is opposite to our recent study [11]. However, their auditory stimuli were completely different from ours: Our stimuli were continuously presented while their stimuli were presented at the duration of 600 ms with a stimulus interval of 2000-3000 ms. Further studies on the effect of the stimulus duration will be necessary to determine the hemispheric specialization for 40 Hz auditory steady-state responses.

Modulative Effect of Spectral Information on Temporal Processing

A reverse in the hemispheric Coh values to the temporal frequency was observed with 500 Hz but not with 2000 Hz carrier frequencies. In addition, the amplitudes in response to 500 Hz TB tended to be larger than those for 2000 Hz. These findings may have resulted from a tonotopic organization in the auditory cortex.

Recent neuroimaging studies, such as MEG, PET, and fMRI, have demonstrated that the activated area for high tones is located more medially and posterior compared with that of the low tone [40,41]. The MEG responses were more pronounced in the right temporal lobe with a slight caudal shift for higher frequencies [22]. In an intracerebral AEP study. [5] showed that the AEPs for high frequencies were recorded medially, whereas AEPs for low frequencies were recorded laterally. These finding were prominent in the right hemisphere but were less significant in the left hemisphere. In addition, the activation area for low tones was larger than that for high tones in fMRI studies [42,43]. [22] showed that the magnitude of the auditory steady-state evoked magnetic fields was greater for lower carrier frequencies than those for higher carrier frequencies, and the direction of the equivalent current dipole flowed in a medial direction as the carrier frequency changed from 250 to 4000 Hz. The combinations of carrier and modulation frequencies resulted in fluctuations in the roughness and residue pitch [44]. From these observations, it is likely that the carrier frequency differentially modulates the temporal processing in the auditory cortex.

Conclusions

The presence of three tuning peaks indicates that neuronal subgroups are present for temporal processing as in the visual system. Our findings indicate and confirm the functional specialization of each hemisphere of auditory cortex. Hemispheric predominance for rapid temporal processing depends on the modulation and carrier frequencies, which thus suggests differential processing of temporal and spectral information in the human auditory cortex.

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