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Research paper

Auditory evoked responses in human auditory cortex to the variation of sound intensity in an ongoing tone

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A B S T R A C T

In daily life, variations of sound intensity, frequency, and other auditory parameters, can be perceived as transitions from one sound to another. The neural mechanisms underlying the processing of intensity change are currently unclear. The present study sought to clarify the effects of frequency and initial sound pressure level (SPL) on the auditory evoked response elicited by sounds of different SPL. We examined responses approximately 100 ms after an SPL change (the $N1m'$). Experiment 1 examined the effects of frequency on the $N1m'$. Experiment 2 examined the effects of initial SPL on the $N1m'$. The results revealed that $N1m'$ amplitude increased with greater SPL changes. The increase in $N1m'$ amplitude with increasing SPL was almost constant for low frequency sounds (250 and 1000 Hz); however, this increase was reduced for high frequency sounds (4000 Hz). The increase in $N1m'$ amplitude was reduced with high initial SPL. The pattern of amplitude change may reflect a difference in activation in the auditory nerve and/or primary auditory cortex.

1. Introduction

Natural sounds in the environment such as speech and music constitute complex acoustic signals involving changes in intensity, frequency, and other features. Changes in sound intensity are highly correlated with changes in perceived loudness, which is one of the most basic perceptual attributes of sound. The neural mechanisms underlying the processing of intensity changes have been the subject of substantial research interest. A large number of studies have examined brain activity accompanying changes of intensity using auditory evoked potentials (AEP) and magnetic fields (AEF) (e.g., Davis et al., 1968; Antonoro et al., 1969; Elberling et al., 1982; Reite et al., 1982; Bak et al., 1985; Pantev et al., 1989a; Vasama et al., 1995; Harris et al., 2007; Lütkenhöner and Klein, 2007; Michalewski et al., 2009; Soeta and Nakagawa, 2009). These studies have focused on the $N1(m)$ response, reporting that $N1(m)$ responses increase with greater intensity. The $N1(m)$ is an auditory evoked response to the transition from silence to sound, and is observed approximately 100 ms after the sound onset in the planum temporale in human auditory cortex. In daily life, abrupt variations of sound intensity are perceived as transitions from one sound to another. However, the effects of variation of sound intensity on human auditory cortex are not well understood.

Functional magnetic resonance imaging (fMRI) has also been used in several studies to investigate the neural mechanisms underlying the processing of intensity changes in the auditory cortex (Jäncke et al., 1998; Hall et al., 2001; Bilecen et al., 2002; Hart et al., 2002; Yetkin et al., 2004; Sigalovsky and Melcher, 2006; Langers et al., 2007). Most studies have demonstrated a systematic increase of brain activation as the SPL increases. Langers et al. (2007) investigated an intensity-activation-function using a wide range of SPLs, reporting a stronger correlation between brain activation increases with loudness level than with SPL. Ernst et al. (2008) investigated signal representation in human auditory cortex for a sinusoidal signal in the presence of a noise masker. They found that brain regions mainly sensitive to SPL changes were located in various parts of the superior temporal lobes, including primary auditory cortex and the planum temporale, while those regions mainly sensitive to changes of signal-to-noise ratios were located at or close to Heschl's gyrus. Although fMRI can localize brain activation with SPL changes over a long period, it cannot measure the neural correlates of rapid changes in SPL. Thus, fMRI is not appropriate for investigating transitions of SPL from one sound to another in a short period.

Some studies have investigated patterns of human brain activity accompanying changes in the intensity of an ongoing continuous tone using AEP (McCandless and Rose, 1970; Jerger and Jerger, 1971;

Abbreviations: ANOVA, analysis of variance; AEP, auditory evoked potential; AEF, auditory evoked field; ECD, equivalent current dipole; fMRI, functional magnetic resonance imaging; MRI, magnetic resonance image; SPL, sound pressure level.

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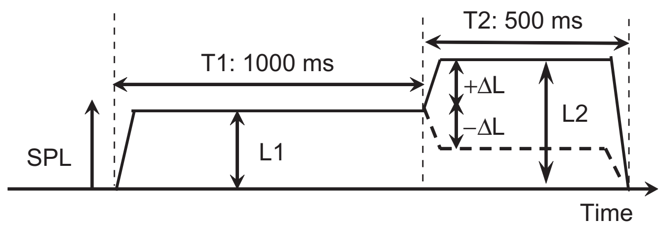

Fig. 1. The temporal change of the SPL of tone stimulus. The tone was initially presented at an SPL of *L*1 dB for *T*1 ms, then changed (±Δ*L* dB) and presented at an SPL of *L*2 dB for *T*2 ms.

Spoor et al., 1971; Martin and Boothroyd, 2000; Harris et al., 2007; Dimitrijevic et al., 2009). Spoor et al. (1971) reported that *N*1−*P*2 amplitude and *N*1 latency increased and decreased, respectively, with increments of SPL with a 1000 Hz tone. The increment and decrement ratio at the SPL of an ongoing continuous tone of 70 dB was greater than that of 30 dB. Several lesion studies reported that the *N*1 and *P*2 receive contributions from different generators (Knight et al., 1980, 1988), suggesting that these potentials combine activity from different processing stages. In addition, the *N*1*m* arises mainly from the planum temporale, whereas the source of the *P*2*m* reflects activity centered on Heschl's gyrus, anterior and inferior to the source of the *N*1*m* (Lütkenhöner and Steinsträter, 1998; Krumbholz et al., 2003; Seither-Preisler et al., 2004). The findings of these two studies suggest that the peak-to-peak amplitude (*N*1−*P*2) measurements commonly used in evoked response studies may be misleading. Harris et al. (2007) reported that *N*1 amplitude in response to an ongoing tone was increased and latency was shortened with increments of SPL for 500 and 3000 Hz tones. The increment of *N*1 amplitude in an ongoing tone with increasing SPL at a frequency of 500 Hz was found to be larger than that at a frequency of 3000 Hz. Dimitrijevic et al. (2009) reported that *N*1 amplitude in response to an ongoing tone increased and latencies were shortened with increasing increments in SPL for 250, 1000, and 4000 Hz tones. The relationship between SPL changes and *N*1 amplitudes/latencies in an ongoing tone did not differ between tone frequencies. Dimitrijevic et al. (2009) used stimuli with a higher SPL (80 dB) compared to the stimuli used by Harris et al. (2007) (70 dB). As such, responses may have been saturated, and results might have been different for tones presented at lower SPL. In addition, the difference between onset *N*1 and *N*1 in response to an ongoing tone has not been examined in previous studies. Soeta and Nakagawa (2009) indicated that the onset *N*1*m* amplitude increased with SPL, reporting that the growth in amplitude with increasing SPL was almost constant with low frequencies (250–1000 Hz); however, this growth decreased with high frequencies (>2000 Hz). This is consistent with the findings of Harris et al. (2007), but not with those of Dimitrijevic et al. (2009).

The current study sought to clarify the effects of changing SPL on the *N*1(*m*) in an ongoing tone in human auditory cortex, hereafter referred to as the *N*1(*m*)′. Although previous studies used tones with a high SPL (70 or 80 dB), sound with lower SPL are often heard in daily life. Thus, we used tones with a lower SPL (50 dB) and examined the effects of frequency on the *N*1*m*′ in Experiment 1. To clarify whether the initial SPL affects the growth in amplitude with increasing SPL, we examined the effects of initial SPL on the *N*1*m*′ in Experiment 2. We hypothesized that cortical amplitude differences would exist between high and low frequency sounds during the encoding of SPL changes in an ongoing tone with a moderate SPL. In addition, we predicted a difference in the growth of cortical amplitude with increasing SPL between high and low initial SPL.

2. Material and methods

2.1. Participants

Ten participants (eight males) with normal hearing (hearing thresholds lower than or equal to 20 dB hearing level at octave frequencies from 125 Hz to 8000 Hz) and no history of neurological disease, aged between 23 and 39 years (median age of 32.5 years), took part in Experiment 1. Ten participants (seven males) with normal hearing and no history of neurological diseases, aged between 23 and 39 years (median age of 34 years), took part in Experiment 2. Seven of the participants took part in both experiments. 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), Japan.

2.2. Stimuli

Pure tones were used as stimuli, and the SPL was experimentally manipulated. The temporal profile of the tone stimulus is shown in Fig. 1. The tone was initially presented at an SPL of *L*1 dB, then changed ±Δ*L* dB (to *L*2 dB). The duration of the initial tone presentation at *L*1 dB (*T*1) was set at 1000 ms. A previous study indicated

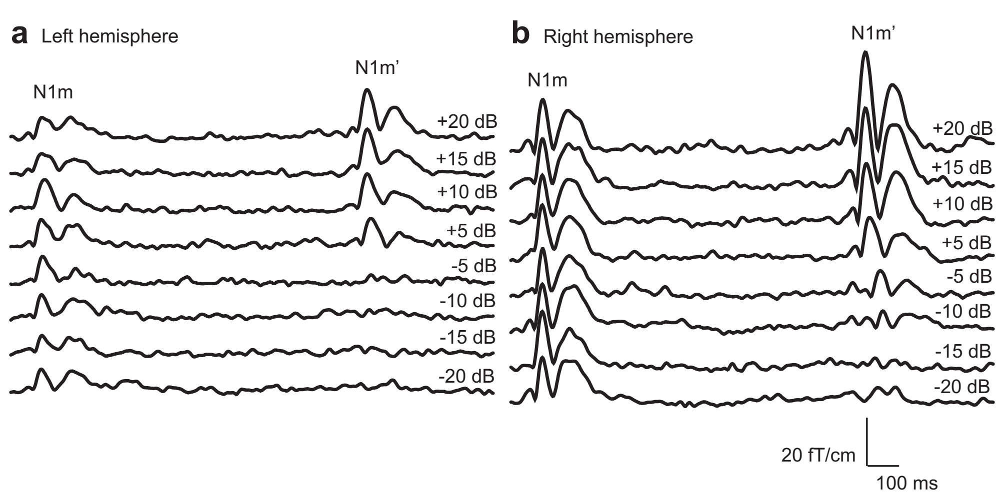

Fig. 2. Typical waveforms of root-mean-square values of the AEFs over the (a) left and (b) right temporal hemisphere obtained by one participant in Experiment 1. The frequency of the tone was 1000 Hz.