Hearing Research 296 (2013) 25–35

Contents lists available at SciVerse ScienceDirect

Hearing Research

journal homepage: www.elsevier.com/locate/heares

Research paper

Steady-state MEG responses elicited by a sequence of amplitude-modulated short tones of different carrier frequencies

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ARTICLE INFO

Article history:
Received 19 June 2012
Received in revised form
28 October 2012
Accepted 5 November 2012
Available online 19 November 2012

ABSTRACT

The auditory steady-state response (ASSR) is a weak potential or magnetic response elicited by periodic acoustic stimuli with a maximum response at about a 40-Hz periodicity. In most previous studies using amplitude-modulated (AM) tones of stimulus sound, long lasting tones of more than 10 s in length were used. However, characteristics of the ASSR elicited by short AM tones have remained unclear. In this study, we examined magnetoencephalographic (MEG) ASSR using a sequence of sinusoidal AM tones of 0.78 s in length with various tone frequencies of 440–990 Hz in about one octave variation. It was found that the amplitude of the ASSR was invariant with tone frequencies when the level of sound pressure was adjusted along an equal-loudness curve. The amplitude also did not depend on the existence of preceding tone or difference in frequency of the preceding tone. When the sound level of AM tones was changed with tone frequencies in the same range of 440–990 Hz, the amplitude of ASSR varied in a proportional manner to the sound level. These characteristics are favorable for the use of ASSR in studying temporal processing of auditory information in the auditory cortex. The lack of adaptation in the ASSR elicited by a sequence of short tones may be ascribed to the neural activity of widely accepted generator of magnetic ASSR in the primary auditory cortex.

1. Introduction

The auditory steady state response (ASSR) of the scalp potential is elicited by repetitive short acoustic stimuli with a maximum response at 35–45 Hz repetition rate (Galambos et al., 1981). Cortical and subcortical origins of the potential ASSR at the thalamus and brainstem have been suggested from cross-modal stimulation (Galambos, 1982), intracranial recording (Lee et al., 1984), patient study (Spydell et al., 1985) and scalp topography (Johnson et al., 1988). The magnetic counterpart of ASSR recorded by MEG (magnetoencephalography) has indicated an auditory cortical generator and has been used to characterize frequency-specific organization of neural activity in the auditory cortex (Romani et al., 1982; Mäkelä and Hari, 1987).

In humans, scalp potential ASSR evoked by a sinusoidal amplitude-modulated (AM) sound has been observed up to a modulation frequency of 400 Hz (Rees et al., 1986). However, the frequency-following response recorded with a subdural electrode from the human auditory cortex showed a steep drop in amplitude above 40 Hz (Lee et al., 1984). Such a difference in auditory responses may be due to the subcortical contribution in the scalp potential. Previous studies using EEG (electroencephalography) and MEG have revealed various aspects of ASSR including the generation mechanism (Pantev et al., 1993; Presacco et al., 2010) and effects of stimulus parameters such as sound level, modulation frequency and carrier frequency (Pantev et al., 1996; Ross et al., 2000; Wienbruch et al., 2006). As for the sound level effect, the amplitude of ASSR increases as the level increases in a logarithmic (dB) manner (Ross et al., 2000), in line with long-latency evoked responses of N1/N1m (Thaerig et al., 2007; Soeta and Nakagawa, 2012), where N1m is the magnetic counterpart of N1 potential. Regarding the dependence of ASSR on carrier frequency, detailed results have been provided by several studies (Pantev et al., 1996; Ross et al., 2000; Wienbruch et al., 2006). As a general trend, the amplitude of ASSR decreases with increase in carrier frequency in the range from about 250 to 4000 Hz, in which the decrease between 500 and 1000 Hz is relatively small. Those results seem to

Abbreviations: AEF, auditory evoked field; AM, amplitude modulation(ed); ANOVA, analysis of variance; ASSR, auditory steady-state response; EEG, electroencephalography; f_c, carrier frequency; f_m, modulation frequency; GOF, goodness of fit; MEG, magnetoencephalography; MR(I), magnetic resonance (imaging); nHL, normal hearing level; SL, sensation level; SPL, sound pressure level.

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http://dx.doi.org/10.1016/j.heares.2012.11.002

depend how the magnitude of sound is controlled in a wide range of frequencies, i.e., whether the sound pressure level (SPL), sensation level (SL) or loudness is kept constant through the carrier frequency. Since SL or loudness is a function of carrier frequency, the effect of stimulus intensity may be mixed in such carrier frequency dependence; the frequency dependence has not been established yet. In most of those studies, repetition of short sound bursts or long-lasting continuous AM sounds typically more than 10 s in length were used.

The ASSR is a clinically useful tool for objective audiometry by evaluating the response threshold (Lins et al., 1996; Picton et al., 2005; Scherf et al., 2006). In such clinical test, delivery of sinusoidal AM tones in a short period while changing the carrier frequencies in an audible range would be a method for fast examination. The ASSR may also be applied in basic studies of temporal processing of input sounds in the auditory cortex. A typical example is the auditory illusion proposed by Deutsch (1974, 1975), in which distinct tonal sequences within about one octave pitch are delivered to the right and left ears. Most listeners hear illusory percepts of smooth contours or stable pitch alternation in the two ears instead of original discontinuous pitch contours. Evoked potential and MEG studies have challenged this phenomenon (Ross et al., 1996; Lamminmäki and Hari, 2000, 2012), but dynamical processes in the right and left auditory cortices underlying the illusion were not clarified. In those studies, the temporal resolution was not sufficient or responses to the right- and left-ear sounds were not separated. In a suitable approach by the ASSR, successive short AM tones with variation in pitch, mimicking the musical tones used in the illusion paradigm, should be used. However, little is known about temporal characteristics of the ASSR elicited by short-sinusoidal AM tones in analyzing the obtained ASSR data in these clinical and basic studies. Specifically, how the amplitude of the ASSR varies when the f_c and/or the sound pressure of the tone are changed from one tone to another in a short time of less than 1 s is a central issue.

Adaptation and transient characteristics by preceding sounds are the key factors that affect the carrier frequency and sound-level dependence of short-tone-elicited ASSR. A behavioral study showed that long exposure to sinusoidal AM stimuli elevated thresholds for detection of subsequent AM sound, where the loss of sensitivity (adaptation) followed a slow asymptotic curve continuing for 20–30 min. In contrast, recovery was rapid, within the first 60 s (Tansley and Suffield, 1983). A neurophysiological study (Bartlett and Wang, 2005) using awake marmosets indicated that about 60% of tested units in the auditory cortex showed significant suppression of firing rate to the second AM sound in a stimulus sequence consisting of two sinusoidal AM sounds. This suppression lasted for more than 1 s. The suppression was often tuned such that the preceding sound whose parameters were similar to the succeeding sound produced the strongest suppression. To our knowledge, corresponding experiments of human ASSR using a sequence of similar/distinct sinusoidal AM sounds have not been reported. For a repetition of pulse AM sounds, it was shown that amplitude of the ASSR of MEG was dependent on the temporal structure of the stimulus sounds, i.e., modulation waveform, even when the amplitude of the wave and spectral properties were kept the same (Simpson et al., 2012). In that experiment, AM sounds of a constant carrier frequency were shaped to be a sequence of short-width pulses at 4 Hz repetition rate. The 4 Hz component of the ASSR was larger when different widths of the AM pulses were variably mixed than when the pulse width was constant. This result suggests a certain effect of temporal structure of AM sound on the adaptation of ASSR. Regarding the transient characteristics, Ross et al. (2005) reported that the amplitude of the ASSR of MEG recovered to its original height in a period of 200–250 ms when the ASSR to continuous AM tone was depressed by desynchronization due to noise-burst perturbation. The recovery form and the time resembled those after initiation of the stimulus sound. Such transient depression and recovery of the ASSR may also be expected at the boundary of frequency change of AM tones, if present, through the variation of the phase of ASSR with the carrier frequency (Ross et al., 2000).

The ASSR measured with MEG shows exclusively the activity of the auditory cortex. Localization of the source of magnetic ASSR on anatomical MR images (Pantev et al., 1996; Engelien et al., 2000; Herdman et al., 2002; Steinmann and Gutschalk, 2011) has consistently indicated a single dipole in the primary auditory cortex, which is known to be located in the medial part of Heschl's gyrus in the superior temporal plane (Galaburda and Sanides, 1980; Hackett et al., 2001; Fullerton and Pandya, 2007). The latency of ASSR, if converted from 40-Hz repetition rate, corresponds to that of the middle latency response. The middle latency responses measured using MEG consisted of three waves having short rise and fall times of 5–10 ms in a period of about 40 ms after the click stimulation (Kuriki et al., 1995). Dipole sources of those waves were located in the medial site of the auditory cortex. This result supports the view that the ASSR originates in the primary auditory cortex.

In contrast to the results of ASSR studies, it is widely accepted that long-latency evoked responses of N1/N1m exhibit strong adaptation in repeated stimulation of sounds in a manner that is frequency-specific, i.e., the response reduction is stronger when the frequency components of preceding sound are closer to those of succeeding sound (Näätänen et al., 1988; Nishimura et al., 2004). The decrement depends on the repetition rate of sinusoidal tone bursts; the amplitude reduction of N1/N1m is larger for shorter inter-stimulus intervals (Budd et al., 1998; Rosburg et al., 2010). The peak amplitudes of N1/N1m/P2m become constant after the first reduction at the second stimulus in repeated stimulation of pure tones and complex tones comprising higher harmonics. This result was interpreted to show the refractory effects of populational neurons rather than habituation (Kuriki et al., 2006; Rosburg et al., 2010). Regarding the frequency dependence, the amplitude/moment of N1m is lower at higher frequencies for pure tone stimulation. It is estimated to be almost independent in a range lower than 1 kHz (Gabriel et al., 2004).

From the aforementioned previous results about ASSR on the behavioral adaptation by long exposure to AM sound, amplitude suppression by dissimilar temporal waveforms, short recovery from desynchronization, and the primary auditory cortical genesis, we hypothesize that the ASSR, especially that of MEG, evoked by sinusoidal AM tones was not attenuated by the change in stimulus parameters of the preceding tone, such as sound level and carrier frequency provided that the length of the AM tone is longer than the recovery time. This may hold even when the AM tones are connected in series with other AM tones having different carrier frequencies and sound levels. The aim of this study was to clarify the basic characteristics of the ASSR elicited by sequential short AM tones having a length of less than 1 s. We examined how the magnitude of ASSR of MEG depended on the carrier frequency and the level of sinusoidal AM sound with a preceding adjacent tone while the modulation frequency was fixed to about 40 Hz. The range of carrier frequencies was restricted to about one octave considering application to basic study of the auditory illusion, in which high spatial resolution of MEG is expected to enable separate detection of activities in the right and left auditory cortices. We measured the amplitude of ASSR in response to paired and consecutive AM tones varying in carrier frequency or sound pressure, in comparison with the corresponding transient evoked response of N1m. Analysis of a single dipole source was also carried