



Amplitude and phase-locking adaptation of neural oscillation in the rat auditory cortex in response to tone sequence



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ABSTRACT

Sensory adaptation allows stimulus sensitivity to be dynamically modulated according to stimulus statistics and plays pivotal roles in efficient neural computation. Here, it is hypothesized that in the auditory cortex, phase locking of local field potentials (LFPs) to test tones exhibits an adaptation property, i.e., phase-locking adaptation, which is distinct from the amplitude adaptation of oscillatory components. Series of alternating tone sequences were applied in which the inter-tone interval (ITI) and frequency difference (ΔF) between successive tones were varied. Then, adaptation was characterized by the temporal evolution of the band-specific amplitude and phase locking evoked by the test tones. Differences as well as similarities were revealed between amplitude and phase-locking adaptations. First, both amplitude and phase-locking adaptations were enhanced by short ITIs and small ΔF s. Second, the amplitude adaptation was more effective in a higher frequency band, while the phase-locking adaptation was more effective in a lower frequency band. Third, as with the adaptation of multiunit activities (MUAs), the amplitude adaptation occurred mainly within a second, while the phase-locking showed multi-second adaptation specifically in the gamma band for short ITI and small ΔF conditions. Fourth, the amplitude adaptation and phase-locking adaptation were co-modulated in a within-second time scale, while this co-modulation was not observed in a multi-second time scale. These findings suggest that the amplitude and phase-locking adaptations have different mechanisms and functions. The phase-locking adaptation is likely to play more crucial roles in encoding a temporal structure of stimulus than the amplitude adaptation.

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1. Introduction

The auditory systems dynamically alter stimulus sensitivity according to stimulus statistics (Smith and Zwislocki, 1975; Kvale and Schreiner, 2004; Dean et al., 2005; King et al., 2011). This coding strategy is referred to as sensory adaptation, and it plays a pivotal role in efficient neural computation (Wark et al., 2007). In the auditory system, adaptation is driven by the spectro-temporal (Fritz et al., 2010) and spatial properties (King et al., 2011) of sound stimuli. This adaptation modulates change detection (Ulanovsky et al., 2004), gain control (Dean et al., 2005; Rabinowitz et al., 2011), auditory short-term memory (Abolafia et al., 2011),

auditory stream segregation (Bregman, 1990; Winkler et al., 2009; Bee et al., 2010), auditory object recognition (Ahveninen et al., 2006), and perception of speech and music (Malone and Semple, 2001; Werner-Reiss et al., 2006).

Adaptation occurs across a wide range of time scales, and the diverse mechanisms underlying adaptation remain to be fully elucidated. Recent studies in the auditory cortex have demonstrated that the adaptation in unit activity is stimulus specific (i.e., stimulus specific adaptation; SSA). The relevant time scales of this adaptation range from hundreds of milliseconds to hours (Ulanovsky et al., 2004; Jääskeläinen et al., 2007; von der Behrens et al., 2009; Farley et al., 2010) or even days (Jääskeläinen et al., 2007). Adaptation can be observed in neural signals from population of neurons, such as local field potentials (LFPs; Farley et al., 2010; Taaseh et al., 2011), current source density (Szymanski et al., 2009), and magnetoencephalography (Christianson et al., 2011). In addition, pioneering studies have demonstrated that neural adaptation occurs in specific neural features, such as a temporal jitter of evoked response (Xu et al., 2007) and spike-gamma field coherence (Hansen and Dragoi, 2011). The adaptation of band-specific oscillatory components may also lend important insight into cortical mechanisms of

Abbreviations: A1, primary auditory cortex; ITI, inter-tone interval; ITPC, inter-trial phase coherence; LFP, local field potential; MUA, multiunit activity; SPL, sound pressure level; SSA, stimulus-specific adaptation; FIR, finite-impulse response.

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adaptation. However, to date, this aspect of adaptation has received little attention.

Neural activity occurring at diverse frequency ranges can be observed in the form of neural oscillations. Neural oscillation is believed to be crucial for a wide array of functions, including sensory encoding (Kayser et al., 2009; Panzeri et al., 2010), binding of elementary features (Gray and Singer, 1989; Engel et al., 2001), attentional control (Snyder and Large, 2005; Jensen et al., 2007). Especially, the phase of ongoing oscillation is strongly correlated with stimulus perception at the moment of stimulus presentation (Luo and Poeppel, 2007; Ng et al., 2012), and is likely to have profound effects on cortical sound processing (Howard and Poeppel, 2010; Vanrullen et al., 2011; Jensen et al., 2012). These suggest that oscillation phase rather than amplitude could contribute to ‘packaging’ incoming sensory information to quasi-periodic stimuli (Giraud and Poeppel, 2012). Neural oscillations are likely closely related to the mechanisms of adaptation because both phenomena occur simultaneously during processing of repeated external stimuli (Matsuzaki et al., 2012). Therefore, oscillatory phase profile like trial-by-trial phase fluctuations must be also influenced by adaptation (Broicher et al., 2012).

In the present study, we tested how neural oscillations in the auditory cortex show adaptation when a tone sequence is presented. We specifically hypothesized that phase locking to test tones, i.e., phase reliability to the stimuli across trials in band specific neural oscillation, would show a different adaptation property from the amplitude of neural signals. We used alternating tone sequences (ABA-ABA-...; known as ABA-tone sequences) as test stimuli (Bregman, 1990), which have long been used to investigate how neural adaptation is involved in auditory streaming. The test frequency and inter-tone interval (ITI) of A and B tones were manipulated as parameters to investigate how neural adaptation depends on the spectro-temporal properties of successive tones. We demonstrate that amplitude and phase-locking adaptation depend differently on these parameters in a band-specific manner. We also show that amplitude adaptation occurs within a second, whereas phase-locking adaptation lasts over seconds.

2. Materials and methods

All procedures were approved by our institutional committee and performed in accordance with “Guiding Principles for the Care and Use of Animals in the Field of Physiological Science” by the Japanese Physiological Society. Every effort was made to minimize the number of animals used and their suffering.

2.1. Animal preparation

Nine adult male Wistar rats, at postnatal week 11–13, with a body weight of 330–380 g, were used in the experiments. Animals were anesthetized with isoflurane (2.5–3.5% at induction and 1.6–2.0% for maintenance) and fixed using a custom-made head-holding device. Atropine sulfate (0.1 mg/kg) was administered at the beginning of the surgery and every 7 h thereafter to reduce the viscosity of bronchial secretions. A heating blanket was used to maintain body temperature at around 37 °C. The temporal muscle, cranium, and dura overlying the auditory cortex were surgically removed, and the exposed cortical surface was filled with saline in order to prevent desiccation. Cisternal cerebrospinal fluid drainage was performed to minimize cerebral edema. Respiratory rate, heart rate, and hind-paw withdrawal reflexes were monitored to maintain an adequate anesthetic level as stably as possible throughout the recording procedure. Another small craniotomy was made near the bregma to embed a reference electrode with an electrical contact to the dura mater. The ground electrode was placed under the

Table 1
Test frequency used in the experiments.

	ABA-condition (ABA-tone sequence)				
A tone (kHz)	20	20	20	20	20
B tone (kHz)	22.5	25.2	28.4	31.9	40.2
ΔF (semitone)	2	4	6	8	12

cervical neck skin. The right eardrum was ruptured and waxed to ensure unilateral sound inputs from the ear contralateral to the exposed cortex.

2.2. Recording and stimulation

All electrophysiological recordings were performed in a sound-attenuated room (AMC-4015, O'hara & Co. Ltd.; Tokyo, Japan). Microelectrode arrays with a grid of 10×10 recording sites and inter-electrode distances of 400 μm (ICS-96 Array, Blackrock Microsystems Inc.; UT, USA) were used, and neural signals were simultaneously obtained from 96 sites out of 100 sites (the 4 corners were excluded from analysis). The electrode impedance was approximately 120 k Ω under 1-kHz, 0.1-V sinusoidal waves.

Both LFPs and multiunit activities (MUAs) were simultaneously measured with an amplification gain of 1000 (Cerebus Data Acquisition System, Cyberkinetics Inc.; UT, USA). LFPs were obtained with a digital filter passband of 0.3–500 Hz and sampling frequency at 1 kHz, while MUAs were obtained with a digital filter of 0.25–7.5 kHz and sampling frequency at 30 kHz.

Based on LFPs on the cortical surface, the electrode array was positioned so as to entirely cover a tone responsive area. The primary auditory cortex (A1) was identified on the basis of short post-stimulus latency in the most dorsal auditory field containing a complete high-to-low tonotopic gradient running along the anterior-to-posterior axis (Takahashi et al., 2005, 2011; Funamizu et al., 2013). The array was then inserted into a depth of about 700 μm from the pial surface.

A function generator (WF1946, NF Corp.; Kanagawa, Japan) presented tonal stimuli in a free field through a speaker (EAS-10TH800, Panasonic Corp.; Osaka, Japan). The speaker was positioned 10 cm in front of the contralateral ear to the exposed cortex. The frequency and intensity of test stimuli were calibrated at the pinna with a microphone (4939, Brüel & Kjær; Nærum, Denmark) and spectrum analyzer (CF-5210, Ono Sokki Co., Ltd.; Kanagawa, Japan).

Tone bursts with varied frequencies (2.0, 5.0, 10, 20, 32, 40, and 50 kHz) were delivered every 1 s to identify the local activation focus for each test frequency. The test intensity was fixed at 70 dB sound pressure level (SPL; in decibels with respect to 20 μPa) and the duration, plateau, and rise/fall times were 30 ms, 20 ms, and 5 ms, respectively.

The main experiments used both isochronous (A-A-) and galloping sequences (AAA-) consisting of a particular tone burst. We used these sequences to investigate how the evoked responses were altered by tone repetitions. In addition, we also applied ABA-tone sequences in which 2 tones with different frequencies (A tone and B tone) were presented alternately (ABA-). This stimulus paradigm was used to investigate how the B tone affected the subsequent A tone-evoked responses with a number of tone repetitions. The A tones preceding and following B tones are referred to as A_1 and A_2 tones (i.e., A_1BA_2 -), respectively, hereafter.

Both A and B tones were tone bursts with 70 dB SPL, 30-ms duration, and 5-ms linear rise/fall ramps. The frequency of the A tone was held constant at 20 kHz, and the frequency of B tone was manipulated in a range between 20 kHz and 40 kHz, with a semitone increment (i.e., 6% frequency difference to the reference tone). The frequency difference (ΔF) between the A and B tones served as a parameter as summarized in Table 1. An ITI, defined as a time

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