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Research Paper

Amplitude modulation rate dependent topographic organization of the auditory steady-state response in human auditory cortex

Nathan Weisz [a, b, *], Chrysoula Lithari [a, b]

[a] University of Trento, Center for Mind/Brain Sciences, Trento, Italy
[b] Paris-Lodron Universität Salzburg, Centre for Cognitive Neuroscience and Division of Physiological Psychology, Salzburg, Austria

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Periodic modulations of an acoustic feature, such as amplitude over a certain frequency range, leads to phase locking of neural responses to the envelope of the modulation. Using electrophysiological methods this neural activity pattern, also called the auditory steady-state response (aSSR), is visible following frequency transformation of the evoked response as a clear spectral peak at the modulation frequency. Despite several studies employing the aSSR that show, for example, strongest responses for ~40 Hz and an overall right-hemispheric dominance, it has not been investigated so far to what extent within auditory cortex different modulation frequencies elicit aSSRs at a homogenous source or whether the localization of the aSSR is topographically organized in a systematic manner. The latter would be suggested by previous neuroimaging works in monkeys and humans showing a periodotopic organization within and across distinct auditory fields. However, the sluggishness of the signal from these neuroimaging works prohibit inferences with regards to the fine-temporal features of the neural response. In the present study, we employed amplitude-modulated (AM) sounds over a range between 4 and 85 Hz to elicit aSSRs while recording brain activity via magnetoencephalography (MEG). Using beamforming and a fine spatially resolved grid restricted to auditory cortical processing regions, our study revealed a topographic representation of the aSSR that depends on AM rate, in particular in the medial-lateral (bilateral) and posterior-anterior (right auditory cortex) direction. In summary, our findings confirm previous studies that showing different AM rates to elicit maximal response in distinct neural populations. They extend these findings however by also showing that these respective neural ensembles in auditory cortex actually phase lock their activity over a wide modulation frequency range.

1. Introduction

Apart from spectral content, temporal amplitude modulations (i.e. derived from the temporal envelope of the signal) constitute an important feature of naturally occurring sounds. An example par excellence is speech, where diverse relevant acoustic features exhibit characteristic modulation rates (Kraus et al., 2000). Of particular importance for the intelligibility of speech appears to be the syllabic rate at ~3–6 Hz corresponding to the neural theta frequency range. Furthermore, higher frequencies in the low gamma range (~30 Hz) have been linked to phonemic processing. Using an amplitude modulated (AM) sound that shifted its modulation frequency across time, Lehongre et al. (2011) were able to show abnormal left-hemispheric processing in a group of dyslexia patients. Underlining the functional relevance of these measures of the brain's ability to follow rhythmic auditory information, the authors reported correlations with deficits in linguistic performance. Another relevant example in which acoustic rhythms play an outstanding role is music (Levitin et al., 2012). Based on observations that relevant acoustic rhythms strongly overlap in their frequency ranges with relevant neural rhythms, a functional link by which perceptual performance can be optimized has been suggested (Giraud and Poeppel, 2012). This is putatively implemented by neural rhythms which provide the auditory system with temporally predictable time windows for sampling the acoustic environment (Arnal and Giraud, 2012). Next to this sensory aspect the rhythmic structure of acoustic stimuli also enables strong integration with the motor system (Fujioka et al., 2009), which shares strong connections to auditory processing regions (Kraus

* Corresponding author. Paris-Lodron Universität Salzburg, Centre for Cognitive Neuroscience, Hellbrunnerstrasse 34, 5020 Salzburg, Austria.
E-mail address: nathan.weisz@sbg.ac.at (N. Weisz).

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and White-Schwoch, 2015). In particular, the idea is gaining increased attention in cognitive neuroscience under the label of “entrainment”, which posits the brain to align temporal high/low excitability phases to (predictable) periods of relevant/irrelevant sensory input respectively.

However, as compared to spectral organization, little is known about the organization of temporal modulations in auditory cortex. An early magnetoencephalography (MEG) study by Langner et al. (1997) hinted at a topographical organization of periodicity in auditory cortex, that was orthogonal to tonotopic representation. This rather crude spatial estimate which used a single moving dipole approach was supported and detailed by later animal neuroimaging studies that illustrated a topographical organization of modulation rates in auditory cortex. In particular, a recent study in awake macaques studying BOLD responses using a 4.7T MRI, Baumann et al. (2015) were able to identify modulation rate (studied between 0.5 and 128 Hz) dependent gradients along the superior temporal plane: while high modulation rates elicited maximal activation in posterior-medial (core) auditory regions, low rates elicited maximal activation in anterior core as well as lateral belt regions of auditory cortex. In humans, while it is generally accepted that sensitivity to faster modulation rates decreases along the ascending auditory system (~2–4 kHz at the level of the auditory nerve to max. 100–200 Hz in auditory cortex; see e.g. (Wallace et al., 2002)), the issue of topographical organization of modulation rates in the auditory cortex is less developed. Using fMRI and modulation rates between 4 and 128 Hz, Giraud et al. (2000) were unable to find a systematic spatial organization of modulation rates, which is in contrast to the macaque work. In another fMRI study, Herdener et al. (2013) observed a spatial organization, in particular along the medial-lateral axis, with higher AM rates being localized more towards medial parts of the auditory cortex. Similar to the macaque work (Baumann et al., 2015), representation of AM rates was orthogonal to the tonotopic organization (see also (Barton et al., 2012)).

A clear disadvantage of the aforementioned studies is that investigating the sluggish BOLD response does not allow to assess to what extent relevant neural populations indeed track AM rates by aligning their activity to the temporal envelope of the acoustic stimulus. These temporal features of neural responses are much better captured using electrophysiological techniques. A classical approach applies rhythmic sensory stimulation to elicit a so-called steady state response (Galambos, 1980). In the auditory modality, the steady-state response (aSSR) appears to elicit a maximum response in auditory cortex at ~40 Hz with a right-sided lateralization (Ross et al., 2005). However, whether the aSSR also exhibits a topographical representation, as suggested by the aforementioned fMRI studies, is not conclusively known. This was also not shown by the classically cited MEG study by Langner et al. (1997), which focused its analysis on low pass filtered transient evoked responses, in particular the M100, M200 and the sustained field. Liégeois-Chauvel et al. (2004) investigated the aSSR in epilepsy patients implanted with stereotactic electrodes, but were unable to identify clear modulation rate dependent spatial gradients. However, it could be argued that the spatial sampling with electrodes was insufficient to uncover fine spatially distributed patterns. In a noninvasive electrophysiological work using electroencephalography (EEG) and a predefined source montage, Herdmann et al. (Herdman et al., 2002) reported that aSSRs driven by a modulation frequency of 39 Hz have generators dominantly in primary auditory cortex (this finding is in line with several other reports also using alternative approaches; see e.g. (Draganova et al., 2007)). A faster modulation at 88 Hz elicits maximum responses in the brainstem, which is conform with the notion outlined previously that the capacity of auditory cortex to track faster amplitude modulations decreases. . In a recent study Farahani et al. (2017) also show responses that suggest aSSRs outside of the classical auditory pathway. However, the approaches in the described studies do not allow for any conclusions regarding a systematic spatial organization pattern for the different modulation frequencies along the supratemporal plane.

The goal of the present work was to elucidate the existence of a topographic organization of amplitude modulation rates in human auditory cortex as captured using the aSSR. By using beamforming applied to MEG data on a spatially fine (2 mm) grid and eliciting aSSRs with modulation frequencies between 4 and 85 Hz, we are able to show a spatial organization along the superior temporal plane, in particular in the medial-alteral and anterior-posterior direction very similar to previously published human and primate fMRI studies (Baumann et al., 2015).

2. Material and methods

2.1. Participants

Nineteen participants took part in the experiment (11 females; mean age: 29.4, SD: ±5 years). All participants reported normal hearing and absence of previous or current psychiatric or neurological problems. All participants gave written informed consent before the experiment. The procedure was approved by the Ethics Committee of the University of Trento.

2.2. Stimuli and procedure

Auditory stimuli were generated in Matlab (MathWorks, Natick, MA) at a sampling rate of 44.1 kHz. For this purpose, a 200 kHz tone of 3 s duration was amplitude modulated (100% modulation depth) at seven different rates: 4, 10, 15, 25,40, 65 and 85 Hz. Stimuli were binaurally presented at an ambient intensity level via air-conducting tubes with ear inserts (SOUNDPixx, VPixx technologies, Canada). Every AM frequency was presented 80 times, pseudo-randomly distributed over four measurement blocks. Intertrial intervals were jittered uniformly between 2 and 4 s. During sound presentation, participants watched a silent movie.

2.3. Data acquisiton

MEG recordings were obtained at a sampling rate of 1 kHz using a 306-channel (204 first order planar gradiometers, 102 magnetometers) VectorView MEG system (Elekta-Neuromag Ltd., Helsinki, Finland) in a magnetically shielded room (AK3B, Vakuumschmelze, Hanau, Germany). Before the experiment, individual head shapes were acquired for each participant including relevant anatomical landmarks (nasion, pre-auricular points) and around 200 digitized points on the scalp with a Polhemus Fastrak digitizer (Polhemus, Vermont, USA). Head positions of the individuals relative to the MEG sensors were continuously controlled using five coils. Head movements did not exceed 1.5 cm within and between blocks.

2.4. Data analysis and statistics

Data were analyzed offline using the Fieldtrip toolbox (Oostenveld et al., 2011). First, a high-pass filter at 1 Hz (6th order Butterworth IIR) was applied on continuous data. Then, trials of 1 s pre- and 4 s post-stimulus were extracted and trials containing physiological or acquisition artifacts were rejected (average number of rejected trials per condition: 6.55; range across all conditions: 0–17). The number of trials were equalized across the seven conditions for each subject to ensure that our results were not confounded by systematic differences in signal-to-noise ratio

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