



Research paper

Auditory cortex tracks the temporal regularity of sustained noisy sounds

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ABSTRACT

Neuroimaging studies have revealed dramatic asymmetries between the responses to temporally regular and irregular sounds in the antero-lateral part of Heschl's gyrus. For example, the magnetoencephalography (MEG) study of Krumbholz et al. [Cereb. Cortex 13, 765-772 (2003)] showed that the transition from a noise to a similar noise with sufficient temporal regularity to provoke a pitch evoked a pronounced temporal-regularity onset response (TRon response), whereas a comparable transition in the reverse direction revealed essentially no temporal-regularity offset response (TRoff response). The current paper presents a follow-up study in which the asymmetry is examined with much greater power, and the results suggest an intriguing reinterpretation of the onset/offset asymmetry. The TR-related activity in auditory cortex appears to be composed of a transient (TRon) and a TR-related sustained response (TRsus), with a highly variable TRon/TRsus amplitude ratio. The TRoff response is generally dominated by the break-down of the TRsus activity, which occurs so rapidly as to preclude the involvement of higher-level cortical processing. The time course of the TR-related activity suggests that TR processing might be involved in monitoring the environment and alerting the brain to the onset and offset of behaviourally relevant, animate sources.

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1. Introduction

Inanimate sources like wind in the trees and waves on the beach generate broadband noises. To communicate in the presence of this background, animals produce distinctive periodic and quasi-periodic sounds, which we hear as, for example, whistling, cooing, purring and hooting; the vowels of speech are also quasi-periodic sounds. Such sounds are characterized by the presence of temporal regularity (TR), which we perceive as pitch. Some aspects of TR processing take place in the cochlea and the brainstem, and they are understood relatively well (Eggermont, 2001). But there is also a cortical component to TR processing that has proven difficult to investigate physiologically. As a result, Griffiths et al. (1998, 2001) turned to brain imaging, which revealed the presence of a TR processing center in the antero-lateral part of Heschl's gyrus, first with Positron Emission Tomography (PET) and then with functional

Magnetic Resonance Imaging (fMRI). The location was subsequently confirmed using fMRI by Patterson et al. (2002), Warren et al. (2003), and Penagos et al. (2004). Bendor and Wang (2005) have found evidence of TR processing in marmosets in the analogous region of auditory cortex. Further evidence has been obtained by depth electrode recordings in human subjects (Schönwiesner and Zatorre, 2008; Griffiths et al., 2010). There is also some evidence to indicate that the TR processing network may be more complex, consisting of multiple sites in the temporal lobe in and around auditory cortex (Hall and Plack, 2009).

MEG research on pitch perception was hampered, until recently, by the use of paradigms in which the pitch response was contaminated by the large non-specific response to the onset of sound. Then Krumbholz et al. (2003) showed how a pitch-related response in auditory cortex can be isolated with a transition from a noise to a Regular Interval (RI) sound having the same intensity and bandwidth, but sufficient temporal regularity to provoking a sensation of pitch. RI sounds are derived from noise by regularizing the temporal fine-structure (Bilsen, 1966; Patterson et al., 1996; Yost, 1996a; Yost, 1996b; Yost et al., 1996). The degree of regularization determines the salience of the pitch. Krumbholz et al. (2003) presented subjects with a 2-s noise that flowed smoothly into a matched 1-s RI sound. This continuous stimulation paradigm

Abbreviations: AEF, auditory evoked field; fMRI, functional Magnetic Resonance Imaging; MEG, magnetoencephalography; N, noise; PET, Positron Emission Tomography; RI, regular interval; RMS, root-mean-square; SR, sustained response; TRon, temporal-regularity onset; TRoff, temporal-regularity offset; TRsus, temporal-regularity sustained.

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represses the large energy onset response that would otherwise contaminate the response to the temporal regularity. The transition from noise to RI sound (N-RI) elicited a prominent TRon response whose latency and size were shown to be directly related to the perceived pitch value and its salience. The response was found to originate in lateral Heschl's gyrus, which is consistent with the previous PET and fMRI studies listed above.

At the same time, there was a puzzling absence of the corresponding TRoff response to the reverse transition, i.e. from RI sound to noise (RI-N); informal listening suggests that the two transitions have about the same salience. A related MEG asymmetry was subsequently reported by Rupp et al. (2004), who also included a continuous transition from one tonal sound to another – in that case, the stimuli were regular and irregular pulse trains. The asymmetry between TR onset and offset responses is the topic of the current study, in which the sensitivity of the MEG measurements was increased by almost an order of magnitude by increasing measurement time and presenting the stimuli at a higher rate.

2. Materials and methods

2.1. Subjects

Six subjects with normal audiological status and no history of neurological disease participated in this study (2 male and 4 female, aged between 23 and 35 years with a median of 26 years). Written informed consent was obtained from all subjects, who were paid for their participation. The experiments were conducted in accordance with the Ethics Commission of the University of Münster and the Declaration of Helsinki.

2.2. Stimulation

The stimulus for a trial was a continuous sequence of three noise (N) bursts interleaved with three bursts of regular interval (RI) sound, as illustrated in Fig. 1; there were no distinguishing changes in the envelope of the stimulus at the transitions between bursts. The bursts had a mean duration of 0.4 s; the duration of the compound stimulus was 2.4 s. The sequence began with an N-burst and so each trial contained three N-RI transitions and two RI-N transitions. The RI sound (Patterson et al., 1996; Yost et al., 1996) was produced from random noise by delaying a copy of the noise by $d = 8$ ms, adding it back to the original, and iterating the process $n = 16$ times. The sound had a strong pitch of 125 Hz. Before presentation, each stimulus was filtered with a 16-th order digital Butterworth filter to remove energy below 800 Hz and above 3200 Hz. It was gated on and off with 5-ms cosine-squared ramps. The crucial property of this stimulus is that the regularity of the sound changes at each transition, without a concomitant change in energy (illustrated in Fig. 1a of Krumbholz et al., 2003). The reason for using a series of transitions rather than a single transition was to create more transitions per unit of time, and thereby increase the power of the experiment. While a continuous stimulation paradigm would have been even more efficient in this respect, it would have rendered comparison with the responses to energy onset and offset impossible. Moreover, and perhaps even more important, the lack

of a silent period would have made it impossible to assess the magnitude of the response in absolute terms since this requires a silent baseline.

Twenty versions of the stimulus were produced from independent realizations of the noise. Although the mean transition time was fixed at 0.4 s, the individual transition times were chosen at random from a uniform distribution 0.1-s wide centered about the mean. The inter-stimulus interval was also chosen at random from a uniform distribution of times between 1.1 and 1.3 s. As a result, the interval between stimulus onsets was uniformly distributed between 3.5 and 3.7 s. The stimuli were presented via a loudspeaker outside the MEG measuring room, which was magnetically shielded, and fed through 6.3 m of plastic tubing to the subject's right ear via a silicon ear piece. The intensity of the stimuli was adjusted to 60 dB above the subject's individual hearing threshold.

2.3. Experiments

The magnetic field was recorded over the subject's left hemisphere using a 37-channel gradiometer system (Magnes I, 4D Neuroimaging, San Diego). The spatial locations of the sensors relative to the subject's head were determined by means of a three-dimensional digitizer (Polhemus 3space tracker). During the measurements, the subjects lay on their right side and watched a movie without sound. To ensure a stable position, their head, neck, and the upper part of the body was supported by a specially fabricated vacuum cushion. The MEG signals were bandpass filtered between 0.1 and 400 Hz and digitized at a rate of 1042 Hz for subsequent offline analysis. Further details of the measurement procedure can be found in Lütkenhöner (1998).

Each subject participated in two separate sessions on each of four days. Between sessions, the subject left the shielded room and used the opportunity to relax. A session was subdivided into five runs of 10 min duration, and 167 stimuli were presented per run so that, all in all, MEG responses to 6680 presentations of the 2.4-s stimulus were recorded from each subject. After the third run of each session, the head position was checked. Between runs, the subjects were contacted via intercom, to keep them informed about the progress of the experiment and to assist them in staying alert.

2.4. Data processing

The data were low-pass filtered using a *fourth-order, zero-phase* Butterworth filter with a cut-off frequency of 100 Hz (50 Hz when considering the first temporal derivative of the response) and averaged separately for seven distinct events: stimulus onset, three N-RI transitions (occurring about 0.4, 1.2, and 2.0 s after stimulus onset), two RI-N transitions (occurring about 0.8 and 1.6 s after stimulus onset), and stimulus offset (occurring precisely 2.4 s after stimulus onset). The event-related epochs extended from 0.2 s before an event to 0.5 s (2 s in the case of the off-response) after it. An additional average was calculated for a time window that extended from 0.2 s before stimulus onset to 3.9 s after it, encompassing the entire 2.4-s stimulus and the following inter-stimulus gap. The resulting average is designated the overall response. Epochs were assumed to be contaminated by artifacts if

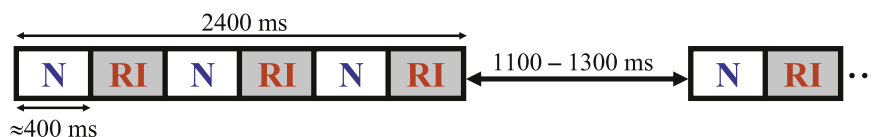


Fig. 1. Stimulus paradigm. The stimulus was a continuous sequence of three noise (N) bursts interleaved with three bursts of regular interval (RI) sound. The durations of the bursts were randomized in the range 350 to 450 ms, with a mean duration of 400 ms. The RI sound was produced with 16 iterations and a delay of 8 ms, resulting in a strong pitch of 125 Hz. The stimulus had a total duration of 2400 ms. It was presented every 3.5–3.7 s to the right ear.

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