Neuromagnetic Representation of Short Melodies in the Auditory Cortex

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Introduction

Neuromagnetic responses to the onset of pitch in a continuous sound typically evoke a negative response at about 100 ms. This component which is refered to as the "Pitch Onset Response" (POR) [1, 2] is found near the medial portion of Heschl's gyrus, close to the regularity-specific generator of the sustained field [3]. The location of the POR is slightly medial to the pitch-specific activation found by functional magnetic resonance imaging (fMRI) of temporal pitch in the human auditory cortex [4]. It was observed that melody-specific activations are found in adjacent areas, lateral and anterior to fixed-pitch activation. Furthermore, melody processing exhibited an asymmetric pattern with higher activations in the right hemisphere. Parallel to the accompanying fMRI-study [5] the current experiment was carried out to study the neuromagnetic POR evoked by melody sequences in contrast to fixed-pitch sequences to allow for a detailed analysis of the specific activation in the left and right auditory cortex with a high temporal resolution. (i) We investigated whether the POR evoked by random melodies exhibits a neuromagnetic representation different to the POR evoked by fixed-melodies by comparing short four-tone melodies with random notes to fixed-pitch sequences of the same length. (ii) We studied the influence of monaural stimulus presentation on the asymmetry of the neuromagnetic representation by presenting the stimuli to the left and right ear separately.

Methods

Stimuli. Regular interval sounds (RIS) were used to create melodies and fixed-pitch sequences, each consisting of four notes. RIS was created using a delay-and-add procedure according to [5]. Each note was 280 ms long and four notes were concatenated to produce short melodies and fixed-pitch sequences, respectively. The pitch of sounds in the fixed-pitch condition was varied randomly to cover the same range as in the melody condition. The melody sequences included all possible permutations of the four notes. The sounds were bandpass filtered (500–4000 Hz) and presented by diotic stimulation of both ears and monaural stimulation to the left and right ear via ER-3 earphones (Etymotic Research, Inc.). The inter-stimulus-interval was set to 340 ms. About 330 averages were obtained for each stimulus condition.

Subjects. MEG data were recorded from nine normal hearing subjects (three female and six male). None of the listeners reported any history of hearing disorders.

MEG methods. The auditory evoked fields were recorded using a Neuromag-122 whole head gradiometer system (Electa Neuromag Oy, Finland) with a sampling rate of 1000 Hz. Data were filtered offline using a zero-phase filter ranging from 2 to 60 Hz. BESA 5.1 (MEGIS Software GmbH) was used to perform the spatio-temporal source analysis [6]. One equivalent dipole in each hemisphere was used for source analysis. The time intervals for the model fit included the specific pitch onset response evoked by the second, third, and fourth note of the diotic melody condition. For each subject this BESA model was held constant and used as a spatial filter to derive the source waveforms for each stimulus condition separately. Bootstrap based confidence intervals were used to assess the significance of the difference waveforms (melody minus fixed-pitch waveforms).

Results

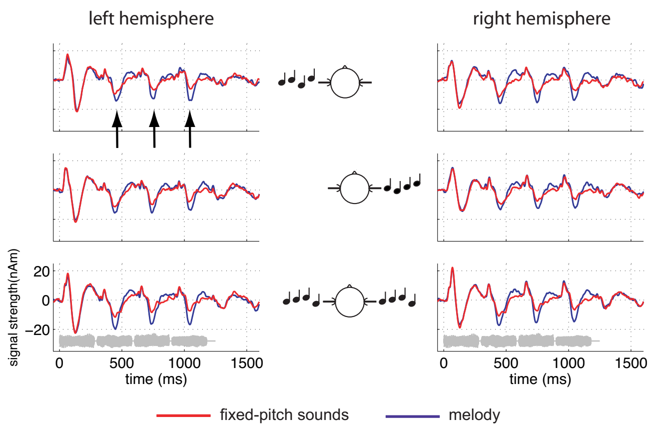

Figure 1: Source waveforms from the two-dipole model based on the fit of the melody-evoked pitch response for the monaural left ear (top), right ear (middle), and diotic stimulation (bottom). Note the specific POR enhancement elicited by the second, third, and fourth note for all melody conditions. The grey lines indicate the temporal position of the notes in the fixed-note and melody sequences.

Figure 1 shows the grand average source waveforms for all stimulus conditions. The waveform morphology indicates that the onset of each sequence elicits a middle latency and late response complex. The POR evoked by each single note is decreasing from the first to the fourth note in the fixed-pitch condition. However, the POR evoked by the short melodies clearly exceeds the POR elicited by the fixed-pitch sounds except for the first note of each melody. The difference source waveforms in Fig. 2 illustrate the statistical significance of the melody-specific activation. This enhancement was found in both hemispheres for all ear-of-entry conditions. Furthermore, this melody specific response exhibits a comparable magnitude for all peaks within the short melodies.

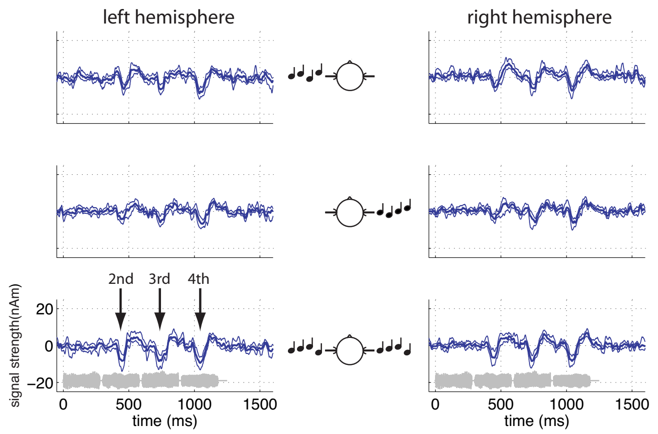

Figure 2: Difference source waveforms (melody - fixed-pitch) for both monaural and the diotic stimulus condition. Thick lines indicate the grand average source waveforms, thin lines represent the upper and lower bootstrap based 95% confidence intervals. The melody specific response reaches statistical significance in all conditions.

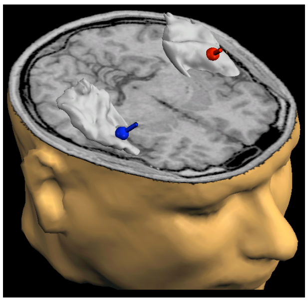

Figure 3: Projection of equivalent dipoles based on the fit of the pitch response evoked by melodies for a single subject onto the individual 3D-reconstruction of T1-weighted MR images. Note that dipoles are located close to the anterior border of Heschl's gyrus.

The difference waveforms depicted in Fig. 4 were computed to investigate the influence of monaural presentation on the representation of melody processing in both hemispheres. The difference waveforms of both monaural conditions show a substantial decrease of the pitch specific response for the POR based on the fixed-pitch and the melody condition, respectively. In contrast, the onset response does not exhibit the same degree of magnitude reduction. This behaviour indicates that the overall onset response of short tone sequences has a stronger representation in the contra-lateral hemisphere.

Discussion

The results of this neuromagnetic study clearly show that melodies elicit an additional activation in the auditory cortex which can be registered from the 2nd note on. The melody specific enhancement of the POR was found to be significant for all stimulus conditions. Source analysis indicates that the generator of this activity is located more anterior as compared to the POR to fixed pitch [2]. Furthermore, the contrasts in Fig. 4 demonstrate that melody processing shows a lower degree of hemispheric asymmetry as compared to the onset response since the POR in the difference waveforms of contra-minus ipsi-lateral hemispheres in the monaural conditions exhibited a substantial decrease. These observations are in line with the fMRI data shown in the accompanying paper [5]. The finding that melody processing is much less sensitive to the ear-of-entry of the sound supports the hypothesis that melody processing is represented at a higher stage in the audiory pathway and thus supports the hypothesis of hierarchical processing of temporal pitch processing.

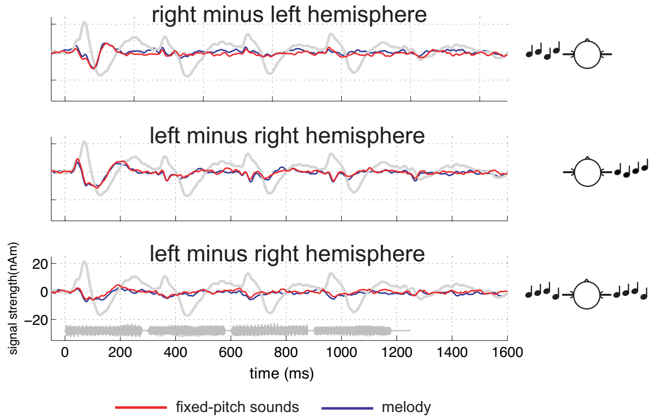

Figure 4: Difference source waveforms (contralateral - ipsilateral hemisphere) for both monaural conditions (top and middle panel). The lower panel shows the difference left-right hemisphere data of the diotic stimulation. In contrast to both monaural stimulations these waveforms exhibit a larger reduction of the onset response. The grey lines depict the original waveforms of the right hemisphere data evoked by the diotic stimulation to allow for a comparison.

References

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