Functional MR imaging of the processing of pitch changes in human listeners

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Introduction

In a previous study, regular interval sounds and functional magnetic resonance imaging (fMRI) had been used to demonstrate a hierarchy of the processing of temporal pitch in human auditory cortex [1, 2]. With diotic stimulus presentation, most subjects in that study showed a bilateral, pitch-specific activation in the lateral edge of the transverse temporal gyrus (Heschl), outside primary auditory cortex. A specific activation in response to changes of the pitch, like in melodies, was located outside of Heschl's gyrus in adjacent cortical areas, mainly in superior temporal gyrus and sulcus. The melody-specific processing appeared to be asymmetric between hemispheres, with more activation in the right hemisphere for most listeners in that study.

The anatomy and physiology of the human brain are characterized by crossed pathways between the two ears and the two sides of the brain, with the main projections from the ears leading to the respective contralateral hemispheres [3]. The recoding of temporal patterns begins as early as cochlear nucleus and is carried forward along the pathway through inferior colliculus and thalamus to auditory cortex [2]. The symmetry between hemispheres of the cortical activation maps in response to diotic sounds with fixed temporal pitch indicates a symmetry in the neural structures for temporal processing along the auditory pathway. The extraction of temporal pitch per se appears to be reflected mainly by sensory coding in these structures. In contrast, the reported asymmetry between left and right hemispheres for the melody specific processing even in the case of diotic stimulation suggests a process that is higher up in the hierarchy, involving cognitive processing, which not only reflects stimulus driven neural excitation but also the way we are listening to melodies. This might be affected by the specific task to the listener and also by some general musical aptitude.

In the current study, fMRI was used to explore the influence of monaural stimulus presentation on the reported hemispheric asymmetry for the processing of sequences of notes with changing pitch. In the accompanying paper [4], a similar experiment was carried out using magentoencephalography (MEG), which allows to explore the timing of pitch specific cortical responses at a high temporal resolution.

Methods

Stimuli. Regular interval sounds were used throughout the experiments. The stimulus generation was very similar to the previous study, and details can be found there [1, 2]. A regular interval sound (RIS) is created by delaying a copy of random noise and adding it back to the original. The resulting sound has some of the hiss of the original noise, but it also has a pitch corresponding to the inverse of the delay [5]. The pitch strength increases when the delay-and-add process is repeated. When the pitch is less then about 125 Hz (corresponding to a delay of 8 ms) and the stimuli are high-pass filtered at about 500 Hz, the RIS effectively excites all frequency channels in the same way as random noise, with no resolved spectral peaks internally. The perception of RIS pitch is probably based on extracting time-intervals from the signal rather than spectral peaks.

The different stimulus conditions in this experiment included melodies and sequences of fixed-pitch notes, with diotic stimulation of both ears, and monaural stimulation just to the left and just to the right ear. Diotic presentation of random noise bursts (no pitch) and silence were also included as controls, giving a total of eight stimulus conditions. The sounds were played as sequences of 32 notes at a rate of four notes/sec. Each note was 210 ms long with 40 ms of silence between successive notes. The pitch range for the melodies was 50 to 110 Hz. The pitch in the 'fixed-pitch' sequences was varied randomly between sequences to cover the same range as the melodies over the course of the experiment. All stimuli were bandpass filtered between 500 Hz and 4 kHz and presented to the subjects at a level of approximately 70 dB SPL via MR-compatible, dynamic headphones mounted into conventional ear defenders (MR confon, Magdeburg). All conditions were repeated 32 times in random order throughout the experiment.

Subjects. Eight normal-hearing listeners volunteered as subjects (seven male, one female). None of the listeners had any history of hearing disorders or neurological disorders.

fMRI methods. Sparse temporal sampling was used to separate the scanner noise and the experimental sounds in time [6]. Blood-oxygenation-level-dependent (BOLD) contrast-image volumes were acquired every 10 s, using a 1.5-T MRI scanner (Siemens SONATA) with gradient-echo-planar imaging. Twenty-one axial slices were acquired covering most of the cortex, including the whole of the temporal lobes. A T1-weighted high-resolution anatomical image was also collected for each subject.

Anatomical and functional data were analysed using SPM99 (http://www.fil.ion.ucl.ac.uk/spm). The preprocesing of the BOLD images included realignment of subject motion, normalisation of individual scans to a standard EPI template, and smoothing with a Gaussian filter of 5 mm full width at half maximum. Fixed-effects analysis was conducted across the whole group of eight subjects (total of 2048 scans), and also for each individual listener (256 scans), using the general linear model.

Results

Figure 1 gives a summary of the results for the whole group of subjects during diotic stimulation with sequences of noise bursts, fixed pitch notes, and melodies. The activation maps were superimposed on the mean of the normalized anatomical images from all eight listeners. While the general activation in response to sound (blue) covers all of the surface of the temporal lobes including Heschl's gyrus and part of the temporal plane in both hemispheres, the pitch specific activation (in red) is largely restricted to the lateral edge of Heschl's gyrus bilaterally. This result is in good agreement with the previous study [1]. Melody specific activation (in green) appears somewhat distributed over several structures adjacent to Heschl, including areas on the temporal plane next to the presumed pitch center (symmetric, see left of Figure 1), and areas in right superior temporal sulcus (STS) and superior temporal gyrus (STG) on both sides.

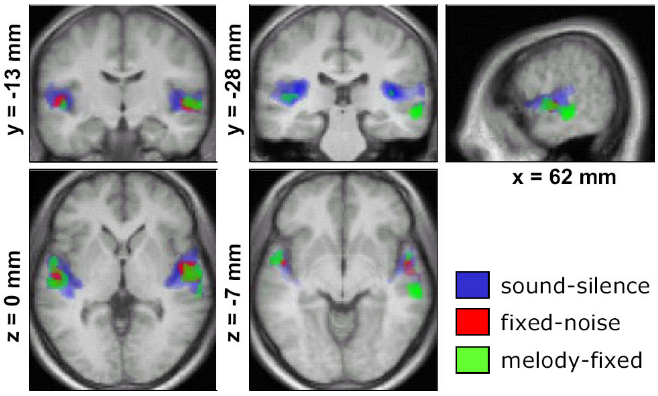

Figure 1: Activation maps for a group of eight listeners for the main contrasts sound vs. silence, fixed pitch vs. noise, and melody vs. fixed pitch, diotic stimulus presentation. Threshold for significance was t=5.13 (p<0.05, corrected for multiple comparisons across the whole brain volume).

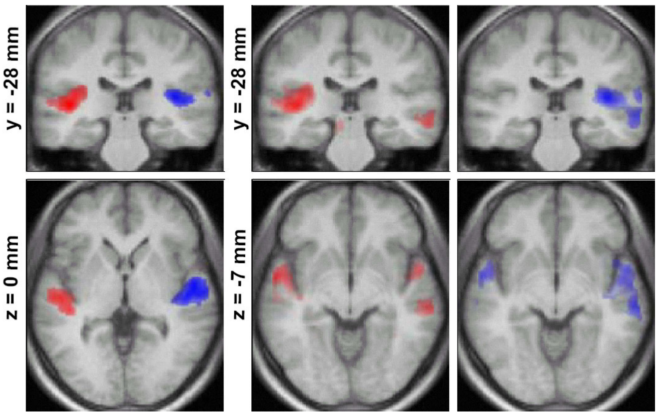

Figure 2: Activation maps (p<0.05, corrected for multiple comparisons across the whole brain volume) for the group of eight listeners, for contrasts between sound to the left ear and sound to the right ear. Left column, red: sound right – sound left; blue: sound left – sound right. Middle column: melody right – fixed pitch left. Right column: melody left – fixed pitch right. Note the additional activity spots for the melody vs. fixed pitch comparisons, that appear to be independent of ear of entry.

Inspection of individual results revealed large differences between subjects for the melody specific activation. Four out of the eight listeners showed preferential activation in the right hemisphere, while two showed bilateral activation and two other had the main activation clusters for melodies in the left hemisphere.

Figure 2 shows the effect of monaural stimulus presentation on the measured activity. A plain contrast between monaural sound in general and silence shows preferential activation of the respective contralateral hemispheres, as expected. A contrast between the conditions with sound in general either to the left or to the right ear results in complete lateralization of the respective activation maps (see Figure 2, left). There is not a single voxel in either hemisphere of the brain, that shows a bigger MR signal for ipsilateral than for contralateral stimulation. The middle and right columns of Figure 2 show the contrasts between the conditions with melodies to one ear and sequences of fixed-pitch notes to the other. Activation around the surface of the temporal lobes, mainly in Heschl's gyrus (see coronal slices, top), is completely lateralized, as before, reflecting the crossed projections from the brainstem to primary auditory cortical areas. However, the melody specific areas outside Heschl's gyrus (the "green areas" from Figure 1) are always activated in both hemispheres, irrespective of the ear of entry.

Discussion

The results from this study for diotic stimulus presentation are completely in line with the previous report [1], and can be interpreted as additional strong evidence for the hierarchical organization of temporal pitch processing. The additional findings for monaural stimulus presentation suggest that the regions specifically responsive to changes of the pitch reflect a higher processing stage, that integrates input from all pitch sensitive areas in the brain, irrespective of the particular ear of entry for the sound. The melody-specific activation seems to reflect the process of feature extraction from a highly processed, recoded sound representation. In conclusion, it can be interpreted as a representation of a cognitive process beyond a purely sensory coding of stimulus properties, probably involving attention and individual musical aptitude.

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