Impact of task difficulty on lateralization of pitch and duration discrimination

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To investigate lateralization of duration and pitch discrimination processing with emphasis on the influences of task difficulty, we used event-related functional magnetic resonance imaging. Seventeen healthy volunteers performed paired auditory discrimination tasks at varying levels of difficulty. Analysis of lateralization effects revealed leftward lateralization within the insular and the temporal cortex under both conditions. Moreover, parametric analysis of haemodynamic responses showed increasing activation within the right temporal cortex correlated to increasing accuracy of stimulus discrimination. Thus, highly differential acoustic stimuli seem to be predominantly processed within the right hemisphere, whereas the detection of slight signal differences might be linked to the left hemisphere. In conclusion, we found evidence for preferential involvement of the right hemisphere in holistic feature processing within the auditory domain. *NeuroReport* 16:239–242 © 2005 Lippincott Williams & Wilkins.

Key words: Acoustic processing; Attention; Auditory cortex; Duration; Frequency; Functional magnetic resonance imaging; Lateralization; Pitch; Task difficulty; Time

INTRODUCTION

The discrimination of acoustic signals is extremely important for humans to cope with various environmental demands. More specifically, acoustic communication depends on correct discrimination of speech sounds at the segmental (phonemes) and suprasegmental (speech melody) level [1]. To extract the appropriate meaning in each situational context, humans depend on intact high-resolution acoustic processes to discriminate speech and acoustic sounds. Among the elementary acoustic categories that have basic as well as higher-order importance are discrimination within the time domain and the frequency domain. In humans, representation of temporal information seems to be subserved by a complex network of cortical and subcortical areas, including the temporal, frontal and parietal cortex and the cerebellum and basal ganglia [2]. Functional imaging studies investigating duration discrimination reported activity in the bilateral dorsolateral prefrontal cortex, parietal lobe, superior temporal gyri (STG), thalamus, basal ganglia, left cingulate cortex [3], and the right inferior and medial frontal areas [4,5].

Concerning differential lateralization effects of sound discrimination, it has been suggested that temporal aspects of acoustic perception are crucial in determining hemispheric lateralization forming also the basis for language and music lateralization. Left hemisphere auditory areas are proposed to subserve short acoustic transitions (e.g. <50 ms) [6–8], whereas the corresponding right hemisphere auditory areas are preferably engaged in decomposing longer time windows (>100 ms) [8–11]. Moreover, emerging evidence shows that not only global stimulus-related aspects (e.g. pitch or duration estimation processes) but also task difficulty level (due to graded levels of stimulus differences) influence the related brain activation patterns. Two recent studies [12,13] found right and left hemisphere fronto-parietal networks correlating with task difficulty in a sound intensity and a duration discrimination task. By assessing graded deviancy between the reference and target sounds, activation within the right STG and inferior frontal gyrus was observed to correlate with sound deviancy. This effect emerged regardless of the stimulus category (duration, pitch and intensity changes were tested). The goal of this study was to investigate, within one and the same study paradigm, the global stimulus-category-related and the detailed task-difficulty-related lateralization effects for both duration and pitch discrimination processing to shed more light on an issue that has so far brought forth contradictory findings that are difficult to compare with one another because of differences in imaging methods, stimulus material and tasks administered. We hypothesized that stimulus-category-related aspects of auditory feature processing (duration discrimination vs. pitch discrimination) would be linked to differential lateralization effects, with increasing sound deviancies (easier discrimination) being related to increasing hemodynamic responses within right-sided temporal and frontal regions during duration and pitch discrimination.

METHODS

In this study, 17 healthy volunteers who gave written informed consent were investigated (eight men, nine women, mean age 25.2 years, range 18–31 years). All participants were strongly right handed as assessed by the Edinburgh handedness scale [14] (laterality index >90%). They had comparable educational status and no psychiatric, neurological or hearing disorders. The experimental paradigm consisted of two paired discrimination tasks: difficulty-varied duration and pitch discrimination. In several separate behavioural experiments on different volunteers (n=30) outside the scanner, the stimulus pairs were pretested for their discriminability, difficulty-balanced according to the resulting performance scores and then used in the follow-up functional magnetic resonance imaging (fMRI) experiment. The acoustic signals were complex harmonic tones consisting of four harmonics: F1–F4 of 500, 1500, 2500 and 3500 Hz manipulated either in duration (signals discretely ranged from 100 to 400 ms, each being compared to a 200 ms reference tone, resulting in duration differences from 0 to 200 ms) or in fundamental frequency (F0), corresponding to the perceived pitch. Fundamental frequency was varied by manipulation of rhythmic intensity changes throughout the signal between 100 and 200 Hz and reference tone was at 150 Hz, which led to pitch differences of 0–50 Hz. Participants had to discern the higher (pitch task) or longer (duration task) of the two stimuli, binaurally presented with a fixed delay of 500 ms (see Fig. 1a). For the

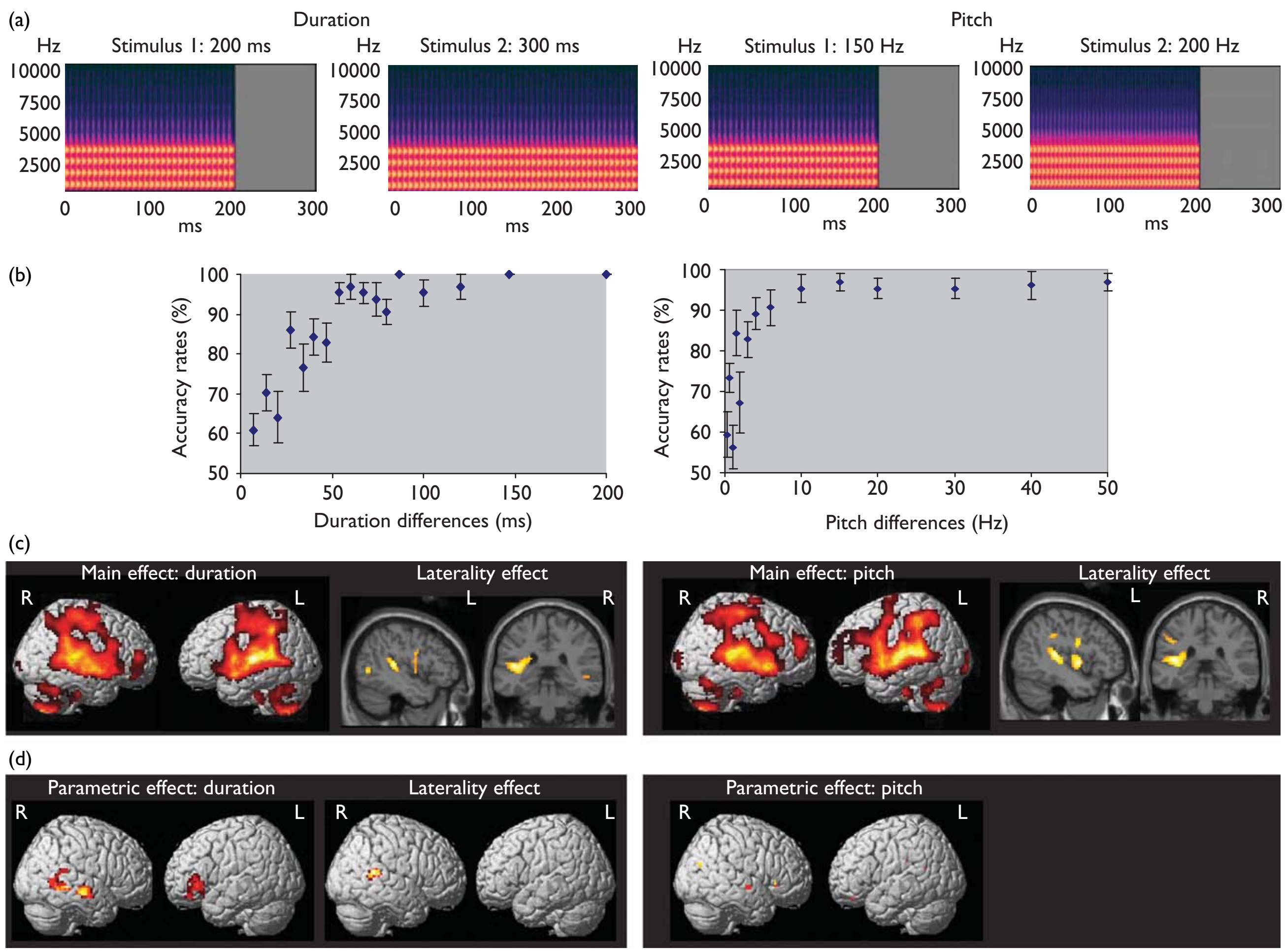

Fig. 1. (**a**) Synthesis of acoustic stimuli: complex acoustic signals comprising four harmonics (500, 1500, 2500, and 3500 Hz) were varied in duration (100–400 ms) or in fundamental frequency (100–200 Hz). Fifty-seven stimuli pairs, exclusively differing in one of these parameters, were used for the respective discrimination task. Left: pair of duration-varied stimuli (200 ms vs. 300 ms); right: pair of F0-varied sample stimuli (150 Hz vs. 200 Hz). (**b**) Behavioural performance: accuracy rates of the duration discrimination (left) and pitch discrimination task (right). Increasing deviance in time and pitch, correlated with higher performance scores. (**c**) Main effect: cerebral activation during pitch and duration discrimination. Significantly activated areas as compared to the rest are projected upon the cortical surface of a template brain. Both tasks yielded a fronto-temporo-parietal activation pattern, with the peak activation residing in left auditory areas. Lateralization effect: activation patterns after a voxelwise comparison of the hemispheres against one another. Laterality analysis showing a similar left-temporal lateralization effect for both tasks (height threshold $p<0.001$, uncorrected; $p<0.05$ corrected at cluster level). (**d**) Parametric effects: significantly activated areas as a function of linear increase with good task performance emerged within the right middle temporal gyrus /superior temporal gyri (STG) and the left inferior frontal gyrus during duration discrimination ($p<0.001$, uncorrected; $p<0.05$ corrected at cluster level) and within the right STG during the pitch discrimination task ($p<0.001$, uncorrected; nonsignificant at cluster level). Laterality analysis: voxelwise comparison of the hemispheres against one another along the x-axis of the Montreal Neurologic Institute coordinate system revealed a significantly activated cluster within the left STG for the parametric effect of duration discrimination ($p<0.001$, uncorrected; $p<0.05$ corrected at cluster level).

acoustic stimulation, special magnetic resonance-compatible earphones, based on piezoelectric signal transmission, were used [15]. After task instruction, earphone volume was adjusted to individual volunteer needs during a test scanning. In each condition, 57 time-jittered stimulus pairs were presented in randomized order with respect to their physical differences (i.e. the difficulty level). Participants pressed a button to indicate their decision after presentation of each stimulus pair. Event-related fMRI was performed using an echoplanar imaging sequence (1.5 T, Siemens Vision, TR=3 s, TE=40 ms, FOV=192 mm, 28 slices, matrix 64×64, flip angle 90°). Four subsequent steps of statistical analysis (random effect analysis) were carried out using SPM2:

Main effects (comparison of task vs. baseline).

Task-specific effects (task vs. task comparisons).

Laterality effects to elucidate left/right hemispheric differences (voxelwise flipping of the contrast images along the x-axis and comparing the inverted against the non-inverted images).

Analysis of parametric effects to extract difficulty-related effects during discrimination of the two acoustic categories: a correlation with the behavioural measure (i.e. identification of cerebral regions characterized by a linear relationship between the blood oxygenation level-dependent signal changes and the behavioural performance score). Corrections for multiple comparisons were performed at cluster level with a height threshold of $p < 0.001$ (uncorrected) and cluster extent threshold $p = 0.05$ (corrected). Finally, the anatomical labelling of the activation maps was performed using the software tools 'Automated Anatomical Labelling' [16] and Cytoarchitectonic Probability Maps [17], both implemented into the toolboxes available for SPM2.

RESULTS

The behavioural data showed comparable hit scores of about 75% for both pitch and duration discrimination. The hit-scores obtained by the fMRI experiment were also comparable to the performance scores of the preceding behavioural experiments outside the scanner, which attenuates objections to the possible influence of scanner noise on acoustic discriminability. For both tasks, the rate of correctly identified stimuli increased with rising physical difference between the two acoustic signals (duration difference or pitch difference, see Fig. 1b).

Considering the imaging results, the main effect was highly similar for both tasks, revealing strong bilateral activations in both primary secondary acoustic cortices – STG and superior temporal sulcus – with the peak activity residing within the left auditory cortex (posterior STG). There was also significant activity in both tasks in bilateral fronto-parietal areas, right and left supplementary motor area, and both hemispheres of the cerebellum. No significant differences were obtained by comparing the pitch against the duration discrimination task and vice versa. The laterality analyses revealed significant leftward lateralization effects at the level of posterior ventral STG and middle temporal gyrus (MTG) – covering planum temporale, Heschl's gyrus and Brodman's area 41 within the primary acoustic cortex – and insula for both tasks similarly (Fig. 1c).

Parametric analysis showed significantly increased activity in the medial and posterior parts of the right dorsal MTG extending to the posterior STG and the left inferior frontal gyrus (IFG) with good task performance for the duration task. Parametric responses during the pitch task were limited to two small clusters (which did not, however, reach statistical significance) within the right IFG and the medial part of the right dorsal STG. When comparing these two parametric effects with one another, no suprathreshold activity emerged, that is, no differences between the linear increases with hit rates for these tasks could be obtained. When computing the laterality analyses, we found a significantly activated cluster in the posterior part of the right STG/MTG (Fig. 1d) for the linear increase, with good performance in the duration task but no significant effect in the pitch condition.

DISCUSSION

The differential lateralization hypothesis of duration and pitch processing [6–10] postulates right hemisphere lateralization for slow acoustic changes (or spectral analysis of acoustic stimuli) and left hemisphere involvement for short acoustic transients (temporal domain) as being the basic prerequisites for the lateralization of speech to the left and music to the right hemisphere. In contrast to these considerations, our results indicate more commonalities than differences for the pitch and duration discrimination tasks concerning their hemispheric lateralization. The main effects of duration and pitch processing activated the same network of cortical areas (including contaminating activity due to motor control requirements of both tasks), culminating in activation bound to the left superior and middle temporal areas and insular cortex. Similar activation patterns for pitch and duration processing were also reported by Nenadic *et al.* [3] and by single-cell recordings in animals, which showed similar processing patterns of frequency-related and time-related features in common spectro-temporal receptive fields. This reflects the theoretical concept that neurons already respond to a combination of spectro-temporal features at a very basic level of feature processing [18]. Furthermore, similar results have been obtained by another series of investigations [15], which reported bilateral activation in the planum temporale with a slight leftward lateralization effect for the analysis of tones and rapidly changing consonant–vowel alterations.

When investigating parametric effects, we obtained more activation within right auditory areas with decreasing task difficulty and increasing task performance, but again similar for the pitch and the duration task. Thus, in line with previous studies on difficulty-dependent effects [12,13], performance level was observed to influence activation within a right hemisphere network (MTG, fronto-parietal) during discrimination of different acoustic parameters. However, performance-dependent modulation of the right hemisphere has been observed to be inversely correlated with discriminability in these studies. The results reported in the study on duration discrimination [13] were, however, described with caution, because significance level was only reached without any correction procedure for multiple comparisons (uncorrected). Furthermore, this study also reported left hemisphere parietal and temporal increases with task difficulty, but no correlations with good performance level. One of the possible reasons for not finding such correlations could have been that the stimuli used for discrimination were altogether easy to discriminate (duration differences: 150–1050 ms). However, other recent work [19], similar in task design and stimulus range to our study, performing a correlation analysis with the physical distances of the stimuli (and not the behavioural measures) to a reference tone, found right hemisphere (STG) involvement with increasing deviancy between the sounds for three categories of auditory stimuli (pitch, duration and sound intensity changes).

Thus, the findings of the present study provide further evidence for a common substrate of duration and pitch processing within left and right auditory areas, shifting its focus as a function of task difficulty. Independent of the acoustic category, large differences between acoustic signals that are easily detected seem to be shifting the common activation more towards the right hemisphere. Our results might indicate that acoustic stimuli that are easier to discriminate, because of either a larger distance in duration or in perceived pitch, are preferentially processed by areas within the right superior temporal gyrus.

This mirrors to some extent the classical general view of 'division of labour' between the hemispheres, with the left hemisphere functioning as the analytical detector of details and the right hemisphere as the holistic device in decomposing the global components of features [20].

Albeit not exactly using this terminology, the differential lateralization hypothesis stated by Zatorre and Belin [6] and Zatorre *et al.* [9] (suggesting that the left hemisphere is selectively better at temporal analysis and the right hemisphere at spectral analysis) and the 'asymmetric sampling in time model' [8] [assuming a short (25 ms) temporal integration window for the left and a long (150–250 ms) one for the right hemisphere] also reconsider this general idea of division of labour from a conceptual point of view.

CONCLUSION

In conclusion, the present results suggest that lateralization effects during pitch and duration discrimination seem to depend rather on task difficulty or ease of processing, than on the acoustic category per se (pitch or duration discrimination).

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