

Focused and Nonfocused Attention in Verbal and Emotional Dichotic Listening: An fMRI Study

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Functional magnetic resonance imaging (fMRI) was used to identify cortical regions which are involved in two dichotic listening tasks. During one task the subjects were required to allocate attention to both ears and to detect a specific target word (phonetic task), while during a second task the subjects were required to detect a specific emotional tone (emotional task). During three attentional conditions of each task, the subjects were required to focus attention to the right (FR) or left ear (FL), while during a third condition subjects were required to allocate attention to both ears simultaneously. In 11 right-handed male subjects, these dichotic listening tasks evoked strong activations in a temporofrontal network involving auditory cortices located in the temporal lobe and prefrontal brain regions. Hemodynamic responses were measured in the following regions of interest: Heschl's gyrus (HG), the planum polare (PP), the planum temporale (PT), the anterior superior temporal sulcus (aSTS), the posterior superior temporal sulcus (pSTS), and the inferior frontal gyrus region (IFG) of both hemispheres. The following findings were obtained: (1) the degree of activation in HG and PP depends on the direction of attention. In particular it was found that selectively attending to right-ear input led to increased activity specifically in the left HG and PP and attention to left ear input increased right-sided activity in these structures; (2) hemodynamic responses in the PT, aSTS, pSTS, and IFG were not modulated by the different focused-attention conditions; (3) hemodynamic responses in HG and PP in the nonforced conditions were the sum activation of the forced conditions; (4) there was no general difference between the phonetic and emotion tasks in terms of hemodynamic responses; (5) hemodynamic responses in the PT and pSTS were strongly left-lateralized, reflecting the specialization of these brain regions for language processing. These findings are discussed in the context of current theories of hemispheric specialization. © 2001 Academic Press

INTRODUCTION

Dichotic listening (DL) is a widely used experimental paradigm in which subjects listen to two different auditory stimuli at the same time, one in each ear, under divided

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attention conditions. The typical finding for verbal stimuli (phonological or language stimuli) is a superior report of the right compared to the left ear items, a finding which is called a right ear advantage (REA). The opposite effect, that is, a left ear advantage (LEA) has been obtained for dichotically presented nonverbal stimuli, e.g., melodies, tonal sequences, or emotional stimuli (Hugdahl, 1992). The most generally accepted explanation for the ear advantage effect in dichotic listening is the "structural model" (Kimura, 1961). The "structural model" assumes that dichotic listening is related to brain asymmetry through predominant contralateral auditory pathways which results in greater representation of verbal stimuli in the language-dominant left hemisphere. This model assumes that the contralateral auditory brain regions are more activated during dichotic stimulations; verbal stimuli presented to the right ear would have direct access to processing centers in the left hemisphere, while left ear stimuli would have to be transferred across the corpus callosum to reach the speech processing areas in the left hemisphere. Similarly, nonverbal stimuli presented to the left ear would have direct access to right hemisphere processing.

An alternative model which was originally proposed by Marcel Kinsbourne (1970) assumes that basic attention and activation mechanisms and not structural constraints are responsible for the ear advantage effect. For example, in situations when the subject is engaged in verbal tasks, brain regions specialized for language and verbal processing are preactivated or primed. Thus, working with verbal material will evoke activation in the language areas predominantly located in the left superior temporal gyrus (STG), and thus direct attention to the stimulus source contralateral to the left hemisphere in verbal tasks and right hemisphere in nonverbal tasks. Due to the predominantly contralateral connection of the auditory cortices with the auditory pathway, right ear verbal input will then be processed more efficiently than left ear input. According to this model, nonverbal stimulation will evoke predominately right hemisphere activation with superior left ear processing.

Empirical validation of these models applying different measures of brain activation are currently scarce. Language dominance evaluation with the sodium-amytal test (Wada test) reveals that subjects with left-hemisphere language dominance exhibit right ear advantages to verbal dichotic stimuli while subjects with right hemisphere language dominance demonstrated left ear advantages to verbal dichotic stimuli (Hugdahl, Carlsson, Uvebrant, & Lundervold, 1997; Zatorre, 1989). At present, seven papers have been published to examine cerebral blood flow during presentation of dichotic stimuli (Coffey, Bryden, Schroering, Wilson, & Mathew, 1989; Tzourio et al., 1997; Hugdahl et al., 2000; O'Leary et al., 1996; Hugdahl et al., 1999; Alho et al., 1999; Hashimoto et al., 2000). In an earlier attempt, Coffey et al. (1989) applied the $^{133}\text{Xenon}$ inhalation technique and revealed increased activation in the right hemisphere for subjects exhibiting a LEA, and a tendency for a reversed pattern of activation for subjects showing a REA. Applying more sophisticated $^{15}\text{O-PET}$ techniques, two recent studies found stronger rCBF activations on the left superior temporal gyrus (STG) during verbal dichotic stimulation (O'Leary et al., 1996; Hugdahl et al., 1999; Hugdahl et al., 2000), a finding which was substantiated in a recent fMRI study (Hashimoto et al., 2000). In the O'Leary et al. study there was also stronger activation on the right STG to dichotically presented environmental sounds, while in the earlier Hugdahl et al. study there was stronger activation on the right auditory cortex to musical stimuli suggesting the processing superiority of the right temporal lobe for nonverbal stimuli. Moreover, four of these recent PET studies also applied a forced-attention paradigm showing that the degree of activation in the auditory cortex depends on the direction of attention. In two studies it was found that attending selectively to the right-ear input activated the auditory cortex predominately in the left hemisphere and vice versa (O'Leary et al., 1996; Alho et al., 1999). A further study

(Tzourio et al., 1997) revealed a trend for a similar effect although this effect was only present in the posterior auditory cortex in the vicinity of the *planum temporale*. On the other hand, a recent paper published by Hugdahl et al. reported a generally decreased bilateral activation within the STG during the focussed attention conditions (Hugdahl et al., 2000). However, all aforementioned brain mapping studies performed group analysis by pooling the stereotactically normalized functional data sets. In the auditory cortex, this technique has the disadvantage that the highly variable gyral and sulcal morphology of the primary and secondary auditory cortex is not taken into account (Steinmetz, Fürst, & Freund, 1990; Westbury, Zatorre, & Evans, 1999).

Taken together, the aforementioned studies revealed results supporting the structural and the attentional model of dichotic listening. However, these models and the above-mentioned studies do not account for the anatomical and functional diversity of the auditory cortex. For example, the volume of the *planum temporale* (a brain region which is thought to be the structural marker of language lateralization) is strongly left-lateralized in right-handers, while there is no consistent volumetric asymmetry of the primary auditory cortex (Steinmetz, Volkman, Jancke, & Freund, 1991; Jancke, Schlaug, Huang, & Steinmetz, 1994a; Steinmetz, 1996). There is however, a volumetric asymmetry of the *planum parietale* favoring the right hemisphere in right-handers (Jancke et al., 1994a). Beside these anatomical diversities there are also conflicting data concerning the involvement of the primary and secondary auditory cortices in attentional processes. Finally, more and more data suggest that language processing is accomplished by brain areas outside the classical speech regions (for example the inferior frontal gyrus and the superior temporal sulcus regions; Binder et al., 2000; Binder, 1997; Buchanan et al., 2000).

This study was designed to reexamine whether ear advantage scores in dichotic listening are related to specific patterns of hemodynamic responses in the auditory cortices. Supplementing previous brain imaging studies, a main purpose of the present study was to precisely map the hemodynamic responses in different parts of the auditory core (Heschl's gyrus), belt (*planum temporale*), parabelt (superior temporal sulcus), and inferior frontal regions in response to dichotic stimuli which were processed in the context of different attentional and perceptual tasks. With these data we aimed to test the plausibility of the structural and attentional model of dichotic listening. The structural model would predict that processing of phonetic dichotic material is associated with left-lateralized activation and processing of emotional dichotic material would lead to right-lateralized activation in the auditory areas and that these activation patterns are not influenced by the side to which attention is directed. On the other hand, the attentional model would predict that lateralized brain activity depends more strongly on the side to which attention is directed, regardless of stimulus type. It might also be that there are interactions between structural and attentional constraints. For example focusing attention to the right ear during phonetic processing might enhance activations on left auditory areas (specialized for phonetic or phonological processing) while focusing attention to the left ear might leave the activation on the right auditory cortex unchanged. A similar but reversed hypothesis can be formulated for the processing of emotional information. In such a situation focusing attention to the left ear might enhance activation on the right auditory cortex but focusing attention on the right ear might leave the activation on the left auditory cortex unchanged. Specifically, we planned to address the following questions: (1) Does the relative ear advantage in verbal and emotional dichotic listening depend on differential and lateralized activity in auditory and prefrontal cortices? (2) Does the allocation of attention to one ear in the context of dichotic listening involve differential activity in specific areas of the auditory and prefrontal cortices?

(3) Does phonetic and emotional processing evoke different activation patterns in the context of dichotic listening?

METHODS

Subject Characteristics

Eleven male volunteers, ranging in age from 22 to 40 years, with no history of neurological or audiological illness were studied. All volunteers were consistently right handed according to standard handedness questionnaires (Peters, 1998). After a full explanation of the nature and risks of the research, subjects gave informed written consent for all studies according to a protocol approved by the Ethics Committee of the Heinrich-Heine University, Düsseldorf. All subjects were native speakers of German.

Stimulus Materials and Experimental Conditions

The auditory stimuli consisted of the four words, “bower,” “dower,” “power,” and “tower,” each originally spoken by a native English-speaking male phonetician in angry, happy, neutral, and sad tones of voices resulting in 16 separate word–emotion combinations. Among the four words, the phonetic pronunciations “bower” and “dower” have meaning in both English and German (although they are spelled differently in German). The other two words, “power” and “tower,” although they are not part of the standard German lexicon, are widely used in the German language and known to all the subjects who participated in this study. These stimuli have been used previously in dichotic listening studies examining verbal and affective laterality effects and have been shown to have adequate discriminative properties (Bryden & MacRae, 1989; Bulman Fleming & Bryden, 1994). The stimuli were edited to a common length of approximately 650 ms and equalized in intensity. They were then stored in 16-bit, digital format on a personal computer.

Each subject was allowed to listen to the sounds of all the stimuli as often as he liked prior to entering the scanner in order to become familiar with both the verbal and affective characteristics of the stimuli. In each of six experimental conditions, subjects were asked to listen for a different target and press a button when that target was detected. One set of conditions involved the detection of the word “power” spoken in any of the four emotional tones (*phonetic detection task*); the second set of conditions required the detection of all words spoken in a “sad” tone (*emotional detection task*). Each task was performed under three different attentional instructions: During the *nonforced attentional* (NF) instruction, the subjects were told that they would be presented with a list of dichotic words. Their task was to attend to both ears and to detect the targets irrespective of to which ear the target was presented. During the *forced-right* (FR) attentional instruction, the subjects were told to pay close attention to the right ear. During the *forced-left* (FL) condition, the subjects were told to pay close attention to the left ear words and only react to targets presented to the left ear. Other than the attentional instructions the procedure in the forced-attention conditions was identical to that for the NF condition. Thus, we applied a total of six experimental conditions:

1. nonforced phonetic (NF-phonetic)
2. forced-right ear phonetic (FR-phonetic)
3. forced-left ear phonetic (FL-phonetic)
4. nonforced emotion (NF-emotion)
5. forced-right ear emotion (FR-emotion)
6. forced-left ear emotion (FL-emotion)

Each experimental condition was specifically designed to fit to the chosen block-design for functional magnetic resonance imaging (see the procedure section below) resulting in the use of less than the whole set of 144 trials as in the original paper using the same stimuli (Bryden et al., 1989). Thus, 96 dichotic stimuli were presented consisting of a random mix of all 16 separate word/emotion combinations, including 48 targets in each (24 for each ear). The order of target stimulus condition as well as the order of stimulus presentation within each condition was randomized for each subject. The interval between words was 1 s. A post hoc experiment assessing behavioral performance on the exact task used in the scanner on a different set of subjects in a normal laboratory setting revealed strong right ear advantages for detecting words and strong left ear advantages for detecting emotional tone. Thus, this slightly modified paradigm revealed basically similar results as in the original paper.

Procedure

Functional MR images (fMRI) were acquired using a 1.5 Tesla Siemens MRI system (SIEMENS Magnetom Vision, Erlangen, FRG), equipped with echo planar imaging (EPI) capability and a standard radiofrequency (RF) head coil for transmit and receive. Pulse sequence parameters were as follows: gradient echo EPI; repetition time (TR) = 6 s; echo time (TE) = 66 ms; field of view (FOV) = 200 × 200 mm; flip angle (α) = 90°; matrix size = 64 × 64; in-plane resolution = 3.125 × 3.125 mm; slice thickness = 5.0 mm; interslice gap = 0.3 mm. Using a midsagittal scout image, 16 axial slices were oriented in the anterior–posterior commissure (AC–PC) plane, with the lowermost slice positioned to be 20 mm below the AC–PC line. In addition, high-resolution, T1-weighted anatomical images of the entire brain were obtained in 3D using the mp-rage (magnetization-prepared, rapid acquisition gradient echo) pulse sequence with the following parameters: TR = 11.4 ms; TE = 4.4 ms; TI = 300 ms; α = 15°; 1 excitation; FOV = 230 mm; matrix = 256 × 256; 128 sagittal slices with 1.25 mm slice thickness.

During scanning the room lights were dimmed and the subjects' eyes were open. Auditory stimuli were presented dichotically using a digital playback system and a magnetically shielded transducer system. The acoustic stimulation system terminated in tightly occlusive headphones allowing unimpeded conduction of the stimulus with good suppression of ambient scanner noise by about 20 dB. During each experimental condition, a series of 78 data sets were acquired. Each series consisted of multiple periods of "baseline" (OFF), during which subjects heard only the ambient machine noise, alternating with periods of "activation" (ON), during which prepared auditory stimuli were delivered. It is worth noting that during the ON-periods the subjects heard the stimuli as well as the ambient machine noise. Each series began with 6 baseline data sets (36-s interval), followed by 72 images during which "rest" alternated with "activation" every 54 s (1 series = 4 cycles, 108 s/cycle, 18 images/cycle, Fig. 1). The total duration of each image series was about 8 min. In order to reduce possible masking effects of scanner noise on the experimental stimuli, a TR of 6 s was adopted (Jancke, Shah, Posse, Grosse-Ryukun, & Muller-Gartner, 1998). Stimulus presentation was triggered by the EPI sequence to start 200 ms after the previous scan and to fall in between the interscan gap of 4 s (sequence scanning time = 2 s) resulting in a nonmasked presentation of the stimuli (3 stimuli per sequence, see also Fig. 1). It is worth noting that we have demonstrated in several experiments that this procedure allows acoustic stimulation within the MRI-scanner with a minimum of masking influence (Shah, Jancke, Grosse-Ruyken, & Muller-Gartner, 1999; Shah et al., 2000; Jancke et al., 1999a; Jancke et al., 1998; Jancke, Mirzazade, & Shah, 1999b).

Because of the limitations involved in taking an SPL meter into an MRI scanner, the intensity of the stimuli [mean signal intensity (SPL) during a 30-s epoch] was determined outside the scanner using an artificial head (Bruel & Kjaer KA637) wearing the headphones. Applying these measurements, intensity of the stimuli was adjusted to be approximately 85 dB (SPL). The acoustic noise level within the MRI

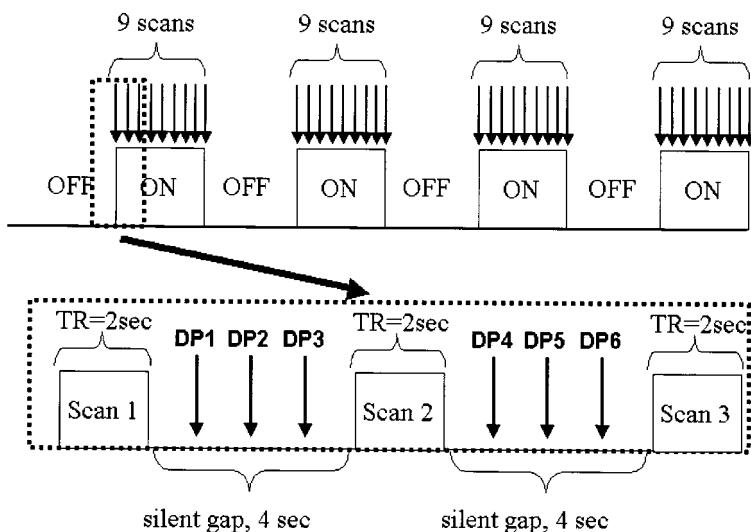


FIG. 1. Schematic view of the fMRI-block design used in the present study. The first row shows the sequence of ON- (during which dichotic stimulation (DP) occurred) and OFF-blocks (no auditory stimulation). The second row shows the detailed timing for three subsequent fMRI-scans with the elongated TR (6 s) allowing the presentation of 3 dichotic stimuli without fMRI-scanner noise.

scanner during an EPI measurement was measured 1 meter from the bore of the scanner magnet with a capacitance microphone revealing a root mean square level of 90 to 100 dB. Because the attenuation factor of the headphones was about 20 dB, the average intensity of the scanner noise perceived by the subjects was estimated to be about 70 to 80 dB. Frequency analysis of the noise generated by the EPI sequence recorded in the scanner revealed five prominent frequencies. The corresponding amplitudes relative to the maximum amplitude were: 612 Hz (-15 dB), 1847 Hz (-29 dB), 3036 Hz (-21 dB), 3365 Hz (-37 dB), and 3644 Hz (-36 dB). This analysis revealed no overlap of the prominent frequencies of the EPI-noise with the formant frequencies of the diphthong /au/ contained within all stimulus words. The diphthong /au/ is generated with downward formant transitions for both formants. At the beginning of the formant, F1 was measured to lie on average at 800 Hz and at the end at 400 Hz. For F2, the beginning was measured to be 1300 Hz and 700 Hz at the end.

Image Analysis

Image analysis was performed on a PC workstation using MATLAB (Mathworks Inc., Natick, MA) and SPM99 software (<http://www.fil.ion.ucl.ac.uk/spm>). For analysis, all images were realigned to the first volume, corrected for motion artifacts, coregistered with the subject's corresponding anatomical (T1-weighted) images, resliced and normalized (4 mm^3) into standard stereotaxic space (template provided by the Montreal Neurological Institute (Evans et al., 1993)), and smoothed using an 8-mm full-width-at-half-maximum Gaussian kernel. The data were analyzed by statistical parametric mapping. The effect of global differences in scan intensity was removed by scaling each scan in proportion to its global intensity. Statistical analysis was performed for each condition in a general linear model, in which regionally specific activation is explored as to how well the reference waveform fits to the observed time series of the fMRI signal (i.e., hemodynamic responses) at each and every voxel (Friston et al., 1995a; Friston et al., 1995b; Friston, Jezzard, & Turner, 1994). The reference waveform was obtained by smoothing a time-dependent parameter of interest (i.e., a box-car waveform with 0s for rest epochs scans and 1s for movement epoch scans) with a Gaussian kernel of a delay and dispersion of the square root of 8 s, modeling the hemodynamic response functions. The time-series fMRI data also were smoothed over observation (time) by use of the same Gaussian kernel as the hemodynamic response function.

Analysis

The spatially normalized fMRI time-series data of each subject were analyzed separately in order to closely examine each individual within the framework of the Talairach coordinates (Talairach & Tournoux, 1988). Significantly activated pixels were searched for using the "General Linear Model" approach for time-series data suggested by Friston and colleagues (Friston et al., 1995a; Friston et al., 1995b; Friston et al., 1994). An ANOVA was calculated for each voxel of the functional data set comparing the six conditions to rest. The resulting set of voxel values for each contrast constitutes a statistical parametric map of the t statistic (SPM $\{t\}$), which was transformed to the unit normal distribution SPM $\{Z\}$. In a first step, a "random effects" procedure was performed in order to search for those regions significantly activated during all dichotic listening conditions compared to rest. For this the adjusted responses obtained for each dichotic condition and each subject were subjected to a t test (66 images). Significant activations were thresholded at $p = 0.05$ (corrected for multiple comparisons) and overlaid on a standard brain and on SPM "glass-brains" (group analysis).

Regions of interest (ROIs) were defined according to the Talairach atlas and prominent sulcal and gyral landmarks (Heschl's gyrus, sylvian fissure, ramus posterior ascendens, ramus posterior descendens, ramus anterior ascendens, ramus anterior descendens, and the superior temporal sulcus) in each brain and hemisphere to include: (1) the primary and immediate auditory area, (2) the planum temporale, (3) the planum polare, (4) the anterior part of the superior temporal sulcus, (5) the posterior part of the superior temporal sulcus, and (6) the inferior frontal gyrus including Broca's area. The exact spatial delineation of the auditory cortices is currently unknown for the following reasons: (i) the spatial extent of the cytoarchitectonic area of the primary auditory cortex is currently unknown, (ii) the exact delineation of the anatomical landmarks is not possible because of the limited spatial resolution of the normalized fMRI images (4 mm^3), (iii) the angulated shape of the Heschl's gyri and the Sylvian fissure vary considerably in horizontal and vertical directions within subjects (left vs. right hemisphere) and between subjects (Jancke et al., 1994a; Ide, Rodriguez, Zaidel, & Aboitiz, 1996). This variability prevents a simple right versus left comparison of the auditory cortices using the standard SPM procedures. Additionally, anterior and posterior auditory cortex activity cannot be quantitatively analyzed using these procedures. Thus, we defined the anterior auditory cortex as a region covering the Heschl's gyrus (HG) defined by Heschl's sulcus as the anterior border and the first transverse sulcus as the posterior border. For each subject, a volume of interest ($24 \times 8 \times 8 \text{ mm}$, 24 voxels of the normalized EPI images) was placed in the HG

from medial to the lateral position with the center of each cube exactly located in the middle of Heschl's gyrus (average center of this cube in MNI coordinates, $x/y/z$: left = 50/-16/8; right: 52/-12/8). In order to define the ROI of the planum temporale (PT) a volume of interest ($16 \times 16 \times 16$ mm, 64 voxels of the normalized EPI images) was placed in the PT with the center of each cube located 10 mm posterior to Heschl's sulcus, thus, minimizing the possibility to detect activation of the primary auditory cortex (average center of this cube in MNI coordinates, $x/y/z$: left = -54/-34/12; right: 56/-34/14). The planum polare (PP) was defined as a cube ($16 \times 16 \times 16$ mm, 64 voxels of the normalized EPI images) with a center located 20 mm anterior to HG on the STG (average center of this cube in MNI coordinates, $x/y/z$: left = -50/4/6; right: 52/8/6). The cube ROI ($16 \times 16 \times 16$ mm, 64 voxels of the normalized EPI images) for the anterior superior temporal sulcus (aSTS) was placed within the dorsal bank of the STS midway between the lateral border and the fundus underneath HG (average center of this cube in MNI coordinates, $x/y/z$: left = -50/-18/2; right: 52/-12/4). The cube ROI ($16 \times 16 \times 16$ mm, 64 voxels of the normalized EPI images) for the posterior superior temporal sulcus (pSTS) was placed within the dorsal bank of the STS midway between the lateral border and the fundus underneath the bifurcation of the Sylvian fissure (average center of this cube in MNI coordinates, $x/y/z$: left = 50/-30/8; right: 52/-12/8). Finally, a larger cube ($20 \times 20 \times 20$ mm, 125 voxels of the normalized EPI images) was placed in the inferior frontal gyrus (IFG) region with the center located within Broca's area according to the probability maps of Broca's area (Amunts et al., 1999) (center of this cube in MNI coordinates, $x/y/z$: left = -56/14/12; right: 56/14/12). For these ROIs mean activation compared to baseline was calculated in terms of mean Z scores. These Z scores were obtained from nonthresholded SPM(Z) maps reflecting the difference between each dichotic listening condition compared to baseline. These mean scores were subjected to further statistical analysis using SPSS Version 10.0. For similar approaches to delineate the auditory cortex and related areas in the context of fMRI-studies see Meyer et al. (2000) and Frederici et al. (2000).

RESULTS

Performance Data

The performance data (number of detected targets: hits, see also Table 1) were subjected to a $2 \times 2 \times 2$ ANOVA with repeated measurements on all three factors (*task*: phonetic vs emotion; *attention*: nonforced vs forced; *ear*: left vs right). This ANOVA revealed significant main effects for the factors *task* [$F(1, 10) = 12.4$, $p = .006$, $\eta^2 = 0.55$] and *attention* [$F(1, 10) = 18.8$, $p < .001$, $\eta^2 = 0.65$]. These main effects were due to superior performance for the emotion task and for the forced attention condition. There were also significant interactions between *task* and *attention* [$F(1, 10) = 6.1$, $p = .03$, $\eta^2 = 0.38$] and between *task* and *ear* [$F(1, 10) = 18.9$, $p < .001$, $\eta^2 = 0.65$]. In order to further evaluate these interactions we calculated separate post-hoc tests (Scheffé test). These tests revealed that there was only a significant performance difference between both attention conditions for the phonetic task [$F(1, 10) = 60.4$, $p < .001$, $\eta^2 = 0.86$] but not for the emotion

TABLE 1
Mean Number and Standard Deviation (*SD*) of Detected Targets during the Two Experimental Tasks (Phonetic and Emotion) and for the Different Attention Conditions

Task	Ear		Total
	Left	Right	
Phonetic			
Nonfocused	8.5 (4.2)	13.0 (7.0)	21.5 (9.2)
Focused	15.3 (5.6)	18.6 (6.1)	33.9 (9.1)
Emotion			
Nonfocused	18.3 (6.5)	14.8 (6.4)	33.1 (10.7)
Focused	19.8 (2.9)	18.2 (5.7)	38.0 (7.2)

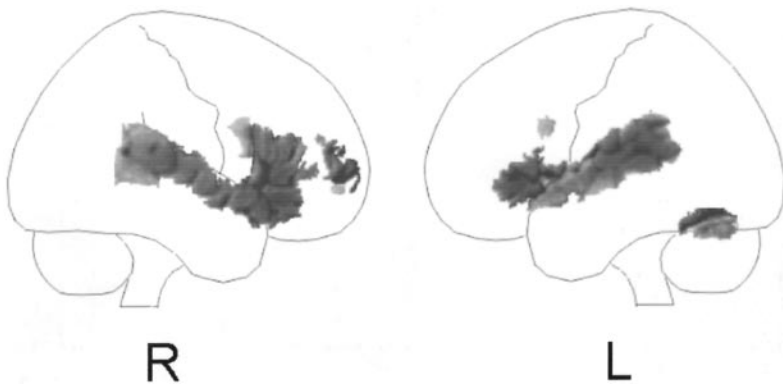


FIG. 2. Average significant hemodynamic responses (gray shading) for the auditory stimulation conditions overlaid on a schematic standard brain. Please note that the activation within the vermis is not depicted in this figure. R, right; L, left.

task [$F(1, 10) = 2.4, p = .15, \text{ETA}^2 = 0.19$]. During the phonetic task there was superior performance for the forced-attention task than during the nonforced task. The *task* and *ear* interaction was qualified by a significant right ear advantage (REA) for the phonetic task [$F(1, 10) = 7.8, p < .02, \text{ETA}^2 = 0.44$] and a significant left ear advantage (LEA) for the emotion task [$F(1, 10) = 7.3, p < .02, \text{ETA}^2 = 0.42$].

Hemodynamic Responses

The group analysis revealed significant bilateral activations in a temporofrontal network comprising the superior temporal gyrus, the superior temporal sulcus, and the inferior frontal region (Fig. 2), thus corroborating findings of previous studies applying verbal stimuli (Binder et al., 1995). The mean stereotaxic coordinates for the peak activations of the ROIs obtained in the present study are tabulated in Table 2. The mean activations of the ROIs within this larger area of activation were subjected to three-way ANOVAs [multivariate model according to (O'Brien & Kaiser,

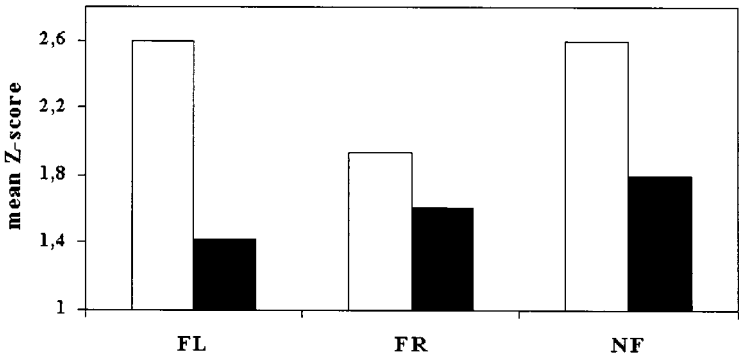
TABLE 2

Mean Coordinates and Standard Deviations (underneath the Means) across All Subjects and Conditions for the Peak Activations within the ROIs

	Left hemisphere				Right hemisphere			
	x	y	z	Z-score	X	y	z	Z-score
HG	-61.9	-14.0	5.1	5.1	61.4	-11.1	8.2	4.5
	2.8	1.9	1.7	1.5	1.9	2.4	0.9	2.1
PP	-59.6	7.2	2.9	5.2	57.8	5.6	4.5	5.2
	3.7	5.0	4.7	1.7	3.8	5.3	4.6	2.1
PT	-61.2	-33.7	12.5	7.4	59.6	-32.7	9.6	6.8
	5.1	8.1	3.9	1.8	5.3	8.7	3.3	1.5
aSTS	-54.5	7.6	-9.8	3.9	57.1	-8.8	-9.7	5.9
	7.8	6.9	3.5	1.7	4.9	6.7	2.4	2.2
pSTS	-59.4	-29.1	5.6	6.8	59.7	-30.1	3.9	7.3
	6.4	7.2	3.0	1.6	6.2	7.5	3.7	1.6
IFG	-55.6	16.2	11.8	6.3	51.4	17.1	15.8	6.9
	7.2	8.3	10.6	1.2	7.6	8.1	10.7	1.6

Note. HG, Heschl's gyrus; PT, planum temporale; PP, planum polare; aSTS, anterior superior temporal sulcus; pSTS, posterior superior temporal sulcus; IFG, inferior frontal gyrus. *x*, *y*, and *z* are the stereotaxic coordinates from the MNI brain. *Z* is the peak activation compared to baseline.

HG



PP

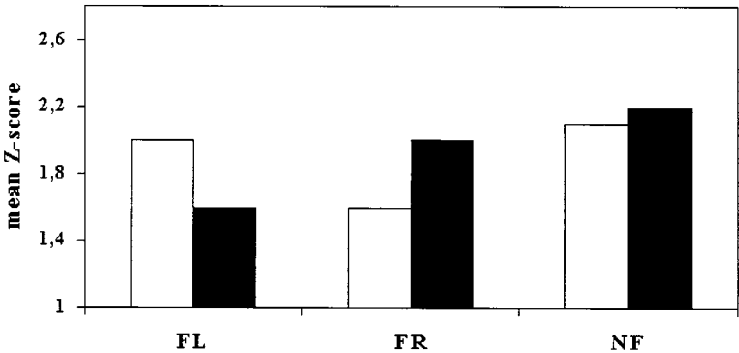


FIG. 3. Averaged hemodynamic response relative to baseline for Heschl's gyrus (HG) and the planum polare (PP) broken down for the right (unfilled bars) and left hemisphere (filled bars) and for the three attention conditions.

1985)] with repeated measurements on each factor (*hemisphere*: left vs right; *attention*: FL, FR, and NF; *task*: phonetic vs emotional task). Both the HG and PP showed increased activity in the contralateral hemisphere during the selective attention to targets presented to the right and left ears, resulting in significant interactions between *hemisphere* and *attention* for HG and PP [HG: $F(2, 9) = 8.34, p \leq .009, \eta^2 = 0.65$; PP: $F(2, 9) = 7.5, p \leq .012, \eta^2 = 0.63$]. Post hoc comparison revealed that the activations in the right HG and PP were stronger during the FL than during the FR condition. Similarly, when attention was focused on the right ear, activation in the right hemisphere drops substantially while activation in the left increases (all p values $< .05$; see Fig. 3).

Contrary to the attentional modulation noted in HG and PP, the other regions of interest did not show attention-dependent differences in activity. There was, however, a pattern of increased left-sided activity across all conditions in the PT and pSTS [PT: $F(1, 10) = 5.4, p \leq .04, \eta^2 = 0.35$; pSTS: $F(1, 10) = 9.4, p \leq .012, \eta^2 = 0.48$]. The opposite pattern was found for the aSTS and the IFG, which both showed increased right-sided activity throughout the conditions [aSTS: $F(1, 10) = 19.1, p < .001, \eta^2 = 0.66$; IFG: $F(1, 10) = 9.6, p \leq .011, \eta^2 = 0.49$] (Fig. 4, Table 3). There were no further significant main effects nor interactions.

DISCUSSION

The present study was designed to answer three basic questions: (1) Does focusing attention on one ear have a substantial influence on the activation within the auditory

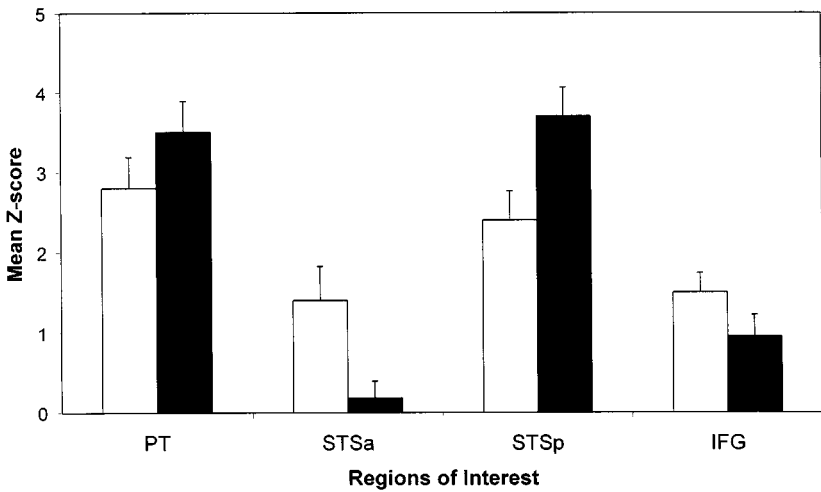


FIG. 4. Averaged hemodynamic response relative to baseline for the planum temporale (PT), the anterior superior temporal sulcus (aSTS), the posterior superior temporal sulcus (pSTS), and the inferior frontal gyrus region (IFG) broken down for the right (unfilled bars), and left hemisphere (filled bars). All between hemisphere differences are significant. Standard deviations are represented as antennas.

cortices? (2) Are the ear advantage scores in the different dichotic tasks related to a specific pattern of hemodynamic response within the auditory cortices? (3) Is there a consistent difference of cortical activation between the phonetic and emotion task? The performance rates for the different dichotic tasks were as expected and resemble those found in previous behavioral studies applying the same stimuli (Bryden et al., 1994; Bulman Fleming et al., 1994). As demonstrated in these studies, there was a significant REA for the phonetic task and a significant LEA for the emotion task. In addition, focusing attention to one ear increased the detection performance of those stimuli presented to the attended ear. Although there was a strong ‘‘focused attention’’ effect for the phonetic task there was no such effect for the emotion task. The better performance on the emotion task compared to the phonetic task suggests that the nonforced attention condition was easy and subjects did not benefit from the

TABLE 3

Mean Hemodynamic Response and Standard Deviation (*SD*) Related to Baseline for the ROIs Broken Down for the Hemisphere (RH and LH), the Task (E: Emotional; PH: Phonetic), and the Attention Condition (FL, FR, and NF)

			HG		PT		PP		aSTS		pSTS		IFG	
			Mean	<i>SD</i>	Mean	<i>SD</i>	Mean	<i>SD</i>	Mean	<i>SD</i>	Mean	<i>SD</i>	Mean	<i>SD</i>
RH	E	FL	2,7	1,5	2,7	0,9	2,1	1,8	1,7	0,9	2,4	1,1	1,4	0,4
		FR	1,8	1,3	2,2	1,3	1,5	1,7	0,9	1,1	2,2	1,0	1,3	0,9
		NF	2,7	1,7	3,0	1,7	2,3	2,4	1,5	2,0	2,8	1,3	1,7	0,9
	PH	FL	2,5	1,1	2,7	1,3	2,0	1,9	1,5	1,3	2,4	1,2	1,5	0,9
		FR	2,4	1,5	2,9	1,2	1,8	1,6	1,3	1,5	2,3	1,3	1,5	1,0
		NF	2,7	1,6	3,2	1,7	2,0	1,8	1,5	1,7	2,4	1,4	1,6	0,9
LH	E	FL	1,6	1,4	3,4	1,2	1,5	1,7	-0,2	0,5	3,5	0,9	0,6	0,9
		FR	1,4	1,6	3,0	0,9	1,7	1,4	-0,4	0,5	3,0	1,5	0,5	1,2
		NF	1,9	2,0	3,7	1,6	2,2	2,0	-0,2	1,0	4,3	1,3	1,1	1,0
	PH	FL	1,6	1,2	3,3	1,1	1,8	1,2	-0,2	0,7	3,5	1,1	1,0	0,7
		FR	2,3	1,6	3,4	1,2	2,4	1,7	0,1	0,8	3,8	1,3	1,3	0,8
		NF	2,0	1,8	3,9	1,7	2,4	1,6	-0,2	0,8	4,1	1,4	1,2	0,8

effect of attention. Future work should attempt to equilibrate task demands in studies of verbal and nonverbal processing.

With respect to our first question we found that the hemodynamic responses within the auditory cortex varied in accordance with the forced attention conditions irrespective of the task. Focusing attention to the left ear revealed strong activation in the contralateral right auditory cortex while allocating the attention to the right ear enhanced activation on the contralateral left auditory cortex (supporting the *attentional* model). Interestingly, the auditory cortex activation ipsilateral to the attended ear decreased significantly in these focused conditions. Thus, this finding is in concordance with previous dichotic listening studies in the context of PET measurements which have shown that the degree of activation in the auditory cortex depends on the direction of attention (O'Leary et al., 1996) (for a different finding see Hugdahl et al., 2000; and Alho et al., 1999). A further PET study revealed a trend for a similar effect although this effect was only present in the posterior auditory cortex in the vicinity of the PT (Tzourio et al., 1997).

A specific goal of our study was to examine this attention-related activation within the auditory cortex more precisely. We therefore defined several regions of interest covering the core, belt, and parabelt regions of the auditory cortex in order to circumvent the likely problem associated with intersubject averaging and to differentiate the activations in the different parts of the auditory cortices. In fact, we found that the anterior parts of the auditory cortices on the superior temporal plane comprising the HG and the PP showed attentional modulation while the hemodynamic responses in the PT, aSTS, pSTS, and IFG did not depend on the direction of attention. In the context of dichotic listening, this is a new finding emphasizing the role of the anterior auditory areas for the control of auditory attention as suggested in earlier fMRI and MEG studies (Fujiwara, Nagamine, Imai, Tanaka, & Shibasaki, 1998; Jancke et al., 1999b; Woldorff et al., 1993). However, the precise mechanism by which early auditory processing is modulated by attention remains unknown. A tonic increase of activity in the primary auditory cortex might occur in anticipation of a stimulus. Alternatively, there could be a phasic modulation such that each target stimulus elicited a larger response in an auditory target area. In future studies it will be necessary to disentangle these two alternatives in more detail. The specific role of the PP for this kind of attentional modulation is not clear at present. However, the PP is strongly interconnected via association and projection fibers with the core and belt regions of the auditory cortex as well as with the brain areas located in the inferior frontal gyrus (e.g., Broca's area; see Sedat & Duvernoy, 1990). Because the PP is located adjacent to HG this region might serve as a kind of interplay station between HG and the other belt and parabelt regions.

With respect to our second question, we found no association between the ear advantage scores and the hemodynamic responses within the auditory cortices. Although there was a clear difference between the phonetic and emotion detection tasks in terms of the direction of the ear advantage during the nonforced conditions (phonetic task: REA and emotion task: LEA), this pattern of performance was not correlated with the hemodynamic responses in any of the ROIs (not supporting both the *attentional* and *structural* models). We rather found strong bilateral activations during the nonforced conditions. This finding, although negative, is interesting. It suggests that a specific level of activation within a neural network does not inevitably determine the performance of this particular network. It rather suggests that during the nonforced conditions, additional processes are involved requiring control resources and thus attenuating detection performance. One possible process might be the control of interhemispheric communication. According to the "callosal relay" model, verbal or phonetic information which has been presented to the subdominant right

hemisphere must be transferred to the dominant hemisphere via callosal channels (Jancke & Steinmetz, 1994b). During the phonetic task stimuli presented to the left ear will be transferred from the right auditory cortices which are not specialized for verbal processing to the specialized auditory areas on the left hemisphere via callosal channels. Conversely, emotional information presented to the right ear will be transferred from the left auditory cortex which might not be specialized for processing this kind of information to the right auditory cortex where the specialized neural networks are presumably located. Such kind of callosal transfer may require additional control demands. For example, the relayed information must be inserted into the ongoing analysis process in the left auditory areas. This insertion process is a likely source of interference. In addition, since only 2% of all cortical neurons are connected via callosal axons, only a fraction of the information could be transferred via the callosum. Finally, the transfer process takes a specific amount of time ranging from 15 to 35 ms, a delay which may also influence the quality of the transferred information (Jancke et al., 1994b; Jancke, Steinmetz, & Volkman, 1992). Taken together, the nonforced conditions reveal bilateral activation in the HG and PP resembling the sum activation of both the FR and FL conditions. Performance in the nonforced conditions, however, is less than for the forced conditions suggesting that the nonforced conditions require more resources than the forced conditions. In conclusion, the ear advantage in both nonforced dichotic tasks are not a simple consequence of asymmetric activations within the auditory cortices nor of directed attention. It is rather obvious that further processes are involved determining the ear advantage.

With respect to our third question concerning the assumed difference in cortical activation for the phonetic and emotional task we did not find any difference. We rather found a general right-sided activation during all tasks of the anterior STS and the IFG across both phonetic and emotion tasks (not supporting the *structural* model). That we found strongly right lateralized activation across both phonetic and emotion tasks might be related to an increased salience of the emotional tone of the words in contrast to the phonetic aspects of the words therefore evoking more right-sided activations in areas known to be involved in emotional processing (Buchanan, et al., 2000; George, Ketter, Gill, Haxby, Ungerleider, & Herscovitch, 1993; George, Ketter, Parekh, Horwitz, Herscovitch, & Post, 1995).

A further finding of the present study is that the PT and the posterior STS revealed an asymmetric activation pattern favoring the left hemisphere irrespective of the dichotic listening condition or the particular task. This lateralized activation pattern might be related to the cytoarchitectonic and structural asymmetry of the PT favoring the left hemisphere in terms of the volume of the association cortex Tpt and the volume of the PT (Galaburda, Sanides, & Geschwind, 1978; Galaburda & Sanides, 1980; Geschwind & Levitsky, 1968; Jancke et al., 1994a; Steinmetz et al., 1991). These anatomical findings support the hypothesis that the left PT and adjacent regions including the posterior STS in close vicinity of the descending ramus of the Sylvian fissure contain neural networks specialized for language processing. Thus, the asymmetric activation pattern found in our study might indicate the processing of this specialized network during processing of verbal dichotic stimuli.

In conclusion, we obtained data supporting the idea that the ear advantage in the nonforced dichotic listening condition is not simply a product of a lateralized activation within the auditory areas (core, belt, and parabelt regions). Thus, the simple assumption of the “structural” model describing the ear advantages is not supported by our data. In addition, the assumption of attention as the main factor determining ear advantage is also not supported because there is virtually no difference between the REA and LEA conditions. It is, however, likely that this behavioral asymmetry is a consequence of several factors comprising callosal transfer as well as different

processing capacities within the bilateral network. A further finding of our study is that focusing attention to one ear has substantial influence on the activation within the anterior auditory cortices comprising HG and PP. These findings extend previous research which has illustrated attentional modulation of the auditory cortex during dichotic listening tasks (Hugdahl et al., 2000; Hugdahl et al., 1999; O'Leary et al., 1996; Alho et al., 1999) by showing that specific regions within the auditory cortex are modulated by lateralized attention. This work further illustrates the influence of higher cognitive processes of attention on the function of selective cortical regions.

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