Auditory Target Detection in Dichotic Listening Involves the Orbitofrontal and Hippocampal Paralimbic Belts

In dichotic listening, two similar, yet different stimuli are presented simultaneously to the left and right ear. When two syllables are presented in this way, they seem to blend and discrimination of syllables presented to one ear is only possible with uncertainty. In this event-related fMRI study, we found that the orbitofrontal and paralimbic belts were involved in target detection in dichotic listening. The posterior orbital gyri bilaterally, the left amygdala, hippocampal formation and the left pregnum paracingulate area (PPA) were activated more strongly during dichotic target detection than during correct rejection of target presence. The right posterior orbital gyrus also showed stronger activation during dichotic compared to diotic target detection. Further analyses showed that the blood oxygen level dependent (BOLD) responses in these areas, with the exception of the right hippocampal formation, varied with the subjective decision on target presence rather than with the physical target presence itself. The left PPA, amygdala and hippocampal formation responded differently to left and right ear target detection, suggesting their involvement in the right ear advantage observed in this task. The data show the importance of the orbitofrontal and hippocampal paralimbic belts for auditory stimulus decision processes based on ambivalent sensory information.

Keywords: auditory, decision, detection, dichotic listening, fMRI, orbitofrontal

Introduction

In noisy environments, it is often difficult to discriminate a particular sound. When many people are talking to each other in a room; for instance, it may be difficult to understand what a particular speaker says. Instead of clearly understanding the words, we may be forced to infer from the noisy auditory input what the speaker may have said. An experimental setting which affords such decisions on auditory stimuli is dichotic listening. In dichotic listening, two different stimuli are presented simultaneously, one in each ear. The blend of the two simultaneously presented stimuli leads to a high degree of uncertainty about which stimuli have been presented. When subjects are asked to detect a target syllable, the numbers of errors sharply increases when compared to diotic presentation, i.e. simultaneous presentation of the same stimulus to both ears. Thus, dichotic listening requires the listener to make a decision on target presence which is based on noisy sensory stimuli.

In the past, dichotic listening has mainly been used as a tool to investigate interhemispheric transfer or auditory attention (for recent reviews, see Hugdahl, 2003; O’Leary, 2003). Disruption of interhemispheric transfer by complete callosal lesions (Milner et al., 1968; Sparks and Geschwind, 1968) or partial callosal lesions affecting the splenium (Sugishita et al., 1995; Pollmann et al., 2002) was found to lead to a left ear suppression, indicating deficient processing of left ear input in the language-dominant left hemisphere. The importance of left-hemispheric language areas for the processing of linguistic material, such as consonant-vowel (CV) syllables or words, was underlined by functional imaging studies which consistently found activation in auditory areas of the superior temporal gyrus, dominantly in the LH (Pugh et al., 1996; Hugdahl et al., 1999, 2000; Hashimoto et al., 2000; Jäncke et al., 2001; Jäncke and Shah, 2002; Lipschutz et al., 2002). In addition, the lateral inferior frontal gyri and inferior posterior parietal cortex were consistently activated. While these studies delineated the neural substrates which are involved in dichotic listening, compared to diotic listening or other low-level auditory baselines, some brain imaging studies found an interaction of sustained attention to one ear and dichotic stimulus presentations (e.g. Hugdahl et al., 2000; Jäncke and Shah, 2002; Lipschutz et al., 2002) in frontal and parietal cortical areas. In addition, Hugdahl et al. (2003) showed that patients with frontal lobe lesions were unable to report the stimulus in the right ear compared to a healthy control group. This points to the involvement of cortical areas beyond the auditory association areas in dichotic listening.

However, to our knowledge, the neuronal circuitry involved in the detection of dichotically presented target syllables is still unknown. In the present study, we ask which brain areas are involved when subjects decide on the presence or absence of a target sound, presented simultaneously with a distractor sound on the other ear. Previous imaging studies of dichotic listening relied on block designs, i.e. blocks of dichotic listening trials were compared to blocks of diotic listening trials (or other control conditions). In this way, blockwise variations of attention, such as attend left versus attend right ear conditions, could be investigated. However, because the order of target presence and ear of target presentation need to be randomized in dichotic listening, only an event-related design, as used in the current study, can capture directly the activation changes which go along with the sensory decision processes leading to a target present or absent judgment.

Which brain areas may support these auditory decision processes? Previous studies in rhesus monkeys (Pandya and Barnes, 1987; Barbas, 1992, 1993) have identified a stepwise projection of connections from the primary auditory cortex ‘down’ to posterolateral orbital cortex. The latter receives the majority of its auditory projections from rostral parts of the superior temporal gyrus, which constitutes the least architectonically differentiated auditory cortex. These stepwise auditory projections may represent a putative auditory object recognition (‘what’) pathway (Romanski et al., 1999; Rauschecker and Tian, 2000) in contrast to an auditory localization (‘where’)
pathway originating in caudal parts of the superior temporal gyrus and projecting mainly to parietal cortex (Zatorre et al., 2002) and to posterior parts of prefrontal cortex (Romanski et al., 1999; for a recent review, see Scott and Johnsrude, 2003). Detection of target stimuli in dichotic listening certainly relies on the ‘what’ pathway rather than the ‘where’ pathway, because the target stimulus needs to be discriminated from a very similar distractor stimulus (whereas localization to the left or right ear is irrelevant in our study). However, we were not interested in auditory stimulus discrimination processes per se, which were probably comparably active in every trial of our demanding dichotic listening task, but rather in the processes leading to a decision on target presence based on the output of auditory discrimination processes. The neural substrate subserving auditory target decision processes may thus be related to the auditory ‘what’ stream.

The difficulty of the decision about target presence in dichotic listening lies in the similarity of the two different stimuli which are presented simultaneously to both ears. A target, in our case the CV syllable /TA/ may be paired with a distractor syllable, e.g. /GA/, on the other ear. Alternatively, a pair of distractor syllables, such as /PA/ and /GA/ may be presented. Under these conditions, decisions about target presence can only be made with a high degree of uncertainty. When we analyze such auditory stimulus decision processes under uncertainty, we are likely to involve brain areas which support decisions based on insufficient information. Notably, the prefrontal endpoint of the putative auditory ‘what’ stream lies in an area which is involved in such decision processes under uncertainty. Lesions of ventromedial prefrontal cortex lead to suboptimal decision making when decisions have to be made on probabilistic information (Bechara et al., 2000). ‘Decisions’ in the absence of relevant information, i.e. guessing, leads to activation of orbitofrontal cortex, with increasing activation as the number of alternatives increases (Elliott et al., 1999). These studies investigated decisions in rather complex card game situations. However, comparable principles may also be involved in stimulus decision processes under uncertainty in dichotic listening.

Materials and Methods

Subjects

Fourteen subjects (six female) participated in the fMRI experiment, each having given prior informed consent according to the Max Planck Institute guidelines. The study was approved by the local ethics review board at the University of Leipzig. All subjects were right-handed, as assessed with a German adaptation of the Edinburgh Inventory (Oldfield, 1971). They had no known hearing deficits. Subject age varied between 20 and 38 years of age, with a mean age of 26 years.

Stimuli

Pairs of CV syllables were presented dichotically via headphones [Sennheiser HD 600 for the training session, Commander XG MRI Audio System (Resonance Technology, California, USA) in the scanner]. Two experimental sets, consisting of three CV syllables each, were used: [/GA/, /PA/, /TA/] and [/BA/, /PA/, /TA/]. Ten subjects received the first set and the remaining four the latter. In the entire experiment the syllable /TA/ was specified as target, because in preliminary testing it produced the most pronounced right ear advantage with a right to left detection ratio of ~2.3:1/3.

Syllable duration was equated as far as possible (range 348–359 ms). The stimuli were digitized (as stereo VOC files, 16 bit/22 kHz) and presented from a PC equipped with a Creative Laboratories SoundBlaster 16PnP board. After digitization, the dichotic syllable pairs were temporally aligned for simultaneous onset in the left and right channels and with regard to initial and final energy release with the aid of a stereo channel editing sound editor (Cool Edit, v. 1.52; Syntrillium Software Corp., Phoenix, AZ). Stimulus presentation was controlled by an ASCII running script made functional through the software package ERTS (Experimental Run Time System; Berisoft Co., Frankfurt am Main, Germany).

Procedure and Design

Each trial started with the presentation of a pair of CV syllables for ~350 ms and lasted for 4 s. Subjects were instructed to press the left button with their right index finger if they heard a /TA/ irrespective of the laterality and the right button with their right middle finger if they did not hear a /TA/. No visual input was given, subjects were instructed to close their eyes during the experiment.

We introduced six experimental conditions (Table 1): (1) right ear target plus left ear distractor (/PA/–/TA/ and /GA/–/TA/); (2) left ear target plus right ear distractor (/TA/–/PA/ and /TA/–/GA/); (3) dichotic distractors (/PA/–/GA/ and /GA/–/PA/); (4) diotic targets (/TA/–/TA/); (5) diotic distractors (/PA/–/PA/ and /GA/–/GA/); and (6) null events (4 s silent periods). All conditions had 48 repetitions over the experiment (except for the diotic targets and distractors with 24 repetitions each), resulting in 240 trials in total. Trial order was pseudo-randomized to control the probability of transitions from one trial to the next (controlled for type of condition, laterality of target syllable and laterality of distractor syllables). Each subject received their own randomization sequence.

The whole experiment was divided in four blocks of 60 trials. Before, after and between blocks, silent intervals of 2–4 s duration were presented. These served as breaks, because the task was very demanding and were not entered in any analysis. After 10 s of break, three repetitions of the diotically presented target /TA/ reminded the subjects of its sound and indicated the start of the next block. The total experiment lasted for 18 min.

Each subject received a training block of 120 trials just before the scanning session. After positioning the subjects in the scanner, a short test of the auditory stimulation system was performed by presenting /TA/ on the left and on the right side alternately, so that the subjects were able to check the fit of the headphones.

Behavioral Data Analysis

Statistical data analyses were performed with matched-pairs t-tests with a significance criterion of α = 0.05. The ratio of left and right ear target detection was computed as a laterality score according to the following formula:

\[
LS = (D_l - D_r)/(D_l + D_r)
\]

Note that for five participants /GA/ was replaced with /BA/.

### Table 1

<table>
<thead>
<tr>
<th>Condition</th>
<th>Stimuli</th>
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<tr>
<td>/TA/ — right</td>
<td>/GA/–/TA/</td>
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<td>/TA/ — left</td>
<td>/PA/–/TA/</td>
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<td>Distractors — diotic</td>
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<tr>
<td>Null events</td>
<td>/PA/–/PA/</td>
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<td>12</td>
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Note: Number of trials per condition.
whereby \( D_i(D_j) \) is the number of correct target detections in the right (left) ear. Positive scores indicate a relative advantage for the right ear stimulus (maximum = 1). Negative scores indicate a relative advantage for the left ear stimulus (minimum = -1), while a score of zero would indicate the absence of an ear advantage.

**MRI Scanning Procedure**

Functional images were collected at 3 T with a Bruker 30/100 Medspec system (Bruker Medizintechnik, Ettlingen, Germany). A gradient-echo EPI sequence was used with \( T_E = 30 \) ms, flip angle = 90°, \( T_R = 3000 \) ms and an acquisition bandwidth of 100 kHz. The matrix acquired was 64 × 64, with a FOV of 19.2 cm, resulting in an in-plane resolution of 3 × 3 mm. The slice thickness was 5 mm with an interslice gap of 2 mm. Eight axial slices were acquired, oriented parallel to the AC–PC plane and covering -2/3 of the temporal lobe, reaching to the upper border of the corpus callosum (Fig. 1). Slice number was limited to eight to reduce the gradient noise and make sufficient perception of the auditory stimuli possible.

To improve the effective sampling rate, the stimulus onset was varied in relation to the timing of image acquisition (Josephs et al., 1997; Miezin et al., 2000). Due to the difference in trial length of 4 s and \( T_R \) of 3 s, one-third each of stimuli was presented at the beginning of image acquisition, or 1 or 2 s later. Image acquisition was continuous, so that the gradient noise was constant in all trials.

**fMRI Data Analysis**

Analysis of fMRI data was performed using the LIPSIA software package (Lohmann et al., 2001). Movement artefacts were corrected using a matching metric based on linear correlation. Then, a correction for slice acquisition order using sinc interpolation was performed. The data were spatially smoothed with a Gaussian kernel with FWHM = 7 mm. All functional data sets were individually registered into a 3D stereotactic coordinate system using the subjects’ individual high resolution anatomical images. The 2D anatomical slices, geometrically aligned with the functional slices, were used to compute a transformation matrix, containing rotational and translational parameters, that registered the anatomical slices with the 3D reference data set. Geometrical distortions of the EPI-\( T_i \) images were corrected using additional EPI-\( T_i \) refinement on the transformation matrices. These transformation matrices were normalized to the standard Talairach brain size (Talairach and Tournoux, 1988) by linear scaling and then finally applied to the individual functional data. The normalized 3D datasets had an isomorphic voxel size of 3 mm side length.

The statistical evaluation was based on the general linear model for serially autocorrelated observations (Friston et al., 1995; Worsley and Friston, 1995). Statistical parametric maps (SPM) were generated for each individual subject. The design matrix for event-related analysis was created using a synthetic model of the hemodynamic response function and its temporal derivative (Josephs and Henson, 1999). The model equation, including the observation data, the design matrix and the error term, was convolved with a Gaussian kernel with a dispersion of 3 s FWHM. The data were high-pass-filtered using filter frequencies which were based on the individual data of each subject, since all subjects had different detection rates of /TA/. The filter frequencies were calculated by multiplying the average individual repetition interval of the dichotic conditions by a factor of 1.5. Frequencies ranged from 1/36 to 1/84 Hz. The model includes an estimate of temporal autocorrelation. The effective degrees of freedom were estimated as described by Worsley and Friston (1995).

A random effects analysis was calculated (Holmes and Friston, 1998), by computing one-sample \( t \) tests of contrast-maps across subjects. The significance criterion was \( \alpha = 0.0005 \), uncorrected for multiple comparisons. To reduce the probability of false positives (type I error), we set a blob size threshold of 135 mm\(^3\) (equal to five contiguous voxels after registration; cf. Forman et al., 1995). All presented SPM\( \{z\} \) were mapped onto an anatomical data set averaged out of the normalized individual high resolution anatomical datasets of the 13 subjects.

All events in the design file were logged to stimulus onset. Only trials with correct detection of /TA/, or correct rejection of /\( \text{GA} \)/ /\( \text{BA} \)/, or /PA/ entered the analysis.

Since dichotic listening with CV syllables typically yields a right ear advantage, i.e., more target detections on the right ear, one could expect that due to the higher number of repetitions, the comparison of conditions is biased toward stronger activations for right ear targets. To avoid this bias, we randomly deleted supernumerary right ear or left ear target trials so that the conditions /TA/-left and /TA/-right had an equal number of repetitions within each subject.

For those areas most strongly activated in the contrasts of correct responses to left and right ear dichotic targets versus dichotic distractors, we extracted the event-related blood oxygen level dependent (BOLD) signal in a voxel of 9 mm side length around the highest group activation. This corresponds to the voxel of peak activation and the directly adjacent voxels in all three dimensions in the registered dataset. The reported signal time courses were obtained after slice-time correction, movement correction and baseline filtering as described above and normalization to the initial timepoint of the event-related response and transformation into percentage signal change. We have analyzed all areas with significant activations in the contrasts of right or left ear targets against dichotic distractors (Table 2b). For reasons of space, we present time courses from those areas in which they contribute to a functional understanding beyond the contrasts used for selection.

The signal time courses were subjected to MANOVAs to assess the contrasts of interest. The MANOVAs were calculated over percentage signal change in a time window of 16 s from trial onset.

**Results**

**Behavioral Performance**

One subject, who had 65% false alarms in dichotic listening, was excluded from further analysis. Right ear targets were detected more often than left ear targets in 8 out of the remaining 13 participants, which led to a marginally significant right ear advantage \( \{ t(12) = 1.72, P = 0.056; \text{one-sided test}\} \). On average, 70% of right ear targets and 59% of left ear targets were detected. False alarms (i.e., false-positive responses) were elicited in an average 17% of trials not containing a target. The substantial amount of misses and false alarms, which illustrates the difficulty of the task, had the benefit of enabling us to analyze the BOLD response obtained during the error trials. Dicot presentation yielded 83% correct detections and 16% misses (neither a present nor an absent response was given in the remaining 1% of trials). False alarms were recorded in 4% of dicotic distractor trials. The percentage of correct detections was significantly higher for dicotic targets than for dichotic right ear targets \( \{ t(12) = 2.73, P = 0.018 \} \) or left ear targets \( \{ t(12) = 4.61, P = 0.001 \} \). Conversely, the percentage of misses of dicotic targets was lower than for dichotic right ear targets \( \{ t(12) = 2.57, P = 0.025 \} \) or left ear targets \( \{ t(12) = 4.28, P = 0.001 \} \). False alarms also occurred in a lesser percentage of dicotic distractor trials than dicotic distractor trials \( \{ t(12) = 4.01, P = 0.002 \} \).

**Functional Imaging**

**Dichotic Listening versus Baseline**

As a first step, we compared trials with correct target detections against a baseline of null events, i.e., periods of silence of equal length and distribution as trials from the experimental conditions. An example for a right ear target contrast is the pair /PA/-/TA/ compared to a silent period.

Target detection, on the left as well as the right ear, elicited activation in the middle portion of left Heschl’s gyrus and adjacent areas of the planum temporale and planum polare, as well as in the entire Heschl’s gyrus on the right, extending into the...
Table 2
List of functional activations

<table>
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<tr>
<th>x</th>
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<th>z</th>
<th>$Z_{\text{max}}$</th>
<th>mm$^3$</th>
<th>Structure</th>
<th>BA</th>
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<td>Left hemisphere</td>
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<td>Right hemisphere</td>
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(a) List of activations for the baseline contrastsa

/\TA/ — left versus null events

1. $-43$ $14$ $18$ $4.4$ $511$ Inferior frontal gyrus BA 09
2. $-47$ $-19$ $12$ $5.24$ $37991$ Transverse temporal gyrus BA 41
3. $49$ $-16$ $3$ $5.22$ $15975$ Superior temporal gyrus BA 22
4. $34$ $-52$ $12$ $4.51$ $188$ Superior temporal gyrus BA 22
5. $13$ $-67$ $38$ $3.76$ $183$ Precuneus BA 07
6. $4$ $-31$ $24$ $3.85$ $513$ Posterior cingulate BA 23

/\TA/—right versus null events

7. $-50$ $-16$ $3$ $5.15$ $22272$ Superior temporal gyrus BA 22
8. $47$ $-22$ $3$ $5.34$ $22072$ Superior temporal gyrus BA 22
9. $31$ $-58$ $38$ $3.81$ $135$ Angular gyrus BA 39
10. $-26$ $-58$ $32$ $3.66$ $153$ Intraparietal sulcus BA 22
11. $13$ $-67$ $41$ $4.21$ $1177$ Precuneus BA 07
12. $-29$ $-64$ $12$ $4.11$ $171$ Posterior cingulate gyrus BA 30
13. $-34$ $23$ $3$ $4.66$ $8783$ Anterior insula BA 13
14. $-26$ $-34$ $27$ $3.71$ $220$ Posterior insula BA 23
15. $28$ $-13$ $21$ $3.95$ $161$ Claustrum BA 23
16. $10$ $11$ $-3$ $3.92$ $207$ Caudate head BA 23
17. $4$ $-55$ $-3$ $4.27$ $679$ Cunmen BA 23

(b) List of activations for target–distractor and target–target contrasts b

/\TA/ — left versus dichotic distractors

18. $-34$ $17$ $-18$ $3.61$ $384$ Posterior orbital gyrus BA 47
19. $-26$ $-10$ $-18$ $4.34$ $205$ Amygdala BA 47
20. $-23$ $-22$ $-12$ $3.8$ $29**$ Hippocampus BA 47
21. $-1$ $53$ $-3$ $3.41*$ Pregen. paracingulate area BA 10
22. $-7$ $32$ $12$ $3.31*$ Anterior cingulate BA 24
23. $-52$ $4$ $-12$ $3.26*$ Superior temporal gyrus BA 38

/\TA/ — right versus dichotic distractors

24. $-5$ $53$ $0$ $3.73$ $206$ Paracingulate area BA 10
25. $-19$ $17$ $-15$ $4.03$ $165$ Posterior orbital gyrus BA 47
26. $13$ $11$ $-15$ $4.2$ $149$ Posterior orbital gyrus BA 47
27. $-26$ $-25$ $-9$ $3.77$ $151$ Hippocampus BA 47
28. $-2$ $-40$ $30$ $3.92$ $688$ Posterior cingulate gyrus BA 23
29. $-49$ $-16$ $-9$ $3.7$ $35**$ Superior temporal gyrus BA 22
30. $-37$ $-76$ $35$ $3.75$ $80**$ Angular gyrus BA 39
31. $-8$ $-67$ $41$ $3.55$ $36**$ Precuneus BA 7
32. $7$ $-69$ $41$ $3.8$ $108**$ Precuneus BA 7

/\TA/ — left versus /\TA/ — diotic

33. $31$ $17$ $-12$ $3.7$ $47500$ Posterior orbital gyrus BA 47

/\TA/ — right versus /\TA/ — diotic

34. $29$ $17$ $-12$ $3.91$ $32700$ Posterior orbital gyrus BA 47

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*Experimental conditions: /\TA/ — left (right) versus null events — targets (/\TA/) presented on the left (right) ear, simultaneously with a distractor syllable on the contralateral ear, were compared to silent periods. x, y, z denote coordinates according to Talairach and Tournoux (1988). $Z_{\text{max}}$ indicates the maximum Z-value. BA, Brodmann area; *P < 0.001. Only activations with an extent ≥135 mm$^3$ are reported.

**Experimental conditions: /\TA/ — left (right) versus dichotic distractors — targets (/\TA/) presented on the left (right) ear, simultaneously with a distractor syllable on the contralateral ear, were compared to dichotically presented pairs of distractors. /\TA/ — left (right) versus /\TA/ — diotic — targets (/\TA/) presented on the left (right) ear, simultaneously with a distractor syllable on the right (left) ear, were compared to presentation of /\TA/ on both ears. The latter analysis was only carried out in the areas activated in the contrasts of left or right dichotic distractors versus pairs of dichotic distractors.

**Activations with an extent < 135 mm$^3$. See also previous note.
Figure 1. Functional activation. (a) Auditory cortex activation elicited by targets plus dichotic distractors versus silent baseline. Detection of targets on one ear, presented simultaneously with a distractor on the other ear, elicited activations in the superior temporal gyri bilaterally. The figure shows activation elicited by dichotic right ear targets minus null-events. The plane was selected to show the maximal activation in left auditory cortex (indicated by crosshairs). The box shows the area in which functional activation was measured. (b) Activation associated with dichotic target detection. Event-related activation observed in trials in which a target, simultaneously presented with a distractor on the contralateral ear, were compared to trials with distractor pairs. Only trials with correct responses, i.e. correct detection and correct target absent responses, were included. Activation is superimposed on the averaged anatomy of the participants. The legends indicate Z-values. PPA, pregenual paracingulate area; PCG, posterior cingulate gyrus. Left hemisphere is on the left. The numbers refer to the activations listed in Table 2b. The graphs show the averaged event-related BOLD time courses for correct detections (CD) and misses (miss) of left and right ear targets, as well as for correct rejection (CR) of target presence and false alarms (FA).
convexity of the posterior superior temporal gyrus (Table 2a; Fig. 1a). In addition, left ear target detection elicited activation of left inferior frontal gyrus (BA 10/9). Further activations were found in right posterior cingulate gyrus and right posterior precuneus (BA 7m).

Right ear target detection activated, in addition to the superior temporal gyri, right angular gyrus and right posterior precuneus (BA 7m). In addition, left posterior cingulate gyrus (BA 30) was activated. Further activations were observed in the left anterior and posterior insula, in the claustrum and in the thalamus, bilaterally, and in the head of the right caudate nucleus. There were also activations in the left mesencephalon and the culmen.

**Dichotic Target Detection**

The baseline contrasts enabled us to demonstrate that the dichotic listening task elicited proper activation of a set of brain areas including auditory cortex in the fMRI experiment. The goal of this study, however, was the investigation of target detection in dichotic listening. To achieve this goal, we needed to compare trials in which targets were presented simultaneously with a distractor syllable on the other ear, with targets in which two dichotic distractors were presented. An example for a right ear target is the pair /PA/–/TA/ compared to /PA/–/GA/.

Right ear targets elicited increased activation (Fig. 1b and Table 2b) in the pregenual portion of the paracingulate area (BA 32/10), in the medial portion of the posterior orbital gyrus, bilaterally and in the left hippocampus proper, in the border region between the hippocampal head and body regions (Fig. 2), as well as more posterior in the left posterior cingulate gyrus (BA 23) and right posterior precuneus. Further activations of small extent were observed in the middle portion of the left superior temporal sulcus, left angular gyrus and in left posterior precuneus.

Detection of left ear targets, compared to dichotic distractors, activated the left posterior orbital gyrus, behind the transverse (H) sulcus of the orbital cortex laterally adjacent to the border of the medial and lateral orbitofrontal portion, as well as the left amygdaloid complex. An activation of small extent was observed in the left hippocampus proper, at the border of hippocampal head and body regions (Fig. 2). In order to explore near-threshold activation, we lowered the significance threshold to $P = 0.001$ to search for additional activations in the areas which were activated during right ear target detection. This analysis yielded additional activations in the left pregenual paracingulate area (PPA), in left anterior cingulate (BA 24) and in the anteriormost portion of the superior bank of the left superior temporal sulcus (BA 38; Table 2b).

**Dichotic versus Diotic Target Detection**

Which of these activations are specific for target detection in dichotic listening? To investigate this issue, we analyzed which of the areas activated in the contrast of dichotic targets versus dichotic distractors showed a significant signal increase when dichotic target detection (e.g. /PA/–/TA/) was compared to diotic target detection (/TA/–/TA/). In both conditions, participants detected the same target and initiated the identical manual response. However, detection of dichotic targets is much more difficult and implies a decision under uncertainty. Increased activation of dichotic target detection over diotic target detection was observed in the right lateral orbital gyrus, both for left ear and right ear targets.

**Target and Response Dependence of Signal Time courses**

Selection of regions was based on the contrasts of correct dichotic target detection versus correct target absent responses in trials with dichotic distractor pairs. However, a substantial percentage of trials led to errors, which enabled us to investigate the contribution of the factor target (present/absent) on the one hand and the factor response (target present/target absent) on the other hand. Figures 1 and 2 show the BOLD time courses in areas with increased responses to dichotic target detection compared to dichotic distractors. We carried out a MANOVA with the factors target (present, absent) and response (present, absent). The main effect of target presence was only significant in the left PPA (Table 3). Activation was higher during target absent trials than target present trials in this area. Thus, signal increases due to target presence were not observed in any area. On the contrary, the main effect of response was significant in all areas but the left hippocampal formation. Target present responses yielded higher activations than target absent responses. In the bilateral orbital gyri and the left amygdala, we observed an interaction between target presence and response, indicating that response-associated activation was modulated by target presence. We therefore calculated separate MANOVAs with response (present/absent) as factor on target present (detection versus miss) and target absent trials (false alarm versus correct rejection) as well as MANOVAs with target (present, absent) as factor on trials with target present responses (detection versus false alarm) and target absent responses (miss versus correct rejection). For the target present analysis, the factor ear of target presentation (left, right) was added.

The nature of the interaction in left orbital gyrus was revealed to be a significant effect of response in target absent trials, with false alarms eliciting a stronger signal than correct rejections, while there was no significant response effect in target present trials. In contrast, right orbital gyrus and left amygdala showed significantly stronger signal increases for target present responses, both for target present and target absent trials. However, whereas they both showed no differences between misses and correct rejections, there were differences between detections and false alarms. In right orbital gyrus, false alarms elicited a higher signal increase than detections, whereas the reverse was observed in the left amygdala.

In target present trials, we could further investigate ear of target presentation as factor. The main effect of ear of target presentation was significant in the left PPA, the left amygdala and the left hippocampal formation. The left PPA and the left amygdala also showed a significant interaction between ear and response. In the left hippocampal formation, response to right ear targets, both detections and misses, were stronger than responses to left ear targets. On the contrary, in the left amygdala, correct detection of left ear targets led to higher signal increase than correct detection of right ear targets, whereas misses of left ear targets led to a stronger signal decrease than misses of right ear targets. In the left PPA the response pattern was reversed, correct detection of right ear targets yielded a stronger signal increase than correct detection of left ear targets, whereas misses of right ear targets yielded a stronger decrease than misses of left ear targets. The same
Figure 2. Activation of the orbitofrontal and hippocampal paralimbic belts associated with dichotic target detection. Event-related activation observed in trials in which a target, simultaneously presented with a distractor on the contralateral ear, were compared to trials with distractor pairs. Only trials with correct responses, i.e. correct detection and correct target absent responses, were included. The left (right) column shows activations associated with dichotic left (right) ear target detection. Legend as in Figure 1.
pattern was observed in the right precuneus. Here, we observed a particularly delayed signal decrease with misses of right ear targets.

Discussion

Our central interest was to investigate target detection processes in dichotic listening. The activations which we found when we compared target detection with correct rejection of target presence coincide very well with the two paralimbic belts which unite cortical and subcortical areas sharing phylogenetic and cytoarchitectural features common to the amygdala/orbitofrontal and hippocampal/cingulate limbic division. The two divisions of the limbic systems work in concert. The posterior orbital gyrus is said to be a gateway for sensory information into the orbitofrontal paralimbic division, which is mediated by higher order association cortices (Mega et al., 1997). It is reciprocally connected with the auditory association cortex of the dorsolateral temporal pole. Both structures were activated in the left hemisphere in our study. The posterior orbital gyrus also has direct and reciprocal connections with the dorsal and caudal regions of the basal, accessory basal and lateral amygdala (Price, 1999). Thus, the amygdala is the subcortical focus for the orbitofrontal paralimbic division, a system primarily associated with the internal relevance that sensory (olfactory, gustatory/visceral, visual and somatic) stimuli have for the organism. In addition, reciprocal connections occur with the cingulate area 24 and 32 (Morecraft et al., 1993), a region that assists attentional mechanisms and effects cognitive engagement. The general pattern of activation, from rostral temporal to orbitofrontal cortex, follows the connectivity found in the monkey brain (Pandya and Barnes, 1987; Barbas, 1992, 1993; Hackett et al., 1999). The pathway from rostral auditory belt and parabelt areas via several relays in the superior temporal gyrus to orbitofrontal cortex may have a specific role in auditory object (‘what’) recognition (Rauschecker and Tian, 2000). Our target decision-related posterior orbital gyrus activation may support this interpretation, because the decision must be based on the output of the ‘what’ stream. The posterior orbital auditory decision-related activations which we have observed may thus receive their input from the orbital endpoint of an auditory object recognition (‘what’) pathway. We also found major components of the hippocampal paralimbic division activated, mainly on the left side. Multimodal sensory information processed in this circuitry enters the anterior thalamus (not seen in our study) and from there it is projected into the posterior cingulate gyrus (BA 23) and then back to the hippocampal formation, including its subsplenial portion. The posterior cingulate is interpreted as a nexus for sensory and mnemonic networks within the hippocampal paralimbic belt. It thus shall facilitate intentional selection, habituation, or episodic encoding of sensory stimuli by the hippocampal/cingulate division (Mega et al., 1997).

The orbitofrontal and hippocampal paralimbic belts intersect in the pregenual cingulate region of BA 24, also activated in this study. The major pathway for information flow is the cingulate bundle. It contains the efferents and afferents of the cingulate to the hippocampal formation, basal forebrain, amygdala and all mesocortical areas (Vogt et al., 1993).

### Functional Characteristics of Orbitofrontal and Paralimbic Brain Areas

All areas of the orbitofrontal and paralimbic belts, with the exception of the left hippocampal formation, showed BOLD responses which varied with the participants’ decision about target presence rather than with target presence itself. Thus, these areas may be actively involved in sensory decision-making, or, alternatively, the paralimbic belts may receive a highly preprocessed perceptual input, which already carries the decision about target presence in it. In any case, they represent the subjects’ perception or perception-based decision processes rather than the stimulus input. This may be best illustrated by false alarms, which were accompanied by the strongest response in absolute terms in all areas but the left

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**Table 3**

Results of MANOVAs carried out over the BOLD response in selected brain areas

<table>
<thead>
<tr>
<th>Factor</th>
<th>Left orbital gyrus</th>
<th>Right orbital gyrus</th>
<th>Left PPA</th>
<th>Left hippocampus</th>
<th>Left amygdala</th>
<th>Left precuneus</th>
<th>Right precuneus</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall analysis</td>
<td>0.327</td>
<td>0.27</td>
<td>0.021*</td>
<td>0.151</td>
<td>0.496</td>
<td>0.275</td>
<td>0.303</td>
<td>1.68</td>
</tr>
<tr>
<td>Target</td>
<td>0.001*</td>
<td>0.001*</td>
<td>0.001*</td>
<td>0.439</td>
<td>0.001*</td>
<td>0.001*</td>
<td>0.001*</td>
<td>1.68</td>
</tr>
<tr>
<td>Response</td>
<td>0.001*</td>
<td>0.002*</td>
<td>0.263</td>
<td>0.293</td>
<td>0.014*</td>
<td>0.09</td>
<td>0.799</td>
<td>1.68</td>
</tr>
<tr>
<td>Target x response</td>
<td>0.001*</td>
<td>0.002*</td>
<td>0.263</td>
<td>0.293</td>
<td>0.014*</td>
<td>0.09</td>
<td>0.799</td>
<td>1.68</td>
</tr>
<tr>
<td>Separate analyses for target present and target absent trials</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Target present (CD/FA)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ear</td>
<td>0.825</td>
<td>0.201</td>
<td>0.001*</td>
<td>0.001*</td>
<td>0.171</td>
<td>0.275</td>
<td>1.44</td>
<td></td>
</tr>
<tr>
<td>Response</td>
<td>0.938</td>
<td>0.001*</td>
<td>0.001*</td>
<td>0.585</td>
<td>0.001*</td>
<td>0.001*</td>
<td>0.001*</td>
<td>1.44</td>
</tr>
<tr>
<td>Ear x response</td>
<td>0.563</td>
<td>0.518</td>
<td>0.001*</td>
<td>0.129</td>
<td>0.001*</td>
<td>0.123</td>
<td>0.005*</td>
<td>1.44</td>
</tr>
<tr>
<td>Target absent (CR/FA)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Response</td>
<td>0.002*</td>
<td>0.001*</td>
<td>0.001*</td>
<td>0.484</td>
<td>0.019*</td>
<td>0.017*</td>
<td>0.016*</td>
<td>1.22</td>
</tr>
<tr>
<td>Separate analyses for positive and negative responses</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Positive response (CD/FA): target</td>
<td>0.003*</td>
<td>0.014*</td>
<td>0.008*</td>
<td>0.834</td>
<td>0.013*</td>
<td>0.667</td>
<td>0.657</td>
<td>1.34</td>
</tr>
<tr>
<td>Negative response (CR/FA): target</td>
<td>0.007*</td>
<td>0.051</td>
<td>0.438</td>
<td>0.001*</td>
<td>0.253</td>
<td>0.051</td>
<td>0.194</td>
<td>1.34</td>
</tr>
</tbody>
</table>

The table contains error probabilities, *P < 0.05. PPA, pregenual paracingulate area; CD, correct detection; M, miss; CR, correct rejection; FA, false alarm; df, degrees of freedom.
amygdala. Future studies may address the functional significance of this strong false alarm response. A potential explanation may reflect differences in uncertainty between correct target present responses and false alarms. Although correct target present responses may sometimes simply be lucky guesses, they are at least in a fraction of trials based on supra-threshold perception of the target. False alarms, in contrast, are necessarily elicited in the absence of a percept of the target and therefore under particularly high uncertainty, which in turn may lead to a particularly high endogenous contribution towards eliciting a positive response.

Based on the current data, we cannot say whether these areas are actively involved in target-present responses under uncertainty, or rather in a subsequent post-decision process, such as error detection. However, whereas the onset of the signal in false alarm trials was delayed in the orbital gyri and the precuneus, which may be expected if these responses were elicited by post-decision processes, this was not the case in the left PPA and hippocampal formation. The prolonged increase of the BOLD response in the latter structures rather resembles the gradual increase of activity which has been interpreted as accumulation of evidence until a sensory decision is reached (Gold and Shadlen, 2001). Furthermore, error detection in general should be accompanied by similar signal increases for false alarms and misses, which was observed in the hippocampal formation, but not in the PPA. Finally, error-related processing was not associated with the PPA, the hippocampal formation or the precuneus in previous imaging and patient studies (Ullsperger and von Cramon, 2001; Garavan et al., 2002; Swick and Turken, 2002; Ullsperger et al., 2002).

Both lateral and medial orbitofrontal activations have been observed in a difficult guessing task (Elliott et al., 1999). However, these activations were in the anterior orbital gyri, whereas ours were in the posterior orbital gyri. From monkey research (Price, 1999) we know that the posterior orbital area provides a basis for convergence onto multimodal areas in the more anteriorly located central orbital cortex. Taken together, these data suggest the involvement of an orbital network in sensory decisions in which the posterior orbital gyrus supports decisions on the basis of noisy sensory input, whereas the anteriorly located central orbital gyri support stimulus decisions in the complete absence of a valid sensory basis, as in guessing. Decisions on target presence in noisy sensory input may be predominantly processed in the right posterior orbital gyrus, because here we found a specific involvement in dichotic target detection which went beyond target detection in diotic listening.

The amygdala responses, in contrast to the orbital responses, were modulated during trials which actually contained a target (correct detections and misses), whereas they were nearly unchanged in trials without a target (correct rejections and false alarms). Thus the amygdala responses appeared not to reflect decision processes about target presence, or subsequent response selection processes, as in the posterior orbital gyri or the PPA, but may rather reflect a stimulus evaluation process. This is suggested by research which showed that the basolateral amygdala is involved in linking a stimulus to a temporary value in the context of a task (Malkova et al., 1997; Baxter and Murray, 2002). In the current experiment, this would mean that the syllable /TA/, which normally is as meaningless as /BA/ or /GA/, gets a specific value in the context of the experiment, because, as the target, it affords a specific response.

Differential Processing of Left and Right Ear Targets

Three areas in the left hemisphere, the PPA, the amygdala and the hippocampal formation, responded differently to left and right ear targets. The PPA and the hippocampal formation responded more strongly to right ear target syllables, which are more easily detected in dichotic listening. In the PPA, an interaction of ear × response was observed in that a stronger response was seen for detection of right than left ear targets, whereas a weaker response was observed for missed right than left ear targets. This may reflect the greater certainty with which subjects made decisions about presence or absence of the target syllable in the right ear. The left amygdala showed the reverse pattern, with a stronger response to detected left than right ear targets and a weaker response when left than right ear targets were missed. We can only speculate that the left amygdala may be important for the detection of the less detectable left ear targets in the presence of dominant right ear input. Contrary to the PPA and amygdala, the left hippocampal formation responded equally strongly to detected and missed right ear targets. This may indicate that the hippocampal formation, in contrast to the other areas of the paralimbic belts, receives input that more directly reflects the sensory stimulation. In fact, auditory association areas have been found to project directly to the hippocampal formation (Room and Groenewegen, 1986).

More posteriorly, the precuneus (in the vicinity of the parieto-occipital sulcus) was bilaterally strongly activated by right ear target detection, whereas misses led to a signal decrease.

The precuneus has been identified as a multimodal association area. Several studies reported that the precuneus plays a role in forming a mental model by integrating the current input with the background knowledge of the previously established situation model (Fletcher et al., 1995; Maguire et al., 1999). More specifically in terms of our study, precuneus activation was previously reported in tone monitoring (Linden et al., 1999), sound recognition (Maeder et al., 2001) and auditory word priming tasks (Badgaiyan et al., 1999). The precuneus may support specific processes of auditory stimulus recognition, in contrast to auditory stimulus localization, which more consistently activates an area along the intraparietal sulcus (Griffiths et al., 1998; Alain et al., 2001; Bremmer et al., 2001).

False alarms elicited an equally strong signal increase than correct detections in the precuneus. The strong activation associated with false alarms and the pronounced difference between the activation elicited by right ear and left ear targets shows that precuneus activation is not directly driven by stimulus input, but rather reflects the participants’ percept. The precuneus may specifically contribute to the right ear advantage in dichotic listening of CV syllables. Patient studies have shown that lesions of the posterior 17–20% of the corpus callosum lead to an exaggerated right ear advantage in dichotic listening (Sugishita et al., 1995; Pollmann et al., 2002) along with comparable visuospatial target detection deficits (Pollmann et al., 2004). Parietal commissures transfer via the splenium (Conturo et al., 1999) and the precuneus, along with the temporo-parietal junction area, is involved in visuospatial (Corbetta et al., 2000) and auditory target detection (Downar et al., 2001). More specifically, the precuneus was found to
support inhibition of irrelevant distractors (Pollmann et al., 2003) in visual search. It is possible that the precuneus supported target detection by distractor inhibition in the auditory domain in the present study. However, further research needs to be carried out to test this hypothesis.

In summary, target detection in dichotic listening was associated with activation of the orbitofrontal and hippocampal paralimbic belts. Within these cortical and subcortical structures, activation strength varied rather with the individual’s decision about target presence than with the physical target presence or absence. The exact nature of the processes subserved by these areas, whether target decisions or post-decision processes, remains to be investigated. Amygdala responses were more strongly modulated by target decisions in target present than target absent trials, which may indicate a role in stimulus evaluation. More posteriorly, the precuneus, possibly in concert with the temporoparietal junction, may play a role in dichotic target detection and specifically the right ear advantage in dichotic listening.

Notes
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