

Human auditory belt areas specialized in sound recognition: a functional magnetic resonance imaging study

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The human primary auditory cortex is surrounded by at least six other, anatomically distinct areas that process auditory information. We have investigated their specialization with respect to sound recognition or sound localization with triple epoch functional magnetic resonance imaging paradigm (recognition–localization–rest) in 18 normal individuals. In each study participant, the pattern of selective activation by the recognition or by the

localization tasks was superimposed on the map of the nonprimary auditory areas, as identified in previous anatomical studies. Two areas, anterior lateral and anterior areas, were activated bilaterally in significantly more individuals by the recognition than by the localization task. They are proposed to be human homologues of macaque anterolateral auditory belt area. *NeuroReport* 17:1659–1662 © 2006 Lippincott Williams & Wilkins.

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Introduction

Electrophysiological and anatomical studies in nonhuman primates have demonstrated a functional specialization within nonprimary auditory areas that is compatible with distinct processing networks for sound recognition and sound localization, the so-called 'what' and 'where' streams, respectively [1,2]. Within the lateral belt, the area surrounding the primary auditory cortex, specific selectivities have been found: an anterolateral area, for species-specific vocalizations independent of their position, and a caudolateral area, for spatial positions independent of the nature of the sound [1,2].

Architectonic studies of the human supratemporal cortex demonstrated heterogeneity that is compatible with the existence of several nonprimary auditory areas. A classical cytoarchitectonic approach [3] identified four areas outside the primary auditory cortex: ProA, PaAI, PaAe and PaAc/d. Another approach using the observer-independent cytoarchitectonic method [4] revealed three areas surrounding Heschl's gyrus: Te3, Te2 and TII. Two histochemical studies [5,6] using cytochrome oxidase, acetylcholinesterase and NADPH diaphorase activity identified in the same region six nonprimary auditory areas: five on the supratemporal plane [anterior (AA), anterior lateral (ALA), posterior (PA), lateral (LA) and medial (MA) auditory areas], and one in the posterior part of the superior temporal gyrus [superior

temporal auditory area (STA)]. Histochemical studies using the calcium-binding protein immunoreactivity [6,7] confirmed a putatively hierarchical organization of these areas; areas AA, ALA, PA, LA and MA are likely to correspond to early stage and area STA to a higher-order area of auditory processing. Several functional studies suggested that early stage areas are tonotopically organized [8,9]. Their proximity and relative position in relation to primary auditory cortex strongly suggest that they are homologous to nonhuman primate auditory belt areas. The question arises whether sound recognition and sound localization are processed independently at the early stage of auditory processing. A strong homology between nonhuman primates and man would predict that some of the human nonprimary areas present specialization in sound recognition and sound localization. We report here on putative involvement of nonprimary auditory areas within auditory 'what' and 'where' processing streams.

Material and methods

Study participants

Eighteen normal individuals, aged 23–47 years, participated in this study; eight were female (mean age 31.1 years, SD = 9.1 years) and 10 were male (mean age 27.7 years; SD = 4.1 years). All study participants had normal audition,

were right-handed and did not have a history of neurological or psychiatric illness; all gave informed consent before testing. The study has been approved by the Ethical Committee of the Medical Faculty of Lausanne.

Experimental protocol

Brain activation associated with sound recognition or sound localization was investigated with a triple epoch functional magnetic resonance imaging (fMRI) study (recognition-localization-rest). Two tasks were active and required a motor response. The stimuli, composed of sound targets superimposed on sound background, were 5 s long. In the recognition task, the background consisted of five different everyday auditory scenes (market place, street, beach, shop and railway station). Targets were meaningful, environmental sounds, lasting 2 s and starting 1.5 s after the background onset. Participants were required to press a pneumatic device, with their right hand, in response to animal cries. Auditory background and targets presented frequency and intensity modulations without spatial cues and contained burst-like (intermittent) sounds (e.g. hammer, church bell, ducks). In the localization task, the background consisted of 25 white noise bursts, each lasting 50 ms, with interaural time differences varying between 0 and 681 μ s and hence stimulating different azimuthal positions. The targets consisted of two 500-ms-long, filtered white noise tracts (low-pass 1000 Hz), the first presented 1.5 s and the second 3 s after the onset of the background. Participants were requested to actively respond when the two targets were presented at the same location. There were semantic cues neither in the background nor in the targets. The activation pattern of this study concerning the cerebral convexities has already been reported as part of a previous publication [10]. Here we concentrate on aspects not reported before, namely the activations on the supratemporal plane and their relationship with nonprimary auditory areas.

Functional magnetic resonance imaging and data analyses

fMRI images were acquired with an echo planar imaging gradient echo T2*-weighted sequence (FA 90, TE 66, pixel size 1.8 \times 1.8 mm, acquisition time 3.95 s) with a head coil on a 1.5-T Siemens Magnetom Vision system (Siemens, Erlangen, Germany) equipped for echoplanar imaging. A sagittal conventional T1-weighted three-dimensional gradient-echo sequence, 128 slices, 1.25 mm thick was acquired for each participant as a structural basis for Talairach transformation [11].

Before performing a first-level statistical analysis, we have co-registered fMRI to MRI and normalized both to the Montreal Neurological Institute standard stereotactic space using SPM99 (www.fil.ion.ucl.ac.uk/spm). We performed a statistical analysis for each participant according to the general linear model. Regions considered significantly activated were those that survived a threshold of $T = 2.37$ ($P < 0.01$ uncorrected with d.f. = 81) and containing a cluster of, at least, 30 contiguous activated voxels. Individual statistical parametric maps (SPMs) were generated for two contrasts of interest (localization vs. recognition, and recognition vs. localization). With MRIcro (<http://www.cla.sc.edu/psyc/faculty/rorden/>) we then rendered SPMs of each participant on the corresponding MRI brain image. In order to determine areas on the supratemporal

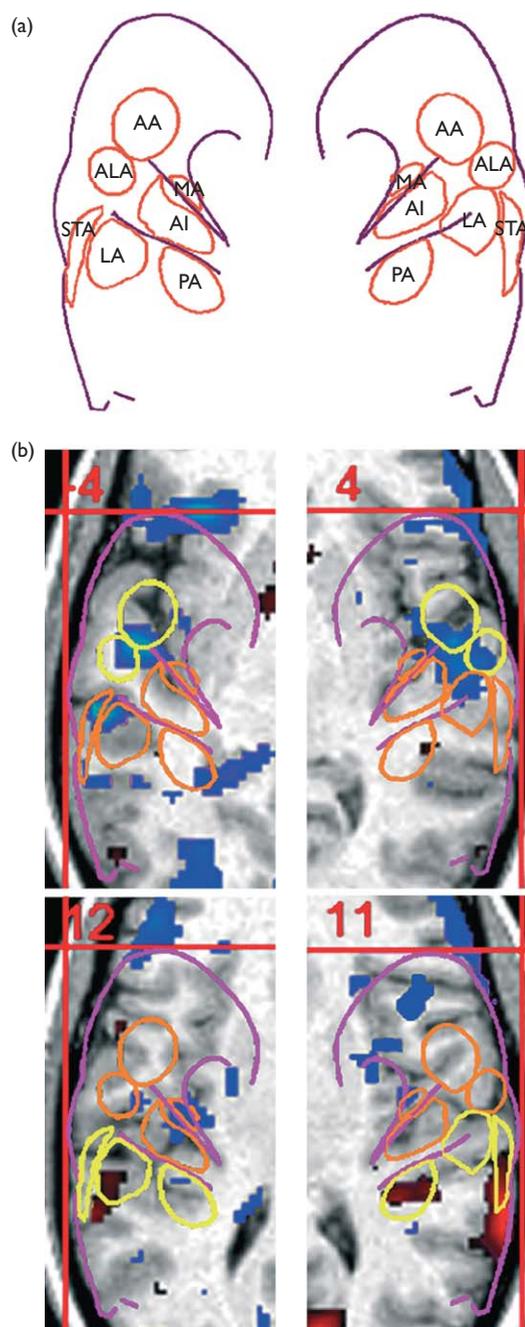


Fig. 1 Location and activation within nonprimary auditory areas: anterior area (AA), anterior lateral area (ALA), medial area (MA), lateral area (LA), posterior area (PA) and superior temporal area (STA). (a) Mask of auditory primary (AI) and nonprimary areas for left (left side) and right (right side) hemispheres as determined in previous anatomical studies [5,6]. (b) Superposition of mask on magnetic resonance imaging statistical parametric maps of the left (left side; two axial slices, $z = -4$, $z = 12$) and the right (right side; two axial slices, $z = 4$, $z = 11$) hemisphere in a representative participant. Red orthogonal lines mark the anterior and lateral extremities of the temporal lobe used for coregistration with the mask. The supratemporal region is oblique in relation to the bicommissural horizontal plane; its anterior part (areas AA and ALA; in yellow) is visible on slices $z = -4$ (left side) and $z = 4$ (right side) and its posterior part (areas PA, LA and STA; in yellow) on $z = 12$ (left side) and $z = 11$ (right side). Clusters more activated by sound localization than recognition are shown in red, clusters more activated by sound recognition than localization in blue. Note that parts of areas AA and ALA are selectively activated by sound recognition. The left side of the figure corresponds to the left hemisphere.

Table 1 Number of participants with activation of nonprimary auditory areas in the left hemisphere

| Left hemisphere | AA | | ALA | | MA | | LA | | PA | | STA | |
|---------------------|-----------------|-----|-----------------|-----|-----|-----|------|-----|------|-----|-----|-----|
| | Rec | Loc | Rec | Loc | Rec | Loc | Rec | Loc | Rec | Loc | Rec | Loc |
| Activating | 12 | 0 | 10 | 1 | 0 | 0 | 3 | 8 | 0 | 3 | 1 | 2 |
| Nonactivating | 6 | 18 | 8 | 17 | 18 | 18 | 15 | 10 | 18 | 15 | 17 | 16 |
| Fisher's exact test | <0.01 | | <0.01 | | 1 | | 0.07 | | 0.11 | | 0.5 | |

Significant interactions are in bold. AA, anterior area; ALA, anterior lateral area; MA, medial area; LA, lateral area; PA, posterior area; STA, superior temporal area; Rec, recognition vs. localization; Loc, localization vs. recognition.

Table 2 Number of participants with activation of nonprimary auditory areas in the right hemisphere

| Right hemisphere | AA | | ALA | | MA | | LA | | PA | | STA | |
|---------------------|-----------------|-----|-----------------|-----|-----|-----|------|-----|------|-----|-----|-----|
| | Rec | Loc | Rec | Loc | Rec | Loc | Rec | Loc | Rec | Loc | Rec | Loc |
| Activating | 8 | 1 | 6 | 0 | 1 | 0 | 7 | 5 | 2 | 4 | 5 | 4 |
| Nonactivating | 10 | 17 | 12 | 18 | 17 | 18 | 11 | 13 | 16 | 14 | 13 | 14 |
| Fisher's exact test | <0.01 | | <0.01 | | 0.5 | | 0.36 | | 0.33 | | 0.5 | |

Significant interactions are in bold. AA, anterior area; ALA, anterior lateral area; MA, medial area; LA, lateral area; PA, posterior area; STA, superior temporal area; Rec, recognition vs. localization; Loc, localization vs. recognition.

plane activated by recognition and/or localization, we employed a mask containing Talairach representation of auditory areas as described in the studies by Rivier and Clarke [5] and Wallace *et al.* [6] (Fig. 1a). This mask contains seven areas, all projected on the same horizontal plane. For each hemisphere, the mask has been superimposed on the MRI-SPM image and transformed by translation, rotation, scaling and shearing in order to match three landmarks: the most anterior and the most lateral plane of the temporal lobe, and the first transverse sulcus on the supratemporal plane (Fig. 1b).

For each auditory area, the total number of pixels and the number of significantly activated pixels was determined using MATLAB (Mathworks Inc., Natick, Massachusetts, USA). The area was considered to be involved in a particular task, when the ratio of activated versus all pixels was at least 0.1 (data not shown). Only activations situated on the supratemporal cortex were taken into account. To investigate whether sound localization and sound recognition activate a given area in a different manner, we examined for each area the significance of the association between two variables, stimuli (localization or recognition) and activation state (activated or nonactivated), in a 2×2 contingency table, using Fisher's exact test.

Results

In the left hemisphere, two areas tended to be activated in more participants by sound recognition than by sound localization in a statistically significant way (Table 1). Area AA was selectively activated by sound recognition in 12 out of 18 participants, but in none by sound localization; area ALA was selectively activated by sound recognition in 10 out of 18 participants and only in one by sound localization. Fisher's exact test showed $P < 0.01$ for both areas confirming the specialization of AA and ALA in sound recognition. Areas LA and STA were activated in several participants either by sound recognition or by sound localization; area PA was activated in three participants by sound localization but the difference was not statistically significant. Area MA

was not activated either during sound recognition or during sound localization.

In the right hemisphere two areas tended to be activated, in a significant way, in more participants by sound recognition than by sound localization (Table 2). Area AA was selectively activated by sound recognition in eight out of 18 participants and in only one by sound localization; area ALA was selectively activated by sound recognition in six out of 18 participants and in none by sound localization; Fisher's exact test showed $P < 0.01$ for both areas. Areas LA, PA and STA were activated in several participants either by sound recognition or by sound localization; area MA was activated in one participant by sound recognition; these differences were not statistically significant (Table 2).

Discussion

Our results strongly suggest that human areas AA and ALA are part of the auditory 'what' stream, as they tend to be selectively activated by an environmental sound recognition task. This interpretation is consistent with previous functional studies (Table 3 [12–18]) showing anterior and lateral regions to the primary auditory cortex being activated during processing of complex features of the sound, particularly involved in speech or speech-like processing [12–15], such as frequency modulation [16], spectral analysis [16], dynamic pitch variation [17], dynamic pitch chroma compared with dynamic pitch height [18], consonant–vowel syllables compared with tones or noise [15], laughter [12] and dichotic [14] processing. With respect to tonotopy, AA and ALA correspond to lower frequency endpoints, 7' and 1', respectively [8], being consistent with speech spectrum situated between 2 and 16 Hz [9,19].

In our study, areas AA and ALA were not selectively activated by spatial aspects of sounds. Auditory spatial processing may implicate more likely auditory areas medial and posterior to the primary auditory cortex, as studies on moving stimuli [20–23] and on active localization of stationary sounds [17,23,24] have shown or tonotopic studies showing these regions activated by higher frequency

Table 3 Review of previous studies showing activation within AA and ALA

| Study | Stimuli | AA | ALA |
|-------------------------------------|--|-----------|--------------|
| Mummery <i>et al.</i> (1999) [13] | Correlation of activity with speech but not to signal-correlated noise Speech vs. signal-correlated noise | L, R | L, R R |
| Hashimoto <i>et al.</i> (2000) [14] | Diotic + dichotic vs. control condition Dichotic vs. diotic | L, R R | L, R L, R |
| Jancke <i>et al.</i> (2002) [15] | Consonant–vowel syllables vs. vowel Consonant–vowel syllables vs. tones | | L L |
| Hall <i>et al.</i> (2002) [16] | Frequency modulated vs. static tone Harmonic complex vs. single tone | | L, R L |
| Warren and Griffiths (2003) [17] | Changing pitch vs. fixed pitch Changing location vs. fixed location | L, R | L, R R |
| Warren <i>et al.</i> (2003) [18] | Changes pitch chroma vs. changes pitch height | L | |
| Meyer <i>et al.</i> (2005) [12] | Laughter vs. sounds Speech vs. laughter | L, R | R L |

AA, anterior area; ALA, anterior lateral area; L, left hemisphere; R, right hemisphere.

that is necessary for spatial localization of sounds [9]. Our study did not demonstrate any specificity of the areas MA, LA, PA and STA for either sound recognition or sound localization, which is compatible with the proposition that the planum temporale acts as 'computational hub' before further processing of complex sounds [25].

Our results are consistent with the processing of the auditory 'what' stream reported in nonhuman primates studies showing anterior regions to the core having greater selectivity for monkey calls, that is species-specific vocalizations, than for spatial analyses [1].

Conclusion

These results suggest that two anatomically identified human nonprimary auditory areas, AA and ALA, are specialized for sound recognition, and are part of auditory 'what' stream.

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