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BEHAVIORAL AND NEURAL CORRELATES OF AUDITORY DISTANCE PERCEPTION

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1. ABSTRACT

The mechanisms and cortical structures underlying human auditory spatial processing are not well understood. For the horizontal localization, the basic perceptual cues have been identified, while functional Magnetic Resonance Imaging (fMRI) studies suggest that posterior aspects of non-primary auditory cortex (AC) areas are the main processing structures. However, very little is known about the mechanisms and structures responsible for sound source distance processing. Here, we present a framework that combines behavioral experiments with fMRI to directly examine both the mechanisms and structures of auditory distance processing. We illustrate the approach on the results of an experiment that studied auditory distance perception for nearby sources in virtual auditory environment. The combined approach allowed us to identify the processing regions and to separate the contribution of individual distance cues to the processing. Regions of most significant activation were found in non-primary AC areas posterior to the AC when contrasting stimuli that varied in distance to stimuli varying in intensity, suggesting that level-independent cortical distance processing occurs in the regions close to the horizontal spatial maps. This result illustrates the potential of our framework for future examination of the three-dimensional representation of auditory space in the human brain.

[Supported by NIH awards R21DC010060, R01MH083744, R01HD040712, and P41RR14075, and the European Community's 7FP/2007-13 grant no PIRSES-GA-2009-247543]

2. INTRODUCTION

BACKGROUND

Spatial auditory processing differs dramatically in the 3 spatial dimensions. For auditory distance perception we don't understand:
- the mechanisms/cues,
- the neural substrates.

In general, distance perception is poor. Nearby, laterally displaced sounds in reverberant rooms represent a special case. They provide multiple robust level-independent distance cues:
- Interaural Level Difference (ILD),
- Direct-to-reverberant energy ratio (D/R).

How the cues are combined is not known. E.g., data of Kopco et al. (2011) suggest that ILD cue is not used in rooms. Direct tests of such hypotheses, e.g., via imaging, are needed.

Probing tuning properties of auditory neurons using adaptation paradigms

Neuronal adaptation reflects suppression of responses to a given stimulus, as a function of its similarity and temporal proximity to preceding stimuli.

Adaptation fMRI indexes properties of neurons at the subvoxel level (Grill-Spector et al., 1999):

Wide tuning: strong adaptation is observed when all neurons within a voxel respond similarly to a series of stimuli.
Sharp tuning: less adaptation occurs when each stimulus in a series activates a specific subpopulation within this voxel --> release from adaptation observed as a function of increasing variance of the relevant feature dimension, such as horizontal localization of sounds (Deouell et al. 2007).

CURRENT STUDY

Use the adaptation fMRI paradigm to examine the neural correlates of auditory distance processing for nearby lateral stimuli.

Two fMRI experiments examining cortical areas responsible for distance processing of:
- stimuli presented at fixed level,
- stimuli presented at random or normalized level.

Behavioral experiment examining the listeners' sensitivity to source distance.

3. METHODS

COMMON METHODS

Twelve normal hearing subjects.

Source Stimuli

300-ms-long broadband noise bursts (100 - 8000 Hz).
Virtual reverberant environment, non-individualized BRIRs.
7 simulated distances: 15, 19, 25, 38, 50, 75, 100 cm.
Simulated direction fixed along right interaural axis.
Stimuli differed by presentation level (Table 1).
Fireface 800 + Kramer 900XL + Sensimetrics S14.
Average presentation level 65 dB SPL(A).

Experimental Session

Each subject performed one 2-hr long session.
Session consisted of
- preparation & practice outside scanner - 45 mins,
- 3 fMRI scanning experimental runs - 1 hr,
- one behavioral experimental run in scanner - 15 mins.

BEHAVIORAL EXPERIMENT (Exp. 1)

Distance Discrimination Experiment

Each trial

Word "Listen" appeared on screen, followed by a sequence two stimuli
- from different distances,
- each presented at a diff. random level (cf. Tab 1).

Subject indicated whether 2nd sound closer or farther away than 1st sound (key press).

Experiment

Four runs of 21 trials.
Each distance pair presented once (random order).

IMAGING EXPERIMENTS

Sparse acquisition design

Each trial

Sound stimulus (7 secs) consisting of 14 noise bursts (2 for each distance), presented with SOA of 0.5 secs.
1 sec quiet gap.
2 secs of fMRI image acquisition.

50% of stimuli contained a deviant, a randomly chosen burst with duration of 150 ms.

Experiment 2

1 run of 36 blocks.

Each block had 2 randomly ordered trials, one of type VarDist2, one of type Const (Table 1).

Experiment 3

2 runs of 18 blocks.

Each block had 4 randomly ordered trials, one of each type VarDist, VarInt, Const, No (Table 1).

Image Acquisition

fMRI was obtained at 3T using a 32-channel coil (Siemens TIMTrio, TR = 12000 ms; TE = 30 ms; flip angle = 90; FOV= 192 mm; voxel size=3 x 3 x 3 mm3, 36 slices with 0.75 mm gap aligned along anterior-posterior commissure line; 97 volumes per run). T1-weighted multi-echo MPRAGE 3D MRIs (TR=2510 ms; 4 echoes with TEs = 1.64 ms, 3.5 ms, 5.36 ms, 7.22 ms; 1×1×1 mm3; FOV = 256 mm; flip angle = 7) were obtained for combining anatomical and functional data.

Image Analysis

Using FSFAST 5, movement corrected, spatially smoothed (Gaussian kernel of FWHM 5 mm), and intensity normalized fMRI time-series were re-sampled to the spherical Freesurfer standard surface representation and entered to a general linear model (GLM) with task conditions as explanatory variables (gamma function delta=2.25, tau=1.25).

TABLE 1 Stimulus types used in imaging experiments (also see Behavioral Exp)

Stimulus type	VarDist	VarInt	Const	No	VarDist2
Distance of bursts in sequence	random	38 cm	38 cm	-	random
Presentation Level of Bursts in sequence	fixed emitted	random	fixed	-	fixed at near ear

4. BEHAVIORAL RESULTS

BEHAVIORAL EXPERIMENT (Exp. 1)

Goal: Validate virtual simulation technique in a task that is more challenging (roved presentation level) than the experimental task.
Possible simulation limitations:
- fMRI-compatible stimulus presentation hardware
- use of non-individualized BRIRs

Estimate d' based on PCC for distance pairs

Assuming that:
- subjects are not biased,
- sensitivity to distance change is independent of baseline distance,
- separation of means of the internal variable is fixed and additive,

sensitivity (d') can be estimated from the percent correct performance values. d' was found for each subject as a non-linear fit of his/her PCC data.

Figure 1a shows that if the individual subjects' d-primes are estimated this way, the modelled across-subject average performance (red) is close to the measured values (black).
Figure 1b shows that individual subjects' sensitivity varied only slightly. Subject S12 (the worst subject) did not perform the task correctly (see next section).

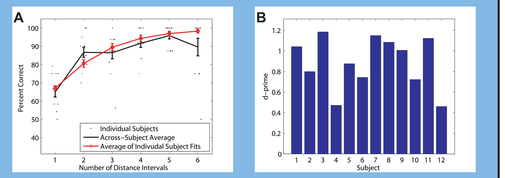

Figure 1. Sensitivity of individual subjects to changes in stimulus distance. (A) Percent correct responses as a function of the number of source distance intervals. Across-subject average (red line), average of a psychophysical model fit to individual data (black line), and individual data (dots). Error bars represent SEM. (B) Individual subjects' d' estimates based on the psychophysical model fit.

Using virtual distance simulation, most subjects can reliably judge relative stimulus distance, even when the overall stimulus level is randomly varied from burst to burst within a stimulus pair.

BEHAVIORAL DATA FROM IMAGING EXP.

Goal: Monitor and analyze deviant detection responses during Imaging Experiment to establish that different conditions are approximately equally demanding, to prevent task difficulty differences from influencing imaging results.

Analysis of Hit Rates (Figure 2A) and Reaction Times (Figure 2B). One subject (S12) excluded from analysis because s/he did not perform the task correctly (Hit Rate 0-20%). For the remaining subjects, task difficulty was similar across the three different stimulus types, suggesting that any fMRI activation differences across conditions cannot be attributed to differences in task difficulty.

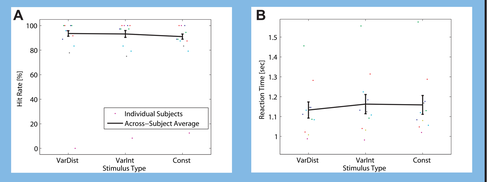

Figure 2. Hit rate (A) and Reaction time (B) in responses to the deviant during the experimental runs. Across-subject averages and SEM are shown across 11 subjects (excluding subject S12).

5. IMAGING RESULTS

Adaptation refers to "repetition suppression" as a function of similarity and temporal proximity of consecutive stimuli. By introducing changes in a specific feature dimension, we expected to reveal fMRI voxels with sharpest tuning to the given feature.

Experiment 2: when sound distance was varied randomly and intensity at the near ear was held constant, we observed a wide spread activation of auditory cortices (red-yellow in Figure 3) presumably reflecting release from adaptation in neuron populations tuned sharply to near-ear intensity-independent distance cues. However, a possible contribution of feature-nonspecific "change detector neurons" cannot be ruled out. Also, contribution of the monaural stimulus characteristics related to varying stimulus intensity at the far ear might influence results.

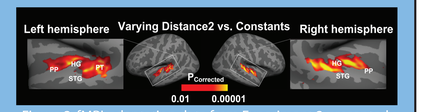

Figure 3. fMRI-adaptation data from Experiment 2 presented on inflated cortical surface representations. The contrast shows activation for sounds varying in distance (with intensity normalized at the near ear, VarDist2) vs. non-varying standard sounds (Const).

Experiment 3: We then compared auditory cortex fMRI activations when sound distance varied randomly (causing variations in D/R, ILD, and intensity cues), or when only sound intensity varied randomly, vs. constant stimulation (Figure 4).

Figure 4A shows a wide-spread release from adaptation, observed in contrasts between conditions with sound changes (Varying Intensity or Varying Distance) and constant stimulation.
Figure 4B The contrast between Varying Distance vs. Varying Intensity was expected to reveal voxels specifically tuned to the level-independent distance processing. These areas are strongest in the left posterior auditory cortex (encircled), contralateral to the simulated direction of the stimuli. They include the planum temporale (PT) and the posterior aspects of the superior temporal gyrus (STG), near the putative "where" auditory stream (Rauschecker, 1998). In contrast, areas showing stronger activations during Varying Intensity than Varying Distance (blue scale) occur mainly in anterior auditory-cortex areas.

The region sensitive to distance, but not to intensity, of lateral sounds is in the contralateral auditory cortex, extending from the planum temporale to the posterior aspects of the superior temporal gyrus.

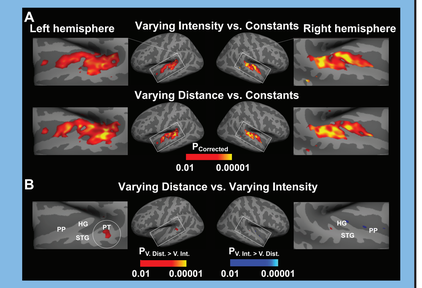

Figure 4. fMRI-adaptation data from Experiment 3 presented on inflated cortical surface representations. (A) The contrasts show activation for sounds varying in distance (VarDist) or varying in intensity (VarInt) vs. non-varying standard sounds (Const). (B) Regions more active during varying distance (VarDist) than varying intensity (VarInt) are shown in red-yellow scale. Regions more active during varying intensity than varying distance are shown in blue scale. Encircled is the area of the strongest activation.

6. SUMMARY

Combined psychophysical and fMRI approach allowed us to identify the distance processing regions and to separate them from the intensity-sensitive regions.

Regions of significant activation were found posterior to the primary auditory cortex (AC) when contrasting stimuli that varied in distance to stimuli varying in intensity. These activations were strongest in the hemisphere contralateral to the direction of sound stimulation.

Level-independent cortical distance processing appears to occur in the regions close to the horizontal spatial maps.

This result illustrates the potential of our framework for future examination of the three-dimensional representation of auditory space in the human brain.

Specifically, for distance processing, it can be used to test contribution of individual distance cues to processing in anechoic and reverberant environments (Kopco et al., 2011).

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