Human cortical auditory motion areas are not motion selective

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The existence of a specialized mechanism supporting auditory motion processing in humans is a matter of debate in the psychophysical literature. Recent functional neuroimaging data appear to have resolved the debate in favor of a specialized motion system in that several studies have found cortical regions that seem to be motion selective. While all these studies contrast some form of moving auditory stimulation with a stationary stimulus, none have adequately controlled for the possibility that these areas are simply computing sound-source location and not motion *per se*: a moving stimulus varies in spatial location as well as motion, and so a system computing spatial location (and not motion) would be activated in response to both a moving and stationary sound source. To control for this possibility, ten subjects were scanned while listening to moving stimuli and while listening to stationary stimuli that varied randomly in spatial location. Consistent with previous imaging studies, we found that a motion stimulus when contrasted with rest (scanner noise) activated STG/planum temporale (bilaterally) and right parietal lobe. However, stationary stimuli presented at varying locations activated these regions equally well, arguing against the existence of specialized motion-processing areas in human cortex. *NeuroReport* 15:1523–1526 © 2004 Lippincott Williams & Wilkins.

Key words: Auditory motion; fMRI; Imaging; Motion selection; Right parietal; STG

INTRODUCTION

The existence of a specialized auditory motion processing system in humans is still a matter of debate. Until recently, the primary source of evidence favoring a specialized auditory motion system came from animal models in which single unit recordings have identified brainstem and cortical neurons in a variety of species that respond preferentially to a specific direction of auditory source movement, and are nonresponsive to stationary sounds [1,2]. Psychophysical evidence from human observers, however, has been equivocal. Some studies have found parallels in the way stationary and moving stimuli are processed (e.g., equivalent spatial acuity thresholds), suggesting a common mechanism [3,4]. These studies propose that auditory motion is inferred from an analysis of position changes of discretely sampled loci in space. Such a snapshot model holds that computational mechanisms supporting sound localization are used to compute sound-source movement. Other psychophysical studies, however, point to findings on the perception of velocity, acceleration, and Doppler-shift phenomena [5,6] as evidence for a specialized motion processing system.

In the last few years, several human functional imaging studies have weighed in on the debate. These studies, which have contrasted various sorts of moving *vs* stationary auditory stimuli, have all identified human cortical regions more responsive to moving *vs* stationary sounds (Table 1). These regions include most prominently, the planum temporale (bilaterally) [7–9], premotor cortex (bilaterally) [10–12], and right parietal cortex [10–13]. However, none of these studies have ruled out a snapshot-like account of motion computation. For example, contrasting a moving sound source with a stationary source at a single location confounds motion *per se* with the presence of a sound source in multiple locations. Thus, the increase in neural activity in the motion condition may be a consequence of a specialized motion processing system, or may result simply from a spatial localization mechanism doing more work localizing multiple *vs* a single sound-source position. The present study sought to disentangle these possibilities by contrasting a moving sound source with stationary sources that vary randomly and discretely in location over time.

MATERIALS AND METHODS

Participants: Ten subjects (four male) participated in this study. Subjects gave informed consent under a protocol approved by the Institutional Review Board at the University of California, Irvine.

Materials: Stimuli were 400 ms bursts of Gaussian noise presented through electrostatic headphones (STAX SR-001) at a sampling rate of 44.1 kHz. Motion was simulated by dynamically changing the stimulus interaural level difference (ILD). Noise bursts were linearly ramped such that the waveforms to the two ears received opposite slopes, e.g. left ear was ramped down while right ear was ramped up in level simulating motion from left to right. The total level

Table 1. Summary of previous auditory motion studies.

Motion stimuli	Control stimulus	Where activated (Talairach coordinates given)	Experiment type
Interaural time differences (ITD) (binaural beats)	Scanner noise	Premotor cortex (bilateral) Right parietal cortex (no coordinates given)	FMRI[12]
ILD (300 Hz sq. wave)	Scanner noise	Right STS (62, −26, 5)	FMRI[8]
ILD (AM tones)	Single stationary stimulus	Right planum (no coordinates given)	FMRI[9]
ITD/ILD (500 Hz tone)	Cancellation motion (ILD-ITD)	Premotor cortex (bilateral) (−36, 0, 58), (58, 8, 46) Right parietal cortex (32, −42, 50)	FMRI/PET[10,13]
Rotating sound field (broadband noise)	Stationary sound field	Premotor cortex (bilateral) (−42, 30, 22), (44, 44, 14) Right parietal cortex (48, −22, 52), (42, −40, 48)	PET[11]
Horizontal/vertical	2 Stationary stimuli (+/− 45 degrees)	PostSTG (bilateral) (−44, −30, 10), (50, −20, 4)	FMRI[7]

Table 2. Talairach coordinates for the voxel of peak activation from each area (either left STG, right STG, or right parietal) for each subject.

Sub Num	LSTG	Location	RSTG	Location	RPAR	Location
1	49, 25, 11	Left transverse temporal gyrus	−46, 29, 11	Right transverse temporal gyrus	−36, 53, 48	Right superior parietal lobule
2	49, 43, 8	Left middle temporal gyrus	−45, 41, 10	Right superior temporal gyrus	−44, 39, 45	Right superior parietal lobule
3	52, 20, 8	Left superior temporal gyrus	−43, 33, 11	Right superior temporal gyrus	−43, 41, 38	Right inferior parietal lobule
4	49, 18, −2	Left superior temporal gyrus	−50, 18, −2	Right superior temporal gyrus	−29, 51, 40	Right sub-gyral white matter
5	54, 27, 20	Left postcentral gyrus	−56, 17, 10	Right transverse temporal gyrus	−47, 36, 36	Right supramarginal gyrus
6	54, 31, 3	Left middle temporal gyrus	−54, 23, 6	Right superior temporal gyrus		
7	41, 29, 2	Left sub-gyral white matter	−52, 17, 15	Right postcentral gyrus	−32, 31, 43	Right sub-gyral white matter
8	52, 16, 11	Left transverse temporal gyrus	−49, 22, 0	Right superior temporal gyrus	−49, 47, 36	Right supramarginal gyrus
9	40, 23, 8	Left superior temporal gyrus	−45, 15, 6	Right insular cortex		
10	56, 17, 14	Left postcentral gyrus	−46, 19, 7	Right superior temporal gyrus		

change was 24 dB in 400 ms (starting 12 dB higher in one ear and ending 12 dB higher in the other ear). These stimuli produce a strong percept of intracranial motion along the interaural axis. For the stationary condition, a fixed ILD was randomly selected on each stimulus presentation from the set −12, −9, −6, −3, 3, 6, 9, and 12 dB (negative and positive signs denote higher intensity at left and right ears respectively). A trial consisted of 8 s stimulation during which noise bursts were presented eight times (400 ms noise followed by 600 ms silence repeated eight times). The 8 s stimulus period was followed by a 12 s rest period. Each run consisted of 12 blocks of 8 s stimulation/12 s silence.

Design and procedure: Sixteen axial slices were collected using a 1.5 T Siemens Vision scanner using an EPI pulse sequence (FOV 256 mm, matrix 64 ± 64, size 4 ± 4 mm, TE 40, slice thickness 6 mm). For each subject, a high resolution anatomical image was acquired with a magnetization prepared rapid acquisition with gradient echo (MPRAGE) pulse sequence.

To correct for subject motion artifacts, the image volumes of each subject were aligned to the sixth volume in the series using a 3D rigid body, six parameter model in the AIR 3.0 program [14]. The volumes were then co-registered to the high resolution anatomical image. After alignment, each volume was spatially smoothed (Gaussian spatial filter, 4 mm FWHM) and the time course of the blood oxygen level dependent (BOLD) signal was temporally filtered (bandpass 0.025–0.1 Hz).

Analysis proceeded in two steps. Initially, we sought to replicate sites of activation during motion perception as found previously [7]. Regression analysis was performed separately on each subject using AFNI software. Two predictor vectors, which represented the time course of stimulus presentations convolved with a standard hemodynamic response function, were entered into the analysis to find the parameter estimates that best explain the variability in the data at each voxel. At each voxel, an F-statistic was calculated and an activation map was created illustrating the areas of activation in each subject during motion perception *vs* rest. These activation maps were thresholded at $p < 0.0001$ (uncorrected). For the next step, we used t-statistics for the motion *vs* stationary condition. To reduce the number of Type II errors, activation maps were thresholded at a higher p-value ($p < 0.025$, uncorrected). In addition, data from individual subjects were transformed into Talairach space using AFNI. Coordinates for areas of interest were calculated in individual subjects.

RESULTS

The motion condition, relative to background scanner noise, showed significant activation bilaterally in the STG/planum temporale (10 subjects showed left activation; nine showed right activation) and in the right parietal lobe (five subjects) at $p < 0.0001$ (uncorrected), consistent with previous studies of auditory motion perception. When the motion condition is contrasted with the stationary condition, however, activation in these locations is eliminated in all but one participant, even at the more liberal threshold of $p < 0.025$ uncorrected. In fact, no consistently activated region was identified in the motion *vs* stationary contrast (Fig. 1, Fig. 2). To ensure further that the lack of a motion selective response in these regions was not a thresholding error, we plotted the timecourse of the top five activated voxels defined by

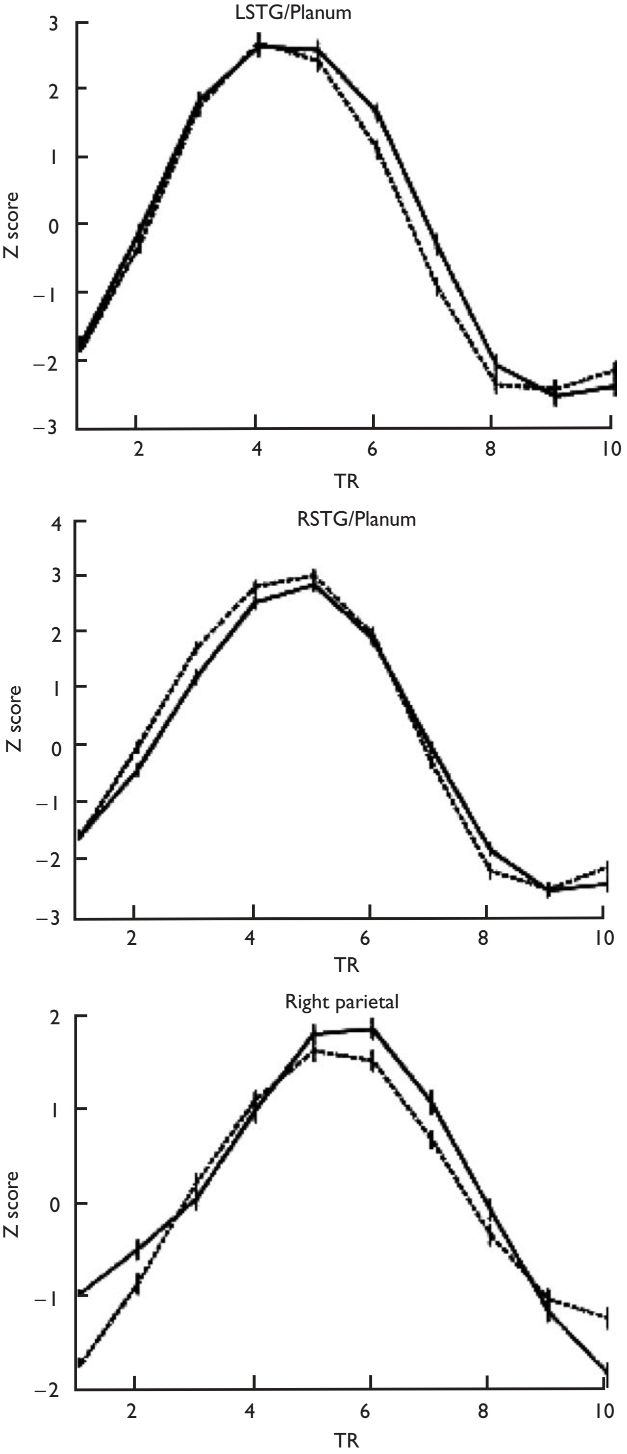

Fig. 1. Activation maps for three subjects in the left STG/planum temporale areas. The top row shows activations for the motion condition (at $p < 0.0001$). The second row shows activations for the stationary condition (at $p < 0.0001$). The bottom row shows the activation associated with the contrast motion–stationary ($p < 0.025$). Each column corresponds to a different subject.

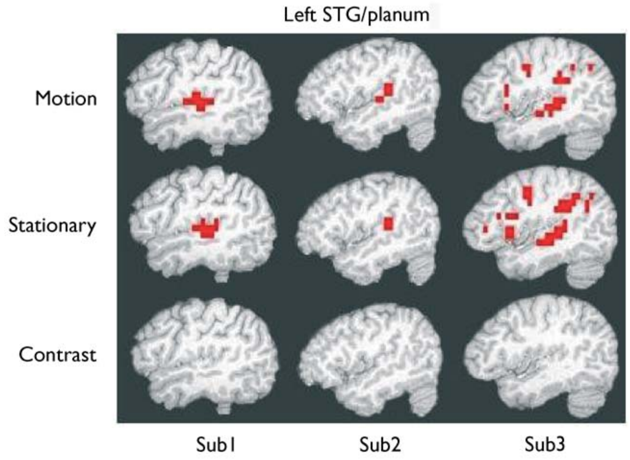

Fig. 2. Activation maps for three subjects in the right STG/planum temporale and parietal areas. The top row shows activations for the motion condition (at $p < 0.0001$). The second row shows activations for the stationary condition (at $p < 0.0001$). The bottom row shows the activation associated with the contrast motion–stationary ($p < 0.025$). Each column corresponds to a different subject.

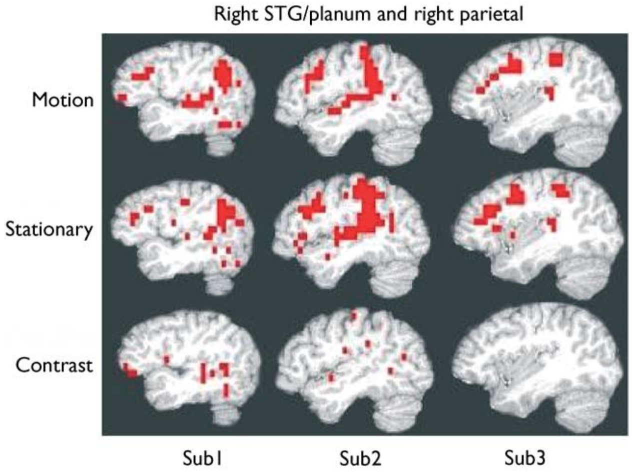

Fig. 3. Group average timecourses from the top five voxels from each subject from each of the three areas (motion=red (solid), stationary=blue (dotted)).

the motion minus rest (scanner noise) contrast, against the activation in the same five voxels in the stationary condition. Note the nearly identical response for both the motion and stationary stimuli in the planum and parietal regions (Fig. 3). Talairach coordinates for the most activated voxel in each of the three areas are presented for each subject in Table 2.

DISCUSSION

When contrasted with background scanner noise, moving auditory stimuli activated regions previously identified as candidates for motion selective cortical fields. However, non-moving but spatially varying stimuli activated these regions to a similar degree, arguing against the view that they are selective for auditory motion processing. Furthermore, no other areas were found consistently across subjects that showed motion selectivity, suggesting that unlike vision, there is not a dedicated region in human cortex specialized for auditory motion processing.

While this finding is consistent with the hypothesis that auditory motion is computed using the same computational mechanisms as non-motion spatial localization processes, it does not rule out the possibility of a specialized motion processing system. For example, neurons that have been found with motion-selective properties are typically interspersed with neurons that do not have motion-selective properties [15]. It is possible that in humans, sound localization and motion perception systems are functionally separate and specialized systems, but that they inhabit the same cortical regions, thus producing indistinguishable responses at the spatial resolution of fMRI.

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