Neural Processing of Auditory Looming in the Human Brain

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Summary

Acoustic intensity change, along with interaural, spectral, and reverberation information, is an important cue for the perception of auditory motion [1–4]. Approaching sound sources produce increases in intensity, and receding sound sources produce corresponding decreases. Human listeners typically overestimate increasing compared to equivalent decreasing sound intensity [5, 6] and underestimate the time to contact of approaching sound sources [2, 7]. These characteristics could provide a selective advantage by increasing the margin of safety for response to looming objects. Here, we used dynamic intensity and functional magnetic resonance imaging to examine the neural underpinnings of the perceptual priority for rising intensity. We found that, consistent with activation by horizontal and vertical auditory apparent motion paradigms [8–10], rising and falling intensity activated the right temporal plane more than constant intensity. Rising compared to falling intensity activated a distributed neural network subserving space recognition, auditory motion perception, and attention [8–23] and comprising the superior temporal sulci and the middle temporal gyri, the right temporoparietal junction, the right motor and premotor cortices, the left cerebellar cortex, and a circumscribed region in the midbrain. This anisotropic processing of acoustic intensity change may reflect the salience of rising intensity produced by looming sources in natural environments.

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Results and Discussion

Rising and falling acoustic intensity are primary cues to approaching and receding auditory motion. Thus, we predicted that changing intensity would activate brain regions concerned with auditory apparent motion, including the temporal plane and areas in the parietal cortex, which represent a functional stream for spatial processing [20–23]. These areas are active during the perception of different kinds of horizontal and vertical auditory motion, such as oscillating motion between the ears, motion from the midline toward one side of the head, or motion around the head [8–16]. Furthermore, we predicted, based on the perceptual priority for rising intensity [5, 6] and its potential biological salience, that rising, but not falling, sound intensity would activate a cortical network that is concerned with space perception and the allocation of sensory attentional resources [17–23].

To identify brain areas that were specifically active during the presentation of rising and falling intensity, we calculated the general linear contrast [24] "changing versus constant" intensity. This yielded activation in the right temporal plane and the right superior temporal sulcus (Figure 1A), where the blood oxygen level-dependent (BOLD) signal time courses were greater for rising and falling compared to constant intensity (Figure 1B). Right temporal plane [8–10] and superior temporal sulcus [12] activation is consistent with previous findings obtained with horizontal and vertical auditory apparent motion. However, this contrast did not yield specific activity for changing intensity in parietal areas more superior to the temporoparietal junction [9, 14]. This may be related to the weaker percept of motion associated with falling sound intensity, as shown below.

To examine whether the perceptual priority for rising compared to falling intensity is reflected in a specific neural network, we compared the responses to rising and falling intensity. We found greater BOLD responses to rising than falling intensity (c.f. Figure 2D) bilaterally in the superior temporal sulci and the middle temporal gyri. In the right hemisphere, activity extended into the temporoparietal junction encompassing the inferior portion of the angular gyrus, into the right central and precentral sulci, and into the right precentral gyrus. In the left hemisphere, cortical activity was found in the frontal operculum and, to a smaller extent than on the right side, in the precentral sulcus (Figure 2A). Additional activity was found in a discrete area of the left superior posterior cerebellar cortex (Figure 2B) and in the midline of the midbrain (Figure 2C; this midbrain region is compatible with the ascending reticular formation [19]). These areas are involved in specific aspects of attentional operations and in the perception of auditory space [17–23, 25, 26]. A similar pattern of right-sided parieto-frontal brain activation has been demonstrated during the perception of horizontal and vertical auditory apparent motion [8–16]. To examine the specificity of this response pattern, we calculated the inverse contrast
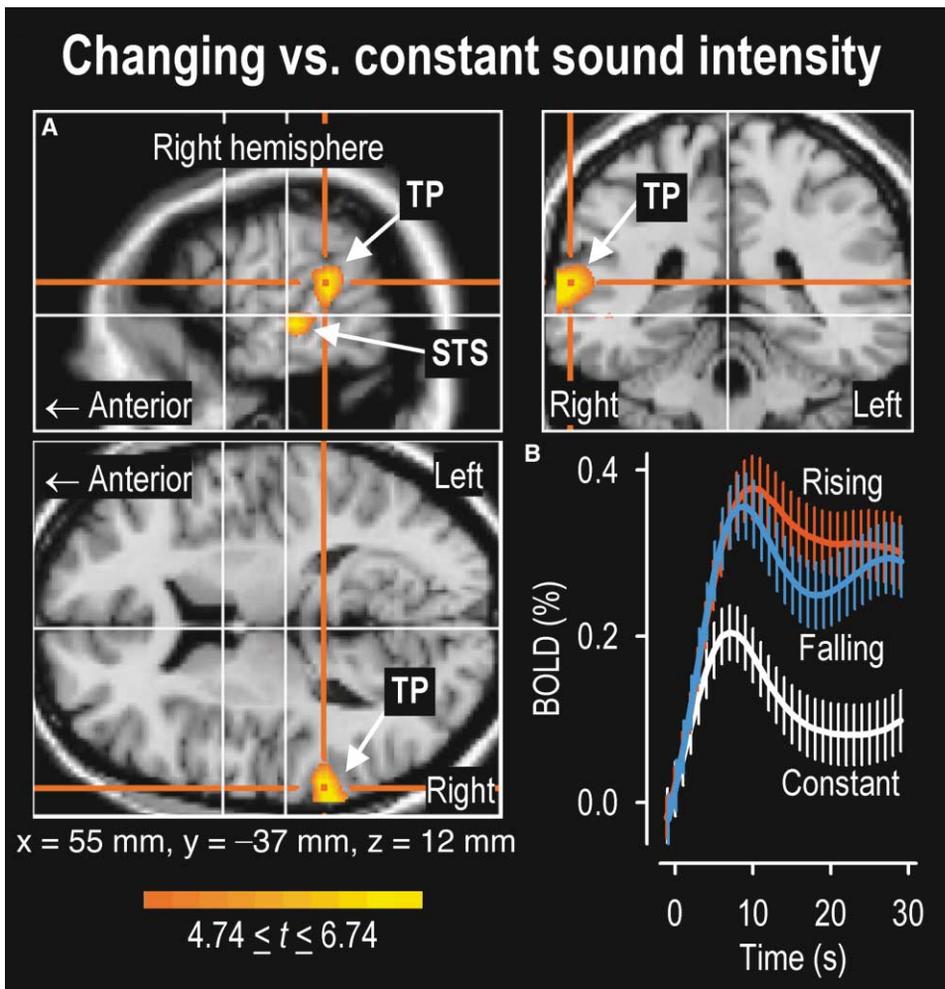
Figure 1. Cortical Activation in Response to Changing Compared with Constant Intensity Tones

(A) The general linear contrast "rising and falling versus constant" intensity tones yielded activation in the right temporal plane and the right superior temporal sulcus.

(B) Condition specific-averaged (and standard errors; linear interpolation to one sample/s) blood oxygen level-dependent (BOLD) signal responses in the right temporal plane (TP) and the superior temporal sulcus (STS). The coordinates are in Talairach space.

"falling versus rising" intensity and found a circumscribed area of activation in the second and third left frontal gyri, but no activity in the temporal and parietal lobes.

In three psychoacoustic experiments, we addressed the possibility that the brain response pattern to our stimuli would be associated with the percept of source motion. We confirmed that rising intensity of pulsed tones is perceived to change in loudness more than falling intensity. Furthermore, we found that changing compared to constant intensity tended to be associated with the percept of a moving source. Motion was reported in 78% of the rising, in 71% of the falling, and in 11% of the constant intensity trials ($\chi^2_2 = 213.4$, p < 0.001, rising versus falling: $\chi^2_1 = 2.55$, p > 0.10). The percentage of trials in which apparent motion was reported did not differ significantly between rising and falling intensity, but its magnitude was significantly greater in the rising intensity trials (Table 1). Finally, we found that 96% of the rising intensity trials were

associated with the percept of approaching motion and 96% of the falling intensity trials were associated with the percept of receding motion. Although the motion percept associated with intensity modulation was not as compelling as more realistic sounds produced by convolving the acoustic signal at the earphones with a generalized head-related transfer function or by using an array of speakers to generate a free-field moving sound [9, 10, 16], and although its direction was only identifiable in an egocentric frame of reference [27], our findings are consistent with evidence that auditory motion can be perceived with stimuli even more impoverished than those used here [28].

Our data converge with studies on the human visual system in which a pattern of anisotropic neural processing has previously been demonstrated. Inward-moving radial dots, perceived as approaching, produced greater activation in the parietal cortex than outward-moving radial dots [29]. In animals, so-called "looming-selective" neurons process specific optical information to
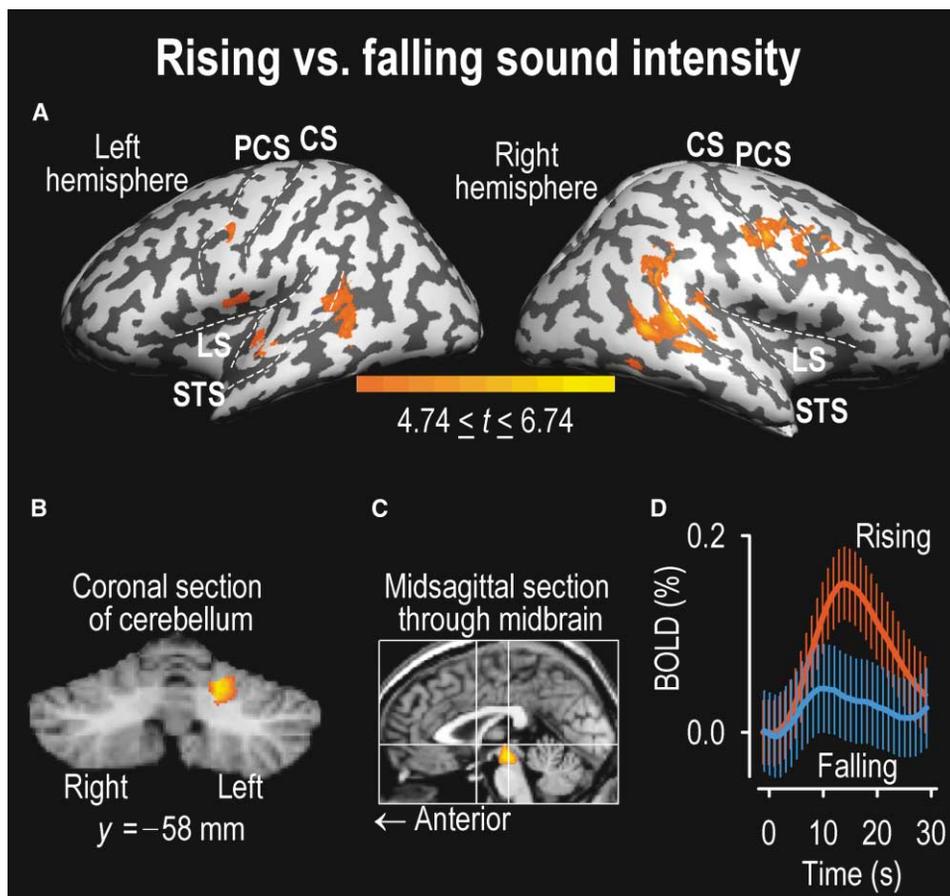
Figure 2. Cortical Activation by Rising Compared with Falling Intensity Tones

(A–C) (A) The general linear contrast "rising versus falling" intensity tones yielded a neural network comprising bilaterally the superior temporal sulci and the middle temporal gyri, the right temporoparietal junction encompassing the inferior portion of the angular gyrus, the right motor and lateral premotor cortices mainly on the right hemisphere, the left frontal operculum, and (B) discrete areas in the left superior posterior cerebellar cortex and (C) in the midbrain (possibly representing the reticular formation).

(D) Condition specific-averaged (and standard errors; linear interpolation to one sample/s) blood oxygen level-dependent (BOLD) signal responses in all areas shown in (A)–(C).

CS, central sulcus; PCS, precentral sulcus; LS, lateral sulcus; STS, superior temporal sulcus.

compute source or self approach [30, 31]. Whereas analogous information about auditory looming has yet to be completely explored, recent electrophysiological work has demonstrated neural specificity for rising and falling sound intensity in the primary auditory cortex of monkeys, independent of sound level or frequency, and that the majority of these neurons prefer rising rather than falling intensities [32]. Behavioral work in monkeys has shown an analogous perceptual bias [33].

The anisotropic neural processing of rising and falling intensity converges with associated perceptual and behavioral anisotropies [5, 6], phenomena that may serve to increase the margin of safety for anticipating approaching sources. Clearly, additional views regarding the significance of rising intensity are to be considered (e.g., aggressive communication, warning signs); however, such alternative interpretations and the collision detection or avoidance hypothesis are not mutually exclusive. Furthermore, our current hypothesis is specifically supported by the fact that humans typically under-

Table 1. Perceptual Bias for Rising Sound Intensity and Related Magnitude of Apparent Auditory Motion

Perception	Sound Intensity		
	Rising (70–85 dB)	Falling (85–70 dB)	Constant (85 dB)
Loudness Change[a]	19.3 (8.3)	16.6 (8.4)	2.8 (5.0)
Perceived Motion[b]	43.1 (18.0)	35.8 (19.9)	12.1 (24.4)

[a]Rising versus falling versus constant: $F_{2,48} = 81.1$, $p < 0.001$; rising versus falling: $F_{1,24} = 6.81$, $p < 0.01$.
[b]Rising versus falling versus constant: $F_{2,18} = 17.8$, $p < 0.001$; rising versus falling, $F_{1,19} = 6.68$, $p < 0.02$.
The data in the table are given as means and standard deviations, which are shown in parentheses.

estimate the time to contact of approaching sound sources [2, 7] and produce, similar to those induced by looming optical stimuli [34, 35], physiological and behavioral signs of preparation for contact in response to rising sound intensity [36]. The prioritization of rising sound intensity is associated with a distributed brain network that modulates attentional and space recognition processes and, as such, is likely to provide an adaptive advantage.

Experimental Procedures

Subjects and Stimuli

We studied healthy volunteers in the imaging (n = 6 females and 10 males; age mean $\pm$ SE, 32.8 $\pm$ 4.7 years) and psychoacoustic studies (n = 30 females and 20 males; age mean $\pm$ SE, 28.2 $\pm$ 13.2 years). Subjects who participated in the imaging studies were not enrolled in psychoacoustic evaluations. Pure tones with 1 kHz carrier frequency were amplitude modulated with a square wave envelope of 5 Hz and a duty cycle of 50%. The pulses were smoothed with exponential onset and offset ramps of 10-ms duration. Pulsed rather than continuous tones were used to improve the hemodynamic signal contrast [37]. Two sound pressure level changes emerging over a period of 2 s (rising, 70–85 dB; falling, 85–70 dB) and constant intensity tones (85 dB) were compared. The slopes of the rising and falling sound amplitudes were exponential, and the stimuli were diotically presented through headphones. In order to map out the time course of activation across the 30-s duration of the stimulus epoch (see below), image volumes were acquired with a brief inter-volume interval. Image acquisition, the gradient switches of which can produce considerable banking background noise depending on the scanner and the sequence [38], reached a sound pressure level that peaked at 100 dB (Brüel & Kjaer 2238 Mediator Sound Level Meter). However, the noise reduction by the headphones (Commander XG) of approximately 30 dB and the spectral composition of the scanner noise enabled a clear perception of all experimental stimuli.

Imaging Studies

For functional imaging, the 2-s sweeps were assembled in 30-s arrays of repeated rising, falling, and constant intensity tones and were implemented in a block design consisting of five randomized repetitions alternating with 30-s resting periods. Subjects were instructed to concentrate on the changes in the auditory signals and to fixate a visual crosspiece to control for eye movements. They were not asked to carry out any output tasks or to make judgments about intensity, auditory motion, or other sound parameters. Electrooculographic recordings carried out in two separate experiments outside the scanner showed no task-related eye movements.

Magnetic resonance images were acquired on a 1.5 T Symphony scanner equipped with a Quantum gradient system and a circularly polarized head coil (Siemens). Anatomical T_1-weighted volumes were obtained with a three-dimensional magnetization-prepared rapid acquisition gradient echo sequence at a voxel size of 1 mm^3 (repetition time TR, 9.7 ms; echo-time TE, 4 ms). Functional T_2*-weighted images were acquired by using gradient-recalled echo-planar imaging (TE, 54 ms; TR, 2675 ms; interslice time, 107 ms). A series of 355 functional whole-brain volumes consisting of 25 contiguous oblique slices that were 5.5 mm thick (field of view, 180 $\times$ 180 mm^2; matrix, 64 $\times$ 64 pixels) were acquired. The first seven volumes were discarded to obtain a steady state regarding longitudinal magnetization and scanner-induced auditory excitation [39].

Images were postprocessed with BrainVoyager v4.4. The 348 functional time series were corrected for slice-acquisition time through linear interpolation, realigned with their corresponding T_1-volumes, warped into Talairach space, resampled into 3-mm isotropic voxels, motion corrected with Levenberg-Marquart's least square fit for six spatial parameters, corrected voxel-wise for linear drifts, and smoothed by using a 6-mm and 3-s full width at half-maximum gaussian kernel. Condition-specific stimulus boxcar func-

tions were convolved with a γ-kernel to model the hemodynamic response behavior. We identified the cortical areas responding to auditory stimulation by applying general linear model analyses [24] to z-transformed time series in each image voxel and used the rising, falling, and constant intensity tone conditions as explanatory variables. For group analyses, the entire imaging time series (5568 T_2*-volumes) were used. Stimulus-specific effects were calculated by using the general linear model contrast. These contrasts were voxel-wise Bonferroni corrected (p < 0.05; t_{5549} = 4.74) and were based on fixed effects analyses. As such, the reported inferences pertain only to the subjects studied here [40]. Statistical maps were superimposed on anatomical sections and inflated cortical surfaces of the standardized Montreal Neurological Institute T_1-weighted brain template.

Psychoacoustic Evaluation

In experiment 1, stimuli of 2-s duration were presented, and the subjects were asked to rate the perceived loudness change on a 100-mm visual analog scale anchored with "no" or "large" change. In experiment 2, stimuli were presented in 30-s arrays of repeated 2-s periods of rising, falling, and constant intensity tones, and subjects were asked to make both a categorical decision as to whether or not they perceived apparent sound motion and to rate the strength of motion on a visual analog scale. The forced-choice procedure included the alternatives "loudness change of a tone that is not moving," "movement of a tone that is not changing in loudness," "no movement and no loudness change," and "movement and loudness change"; the visual analog scale was anchored with "no" and "strong" sound movement. In experiment 3, 30-s arrays of rising, falling, and constant intensity tones were presented, and subjects were asked to indicate by hand the trajectory of perceived sound motion relative to their head. Inferential statistics were based on repeated measures analysis of variance and χ^2 tests (2-tailed p < 0.05).

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