

Auditory Neuroscience: The Salience of Looming Sounds

Dispatch

Deborah A. Hall and David R. Moore

Sounds that move towards us have a greater biological salience than those that move away. Recent studies in human and non-human primates have demonstrated a perceptual and behavioural priority for such looming sounds that is also reflected in an asymmetric pattern of cortical activation.

The ability to localize sound sources in the environment is of considerable importance to both humans and animals because it determines the direction of predators and of prey and it also indicates where to focus visual attention. The auditory system is able to use a range of physical cues to determine the location and movement of a sound source. One set of cues are 'monaural' and are provided by the level of a sound, directional filtering of the spectral composition of sounds as a result of the head shadow and effects of the outer ear, other spectral cues and the ratio of direct-to-reverberant sound energy. Another set of cues are 'binaural' and depend upon the neural computation of differences in the time and the level of auditory signals reaching the two ears [1]. These cues contribute to the perception of the horizontal position, vertical position and distance of a sound source.

The study of distance perception has received much less research attention than has the study of horizontal and vertical position. One clearly consistent phenomenon, however, is that of a distance judgement asymmetry — human listeners systematically underestimate the time to contact of an approaching sound source [2,3] and overestimate the change in loudness for sounds that increase in level compared to those that decrease by an equivalent amount [4]. Two recent studies [5,6] have contributed to the debate about the perceptual salience of approaching ('looming') versus receding sound sources by exploring perceptual biases for auditory looming in primates [5] and its neural basis in humans [6].

Behavioural Bias for Looming Sounds

Sound level generally increases when the distance between the listener and the sound source is decreased. This simple manipulation is often used to generate the sensation of auditory looming in psychophysical studies. In their paradigm, Seifritz *et al.* [6] presented an amplitude-modulated 1 kHz carrier tone diotically through headphones. The 'distance' changes were therefore perceived as internalised, rather than in external space. Nevertheless, listeners showed a perceptual bias for auditory looming, judging both the magnitude of the level change and the magnitude of the

apparent motion to be greater for the rising than the falling sounds for the same overall 5 dB change in level. In contrast, Ghazanfar *et al.* [5] presented rising and falling level sounds from a hidden loudspeaker situated 75 cm behind and to the right of the primate listeners. Thus, the sound source was in the animal's free field. A perceptual bias was observed for rising level harmonic-complex tones, but not for white noise, as measured by the duration of a head-orienting response.

The interpretation of the perceptual asymmetry in terms of an adaptive salience for looming sounds is certainly parsimonious, but the manipulation of sound level to evoke the percept of an approaching object provides, at best, an impoverished one. Sound level is a salient cue for auditory distance perception, but it is not the only cue. The frequency spectrum, reverberant energy and interaural level differences of a sound reaching the ears can all vary as a function of the distance of a sound source [7]. No single sound property provides a definitive cue for distance, because they are all influenced by factors other than source distance. For example, in a reverberant space, sound level does not follow the normal inverse-square law of level loss as a function of distance. Measures of level at the ear also confound source distance and source energy, especially for pure tones, so the auditory system may have to make certain assumptions about the source energy to use level reliably as a distance cue. Zahorik [7] has shown that judgements of distance in the real world are more likely to combine and weight the multiple cues that are available.

Neural Encoding of Sound Source Movement and Sound Level

Ghazanfar *et al.* [5] speculate that the perceptual bias for auditory looming might have a neural basis, such as that seen in the primary auditory cortex of marmoset for rising, compared to falling, level sinusoids [8]. However, in the work of Seifritz *et al.* [6] on human listeners, rising and falling level sounds were found to generate equivalent auditory cortical activation, as measured using functional magnetic resonance imaging (fMRI) [6]. So it is possible that the primary auditory cortex provides part of the *input* to those cortical areas that compute changes in distance.

Seifritz *et al.* [6] found that rising sounds differ from falling sounds in the way they engage a widespread network of activity elsewhere in the brain, including the superior temporal sulcus, middle temporal gyrus, right premotor cortex and right temporo-parietal junction (Figure 1). They suggest that this network might subserve auditory space perception and attention, and so we might expect a number of these brain areas also to be activated by sound movement in the horizontal and vertical planes.

There is a body of imaging research using virtual externalised acoustic space [9–11]. These earlier studies found that, relative to stationary sounds,

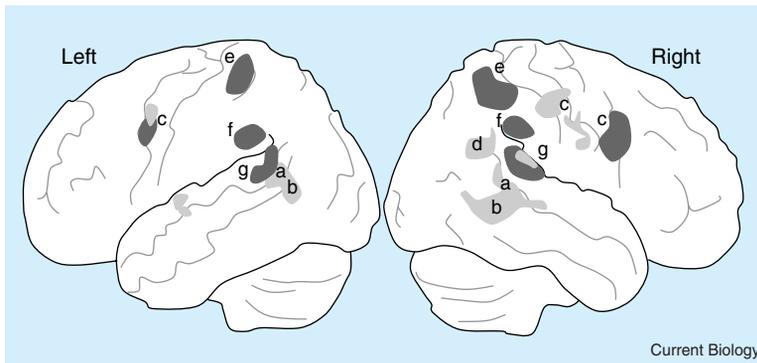


Figure 1. Left and right views of the lateral surface of the human brain summarizing the relative distribution of the networks of activity associated with auditory looming and horizontal and vertical motion perception.

Brain areas shaded in dark grey are those evoked by 1 kHz tones that rise in level relative to those that fall in level [6]: (a) superior temporal sulcus; (b) middle temporal gyrus; (c) premotor cortex; and (d) right temporoparietal junction. Brain areas shaded in pale grey represent the network described in the review by Warren *et al.* [10] and include: (c) premotor cortex; superior (e) and inferior (f) parietal areas; and the planum temporale (g)

horizontal and vertical sound movements generally engage bilateral inferior parietal areas, premotor areas, planum temporale and the superior posterior parietal cortex (Figure 1). The network described by Seifritz *et al.* [6] involves different brain areas. One explanation for the different results may be that the looming-specific activation largely reflects the processing of a semantic message – an ‘approaching object’ – and the decision for action, rather than the acoustic information about the change in spatial location conveyed by a rising sound level.

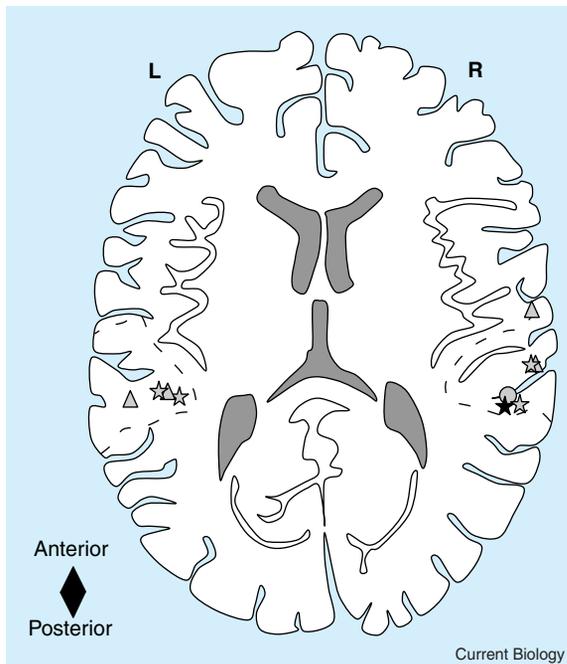


Figure 2. Axial outline showing the co-localization of peak activity within the planum temporale (dotted lines).

The black star indicates where activation was significantly greater for sounds that moved in distance relative to those that were stationary [6]. Grey triangles show where activation was greater for both horizontal and vertical motion relative to stationary sound [11], and grey stars for horizontal motion relative to stationary sound [10]. The circle shows where activation was significantly greater for sound level discrimination than for passive listening [13]. Activation peaks vary in the axial dimension between 0 and 14 mm, but for display purposes are overlaid onto the brain at 12 mm.

A more appropriate basis for comparison across studies may be to consider the activation by both rising *and* falling level sound relative to that induced in response to a constant level (stationary) sound. This contrast revealed a discrete region in a part of the right planum temporale where activation seems to be specific for sound of changing level, regardless of the direction of that change [6]. A comparison between studies (Figure 2) suggests that this area is sensitive to sound motion in any direction [10–12] and it might generally subserve auditory space perception.

The results reported by Baumgart *et al.* [12] are particularly intriguing in light of the study by Seifritz *et al.* [6]. Baumgart *et al.* [12] reported significantly greater activation in the right planum temporale for a horizontally moving sound (generated using an amplitude-modulated envelope 90° out of phase at the two ears) than for an approaching or receding sound (the same carrier but in phase at the two ears). This raises the possibility that the right planum temporale has a preference for sounds that move more in azimuth than in distance. The right posterior planum temporale has also been implicated in the discrimination of discrete changes in sound level [13], so its role in auditory processing is likely to be complex [14].

In summary, imaging data indicate that the processing of the distance, horizontal and vertical motion, and level of a sound share a common location in the right planum temporale. Beyond this, auditory looming generates a specific and distinctive pattern of distributed brain activity. Further work is required to achieve a precise functional description of this network and to search for additional modes for its activation.

References

1. Moore, D.R. and King, A.J. (1999). The near and far of sound localization. *Curr. Biol.* 9, R361–363.
2. Rosenblum, L.D., Carello, C. and Pastore, R.E. (1987). Relative effectiveness of three stimulus variables for locating a moving sound source. *Perception* 16, 175–186.
3. Schiff, W. and Oldak, R. (1990). Accuracy of judging time to arrival: Effects of modality, trajectory and gender. *J. Exp. Psychol. Hum. Percept. Perform.* 16, 303–316.
4. Neuhoff, J.G. (1998). Perceptual bias for rising tones. *Nature* 395, 123–124.
5. Ghazanfar, A.A., Neuhoff, J.G. and Logothetis, N.K. (2002). Auditory looming perception in rhesus monkeys. *Proc. Natl. Acad. Sci. U.S.A.* 99, 15755–15757.
6. Seifritz, E., Neuhoff, J.G., Bilecen, D., Scheffler, K., Mustovic, H., Schächinger, H., Elefante, R. and Di Salle, F. (2002). Neural processing of auditory looming in the human brain. *Curr. Biol.* 23 2147–2151.

7. Zahorik, P. (2002). Assessing auditory distance using virtual acoustics. *J. Acoust. Soc. Am.* *111*, 1832–1846.
8. Lu, T., Liang, L. and Wang, X. (2001). Neural representations of temporally asymmetric stimuli in the auditory cortex of awake primates. *J. Neurophysiol.* *85*, 2364–2380.
9. Griffiths, T.D. and Green, G.G.R. (1999). Cortical activation during perception of a rotating wide-field acoustic stimulus. *Neuroimage* *10*, 84–90.
10. Warren, J.D., Zielinski, B.A., Green, G.G.R., Rauschecker, J.P. and Griffiths, T.D. (2002). Perception of sound source motion by the human brain. *Neuron* *34*, 139–148.
11. Pavani, F., Macaluso, E., Warren, J.D., Driver, J. and Griffiths, T.D. (2002). A common cortical substrate activated by horizontal and vertical sound movement in the human brain. *Curr. Biol.* *12*, 1584–1590.
12. Baumgart, F., Gaschler-Markefski, B., Woldorff, M.G., Heinze, H.-J. and Scheich, H. (1999). A movement-sensitive area in auditory cortex. *Nature* *400*, 724–726.
13. Belin, P., McAdams, S., Smith, B., Savel, S., Thivard, L. and Samson, S. (1998). The functional anatomy of sound intensity discrimination. *J. Neurosci.* *18*, 6388–6394.
14. Griffiths, T.D. and Warren, J.D. (2002). The planum temporale as a computational hub. *Trends Neurosci.* *25*, 348–353.