Title : **Auditory Neuroscience : The salience of looming sounds**

Authors : Deborah A Hall and David R Moore

Address : MRC Institute of Hearing Research, University Park, Nottingham, NG7 2RD, UK.

Summary : **Sounds that move towards us have a greater biological salience than those that move away. Recent studies in human and non-human primates demonstrate 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 (‘monaural’) cues is provided by (i) the level of a sound, (ii) directional filtering of the spectral composition of sounds due to the head shadow and effects of the outer ear, (iii) other spectral cues and (iv) the ratio of direct-to-reverberant sound energy. Another set of (‘binaural’) cues depends 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 scientific attention than has the study of horizontal and vertical position. However, a consistent phenomenon 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 papers 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 harmonic-complex tones 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. In addition, measures of level at the ear 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 distance, lateral motion and sound level

Ghazanfar et al. [5] speculated 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, when measured using fMRI in human listeners, rising and falling level sounds generated equivalent auditory cortical activation [6]. Thus, it is possible that the primary auditory cortex provides part of the *input* to those cortical areas that compute changes in distance. Unlike falling level sounds, rising sounds engaged 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). Seifritz et al. [6] suggested 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]. Relative to stationary sounds, 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 is that the looming-specific activation largely reflects the processing of a semantic message (“approaching object”) and the decision for action, rather than the acoustic information about the change in spatial location conveyed by a rising sound level.

Perhaps a more appropriate basis for comparison across studies is to consider the activation by both rising *and* falling level relative to a constant level (stationary) sound. This contrast revealed a discrete region in a part of the right planum temporale [6]. A comparison between studies (see Figure 2) suggests that this area is sensitive to sound motion in any direction [10-12] and 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 that was 90˚ out of phase at the two ears) than for an approaching and receding sound (the same carrier that was 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] and so its role in auditory processing is likely to be complex [14].

In summary, imaging data indicate that the processing of distance, horizontal and vertical motion, and level 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.

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Figure legends

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 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 temporo-parietal junction)). Brain areas shaded in dotted 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**).

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.

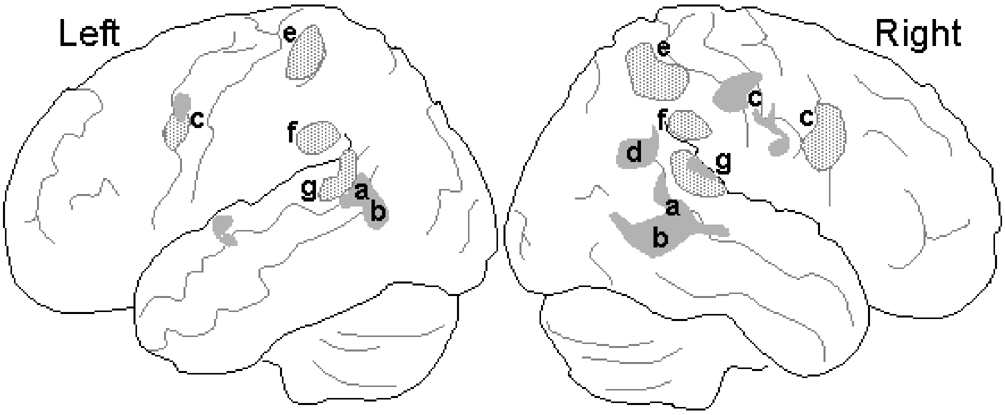


Figure 1

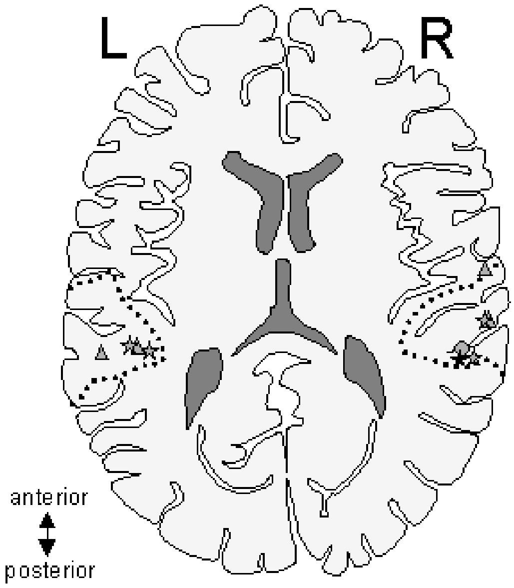
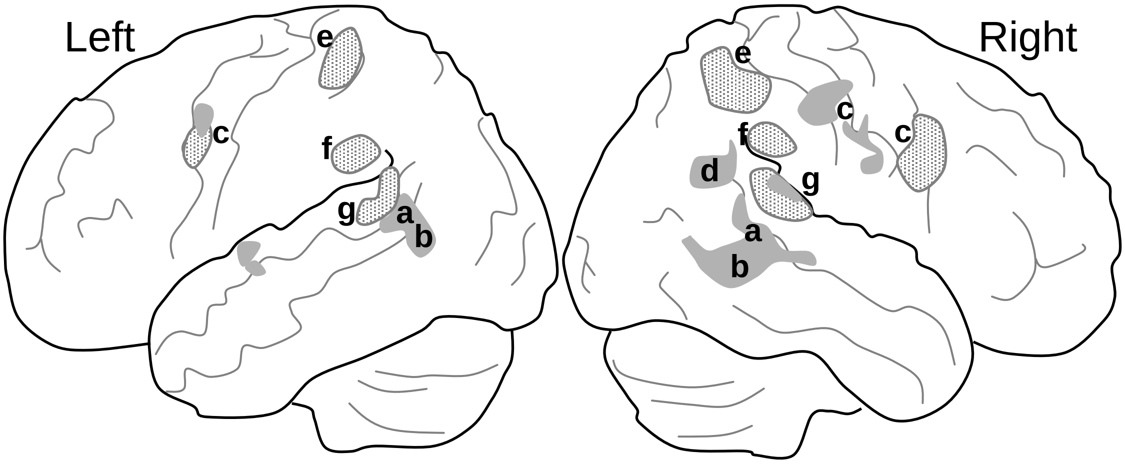


Figure 2



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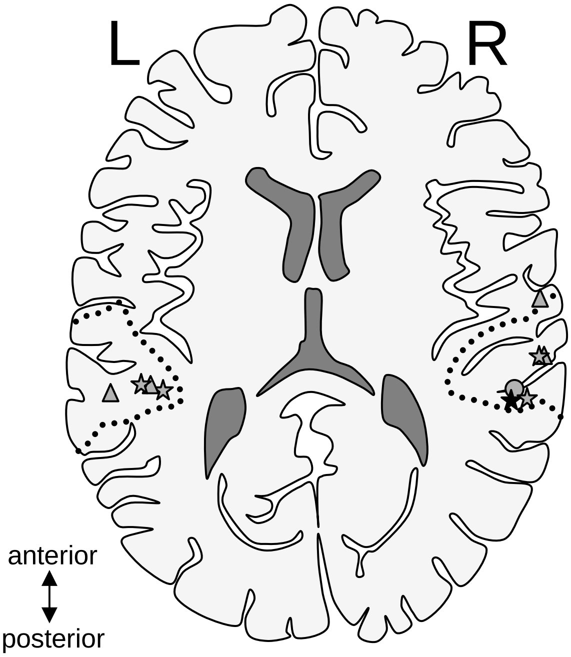

Figure 2