each neuron, a sound from a particular location, which generates a particular ITD, will produce coincident inputs in only one neuron (or a subset of neurons); all other neurons will receive non-coincident inputs and fire weakly. Changing the location of the sound, and hence the ITD, results in coincidence at a different neuron, and thus at a different place in the array. In this way, the ITD received is encoded by the place in the array at which neurons fire maximally. This arrangement is reiterated for each frequency.

So, for example, a sound emanating from directly ahead will generate an ITD of 0 μs, and coincidence will occur only at those auditory neurons with equal axon lengths. Neurons in each frequency array that are 'tuned' to 0 μs will fire maximally, and all other neurons will fire weakly. In this way, a complex sound originating directly in front of the animal will evoke maximal activity at one place across frequency arrays.

These features appear in the first brain region innervated by the two ears: the medial superior olive (MSO) in mammals and the nucleus laminaris in reptiles and birds. As early as 1953, Stotler[5] reported a striking binaural innervation of MSO neurons. Subsequent neurophysiological studies all showed that these neurons respond to the coincidence of excitatory inputs and are exquisitely sensitive to ITDs in the microsecond range — properties consistent with the Jeffress model[6]. Even more compelling are studies of the nucleus laminaris in birds. There, the Jeffress-type delay lines have been demonstrated anatomically[7], and the place coding of ITDs, resulting from coincidence of excitatory inputs, has been shown with physiological recordings[8–10].

But Brand *et al.*[4] now provide evidence that the MSO in mammals might not work as previously supposed. The authors recorded the electrical activity of MSO neurons in gerbils, animals that are known to localize low-frequency sounds by means of ITDs, and confirmed that each neuron fires maximally at a particular ITD. Yet — and here's the rub — the peak firing occurred at long ITDs that gerbils almost never experience, because their headwidths are too small to generate them. So it is difficult to imagine that ITDs are indeed represented by the place code envisaged by Jeffress.

Brand *et al.* also report that the ITDs that produce maximal firing are closely correlated with the frequency to which each neuron is tuned. Neurons that fire maximally at relatively small ITDs are almost always tuned to higher-frequency sounds, whereas neurons that fire maximally at progressively longer ITDs 'prefer' progressively lower frequencies. So the peak firings generated by a particular ITD are not represented equally in each frequency array of the MSO, as predicted in a Jeffress-like arrangement. Instead, each frequency array responds to a small range of ITDs over which the neuronal firing rate changes markedly.

This leads Brand *et al.* to suggest that, in mammals, the location of a sound is encoded not by the place of maximal firing but rather by the activity pattern across the entire population of auditory neurons, with these neurons changing their firing rates as ITDs change. In their model, high frequencies, which generate the steepest changes in firing rate with ITD, are scaled to peak at small ITDs so that the steep rate changes occur within the biologically relevant ITD range. Conversely, low frequencies, which generate the shallowest rate changes with ITD, are scaled to peak at longer ITDs so that the largest changes in firing also occur within the biologically relevant ITD range.

But the most surprising result occurred after Brand *et al.* blocked inhibitory inputs to MSO neurons. They found that all neurons tested, regardless of their usual behaviour, now fired maximally at ITDs of and around 0 μs. Although the authors blocked inhibition in only a few MSO neurons, their results suggest that delay lines of excitatory inputs are not arranged to produce a range of ITD sensitivities, as Jeffress proposed. Rather, the implication is that, regardless of their arrangement, all neurons fire maximally at ITDs of 0 μs. Inhibition, or more specifically its timing relative to excitation, then sculpts a variety of ITD sensitivities out of the common 0-μs sensitivity produced by the excitatory inputs.

This work raises several questions. Why do mammals and birds have different mechanisms for localizing sounds? And what structural features underlie the inhibitory delay lines suggested by Brand *et al.*? Finally, gerbils are small mammals with small headwidths, and their peak neuronal firing occurred at ITDs that their headwidths could not generate. But what about larger mammals, whose headwidths generate much longer ITDs — does inhibition have a role to play here, too? All in all, the study by Brand *et al.* will no doubt generate considerable discussion about mechanisms that many had thought were already solved. ■

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1. Rayleigh, Lord. *Phil. Mag.* 13, 214–232 (1907).
2. Klumpp, R. *et al. J. Acoust. Soc. Am.* 28, 215–232 (1956).
3. Jeffress, L. A. *J. Comp. Physiol. Psychol.* 41, 35–39 (1948).
4. Brand, A., Behrend, O., Marquardt, T., McAlpine, D. & Grothe, B. *Nature* 417, 543–547 (2002).
5. Stotler, W. *J. Comp. Neurol.* 98, 267–285 (1953).
6. Joris, P. X., Smith, P. H. & Yin, T. C. *Neuron* 21, 1235–1238 (1998).
7. Parks, T. N. & Rubel, E. W. *J. Comp. Neurol.* 164, 435–448 (1975).
8. Carr, C. E. & Konishi, M. *Proc. Natl Acad. Sci. USA* 85, 8311–8315 (1988).
9. Overholt, E. M., Rubel, E. W. & Hyson, R. L. *J. Neurosci.* 12, 1698–1708 (1992).
10. Reyes, A. D., Rubel, E. W. & Spain, W. J. *J. Neurosci.* 16, 993–1007 (1996).

Daedalus

Spatial audio

In electron spin resonance (ESR), a chemical sample is placed in a strong magnetic field and irradiated with microwaves. Unpaired electrons in the sample reveal themselves by resonating. Daedalus has been musing on interstellar space, and its content of hydrogen atoms. Each has an unpaired electron (indeed, it is the only one it has). In the low magnetic field of space, each electron should resonate feebly at some audio frequency. Yet the total signal might be quite strong: there are cubic light-years of this specimen. Indeed, the distribution of monatomic hydrogen, and the range and intensity of the interstellar magnetic field itself, are all hot astronomical topics. Daedalus reckons that audio frequencies from space are well worth looking for.

An audio signal would have a very long wavelength — 200 km or thereabouts. A directional parabolic aerial, which must be many wavelengths across, could never be made big enough. Even a conventionally resonant quarter-wave aerial of 50 km would be hard to build. But Daedalus recalls that power-lines and telegraph cables, thousands of kilometres long, already span the globe. Furthermore they are liable to dangerous surges when solar magnetic effects induce big voltages in them. This astrophysical phenomenon suggests to him that a careful search should be made on these conductors, looking for another astrophysical effect: small but detectable audio frequencies from space.

Of course 50 Hz and 60 Hz, the main human power frequencies, will contribute hugely, and will have to be well filtered out. These, however, will have their own human rhythm, caused by the known changing load. The audio spectrum to be studied is wide, too. Furthermore, the system as a whole will be steadily scanned in longitude by the rotation of the Earth, and in latitude by choosing the right conductors to listen to. Circumpolar ones, for example, should discriminate rather well against equatorial signals or ones from the wrong hemisphere.

Here, says Daedalus, is a new way of testing the theory of 'steady-state continuous creation'. It holds that monatomic hydrogen is appearing steadily throughout space, at just the rate needed to compensate for spatial expansion. The Universe has no beginning and no end. If the Earth is indeed receiving a steady ESR hydrogen signal from every point in space, the implications would be cosmologically profound indeed. **David Jones**