

# Of vulcan ears, human ears and 'earprints'

Fred Wightman and Doris Kistler

Our outer ears are critical for localizing sound elevation. Van Opstal and colleagues show that humans adapt to new ear shapes. This process resembles learning a second language because after adaptation people can localize equally well with their own or modified ears.

As any Star Trek fan can tell you, First Officer Spock's ears are decidedly non-human. Whether or not Vulcans hear things differently (or better) than we do is hard to know, but for humans and some other Earthly creatures, ear shape is important to our perception of the auditory world. For example, our ability to localize a sound is determined in

ability, as previous research would suggest<sup>1,2</sup>. After six weeks of wearing these molds continuously, though, all four listeners seemed to have learned the new ears, so that their localization was normal again.

Even more surprising was that when the molds were removed, localization was still normal. In other words, there

differences is that they are ambiguous cues. Consider interaural time difference. This sub-millisecond difference in time of arrival of a sound wave at a person's two ears does depend on sound source direction, and thus is a potential cue for direction. Figure 2 shows interaural time differences actually measured from a person's ears and plotted as a function of source position. Contours of constant ITD are plotted underneath the colored surface. These contours mark off sound-source azimuths and elevations for which the ITD cue is constant, and thus clearly reveal the ambiguity of this cue. Note that the contours are roughly circular, suggesting that the ITD produced by a source at 90 degrees azimuth and 30 degrees ele-

## Pinna cues... are as individual as fingerprints, thus the term 'earprints'

large part by what happens when a sound wave reflects off the ridges and folds of our outer ears, the pinnae. Pinna shapes vary tremendously from person to person (Fig. 1), and to localize accurately we must learn the acoustical characteristics of our own pinnae. Mr. Spock would be the first to point out that it is logical to assume that he has learned his own ears, in spite of their very different shape, and that he can localize at least as well as we Earthlings. One wonders how well Leonard Nimoy can localize when he is using Spock's ears rather than his own.

In this issue of *Nature Neuroscience*, Hofman, Van Riswick and Van Opstal (pp. 417–421) offer an intriguing new insight into how our brains learn the characteristics of our own ears and how we might learn to use a different set of ears. They measured the localization ability of four people before and after the shapes of their ears were changed by inserting plastic molds into the pinna cavities. Changing ear shape had a dramatic deleterious effect on localization

was no aftereffect of the kind typically reported in sensory adaptation studies. It was as if the listeners had learned a new 'language' and now had two sets of ears with which they were proficient. Acquisition and maintenance of a second mapping without erasing the first seems more like learning a second language than like learning a sensory perceptual transformation.

Auditory researchers understand roughly how people localize sounds, but some puzzles remain. The process is very different from visual localization, in which the location of an object in the environment directly corresponds to the retinal location of the image of that object. Audition has no such direct representation of the spatial arrangement of objects. Instead, apparent sound direction must be derived from the neural representations of incoming sound waves. Until recently, the apparent direction of a sound was thought to be determined mainly by two acoustical cues that have neural representations: the interaural differences in the time of arrival of a sound wave at the two ears and the interaural differences in level or loudness.

The problem with interaural

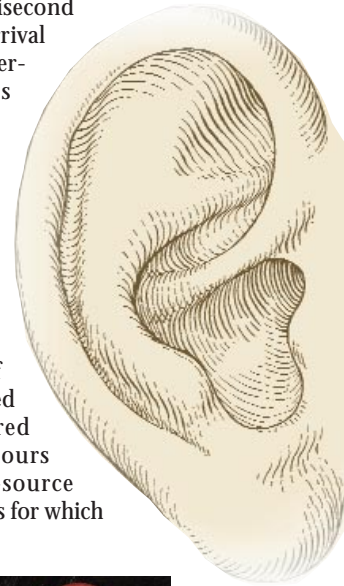


Fig. 1. The shape of the outer ear or pinna varies substantially among individuals.

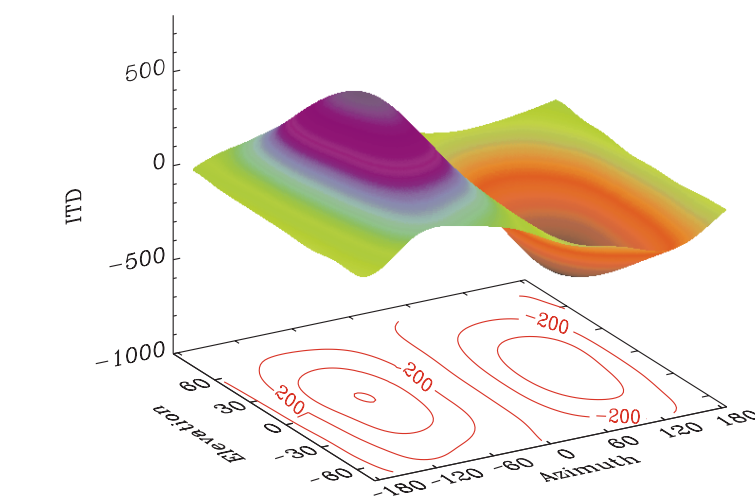
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vation (90,30) would be about the same as the ITDs produced by sources at (90,-30), (60,0) and (120,0). The other interaural difference cue, in sound level, is similarly ambiguous.

To the extent that listeners rely on interaural difference cues to determine sound source direction, they should make localization errors that reflect the ambiguity of the cues. Although such errors do not seem to be a problem in real life, they are not infrequent in laboratory studies of sound localization. Most numerous are those called 'front-back confusions'. An example of a front-back confusion would be a listener's report that the apparent direction of a sound was 120 degrees to the right of straight ahead (thus, in the rear hemifield) when in fact the source was only 60 degrees to the right. Both azimuths would produce roughly the same interaural time difference. Some listeners make large numbers of front-back confusions, and some listeners make very few. If apparent sound position were determined mainly by interaural differences, one would expect many more confusions than are observed. Clearly some other source of information is used to resolve ambiguities.

This is where ear shape enters the picture. In recent years, a great deal of research has focused on the acoustical cues to sound direction produced by our pinnae. Diffraction of a sound wave around the shoulders, head and pinnae introduces large changes into the frequency content of the sound wave at each ear. These changes, 'pinna cues', are exactly analogous to what would happen if the sound were passed through a pair of electronic filters: certain frequencies are amplified and others are attenuated. The frequency response of these 'filters', commonly called 'head-related transfer functions' or HRTFs for short, are highly dependent on sound direction and thus offer potential localization cues. Not only are pinna cues used to determine the direction of a sound, they are essential. Among other things, pinna cues are required for accurate perception of sound source elevation<sup>3</sup>, and they seem to be needed to give us the 'out there' character of everyday sounds. When pinna cues are stripped away and sounds are presented to listeners over headphones, the most common report is that the sounds are heard inside the head<sup>4</sup>.

Pinna cues are idiosyncratic. Because there is a wide variety of ear shapes in the population, the laws of acoustics dictate



**Fig. 2.** The difference in time of arrival of a sound wave at the two ears (ITD) plotted as a function of the azimuth (left–right) and elevation (up–down) of the sound source relative to the listener's head. The ITD is given in microseconds, and azimuth and elevation in degrees. At zero degrees azimuth and zero degrees elevation, the source is directly in front of the listener. Positive angles are to the right and above. The ITDs are computed relative to the left ear, so when the source is on the left (negative azimuths), ITD is positive (blue). Note that for this listener, ITD reaches a maximum of about 500  $\mu$ s at an azimuth of about  $-90^\circ$  and an elevation of  $0^\circ$ . An ITD of 500  $\mu$ s implies roughly that the sound wave must travel an extra 17 cm to get to the opposite ear. The red contours plotted beneath the colored surface illustrate the ambiguity of ITD as a localization cue. All locations defined by each contour line have the same ITD.

that HRTFs will also vary a great deal from individual to individual. They are as individual as fingerprints, thus the term 'earprints'. The perceptual relevance of the individual differences in pinna cues has been demonstrated in a number of ways, but perhaps most convincingly in experiments using virtual auditory space techniques<sup>5,6</sup>. With these virtual techniques, pinna cues are synthesized from individually measured HRTFs and then added to sounds presented through headphones. Thus, it is possible to present sounds to listeners that simulate the effect of 'listening through someone else's ears'. The results of such experiments<sup>1,2</sup> suggest that the most accurate localization is always achieved when one's own HRTFs are used, and that localization accuracy progressively deteriorates as the HRTFs used to synthesize sounds in virtual auditory space increasingly differ from one's own<sup>2</sup>. The most frequent kind of error made when listening through other people's HRTFs is the front-back confusion. This result suggests that pinna cues are indeed used to resolve front-back ambiguities.

Most theoretical accounts of how the brain might use pinna cues include the concept of a central repository of direc-

tion templates, derived either from the HRTFs or a transformation of them<sup>7-9</sup>. The idea is that the frequency content of an incoming sound is compared to each of the templates, and the one that fits the best then codes the direction of the incoming sound. Presumably the template bank is built up through long experience listening to sounds (with one's own HRTFs) in everyday life, where visual or other cues give the listener feedback about actual sound source direction. Nothing is known for certain about either how the templates are formed or how the brain uses the templates to determine a sound's direction. At this point the template theory is simply an untested hypothesis that seems to be consistent with much of the empirical data. Among the many important, but as yet unexplored, issues is how templates might develop in the early years of life when changes in head and pinna size and shape produce significant changes in the HRTFs. One obvious possibility is that the mechanism is adaptable, at least during development. The study by Hofman and colleagues offers convincing evidence for the adaptability of pinna cue processing.

There is no doubt that pinna cues

offer sufficient information for resolving the ambiguities produced by interaural difference cues, and thus for reducing front-back confusions. However, because many listeners make large numbers of front-back confusions even when their own pinna cues are available, more information must be necessary for resolving front-back confusions, at least for these listeners. It is possible that they use dynamic cues. Hans Wallach<sup>10</sup> originally articulated the theory that head movements could provide the information needed to resolve the ambiguity in interaural difference cues. The basic idea is that, given a fixed sound source, the way the interaural differences change during a head movement uniquely determines whether the sound is in the front or rear hemisphere. Indeed, front-back confusions nearly disappear when head movements are allowed<sup>11–13</sup>.

Our own recent work<sup>13</sup> suggests that there are large individual differences in how pinna cues and dynamic cues are used. In the 'freestyle' condition of this experiment, listeners were encouraged to move their heads, but only if they felt it would help them localize the sounds, and in a control ('restricted') condition, listeners were told not to move their heads. The 2.5-second wideband noise bursts were presented from one of several hundred possible locations all around the listener, starting when the listener was facing straight ahead. Head position was continuously monitored with a magnetic tracker. The striking result was that only those listeners who made frequent front-back confusions in the 'restricted' condition moved their heads in the 'freestyle' condition, implying that even without feedback some listeners know that they make front-back confusions and that head movements can help them avoid such errors. Subjects in the Hofman study moved freely as they learned the new mapping, so presumably they could have used movement cues to help calibrate their new pinnae.

Modern research on sound localization is informing us of the importance of 'earprints' and providing new understanding of how they are processed. The suggestion from this new study that learning earprints is like learning a second language is especially exciting in this regard. This and other research demonstrates that sound localization involves an individual-specific integration of several different kinds of information, including interaural difference

cues, pinna cues and dynamic cues. "Fascinating!", Spock would say.

1. Wenzel, E. M., Arruda, M., Kistler, D. J. & Wightman, F. L. *J. Acoust. Soc. Am.* **94**, 111–123 (1993).
2. Wightman, F. L. & Kistler, D. J. in *Proceedings of the ASSP (IEEE) Workshop on Applications of Signal Processing to Audio and Acoustics*. (IEEE Press, New York, 1993).
3. Gardner, M. B. & Gardner, R. S. *J. Acoust. Soc. Am.* **53**, 400–408 (1973).
4. Plenge, G. *J. Acoust. Soc. Am.*, **56**, 944–951 (1974).
5. Wightman, F. L. & Kistler, D. J. *J. Acoust. Soc. Am.* **85**, 858–867 (1989).
6. Wightman, F. L. & Kistler, D. J. *J. Acoust. Soc. Am.* **85**, 868–878 (1989).
7. Macpherson, E. A. *J. Acoust. Soc. Am.* **101**, 3105 (1997).
8. Middlebrooks, J. C. *J. Acoust. Soc. Am.* **92**, 2607–2624 (1992).
9. Zakarauskas, P. & Cynader, M. S. *J. Acoust. Soc. Am.* **94**, 1323–1332 (1993).
10. Wallach, H. *J. Exp. Psychol.* **27**, 339–368 (1940).
11. Perrett, S. & Noble, W. *J. Acoust. Soc. Am.* **102**, 2325–2332 (1997).
12. Perrett, S. & Noble, W. *Percept. Psychophys.* **59**, 1018–1026 (1997).
13. Wightman, F. L. & Kistler, D. J. *J. Acoust. Soc. Am.* (in press).

## Opening the third eye

Fred Rieke

Dark-adapted parietal-eye photoreceptors depolarize in response to light. A new study reveals that an unusual G-protein signaling pathway mediates this response.

In Hindu mythology, the god of destruction, Shiva, is often depicted with a third eye in the middle of his forehead. Legend has it that when this third eye is opened, it can destroy anything it sees. Humans, perhaps fortunately, have no such third eye, but some lizards do have a parietal or third eye on top of their head (Fig. 1). In this issue of *Nature Neuroscience* (page 359–365), Xiong, Solessio and Yau describe the unusual transduction cascade that underlies the response to light in photoreceptors from the lizard parietal eye.

The function of the parietal eye is not entirely clear, although it seems likely to detect day/night changes in light intensity and spectral composition<sup>1</sup>. The retina of the parietal eye has two types of cells, photoreceptors and ganglion cells, but lacks the bipolar, horizontal and amacrine cells found in the retina of the vertebrate lateral eye. A curious feature of the dark-adapted parietal photoreceptors is that they depolarize when exposed to light<sup>1</sup>, whereas other vertebrate photoreceptors hyperpolarize in response to a light flash.

As with vertebrate and invertebrate lateral-eye photoreceptors, phototransduction in the parietal-eye photoreceptors is

mediated by a G-protein intracellular signaling cascade. However, Xiong and colleagues show that the parietal-eye phototransduction cascade differs from other known G-protein cascades in two important ways. First, G-protein activation increases the cGMP concentration by inhibiting the cGMP phosphodiesterase (PDE, the enzyme that hydrolyzes cGMP). G-protein inhibition of PDE has not been observed previously<sup>2</sup>. Second, the PDE activity in parietal-eye photoreceptors is regulated by two G proteins operating



Fig. 1. Photograph of a side-blotched lizard, showing the parietal (third) eye on the top of its head. Photograph provided by John Finn and King-Wai Yau.

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