

- Langendijk, E.H.A., Bronkhorst, A.W., 2002. Contribution of spectral cues to human sound localization. *J. Acoust. Soc. Am.* 112, 1583–1596.
- Lawrence, B.C., Simmons, J.A., 1982. Echolocation in bats: the external ear and perception of the vertical positions of targets. *Science* 218, 481–483.
- Møller, A.R., 2000. *Hearing: Its Physiology and Pathophysiology*. Academic Press, San Diego, CA, pp. 30–36.
- Shaw, E.A.C., 1974. The external ear. In: Keidel, W.D., Neff, W.D. (Eds.), *Handbook of Sensory Physiology*, vol. V(1). Springer, New York, pp. 450–490. pp. 450–490.
- Wightman, F.L., Kistler, D.J., 1989. Headphone simulation of free-field listening. I: stimulus synthesis. *J. Acoust. Soc. Am.* 85, 858–867.
- Wotton, J.M., Haresign, T., Simmons, J.A., 1995. Spatially dependent acoustic cues generated by the external ear of the big brown bat, *Eptesicus fuscus*. *J. Acoust. Soc. Am.* 98, 1423–1455.
- Wotton, J.M., Simmons, J.A., 2000. Spectral cues and perception of the vertical position of targets by the big brown bat, *Eptesicus fuscus*. *J. Acoust. Soc. Am.* 107, 1034–1041.

J. Guo

Y. Chen

Department of Physics, Tsinghua University

Beijing 100084, PR China

E-mail address: guoj01@tsinghua.edu.cn

(J. Guo)

Available online 26 October 2004

0378-5955/\$ - see front matter © 2004 Published by Elsevier B.V.  
doi:10.1016/j.heares.2004.05.001

## Reply to the letter of J. Guo and Y. Chen

It is not unusual for the high-frequency half of mammalian audiograms to show minor dips and peaks in sensitivity and it has been shown that they change with the elevation of the sound source relative to the animal (e.g., Heffner et al., 2003). This suggests that they are due to the pinna and may provide sound localization cues for elevation. As Guo and Chen (in press) note, the high-frequency portion of an animal's audiogram may also provide pinna cues necessary for front-back localization, a point that has been demonstrated in chinchillas and other animals (e.g., Heffner and Heffner, 2003; Heffner et al., 1995). Applying to animals the results of a virtual localization study conducted on humans by Langendijk and Bronkhorst (2002), Guo and Chen suggest that the high-frequency portion of an animal's audiogram can be divided into two bands, one band providing the major spectral cues for elevation and a higher band providing the major cues for front-back localization. They then suggest that the location of these bands can be determined from the position of the first and second peaks of the audiogram.

The question is whether results obtained on humans can be easily generalized to other mammals. In this case, the erect and mobile pinnae of most mammals are quite different from ours, which are fixed and set in the shadow of the head. Thus, the way in which those animals make use of different frequencies for pinnae cues is most likely different. Moreover, some animals, including a number of bats, have more than two peaks

of sensitivity, making placement of the spectral bands problematic (e.g., Koay et al., 2003; Long and Schnitzler, 1975). Finally, the little evidence available on animals suggests that neither front-back nor vertical localization is restricted to particular frequency bands. For example, the ability of chinchillas to perform either localization task declines steadily as the high-frequency content of a noise signal is progressively filtered out from 40 to 5 kHz, an observation which indicates that they use the entire range to obtain both elevation and front-back locus cues (Heffner et al., 1995).

It is important to realize that mammals vary greatly in their use of sound localization cues. For example, some animals do not use binaural time cues (e.g., hedgehog), others do not use the binaural intensity cue (e.g., horse), and still others have completely relinquished the ability to localize sound (underground animals such as mole rats). And contrary to what has sometimes been suggested (e.g., Jeffress, 1975), the possession of erect and highly mobile pinnae does not guarantee good sound localization as demonstrated by poor sound localization ability of horses and cattle, who have left-right sound localization thresholds of 25 and 30, respectively (for a review, see Heffner and Heffner, 2003). Thus, although it is not impossible that some mammals rely on one band of high frequencies for vertical localization and another band for front-back localization, this has so far not been demonstrated and would require detailed behavioral testing to do so.

**References**

- Guo, J., Chen, Y., this issue. Comments on “Hearing in American leaf-nosed bats. III: *Artibeus jamaicensis*”. *Hear. Res.* 184, 113–122.
- Heffner, H.E., Heffner, R.S., 2003. Audition. In: Davis, S. (Ed.), *Handbook of Research Methods in Experimental Psychology*. Blackwell, Oxford, pp. 412–440.
- Heffner, R.S., Heffner, H.E., Koay, G., 1995. Sound localization in chinchillas, II: front/back and vertical localization. *Hear. Res.* 88, 190–198.
- Heffner, R.S., Koay, G., Heffner, R.S., 2003. Hearing in American leaf-nosed bats. III: *Artibeus jamaicensis*. *Hear. Res.* 184, 113–122.
- Jeffress, L.A., 1975. Localization of sound. In: Keidel, W.D., Neff, W.D. (Eds.), *Handbook of Sensory Physiology*, vol. V/2. Springer, New York, pp. 449–459.
- Koay, G., Heffner, R.S., Bitter, K.S., Heffner, H.E., 2003. Hearing in American leaf-nosed bats. II: *Carollia perspicillata*. *Hear. Res.* 178, 27–34.
- Long, G.R., Schnitzler, H.-U., 1975. Behavioral audiograms from the bat, *Rhinolophus ferrumequinum*. *J. Comp. Physiol.* 100, 211–219.

H.E. Heffner

R.S. Heffner

G. Koay

*Department of Psychology, University of Toledo**Toledo, OH 43606, USA**E-mail address: rickye.heffner@utoledo.edu*

(R.S. Heffner)

Available online 18 October 2004