3. Results

In a typical test session lasting approximately 1.5^2 h, each bat consumed up to 9 ml of juice ^ enough to permit presentation of 40^50 warning trials (together with 160^200 safe trials) and to determine a threshold for a single frequency. Because their natural fruit diet is relatively low in nutrients, this species must consume a larger volume of food than it can ingest in one feeding bout (Gardner, 1977). Thus each session included at least two bouts of feeding, with 20- to 30-min pauses in between, during which the food cleared their digestive system.

The audiograms of the two *C.* are illustrated in Fig. 1. The mean values for each bat after the thresholds had reached asymptote (three thresholds within a range of 3 dB) are listed in Table 1. The two individuals showed good agreement, as is expected for young, healthy, and well-motivated animals of the same species. Beginning with a mean threshold of 72 dB at 4 kHz, the audiogram shows a comparatively rapid improvement in sensitivity up to 25 kHz, the frequency of best hearing, with a mean threshold of 0 dB SPL. Hearing sensitivity then steadily decreased to 36.5 dB at 50 kHz but improved again as frequency further increased to 71 kHz, forming a secondary peak of sensitivity with an average threshold of 16.5 dB. Above 71 kHz, sensitivity again declined slowly with increasing frequency up to 125 kHz (29 dB), then steeply to 80 dB at 160 kHz, the highest frequency tested. At an intensity of 60 dB SPL, *C.* can hear frequencies from 5.2 kHz to 150 kHz, a range of 4.85 octaves.

To explore the possibility that the decrease in sensitivity centered at 50 kHz may have been due to pinna directionally, additional thresholds at 25, 40, 50, 71, and 125 kHz were determined at di¡erent sound source elevations in the median sagittal plane for Bat B (Fig. 2). *E* the sound source 30‡ above the horizon did not improve detectability at 50 kHz (the peak of insensitivity), but did decrease detectability by 10^27 dB at £anking frequencies of 25, 40, and 71 kHz. As a result, the sharp peak in the audiogram became less prominent. *L* the sound source 30‡ below the horizon enhanced the insensitivity peak and shiftDbyW)/x/511/D

by less than 10 dB. At 125 kHz, the highest frequency tested, neither raising nor lowering the sound source a¡ected the thresholds. This limited change in threshold at high frequencies is supported by direct measures of pinna directionality in this species, in which 30‡ changes in elevation near the midline resulted in changes in amplitude of less than 5 dB at the tympanic membrane for frequencies of 45 kHz or higher (Jen and Chen, 1988).

The di¡erences in threshold as a function of elevation cannot be attributed to variation in the animals' performances over time, as re-testing with the speakers at the horizon (0‡ elevation) produced thresholds that differed by no more than 2.5 dB from the original (see Fig. 2). Thus, the systematic changes in thresholds at di¡erent speaker elevations suggest that the irregular shape of the audiogram in the mid-frequency range is largely a result of the ¢ltering characteristics of the pinnae at these frequencies.

4. Discussion

4.1. A

The best sensitivity of *C.* is 0 dB (at 25

from 56 to 125 kHz that corresponds to the dominant second and third harmonics of its echolocation call (sweeping from 80 to 48 kHz and from 112 to 80 kHz, respectively; Gould, 1977; Grinnell, 1970; Pye, 1966). The reduced sensitivity in the range of its weak ¢rst harmonic (sweeping from 50 to 25 kHz) was shaped in part by pinna directionality, as it could be altered by changing the elevation of the sound source relative to the pinnae (Fig. 2). The increased thresholds seen here following both raising and lowering the speaker are in accord with physical measures of pinna directionality in this species (Jen and Chen, 1988) that show greater amplitudes when the sound source is at or near the horizon. These spectral transformations of sound by the pinnae generate pinna cues known to be especially important for localizing sound sources in the vertical plane (e.g., Lawrence and Simmons, 1982; Middlebrooks and Green, 1991; Ro¥er and Butler, 1968; Wotton et al., 1996; Wotton and Jenison, 1997).

4.2. H - - -

C. has very good high-frequency hearing. Its high-frequency hearing limit (the highest frequency audible at 60 dB SPL) is 150 kHz, the highest so far reported for a bat or for any other mammal that hears in air. The ability to perceive such high frequencies has implications for the study of auditory mechanisms. For example, the cochlear ampli¢er must either be capable of functioning at higher frequencies than previously thought (Gale and Ashmore, 1997), or else is not necessary for hearing these frequencies.

Although it may seem that the excellent high-frequency hearing of *C.* is due to its use of echolocation, it should be noted that when functional head size is taken into account, neither *C.* nor any other bat has unusually good high-frequency hearing. Good sensitivity to high frequencies is common in small mammals because of the selective pressure to detect high frequencies for use in passive sound localization. This selective pressure on passive hearing applies to all mammals studied so far, except those that do not localize sound (He¡ner and He¡ner, 1993). Small mammals must hear frequencies that are e¡ectively shadowed by their small heads and pinnae in order to produce interaural intensity/spectral di¡erences and monaural pinna cues large enough to be e¡ective indicators of locus (He¡ner and He¡ner, 1998; Masterton et al., 1969). Thus, mammals with small interaural distances, including bats and aquatic mammals (whose interaural distances are functionally small because of the faster travel time of sound in water), are under selective pressure to hear frequencies high enough to be useful in sound localization. Among mammals, there is a high correlation between functional head size (the time required for a sound to travel from one auditory meatus to the other) and the highest frequency audible at 60 dB ($=-0.787$, $P \leq 0.0001$), and *C.* does not deviate signi¢cantly from this relationship ($=1.49$, P

These overestimates are likely due to di¡erences in sound calibration and the orientation of the pinnae, as well as to the use in physiological studies of tones with abrupt onsets that generate additional frequencies (sometimes referred to as 'spectral splatter'). The remaining two curves showed less similarity to the behavioral audiograms. Whereas the gross electrode recordings from the inferior colliculus (Grinnell, 1970) re£ect

in American leaf-nosed bats. I: *P* . Hear. Res. 171, 97^103.

Koay, G., He¡ner, R.S., Bitter, K., 2002b. Hearing in the greater spear-nosed bat, *P* : Audiogram, temporal integration, sound localization, and use of binaural cues. Assoc. Res. Otolaryngol. Abstr. 25, 210.

Lawrence, B.D., Simmons, J.A., 1982. Echolocation in bats: The external ear and perception of the vertical position of targets. Science 218, 481^483.

Masterton, B., He¡ner, H., Ravizza, R., 1969. The evolution of human hearing. J. Acoust. Soc. Am. 45, 966^985.

Middlebrooks, J.C., Green, D.M., 1991. Sound localization by human listeners. Annu. Rev. Psychol. 42, 135^159.

Pye, A., 1966. The structure of the cochlea in Chiroptera III. Microchiroptera: Phyllostomatoidea. J. Morphol. 121, 241^254.

Ro¥er, S.)jLj1^6D24j1^28utlW)j561z6R.S., iP66.24j1/DFa/tureorsL51/DIIIthF/1x1PDt6W)j£uCF/eWD*x1PDofWW)jLj1zDexcalizatWFP