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Behavioral hearing range of the chinchilla

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The audiograms of three chinchillas were determined using pure tones ranging from 32 Hz to 45 kHz. The animals were tested with a conditioned avoidance procedure in which their heads were fixed within the sound field by requiring them to place their mouths on a water spout. At a level of 60 dB SPL the average hearing range extended from 50 Hz to 33 kHz with none of the animals able to hear 45 kHz at 89 dB. Overall, the audiogram of the chinchilla appears to resemble the human audiogram more closely than do other rodent audiograms. An analysis of ten published chinchilla audiograms indicates that those procedures which do not fix an animal within the sound field may overestimate their sensitivity.

Rodent; Human; Psychophysics; Method; Audiogram; Threshold

Introduction

Chinchillas (*Chinchilla laniger*) have been common laboratory animals for the study of the auditory periphery for over 20 years. The many reasons for their popularity have been described by Miller (1970): they are a convenient laboratory species; easy to maintain and breed in captivity, long-lived, and less subject to ear infections than laboratory rats; their middle ear and cochlea are convenient for electrophysiological studies, offering easy access for recording electrodes; they are easily trained for behavioral studies; and finally, their audibility curve is more like that of man than any of the other common laboratory species (e.g., mouse, rat, cat, guinea pig).

Despite the widespread use of the chinchilla in auditory studies, there remain some questions concerning their audiogram. First, the complete hearing range for chinchillas has never been established. Indeed, most audiograms for the chinchilla were obtained for the purpose of determining the effects of various physiological manipulations on hearing and determined thresholds only for mid-range frequencies (e.g., Clark and Bohne, 1978; Davis and Ferraro, 1983). The most complete audiogram to date is that by Miller (1970) who tested chinchillas at frequencies from 90 Hz to 32 kHz. However, chinchillas are remarkably sensitive to low frequencies and their good sensitivity (approximately 32 dB) at 90 Hz does not give a complete indication of their low-frequency hearing range. Further, Miller considered the thresholds at 16 kHz and above to be tentative because of difficulties in accurately specifying the intensity of these high-frequency tones (Miller, 1970, p. 517). However, if those thresholds are correct, then the chinchilla may be unique among rodents in that it does not appear to be able to hear much above 32 kHz. Thus, not only is the chinchilla's low-frequency hearing limit unknown, but its high-frequency hearing is sufficiently unusual to warrant further examination.

Second, there exists variability between studies regarding the absolute sensitivity of the chinchilla, particularly at frequencies above 2 kHz where differences of up to 35 dB can be found (cf. Ades, Trahiotis, Kokko-Cunningham, and Averbuch, 1974; Blakeslee, Hynson, Hamernik, and Hender-

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son, 1978). Although there are a number of possible causes of such variation, one obvious source is the heterogeneity of the sound field to which the animals are exposed. In studies in which the animals are permitted to move about the test cage, the sound field may vary by as much as 15 dB (e.g., Miller, 1970). Since thresholds are usually specified relative to an average sound field intensity, it is possible that some of the variability between studies and between individuals may have been due to variation in the sound field and the position of the animal within it.

Finally, in many cases, the primary goal of the experiments called for control audiograms to be obtained for monaurally deafened animals and these have been used as the estimate of normal hearing (e.g., Ades et al., 1974; Blakeslee et al., 1978; Clark and Bohne, 1978; Davis and Ferraro, 1983; Miller, 1970; Salvi, Hamernik, and Henderson, 1983; Saunders, Mills, and Miller, 1977). Although, as demonstrated by Miller (1970), there seems to be little difference in sensitivity between monaural and normal animals, ideally the audiogram for a species should be based on animals with normal ears.

Materials and Methods

The purpose of this paper is to report the complete hearing range of normal chinchillas which was determined using a procedure which maintains their heads in a fixed position within a known and constant sound field. Three chinchillas (*Chinchilla laniger*) were tested using a conditioned avoidance procedure (for details see Heffner and Heffner, 1985a). A thirsty animal was placed in a cage constructed of 1/2-inch (1.27-cm) hardware cloth mounted on a tripod in the center of a sound chamber (IAC model 1204) with carpeted floor and eggcrate foam on the walls and ceiling to reduce sound reflections.

Thresholds were determined behaviorally by training the chinchillas to indicate the presence of a pure tone by momentarily ceasing to drink from a water spout (a detection response) in order to avoid a mild shock from the spout. Drinking from the spout served to fix the heads of the animals in the sound field. Test sessions were divided into 2.5-s trials separated by 1.5-s intertrial intervals and a contact circuit indicated whether an animal was in contact with the spout during the last 150 ms of each trial. If an animal broke contact for more than half of this 150-ms response period, a response was recorded.

Each trial had a 22% probability of containing a pulsing tone (400 ms on, 200 ms off, 10 ms rise/decay for frequencies of 4–45 kHz and 20–160 ms rise/decay for progressively lower frequencies). Responses during "tone" trials were recorded as hits, and responses during "no-tone" trials were recorded as false alarms. The hit rate was corrected for false alarm rate to produce a performance measure according to the formula: Detection Performance = Hit rate − (False alarm rate × Hit rate). This measure varies from zero (no hits) to unity (100% hit rate with no false alarms).

Blocks of trials were presented at decreasing intensities in 5-dB steps until an animal's performance during tone trials did not differ significantly from its performance during no-tone trials. Threshold was defined as the intensity at which the detection performance was 50%.

The sound system was calibrated with either a Brüel and Kjaer 1-inch (2.54 cm) microphone (B and K 4131), sound level meter (B and K 2203) and octave filter (B and K 1613) or a 1/4-inch (0.64 cm) microphone (B and K 4135), preamplifier (B and K 2608), and filter (B and K 1613 or Krohn-Hite 3202). Sound measurements were taken in the position occupied by an animals's ears when it was drinking, and care was taken to ensure that the sound field was homogeneous (no more than 2-dB variation) in the area occupied by the animal. The intensity of ambient noise in the test chamber was measured at one-sixth octave steps throughout its measurable range. To reduce the intensity of low-frequency ambient noise in the test chamber, the air conditioning system for the building was turned off during testing of low frequencies. Background noise was at least 20 dB below threshold at all frequencies at which it was of measurable intensity (see Heffner and Heffner, 1985b, for measurements).

Results and Discussion

The audiograms of the three chinchillas are shown in Fig. 1. Beginning at the low frequencies,

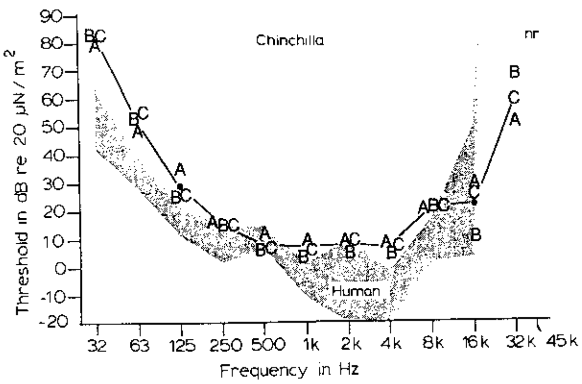

Fig. 1. Audiograms for three chinchillas (letters indicate individual animals) compared with the range of audiograms obtained for six humans in the same listening situation (shaded area).

the animals were able to hear 32 Hz with an average threshold of 82 dB SPL thus confirming the belief that chinchillas are very sensitive to low frequencies. Their sensitivity improved as frequency increased, and the audiogram shows a broad range of good sensitivity from 250 Hz to 16 kHz. Above 16 kHz, the chinchillas' sensitivity decreased rapidly to 32 kHz with none of the animals responding to 45 kHz at 89 dB SPL. Therefore, at a level of 60 dB SPL, the average hearing range of chinchillas extends from 50 Hz to 33 kHz giving them a range of hearing spanning more than 9 octaves.

Fig. 1 also allows a comparison of the chinchilla audiogram to audiograms obtained for 6 humans in the same listening environment (shaded area). Unlike most rodents (cf. Heffner and Heffner, 1985a), chinchillas have a hearing range very close to that of humans, the main difference being a shift of their hearing range approximately 1 octave into the higher frequencies. The best sensitivity range of the chinchilla is coincident with the best sensitivity range for man, approximately 125 Hz to 16 kHz, although they are generally not quite as sensitive as humans.

A comparison of the present audiogram with those published previously for chinchillas is shown in Fig. 2. First, it should be noted that our 32 kHz threshold of 59 dB is similar to the 56-dB threshold obtained by Miller (1970). Thus our results confirm his finding concerning the relatively restricted high-frequency hearing of chinchillas. The second point to be noted is the wide variation in sensitivity. Fig. 2 reveals a range of reported sensitivity of as much as 35 dB that is most marked at the upper frequencies. Much less variation is typically observed between individuals within an experiment where the average range of thresholds is approximately 6 dB and rarely greater than 10 dB (present report; Davis and Ferraro, 1983; Saunders et al., 1977).

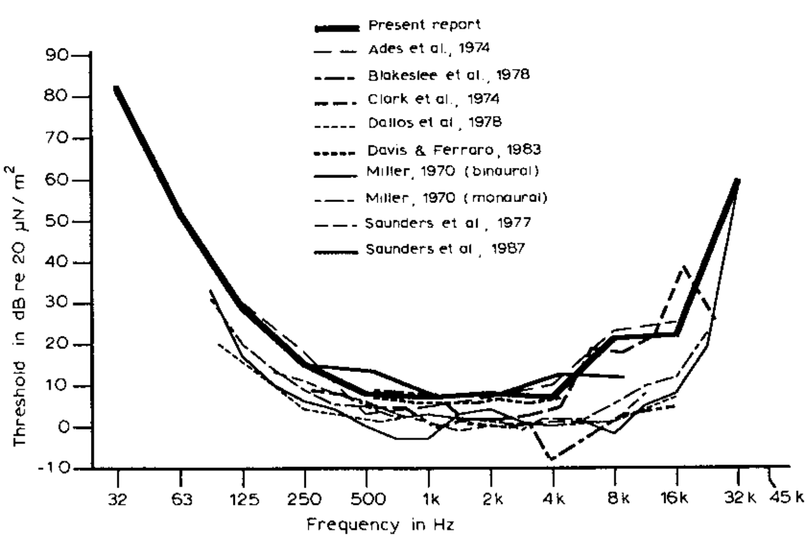

Fig. 2. Audiogram for the chinchillas reported here compared to nine previously-reported audiograms.

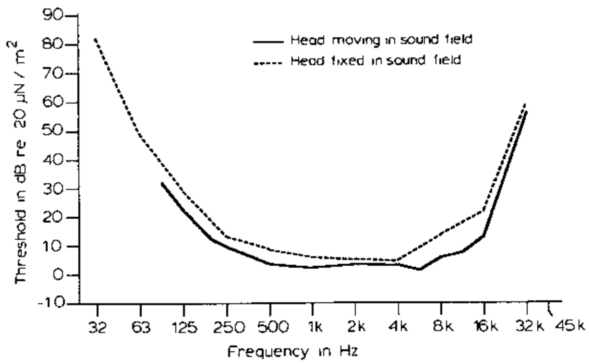

Fig. 3. The average of four audiograms obtained with the chinchillas' heads fixed in the sound field (dashed line; present report; Blakeslee et al., 1978; Clark et al., 1974; Saunders et al., 1987) compared to the average of six audiograms in which the animals were allowed to move about in the sound field [solid line; Ades et al., 1974; Dallos et al., 1978; Davis and Ferraro, 1983; Miller, 1970 (monaural and normal); Saunders et al., 1977].

One possible source of the difference between the reported sensitivity curves is the acoustic environment. Fig. 3 compares the average audiograms from six procedures in which the animals were allowed to move about within the sound field (double grill-box method) to four in which the animals' heads were fixed in the sound field either by restraining them, or by requiring them to hold down a lever or drink from a spout. Those test procedures which allowed an animal to move about in the sound field produced on average lower thresholds than those which did not (binomial test, one tailed $P < 0.004$).

One explanation for this difference in thresholds is the opportunity for the animals to choose a favorable listening position in the sound field where the intensity of the signal is loudest. Sound pressure level measurements taken at numerous positions in a grill box vary by as much as 15 dB (Miller, 1970), and thresholds are typically calculated based on a mean or median intensity which is necessarily lower than the loudest intensity available to the animal. Because small changes in the acoustic environment can result in significant differences in intensity, it is also possible that differences in the sound field contributed to the unexplained difference between the two groups of normal chinchillas tested in two different apparatus reported by Miller (1970). In contrast, procedures in which an animal must maintain its head and ears in a single position can achieve sound fields which vary by less than 2 dB even for relatively high frequencies. Thus it is likely that allowing an animal to move about the sound field results in an overestimation of its sensitivity.

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