Hearing in prairie dogs: Transition between surface and subterranean rodents

Rickye S. Heffner *, Henry E. Heffner, Christopher Contos, Dara Kearns

Department of Psychology, University of Toledo, Toledo, OH 43606, USA

Abstract

Behavioral audiograms were determined for four black-tailed and one white-tailed prairie dogs (*Cynomys ludovicianus* and *C. leucurus*) using a conditioned avoidance procedure. The hearing of black-tailed prairie dogs ranges from 29 Hz to 26 kHz and that of the white-tailed prairie dog from 44 Hz to 26 kHz (at sound pressure levels of 60 dB). Both species have good low-frequency hearing, especially black-tailed prairie dogs which can hear as low as 4 Hz and are more sensitive than any other rodent yet tested at frequencies below 63 Hz. In contrast, prairie dogs are relatively insensitive in their midrange and have poor high-frequency hearing. It is suggested that the reduced midrange sensitivity and high-frequency hearing are related to their adaptation to an underground lifestyle with its reduced selective pressure for sound localization. In this respect they appear to be intermediate between the more exclusively subterranean rodents (such as gophers and mole rats) and surface dwellers (such as chinchillas and kangaroo rats).

Key words: Audiogram; Rodent; Squirrel; *Cynomys*; Infrasound; Localization

1. Introduction

Rodents are a varied and successful order of mammals. Not only are they widespread geographically, but they inhabit nearly all the major ecological niches including nocturnal and diurnal, predator and prey, arboreal, terrestrial, subterranean, and semiaquatic. Similarly, rodents are morphologically diverse and range in size from small mice weighing less than 10 g to large beaver and capybara weighing more than 10 kg – a range of four orders of magnitude.

Of the 33 different families of rodents, the squirrel family (Sciuridae) is the third largest, comprising 51 genera with 280 species (Hartenberger, 1985). Although sciuridae diverged from a common ancestor as recently as the Oligocene and consequently have a close phyletic affiliation with each other, they are nevertheless a very diverse group. Indeed sciurids encompass nearly the entire range of body sizes and lifestyles present in the entire order Rodentia. They include small ground squirrels and large groundhogs, species

that live in trees and even glide from branch to branch, as well as species that are terrestrial and fossorial. Finally, although a few of the sciurids are nocturnal, most are diurnal – a character otherwise common in mammals only among primates. Because of the remarkable variety of lifestyles among a group of species sharing a long common evolutionary history, the Sciuridae seem an appropriate group in which to examine the effects of lifestyle on hearing with relatively limited influence of genetic variation. That is, any differences in hearing in this varied group are likely to have resulted from adaptation to specific habitats and lifestyles that took place after divergence from a common sciurid ancestor and thus are not attributable to differences in phyletic heritage (Hartenberger, 1985).

This study of black-tailed prairie dogs and a white-tailed prairie dog is the first in a series examining auditory sensitivity and sound localization in the squirrel family. Both species of prairie dogs are colonial and spend much of their time in large underground burrow systems but forage on the surface, usually within close range of a burrow entrance. Their strong, but not exclusive, adaptation to an underground habitat makes them intermediate between surface dwellers and sub-

terranean species, a feature which is reflected in their audiogram.

2. Materials and methods

2.1. Animals

Four young adult black-tailed prairie dogs (*Cynomys ludovicianus*) and one white-tailed prairie dog (*Cynomys leucurus*) served as subjects. The white-tailed and two of the black-tailed prairie dogs (C and D) were wild-caught and the other two black-tailed prairie dogs (A and B) were zoo-bred. The animals were housed in pairs in wire-covered glass tanks (32 × 76 × 31 cm high) with pelleted corn cob bedding and given free access to rat chow and rabbit pellets. They were given small amounts of fruit, vegetables, seeds, and nuts as supplements to assure good health. Water was used as a reward and was available only during the test sessions. The animals were weighed daily to monitor their deprivational state. Prior to testing the animals weighed 1.0–1.2 kg, and during testing they maintained 85–94% of their freefeed body weights, which is comparable to that of individuals in the wild.

2.2. Apparatus

The test apparatus and environment were identical to those described previously (e.g., Heffner and Heffner, 1990) and consisted of a large sound attenuating, low-reflective test chamber, a sound-transparent wire mesh test cage, and a reward delivery spout that kept the heads of the animals fixed relative to the sound source (cf. Heffner and Heffner, 1991). The acoustic apparatus was the same as that described in Heffner and Heffner (1993), including the daily measurement of sound pressure levels. Special precautions for the low-frequency thresholds included rise decay times as long as 300 ms for the low-frequency tone pulses (and compensatory lengthening of the tone durations) and a spectral analysis for distortion and overtones at frequencies below 125 Hz. In addition, thick foam cushions were placed under the cage and under the loudspeaker as a precaution against substrate vibration at low frequencies.

2.3. Behavioral procedure

The animals were tested using a conditioned avoidance procedure in which an animal that had been deprived of water for 23 hours was placed in the test cage and allowed to consume a steady trickle of water from the spout. It was then trained to respond by breaking contact with the spout momentarily whenever an obviously suprathreshold sound was presented in order to avoid a mild electric shock from the spout. This response was classified as a 'hit' if the trial contained a pulsing tone, and as a 'false alarm' if no tone was presented. Each trial had a 22% probability of containing a tone. Both the hit and false alarm rates were determined for each block of 6–8 warning trials (which also included approximately 25 safe trials) for each stimulus condition. The hit rate was corrected for false alarms to produce a performance measure according to the formula: Performance = Hit rate − (False alarm rate × Hit rate). This measure proportionately reduces the hit rate by the false alarm rate observed under each stimulus condition and varies from zero (no hits) to unity (100% hit rate with no false alarms) (cf. Heffner and Heffner, 1988 for additional details).

Auditory thresholds for each frequency were determined by reducing the intensity of the tone in successive blocks of 6–8 warning trials until an animal no longer responded to the tone above the level expected by chance (i.e., responses during tone and no-tone trials did not differ significantly, $P > 0.01$). Threshold was defined as the intensity corresponding to a performance of 0.50. Testing for a frequency was considered complete when the thresholds no longer improved with practice and those obtained in at least two different sessions were within 3 dB of each other. Once stable thresholds had been determined throughout the hearing range, each frequency was retested to ensure reliability. The final threshold for each animal at each frequency was the average of the best two thresholds after asymptote had been reached.

The care and use of the animals in this study were approved by the University of Toledo Animal Care and Use Committee which adheres to the guidelines of the Declaration of Helsinki (NIH DC00179).

3. Results

The audiogram for the black-tailed prairie dogs is illustrated in Fig. 1. That the animals from different sources show good agreement throughout their hearing range suggests that these individuals are probably representative of their species. Two individuals were tested only in the midrange of the audiogram (owing to hibernation before testing could be extended to the farthest limits of their sensitivity). Of the two individuals tested (during non-hibernating months) at the extremes of the hearing range, consistent responses were obtained for frequencies of 4 Hz to 22.4 kHz. Prairie dog A also responded to 32 kHz, but B did not respond even at an intensity of 92 dB. The prairie dogs did not have a distinct point of best sensitivity, but rather had a rela-
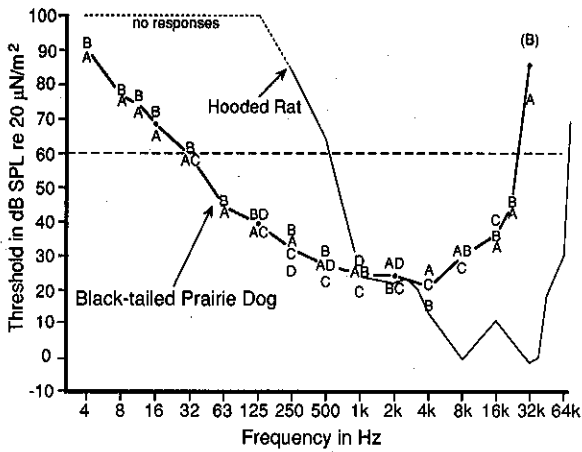
Fig. 1. Audiograms for four black-tailed prairie dogs (A, B, C, and D represent individual animals). Note the good sensitivity to frequencies below 63 Hz but relatively restricted sensitivity to middle and high frequencies (the inability of prairie dog B to respond to 32 kHz at 92 dB is indicated by parentheses). The solid line represents the audiogram of hooded rats (Heffner et al., 1994) and its dotted extension indicates that the hooded rats were unable to respond to any frequencies of 125 Hz and below at intensities of 99–101 dB. Dashed line indicates the 60-dB SPL level of hearing.

Fig. 3. Audiograms of two species of prairie dogs relative to the audiograms of other rodents capable of hearing low frequencies, (i.e., below 250 Hz; Heffner and Heffner, 1991; Heffner et al., 1971; Heffner and Masterton, 1980; Ryan, 1976; Webster, 1962). Note that both prairie dogs are more sensitive than other species to frequencies of 63 Hz and below (with the one exception that naked mole rats are more sensitive than the white-tailed prairie dogs at 32 Hz). At the middle and upper frequencies, prairie dogs appear to be intermediate in sensitivity between the surface-dwelling species (dark shading) and the species adapted exclusively to an underground lifestyle (light shading).

tively flat audiogram in their midfrequency range with thresholds between 500 Hz and 8 kHz varying by less than 10 dB. The lowest average threshold was 20.3 dB SPL at 4 kHz. The range of frequencies audible at 60 dB SPL extended from 29 Hz to 26 kHz for the black-tailed prairie dogs.

Perhaps the most remarkable aspect of the audiogram of the black-tailed prairie dogs is the extension of sensitivity far into the low frequencies. They continued to respond and produce reliable psychophysical functions to frequencies as low as 4 Hz. Because of this unexpected sensitivity to low frequencies, Norway rats, a species known to have limited low-frequency hearing,

were tested concurrently in the same apparatus as a control (Heffner, 1994). However, unlike the prairie dogs, the rats were unable to respond to frequencies below 250 Hz even at intensities of 99–101 dB SPL (dotted line in Fig. 1). Thus the low-frequency thresholds of the prairie dogs cannot be attributed to artifacts or to any unusual aspects of the behavioral or acoustic procedure.

The audiogram of the white-tailed prairie dog is illustrated in Fig. 2. Overall, its sensitivity and range of hearing is similar to that of the black-tailed prairie dogs, although it is somewhat less sensitive to low frequencies so that thresholds were determined only for frequencies down to 32 Hz. Again there is a broad range of best sensitivity and the white-tailed prairie dog's lowest threshold (at 8 kHz) is only 24 dB SPL. Its hearing range at 60 dB SPL extends from 44 Hz to 26 kHz.
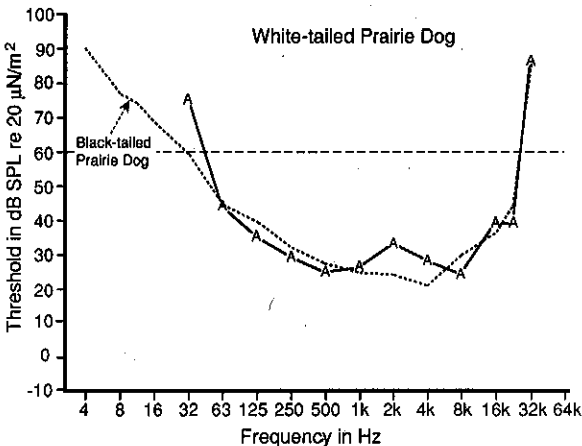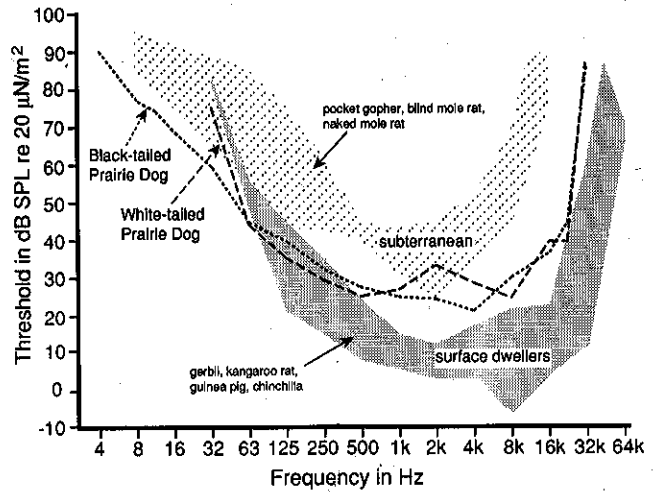

Fig. 2. Audiogram of a white-tailed prairie dog. Note relatively good low-frequency sensitivity, but poor hearing for the middle and high frequencies. Dashed line indicates the 60-dB SPL level of hearing.

4. Discussion

The most striking aspect of these results is the unexpected sensitivity of black-tailed prairie dogs to very-low-frequency sounds. At 63 Hz and lower frequencies they are more sensitive than any other rodents tested so far. Fig. 3 illustrates audiograms of the prairie dogs in relation to the audiograms of all other rodents previously reported to have good low-frequency

hearing (cf. Heffner and Heffner, 1992). The single white-tailed prairie dog, while more sensitive at low frequencies than most rodents, is not as sensitive as the black-tailed prairie dog at 32 Hz. Whether this difference is reliable, however, cannot be determined until additional white-tailed individuals have been tested. Above 32 Hz, however, the hearing of the two species appears to be indistinguishable.

Among rodents, good low-frequency hearing has previously been associated with anatomical specializations believed to enhance low-frequency sound transduction (e.g., Fleischer, 1978). Such specializations include the large bullae and tympanic membranes found in chinchillas, gerbils, guinea pigs, and kangaroo rats (Fleischer, 1978; Webster, 1984). Good low-frequency sensitivity has also been documented for two subterranean species, blind and naked mole rats (Bronchti et al., 1989; Heffner and Heffner, 1992, 1993), which, although lacking large bullae, have cochlear specializations thought to favor low-frequency hearing (Raphael et al., 1991). However, in contrast to the morphological specializations found in these rodents, no such specializations have been observed in the auditory apparatus of prairie dogs (Peterson et al., 1974) despite their superior low-frequency sensitivity. This finding suggests that the morphological, and perhaps neurological, mechanisms that subserve low-frequency hearing in small mammals may not yet be fully understood (cf. Heffner and Heffner, 1985).

Turning to the midrange of the audiograms, it can be seen that both species of prairie dogs are less sensitive than most of the low-frequency surface-dwelling rodents between 250 Hz and 16 kHz (Fig. 3). Indeed, prairie dogs are relatively insensitive compared to *all* other surface-dwelling rodents; their best sensitivity is only 20.3 dB (black-tailed) and 24 dB (white-tailed) whereas the mean best sensitivity for all other terrestrial rodents is −0.3 dB (cf. Heffner and Heffner, 1985). Thus the good low-frequency hearing of prairie dogs is accompanied by relatively poor sensitivity in the midrange. On the other hand, the prairie dogs are more sensitive than the subterranean rodents whose hearing can be considered vestigial (Heffner and Heffner, 1990, 1992, 1993). As indicated in Fig. 3 (lighter shading), the three subterranean species (pocket gopher, naked mole rat, and blind mole rat) have an even greater reduction in sensitivity to mid-frequency sounds with a mean best sensitivity of only 30 dB.

In sharp contrast to their excellent low-frequency hearing, the high-frequency hearing of prairie dogs is unusually limited (cf., Heffner and Heffner, 1985, 1992). This behavioral finding corresponds to the relative insensitivity of the cochlear microphonic responses in black-tailed prairie dogs to frequencies above 20 kHz (Peterson et al., 1974). As shown in Fig. 3, the observed high-frequency limit of prairie dogs, with their strong (but not exclusive) commitment to an underground habitat, is significantly lower than that of the other surface dwelling rodents specialized for low-frequency hearing. However, their high-frequency hearing remains superior to that of rodents which are exclusively subterranean.

One explanation for the limited high-frequency hearing of prairie dogs, and indeed all species which spend much of their time below ground, may lie in their vestigial pinnae. That is, a major advantage of hearing high frequencies is the resulting availability of monaural pinna cues for localizing sound – cues based on the high-frequency filtering characteristics of the pinnae (e.g., Carlile and Pettigrew, 1987; Musicant and Butler, 1984; Rice et al., 1992). The absence of pinnae would result in reduced selective pressure to hear high frequencies.

It is likely that the reduction of the pinnae and the loss of high-frequency sensitivity have both been affected by the reduced utility of sound localization in a largely one-dimensional underground world. This reduction in sound localization and high-frequency sensitivity is extreme in the exclusively subterranean species, but intermediate in the prairie dogs which continue to spend some time subject to selective pressures above ground. The limited ability of prairie dogs to localize sounds in azimuth and elevation (Heffner, unpublished; Koay et al., 1993) are consistent with the reduced utility of both the binaural and monaural high-frequency sound-localization cues.

In summary, just as prairie dogs are intermediate in their specialization for an underground lifestyle between surface dwelling species and the strictly subterranean species, they also seem to be intermediate in their overall sensitivity to sound. Specifically, it appears that poor sensitivity to middle and high frequencies of airborne sound occurs in species which spend much of their time in burrow systems such as prairie dog towns and mole rat tunnels, where the propagation of low frequencies is favored (cf., Heth et al., 1986; Narins et al., 1992). In addition, it should also be noted that a well-developed system of vocalizations (Waring, 1969) has not been sufficient to sustain sensitivity to middle and high frequencies in prairie dogs, just as it was not sufficient in naked mole rats (Heffner and Heffner, 1993). Finally, it is likely that the acoustic characteristics of an underground habitat may help account for the unusual insensitivity to most airborne sound while retaining good sensitivity only to low frequencies.

5. Acknowledgement

6. References

Bronchti, G., Heil, P., Scheich, H. and Wollberg, Z. (1989) Auditory pathway and auditory activation of primary visual targets in the blind mole rat (Spalax ehrenbergi): I. 2-deoxyglucose study of subcortical centers. J. Comp. Neurol. 284, 253–274.

Carlile, S. and Pettigrew, A.G. (1987) Directional properties of the auditory periphery in the guinea pig. Hear. Res. 31, 111–122.

Fleischer, G. (1978) Evolutionary principles of the mammalian middle ear. Adv. Anat. Embryol. Cell Biol. 55, 5–64.

Hartenberger, J.-L. (1985) The order Rodentia: Major questions on their evolutionary origin, relationships and suprafamilial systematics. In W.P. Luckett and J.-L. Hartenberger (Eds.), Evolutionary Relationships among Rodents, Plenum, New York, pp. 1–34.

Heffner, H.E. and Heffner, R.S. (1985) Hearing in two cricetid rodents: Wood rat (*Neotoma floridana*) and grasshopper mouse (*Onychomys leucogaster*). J. Comp. Psychol. 99, 275–288.

Heffner, H.E. and Masterton, R.B. (1980) Hearing in Glires: Domestic rabbit, cotton rat, feral house mouse, and kangaroo rat. J. Acoust. Soc. Am. 68, 1584–1599.

Heffner, R.S. and Heffner, H.E. (1985) Hearing in mammals: The least weasel. J. Mammal. 66, 745–755.

Heffner, R.S. and Heffner, H.E. (1988) Sound localization in a predatory rodent, the northern grasshopper mouse (*Onychomys leucogaster*). J. Comp. Psychol. 102, 66–71.

Heffner, R.S. and Heffner, H.E. (1990) Vestigial hearing in a fossorial mammal, the pocket gopher, (*Geomys bursarius*). Hear. Res. 46, 239–252.

Heffner, R.S. and Heffner, H.E. (1991) Behavioral hearing range of the chinchilla. Hear. Res. 52, 13–16.

Heffner, R.S. and Heffner, H.E. (1992) Hearing and sound localization in blind mole rats, *Spalax ehrenbergi*. Hear. Res. 62, 206–216.

Heffner, R.S. and Heffner, H.E. (1993) Degenerate hearing and sound localization in naked mole rats (*Heterocephalus glaber*) with an overview of central auditory structures. J. Comp. Neurol. 331, 418–433.

Heffner, R.S. and Heffner, H.E. and Masterton, B. (1971) Behavioral measurements of absolute and frequency-difference thresholds in guinea pigs. J. Acoust. Soc. Am. 49, 1888–1895.

Heffner, H.E., Heffner, R.S., Contos, C. and Ott, T. (1994) Audiogram of the hooded Norway rat. Hear. Res. 73, 244–247.

Heth, G., Frankenberg, E. and Nevo, E. (1986) Adaptive optimal sound for vocal communication in tunnels of a subterranean mammal (*Spalax ehrenbergi*). Experientia 42, 1287–1289.

Koay, G., Heffner, R.S. and Heffner, H.E. (1993) Vertical sound localization in chinchillas and prairie dogs. Abstr. Assoc. Res. Otolaryngol. 16, 49.

Musicant, A.D. and Butler, R.A. (1984) The influence of pinnae-based spectral cues on sound localization. J. Acoust. Soc. Am. 75, 1195–1200.

Narins, P.M., Reichman, O.J., Jarvis, J.U.M. and Lewis, E.R. (1992) Seismic signal transmission between burrows of the Cape mole-rat, *Georychus capensis*. J. Comp. Physiol. A 170, 13–21.

Peterson, E.A., Levison, M., Lovett, S., Feng, A. and Dunn, S.H. (1974) The relation between middle ear morphology and peripheral auditory function in rodents, I: Sciuridae. J. Aud. Res. 14, 227–242.

Raphael, Y. Lenoir, M., Wroblewski, R. and Pujol, R. (1991) The sensory epithelium and its innervation in the mole rat cochlea. J. Comp. Neurol. 314, 367–382.

Rice, J.J., May, B.J., Spirou, G.A. and Young, E.D. (1992) Pinna-based spectral cues for sound localization in the cat. Hear. Res. 58, 132–152.

Ryan, A. (1976) Hearing sensitivity of the mongolian gerbil *Meriones unguiculatis*. J. Acoust. Soc. Am. 59, 1222–1226.

Waring, G.H. (1969) Sound communications of black-tailed, white-tailed, and Gunnison's prairie dogs. Am. Midland Naturalist 83, 167–185.

Webster, D.B. (1962) A function of the enlarged middle ear cavities of the kangaroo rat. Physiol. Zool. 35, 248–255.

Webster, D.B. and Webster, M. (1984) The specialized auditory system of kangaroo rats. Contribut. Sensory Physiol. 8, 161–196.