

BRIEF COMMUNICATIONS

Audiogram of the Fox Squirrel (*Sciurus niger*)

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The behavioral audiograms of 2 fox squirrels (*Sciurus niger*) were determined with a conditioned avoidance procedure. The squirrels were able to hear tones ranging from 113 Hz to 49 kHz at a level of 60 dB sound-pressure level or less, with their best sensitivity of 1 dB occurring at 8 kHz. Their ability to hear frequencies below 150 Hz indicates that they have good low-frequency hearing, as do the 2 other members of the squirrel family (black-tailed and white-tailed prairie dogs) for which audiograms are available. This suggests that the ancestral sciurid may also have had good low-frequency hearing.

The taxonomic order Rodentia is a varied and successful group of animals comprising 33 families with more species than any other mammalian order. In addition to being distributed nearly worldwide, these species inhabit many diverse ecological niches, including nocturnal and diurnal, predator and prey, arboreal, terrestrial, subterranean, and semiaquatic (Nowak, 1991). They also possess a variety of adaptations for leaping, running, climbing, burrowing, swimming, and gliding. In terms of body sizes, rodents range from small mice weighing less than 10 g to large beaver and capybara weighing more than 10 kg—a morphological diversity encompassing a range of four orders of magnitude.

Among rodents the squirrel family, Sciuridae, is the third largest family with 51 genera and 280 species (Hartenberger, 1985). Although the squirrel family is of relatively recent origin, having diverged from a common ancestor during the Oligocene, it is an ecologically and morphologically diverse group. The squirrel family includes small ground-dwelling chipmunks and large groundhogs, prairie dogs that live underground but forage on the surface, and tree-dwelling squirrels. Indeed, the variety of body sizes and lifestyles within this closely related family makes it possible to examine the effects of lifestyle on hearing within the constraints of a comparatively limited phyletic heritage. As a result, differences in the auditory abilities of different sciurids are likely to have resulted from adaptation to specific habitats, lifestyles, and body sizes that took place after divergence from a common squirrel ancestor rather than to differences in phyletic heritage.

This report is the second in a series that examines the hearing abilities of a sciurid chosen on the basis of its

habitat (cf. R. S. Heffner, Heffner, Contos, & Kearns, 1994). Here we present the first audiogram of an arboreal rodent, the tree-dwelling fox squirrel, *Sciurus niger*, and compare its hearing with that of other rodents, particularly that of other sciurids.

Method

The animals were tested with a conditioned avoidance procedure with a water reward (H. E. Heffner & Heffner, 1995). Briefly, the animals were trained to maintain steady contact with a water spout to obtain water and to break contact whenever they detected a tone to avoid a mild shock delivered through the water spout.

Subjects

Two wild-caught fox squirrels (*Sciurus niger*), a male and female (designated as A and B, respectively), were used in this study. Both animals were approximately 4 months old at the beginning of testing. Each animal was housed in a cage (50 × 55 × 28 cm) constructed of 1-in. (2.54 cm) wire mesh. A 12-cm diameter PVC pipe (30 cm long and closed on one end with wire mesh) was attached to the side of the cage to serve as a nest box. The animals' diet consisted of dog biscuits, monkey chow, and rat chow supplemented with fruit, vegetables, and nuts. Water was used as a reward and was available only during the test sessions. The animals were weighed daily to monitor their deprivational state.

Behavioral Apparatus

Testing was conducted in a double-walled acoustic chamber (IAC model 1204, Industrial Acoustics Co., Bronx, NY; 2.55 × 2.75 × 2.05 m). The chamber floor was carpeted, and the walls and ceiling were lined with eggcrate foam to reduce sound reflections. The electronic equipment and microcomputer used for behavioral and stimulus control were located outside the chamber, and the animals were observed over closed-circuit television.

The squirrels were tested in a cage (38 × 21 × 23 cm) constructed of 0.5-in. (1.27 cm) hardware cloth (Figure 1). The cage was mounted on a camera tripod 71 cm above the chamber floor. A water spout was mounted vertically in the front of the cage, coming up through the floor to a level 8 cm above the cage floor.

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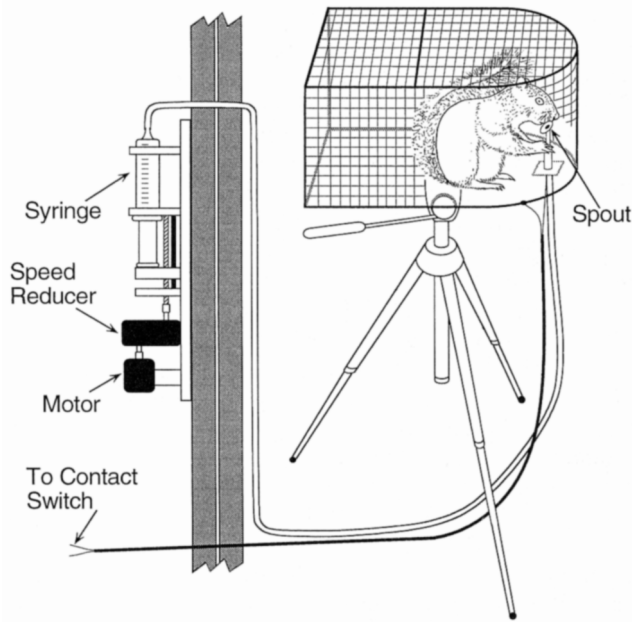


Figure 1. Diagram illustrating the arrangement of the behavioral test apparatus (not to scale).

The water spout consisted of a brass tube (3 mm outer diameter) with an oval brass disk (2 cm \times 2.5 cm) mounted on the top of the spout at a 50° angle sloping down toward the animal. This arrangement allowed the animal to face the front of the cage and hold its head in a normal posture while drinking from the water spout. The water spout was connected by plastic tubing to a syringe pump located outside the chamber. A contact switch connected between the spout and the cage floor indicated when a squirrel was in contact with the spout and activated the syringe pump. Thus, the squirrels received a steady trickle of water whenever they were in contact with the water spout. They typically received 35–40 ml of water in a session lasting 60–90 min.

A mild electric shock was delivered by a constant-current shock generator connected between the water spout and the cage floor. The duration of the shock pulse was 0.3 s, and the squirrel could escape it by breaking contact with the spout. The delivery of the shock was accompanied by turning on a 15-watt light bulb located beneath the front of the cage—the light thus served as a signal that the shock was being delivered, and turning it off signalled that the shock was over and the squirrel could return to the spout.

Acoustical Apparatus

Sine waves were generated by a signal generator (Krohn-Hite 2400, Krohn-Hite, Avon, MA), which was calibrated daily with a frequency counter (Fluke 1900A, John Fluke Manufacturing, Seattle, WA). The electrical signal was gated on and off with a rise-fall gate (Coulbourn S84-04, Coulbourn, Lehigh Valley, PA), bandpass filtered at one-third octave centered on the test frequency (Krohn-Hite 3550 filter, Krohn-Hite, Avon, MA), attenuated (Hewlett Packard 350D, Hewlett Packard, Loveland, CO), and connected by an amplifier (Adcom GFA 545, Adcom, East Brunswick, NJ) to a loudspeaker. The electrical signal to the loudspeaker was monitored with an oscilloscope. A loudspeaker was placed approximately 1.0 m in front of the cage and oriented toward the position occupied by the squirrel's head when it was drinking from

the water spout. The distance of the loudspeaker was varied by as much as 0.5 m as needed to achieve an even sound field of sufficient intensity around the squirrel's head. The loudspeakers used included a 15-in. (38-cm) woofer for 63 Hz to 8 kHz, and a ribbon tweeter for 8 kHz to 56 kHz. Pure-tone thresholds were obtained at octave intervals ranging from 63 Hz to 32 kHz, with additional thresholds at 45, 50, and 56 kHz. The tones were pulsed, 400 ms on and 100 ms off for 4 pulses, with rise-fall times of 100 ms for 63 Hz, 40 ms for 250 Hz, 20 ms for 500 Hz, and 10 ms for frequencies of 1 kHz and higher. The sound-pressure level (SPL re 20 $\mu\text{N}/\text{m}^2$) was measured daily with a .25-in. (.64 cm) microphone (Brüel & Kjaer 4135, Brüel & Kjaer, Naerum, Denmark), microphone amplifier (Brüel & Kjaer 2608, Brüel & Kjaer, Naerum, Denmark), and filter (Krohn-Hite 3202, Krohn-Hite, Avon, MA) set to pass one octave above and below the test frequency. The measuring system was calibrated with a pistonphone (Brüel & Kjaer 4230, Brüel & Kjaer, Naerum, Denmark). Sound measurements were taken by placing the microphone in the position occupied by the squirrel's head and pointing it directly toward the loudspeaker (0° incidence). Care was taken to produce a homogeneous sound field (± 1 dB) in the area occupied by the squirrel's head and ears while it was drinking from the spout. As a precaution against transmission of low-frequency substrate vibrations to the squirrels through the floor, thick foam was placed under the 15-in. woofer used for low-frequency testing. In addition, the linearity of the attenuator was verified over the range of attenuation used for threshold testing at each frequency by measuring its output voltage and the resulting sound pressure level.

Psychophysical Procedure

A thirsty squirrel was placed in the test cage and allowed to drink from the water spout. Tones were presented at random intervals and followed at their offset by mild electric shock delivered through the spout. The squirrels quickly learned to avoid the shock by breaking contact with the spout whenever they heard a tone. The shock was adjusted for each individual to the lowest level that would reliably produce an avoidance response. The mildness of the shock was attested by the fact that neither squirrel developed a fear of the spout; both returned to it without hesitation after a shock had been delivered.

Test sessions were divided into 2.0-s trials separated by 1.5-s intertrial intervals. Each trial contained either a pulsing tone (the warning signal) or silence (the safe signal), with 22% of the trials containing a tone. A response was recorded if a squirrel broke contact for more than half of the last 150 ms of a trial (as determined by the microcomputer). The response was classified as a hit if the trial contained a tone and as a false alarm if no tone had been presented. 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 according to the following formula: performance = hit rate - (false-alarm rate \times hit rate), with the hit and false-alarm rates expressed as percentages. This measure proportionately reduces the hit rate by the false-alarm rate observed under each stimulus condition and varies from 0 (no hits) to 1 (100% hit rate and 0% false-alarm rate).

Absolute thresholds were determined by reducing the intensity of a tone in successive blocks of 6–8 warning trials until the squirrel no longer responded to the signal above the .01 chance level (binomial distribution). Once a preliminary threshold had been obtained, final threshold determination was conducted by presenting tones varying in intensity in 5-dB increments extending from 10 dB below to at least 10 dB above the estimated threshold.

Threshold was defined as the intensity corresponding to a performance of .50. Threshold testing for a particular frequency was considered complete when the thresholds obtained in at least two different sessions were within 3 dB of each other. Once an audiogram had been completed, each threshold was rechecked to ensure reliability.

Results

The avoidance task was an easy one for the squirrels to learn, and they were reliably avoiding the shock within the first session. The squirrels trained quickly and were giving reliable and valid thresholds within 3–10 sessions. Moreover, the squirrels worked steadily for 60–120 min without misses or false alarms at easily detectable intensities. Our impression is that squirrels are better subjects for psychophysical experiments than most other rodents, including laboratory rats, because of their quick learning and consistently perfect performance on suprathreshold stimuli. The audiograms of the two squirrels are shown in Figure 2. Beginning at the low frequencies, the squirrels were able to hear 63 Hz with an average threshold of 79 dB SPL and with sensitivity improving as frequency was increased. The squirrels showed a broad range of good sensitivity extending from 500 Hz to 32 kHz, with their best threshold of 1 dB at 8 kHz. Above 32 kHz, their sensitivity decreased rapidly, with Squirrel A able to hear 50 kHz at a level of 69 dB and Squirrel B able to hear as high as 56 kHz at a level of 85 dB. Overall, at an intensity of 60 dB, the average range of hearing for the two squirrels, extended from 113 Hz to 49 kHz.

Discussion

Hearing in Rodents

The addition of the fox squirrel brings the total number of rodents for which behavioral audiograms are available to 17. In making comparisons among rodents, we have come to classify them into one of three groups based on their

hearing abilities: good low-frequency hearing, poor low-frequency hearing, and degenerate hearing. The good low-frequency rodents are those with the ability to hear below 150 Hz at an intensity of 60 dB while retaining good high-frequency hearing. These are the chinchilla, gerbil, guinea pig, and kangaroo rat (H. E. Heffner & Masterton, 1980; R. S. Heffner & Heffner, 1991; R. S. Heffner, Heffner, & Masterton, 1971; Ryan, 1976). The poor low-frequency rodents are those whose 60-dB low-frequency cutoff is above 500 Hz. These rodents tend to be smaller and to have slightly better high-frequency hearing than those with good low-frequency hearing—a finding consistent with the inverse relationship between interaural distance and high-frequency hearing that has been observed in mammals (e.g., R. S. Heffner & Heffner, 1992). These rodents include the cotton rat, grasshopper mouse, domestic house mouse, wild house mouse, albino Norway rat, pigmented Norway rat, and wood rat (H. E. Heffner & Heffner, 1985; H. E. Heffner, Heffner, Contos, & Ott, 1994; H. E. Heffner & Masterton, 1980; Kelly & Masterton, 1977; Markl & Ehret, 1973). Finally, the third group consists of rodents with degenerate hearing and includes the blind mole rat, naked mole rat, and pocket gopher (R. S. Heffner & Heffner, 1990, 1992, 1993). The range of auditory sensitivities for each of these groups is shown by the shaded areas in Figure 3.

In making this classification, the question arises as to what ecological, anatomical, or phylogenetic factors may account for the three groupings. In the case of the rodents with degenerate hearing, it can be seen that they share a common habitat—the blind mole rat, naked mole rat, and pocket gopher are all subterranean rodents. Underground burrows provide a very different acoustic environment than above-ground habitats, and we have noted elsewhere that animals adapted exclusively to an underground habitat lose much of their overall sensitivity and high-frequency hearing due in part to the apparent absence of selective pressure to localize brief sounds (R. S. Heffner & Heffner, 1990, 1992, 1993). With regard to the other two groups, the use of 150 Hz to define good and poor low-frequency rodents is based on an apparent gap in the distribution of mammalian low-frequency cutoffs. In a sample of 61 mammals (excluding those adapted to underwater hearing), we have found that the lowest frequencies audible at a level of 60 dB are evenly distributed with the exception of a 1.75-octave gap between 150 Hz and 500 Hz (the probability of such a gap occurring by chance is $p < .001$, Monte Carlo method; cf. Simon, 1992). There currently is no recognized factor that can explain why some rodents (or mammals in general) have better low-frequency hearing than others. That is, there appears to be no ecological or phylogenetic basis for this grouping. Nor is there any obvious anatomical basis—although it appears that the enlarged bullae of the kangaroo rats and gerbils is a morphological adaptation for low-frequency hearing (Webster & Webster, 1984), not all mammals with good low-frequency hearing possess this specialization (R. S. Heffner et al., 1994). One alternative is that these two groups may simply represent two ends of a continuum, with the possibility that future studies may

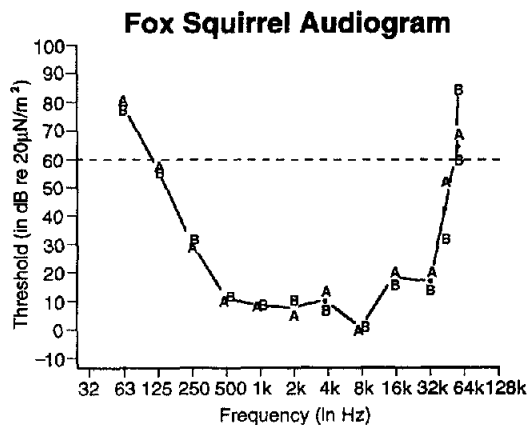


Figure 2. Absolute thresholds of two fox squirrels (A and B). Dashed line indicates the 60-dB sound-pressure level.

Squirrels Compared with Other Rodents

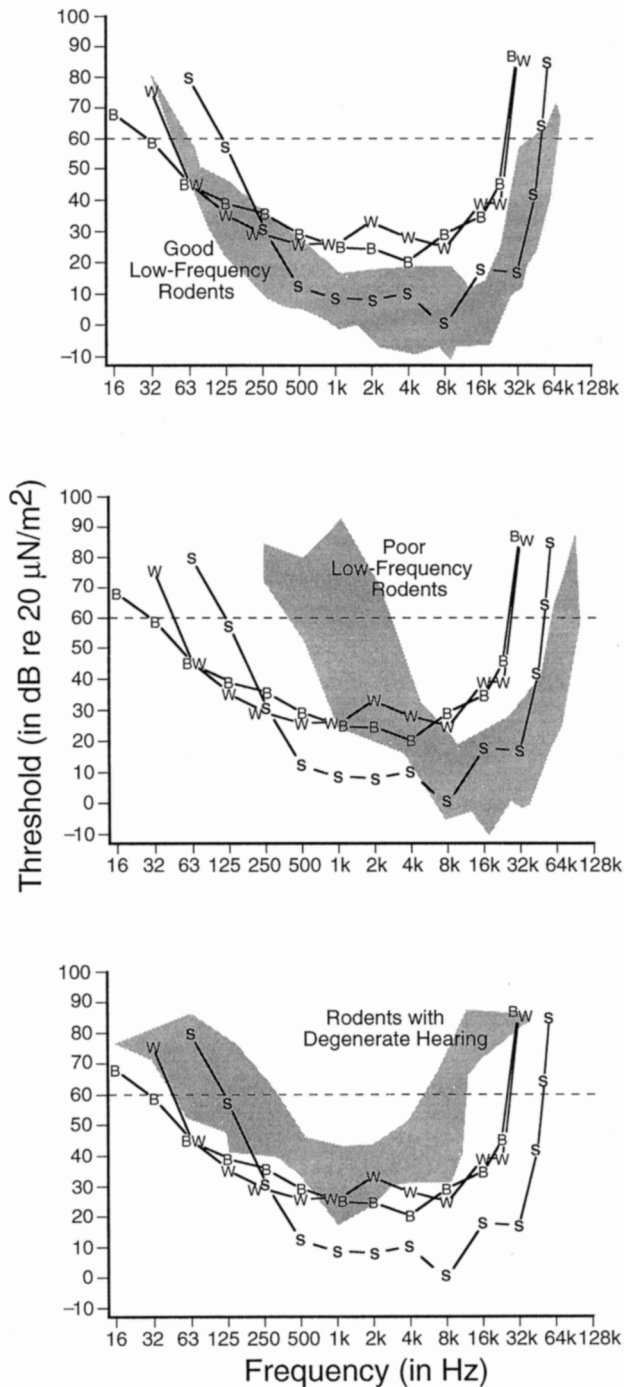


Figure 3. Average fox squirrel audiogram (S) compared with the audiograms of other rodents, black-tailed prairie dogs (B; *Cynomys ludovicianus*), and white-tailed prairie dogs (W; *Cynomys leucurus*). Horizontal dashed lines indicate 60-dB sound-pressure level. See text for references to individual audiograms. Top: Shading indicates rodents with good low-frequency hearing—chinchilla (*Chinchilla laniger*), gerbil (*Meriones unguiculatus*), guinea pig (*Cavia porcellus*), and kangaroo rat (*Dipodomys merriami*). Middle: Shading indicates rodents with poor low-frequency hearing—albino and pigmented rat (*Rattus norvegicus*),

reveal rodents whose hearing falls intermediate to them. However, this distinction is currently useful as a reminder that the hearing ability of rodents is quite varied and that rodent hearing cannot be adequately represented by a single species, such as the laboratory rat.

Comparison of Fox Squirrels With Other Rodents

The audiogram of the fox squirrel is compared with each of the three groupings of rodents in Figure 3. As shown in the top graph of Figure 3, the ability of the fox squirrel to hear below 150 Hz at a level of 60 dB places it with the good low-frequency rodents. Although its low-frequency hearing is not as good as the four species represented by the shading, or the two species of prairie dogs also shown in Figure 3 (indicated by the letters B and W), the squirrel hears nearly 2 octaves lower than the high-frequency rodents (middle graph of Figure 3). In addition, its high-frequency hearing is within the range of the other low-frequency rodents. Thus, it appears that the fox squirrel belongs among the low-frequency rodents.

Hearing in Sciurids

A comparison of the fox squirrel with the two other sciurids for which data are available, the black-tailed and white-tailed prairie dogs (R. S. Heffner et al., 1994), reveals both similarities and differences. Prairie dogs, like squirrels, fall into the good low-frequency group of rodents (cf. Figure 3). This finding raises the possibility that the ancestral sciurid was also a good low-frequency animal, a point that will require the examination of additional sciurids before it can be accepted. Fox squirrels and prairie dogs differ on two important parameters: high-frequency hearing and absolute sensitivity. In terms of the 60-dB high-frequency cut-off, fox squirrels hear up to 56 kHz whereas prairie dogs hear only as high as 26 kHz, a difference of slightly more than an octave. This difference is notable because there is an inverse relationship between interaural distance and high-frequency hearing, which would predict that, if anything, prairie dogs with their slightly smaller interaural distance should have somewhat better high-frequency hearing than fox squirrels (H. E. Heffner & Heffner, 1985). In addition, prairie dogs are far less sensitive than fox squirrels, with their best sensitivity of 20–24 dB contrasting with the fox squirrels' best sensitivity of 1 dB. The bottom graph in Figure 3 shows that the comparatively poor absolute sensitivity and high-frequency hearing of the prairie dogs place them intermediate between fox squirrels and subterranean rodents. Although prairie dogs are not subterranean animals, they do spend much of their

wild and domestic house mouse (*Mus musculus*), cotton rat (*Sigmodon hispidus*), grasshopper mouse (*Onychomys leucogaster*), and wood rat (*Neotoma floridana*). Bottom: Shading indicates subterranean rodents with degenerate hearing—blind mole rat (*Spalax ehrenbergi*), naked mole rat (*Heterocephalus glaber*), and pocket gopher (*Geomys bursarius*).

time in underground burrows. This suggests that the hearing of prairie dogs may be an intermediate adaptation between surface-dwelling and subterranean rodents. It also suggests that good absolute sensitivity and high-frequency hearing are either not necessary for, or else are somehow incompatible with, an underground lifestyle. Thus, although the recent common ancestry of the fox squirrel and the prairie dog may be responsible for the fact that they all have good low-frequency hearing, the differences in absolute sensitivity and high-frequency hearing may be the result of divergent adaptations to different lifestyles. These differences in closely related animals indicate that hearing range and sensitivity are relatively plastic behavioral traits. An identification of the selective pressures that lead to such differences should provide insight into the evolution of mammalian hearing.

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