Sound localization in chinchillas. I: Left/right discriminations

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Abstract

The ability of chinchillas to localize sound was examined behaviorally using a conditioned avoidance procedure in which the animals were trained to discriminate left from right sound sources. Their minimum audible angle was 15.6° for 100-ms broadband noise making them one of the more accurate rodents, although they are not as accurate as primates and carnivores. Thresholds obtained for filtered noise stimuli demonstrated that chinchillas are equally accurate in localizing either low- or high-frequency noise. Further, they are able to use both interaural phase-difference and interaural intensity-difference cues as demonstrated by their ability to localize both low- and high-frequency pure tones. Finally, analysis of the chinchilla retina supports the hypothesis that the role of auditory localization in directing the eyes to sound sources played a role in the evolution of auditory spatial perception.

Keywords: Evolution; Comparative; Retina; Ganglion cells; Vision; Binaural cues; Pinna

1. Introduction

Because of their widespread use in anatomical and electrophysiological studies of the auditory periphery, chinchillas have become a common species for use in behavioral studies of hearing. As a result, more is known about the hearing abilities of chinchillas than about those of most other species of mammal. Not only have chinchillas been tested for their ability to perform basic discriminations of frequency, intensity, and time, but they have also been used in studies of masking, noise exposure, and speech perception (for references, see Fay, 1988). However, in spite of their wide use, there is one major aspect of their hearing which has remained unexamined, specifically, their ability to localize sound. In view of the recent use of chinchillas in the study of the central auditory system, particularly the neural basis for sound localization (e.g., Benson and Teas, 1976; Finlayson and Caspary, 1989, 1991; Langford, 1984), information regarding their basic sound-localization abilities is needed to more fully appreciate the electrophysiological data.

In addition, the ability to localize sound is a fundamental function of hearing, of interest in its own right, and has been subject to detailed comparative analyses (for recent reviews, see Brown and May, 1990; Heffner and Heffner, 1992a). One result of these analyses has been the realization that the sound-localization abilities of mammals are not uniform, but vary greatly between species. Mammals vary not only in acuity, but also in the degree to which they rely on the different cues for sound localization. Thus, given the importance of chinchillas in auditory research, it would be useful to determine their sound-localization abilities thereby gaining some understanding as to how their abilities compare to those of other mammals, including humans.

The present report is the first in a series of three papers describing the sound localization ability of chinchillas. The experiments reported here were undertaken to determine: 1) left/right sound-localization acuity for broadband noise (i.e., minimum audible angle around the median sagittal plane), 2) the ability to use binaural time- and intensity-difference cues as indicated by the ability to localize low- and high-frequency tones, and 3) the importance of low and high frequencies in performing a left/right locus discrimination. Finally, in order to further examine the hypothe-

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sis that a primary function of sound localization is to direct the gaze to a sound source (Heffner and Heffner, 1992b), we present retinal ganglion cell isodensity contours for a chinchilla and describe how the width of the field of best vision is related to sound localization acuity.

2. Methods

A conditioned avoidance procedure was used in which an animal learned to drink steadily from a water spout while sounds were presented from a loudspeaker to its right, and to cease drinking when a sound was presented from a loudspeaker to its left in order to avoid a mild shock.

2.1. Subjects

Altogether five adult pigmented male chinchillas were tested. They were housed individually in glass tanks with wire mesh tops and given free access to rabbit chow supplemented by one raisin daily and occasional greens. They received most of their water in the test sessions with additional water provided as needed to maintain health. They typically consumed 5-10 ml of water during test sessions lasting 30-45 min. The animals were weighed daily to monitor their deprivational status; well trained chinchillas usually did not require deprivation below 90% free-feed body weight for good performance.

2.2. Behavioral apparatus

All testing was conducted in a double-walled sound-attenuating chamber (IAC model 1204; 2.55 × 2.75 × 2.05 m). The floor of the chamber was carpeted and the walls and ceiling were covered with eggcrate foam to reduce sound reflections. The equipment for behavioral control and stimulus generation was located adjacent to the chamber and the animals were observed over a closed-circuit television system during testing.

The animals were tested in a cage (38 × 21 × 23 cm) constructed of half-inch (1.26-cm) hardware cloth. The cage was mounted on a camera tripod 86 cm above the floor. In order to minimize obstructions between an animal's ears and the loudspeakers, a 15-gauge stainless steel waterspout was mounted vertically in the front of the cage so that it projected 9 cm above the cage floor. An oval metal disk (1.5 × 2.5 cm) was mounted on top of the spout so that a chinchilla could lick water off the disk while holding its head in a normal position. To prevent the animals from turning their heads while drinking, a 5-cm high hardware cloth barrier was placed 3 cm from the spout so that they

had to extend their heads over the barrier in order to reach the waterspout. The waterspout was connected via plastic tubing either to an electrically operated water valve and a 25-ml water reservoir or to a 25-cc syringe pump located outside the chamber. The chinchillas received a steady trickle of water as long as a contact circuit connected between the spout and the cage floor detected that they remained in contact with the waterspout. (For an illustration of the test cage, see Heffner et al., 1994.)

A mild shock was delivered by a constant-current generator connected between the spout and the floor of the cage. The shock was adjusted for each individual to the lowest level that produced a consistent avoidance response to a readily detected signal. The mildness of the shock was indicated by the fact that the animals did not develop a fear of the spout but returned to it immediately after the shock had been delivered. A 25-watt light bulb located beneath the cage was turned on whenever the shock was on so that turning off the light indicated that the shock was over and that the animal could return to the waterspout.

2.3. Acoustic apparatus

Noise

A broadband electrical signal was generated by a Grason-Stadler noise generator (GS 1285) and led to a programmable attenuator (Coulbourn S85-08) which randomly attenuated the signal by 0-7 dB in 1-dB steps in order to reduce the possibility that the animals could distinguish between the loudspeakers on the basis of small intensity differences. In order to ensure that an animal was not discriminating possible differences in quality between speakers, the signal was randomly sent through one of two equalizers (Symmetric Sound Systems EQ3) which varied the spectrum of the signal by up to 1 dB in 24 bands extending from 200 Hz to 20 kHz (Fig. 1a).

The electrical signal was filtered (Krohn-Hite 3202) using one of three settings: broadband noise (Fig. 1a); high-pass noise, pass above 8 kHz (48 dB per octave roll off) (Fig. 1b); and low-pass noise, pass below 500 Hz (48 dB per octave roll off) (Fig. 1c). The broadband signal was switched by a rise/decay gate (Coulbourn S84-04) set on 0 (0.1 ms) rise/decay, 100 ms duration. A 50-ms rise/decay (50 ms full amplitude) was used for the high- and low-pass filtered signals to avoid high-frequency onset transients.

Finally the signal was split into left and right channels, separately amplified (Coulbourn S82-24), and sent to one of three pairs of matched loudspeakers. The speakers were placed on a perimeter bar 103 cm in radius centered on the position of an animal's head while it drank from the spout. Dome speakers were used for the broadband tests, piezoelectric tweeters for
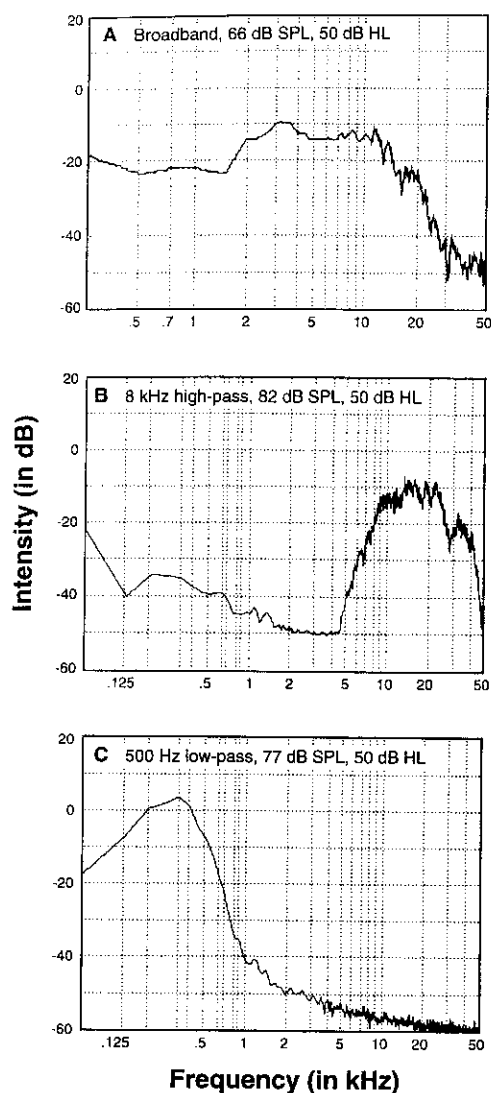
Fig. 1. Spectra of noise bands used for sound localization. There was no overlap in the frequency content of the high-pass and low-pass noise bands. All three noise bands were presented at 50 dB above the chinchillas' thresholds. Note that at 60 dB SPL the hearing range of chinchillas extends from 50 Hz to 33 kHz (Heffner and Heffner, 1991).

the high-pass noise, and 3-in woofers for the low-pass noise. The signals from all six speakers were matched in intensity within 1 dB and set at 50 dB above the average detection threshold which had been behaviorally determined prior to testing.

Tones

Sine waves were generated by a function generator (Hewlett-Packard 200 CD), randomly attenuated over a 4-dB range, shaped by the rise/decay gate (50 ms rise-fall, 150 ms on full), and filtered (2/3 octave bandpass centered on the frequency of the tone, 24 dB per octave roll-off). Finally, the electrical signal was split and sent to the two amplifiers with the intensity of

the tone set at 50 dB above the average threshold for chinchillas (Heffner and Heffner, 1991). A variety of loudspeakers was used to produce the wide range of frequencies at the required intensities: 5.5-in. (14-cm) woofer for 125 Hz and 180 Hz, 3-in. (7.5-cm) woofer for 250 Hz to 1 kHz, dome speakers for 2 kHz to 4 kHz, and leaf tweeters for 8 kHz to 22.4 kHz. The speakers were separated by 60° (30° to the left and right of midline) and placed 103 cm from the center of the animal's head. Testing was conducted in octave steps from 125 Hz to 16 kHz with additional testing at the intermediate frequencies of 180 Hz, 1.4 kHz, 2.8 kHz, 11.2 kHz, and 22.4 kHz.

Sound level measurement

The sound pressure levels of the stimuli were equated and measured at the position occupied by the animal's ears using a sound level meter (Brüel and Kjaer 2203 or 2608 microphone amplifier, 4131 or 4135 microphone, and a Krohn-Hite 3202 filter). Spectra were obtained for the acoustic signals using a Zonic 3525 FFT spectrum analyzer.

2.4. Psychophysical procedure

A thirsty animal was trained to make steady contact with the water spout by providing a steady trickle of water (approximately 0.2 ml/min) as long as it was in contact with the spout. The animals were then accustomed to drinking while broadband noise bursts were presented once every 3.3 s from their right. They were then trained to break contact with the spout (a 'detection response') whenever a noise burst was presented from their left in order to avoid a mild electric shock from the spout which followed 1.8 s after left signal onset.

Test sessions consisted of a series of trials which began with the onset of a stimulus and ended 1.8 s later. Trials were separated by 1.5-s intertrial intervals (i.e., one trial every 3.3 s). The response of an animal on each trial (i.e., whether or not it made a detection response) was determined by whether it 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 detection response was recorded and classified as a 'hit' if the preceding signal had been a warning signal and as a 'false alarm' if the preceding signal had been a safe signal. Each trial had a 22% probability of containing a warning signal. The schedule was quasi-random and included the restriction that no more than 13 safe signals could occur consecutively. Both the hit rate and false alarm rate were determined for each block of 8–10 warning trials for each stimulus condition. The hit rate was corrected for false alarms to produce a corrected detection measure according to the formula: Performance = Hit rate − (False alarm

rate × Hit rate) (Heffner and Heffner, 1988a). This performance measure varies from zero (no hits) to unity (100% hit rate with no false alarms). Note that this calculation proportionately reduces the hit rate by the false alarm rate observed under each stimulus condition rather than the false alarm rate averaged for the session as a whole.

For the noise localization thresholds, blocks of trials containing 8–10 warning signals were presented at one angle of separation before changing to a different angle. The angle was decreased until the corrected detection measure fell below 25% and the hit rate was no longer significantly different from the false alarm rate (binomial distribution, p > 0.05). Daily testing continued until performance no longer improved at any angle. The mean of the best three sessions was then plotted as the asymptotic performance curve for each individual. Threshold was defined as the angle at which the corrected detection score equaled 0.50.

Tone-localization tests were conducted at a fixed angle of 60°. Testing was carried out using a single frequency per session with the animal's performance calculated for blocks of 10 warning trials. Each frequency was tested over several non-consecutive sessions for a total of 100 warning trials. The three best performance scores for blocks of 10 consecutive warning trials were averaged to represent the best performance of which the animals were capable.

2.5. Histological procedure

A chinchilla was anesthetized with an overdose of barbiturate and perfused through the heart with 0.9% saline followed by 4% formalin. The superior surfaces of the eyes were marked with suture prior to their removal. The retinae were dissected free from the sclera, mounted on gelatinized slides with the ganglion-cell layer uppermost, and stained with thionine according to the procedure of Stone (1981). The density of the ganglion cells was determined throughout the retina in 0.1-mm steps using a 40 × immersion objective and a sampling area of 0.0062 mm^2. The horizontal width of the region encompassing densities equal to or greater than 75% of maximum density was determined as an indication of the width of the field of best vision as described previously (Heffner and Heffner, 1992b). Maximum density was used to calculate the maximum theoretical acuity of chinchillas using Shannon's sampling theorem (e.g., DeBruyn et al., 1980): $(\sqrt{x})/2$ = maximum theoretical resolvable spatial frequency in cycles/degree, where x = number of ganglion cells per deg^2.

The care and use of the animals in this study were approved by the University of Toledo Institutional Animal Care and Use Committee, which abides by the Helsinki agreement (NIH DC00179).

3. Results

3.1. Noise localization

The ability of three chinchillas to discriminate sound sources centered symmetrically around midline is illustrated in Fig. 2 for each of the three noise stimuli: broadband, 8-kHz high-pass, and 500-Hz low-pass noise. In each test the three individuals showed good agreement with good performance at angles of separation of 30° or greater. Performance fell rapidly at smaller angles with chance performance usually reached by 10°. Average thresholds are: for the broadband noise, 17.5°; for the 8-kHz high-pass noise, 13.7°; and for the 500-Hz low-pass noise, 15.7°. However, the
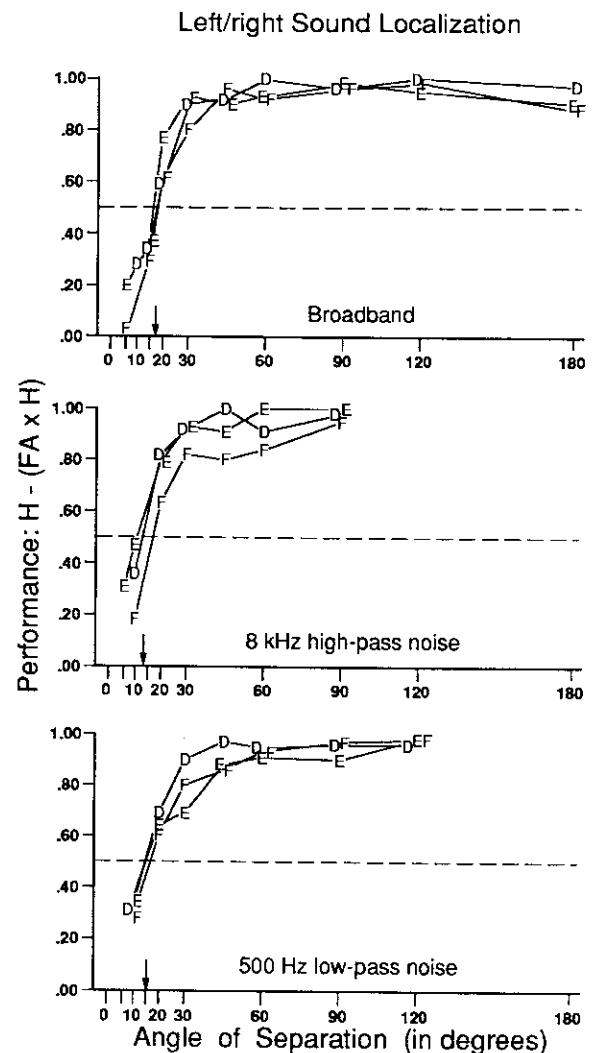

Fig. 2. Left/right sound-localization performance of three chinchillas as a function of angle of separation for three noise bands. Note that thresholds do not differ significantly for the different noise bands. Letters represent individual animals and dashed lines indicate the 0.50 performance level used to define thresholds, which are indicated by arrows.

differences between the thresholds for the three different noise stimuli are not statistically reliable and no significance should be attached to them (Mann-Whitney U, p > 0.05). It should be noted that testing was carried out first with the broadband signal followed by the high-pass and then the low-pass noise. Although the animals were experienced listeners when testing began, and testing was continued at each stimulus until performance no longer improved, the possibility of a practice effect cannot be ruled out. Accordingly, for comparison to other species, we will use the mean threshold of 15.6° to represent the acuity of chinchillas.

3.2. Pure-tone localization

In order to explore the ability of chinchillas to localize sound sources using binaural time and intensity cues alone, the animals were tested for their ability to localize brief tone pips at frequencies from 125 Hz to 22.4 kHz. This test takes advantage of the fact that intensity-difference cues are not produced by low-frequency tones because low frequencies bend around the head with little attenuation (for direct measures of the absence of interaural intensity differences, see Carlile and Pettigrew, 1987; Harrison and Downey, 1969; Heffner and Heffner, 1992a; Musicant et al., 1990; Rice, et al., 1992). On the other hand, phase-difference cues become ambiguous at high frequencies. At a 60° angle of separation between sound sources, the calculated frequency above which the phase cue becomes physically ambiguous for an animal with a spherical head and the 224-μs interaural distance of an adult chinchilla is 5.5 kHz (indicated by the vertical stippled bar in Fig. 3; for the formula for calculating the frequency of ambiguity, see Kuhn, 1977). Thus, the
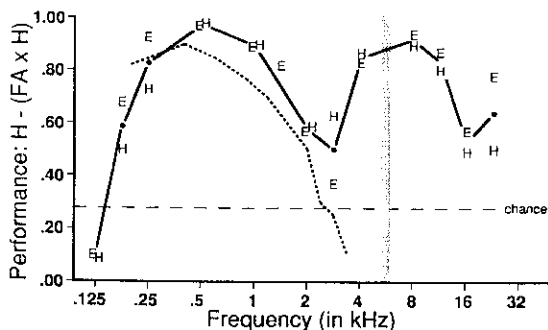

Fig. 3. Sound localization performance of two chinchillas as a function of the frequency of a pure-tone stimulus. Letters represent individual animals and the stippled bar indicates the upper limit of physical availability of the interaural phase-difference cue. The dotted line indicates the coefficient of synchrony (ranging from 0 to 1.0) of phase locking in eighth nerve fibers in chinchillas (from Woolf et al., 1981). Note that both localization performance and phase locking decline above and below 500 Hz and 400 Hz, respectively, even though a phase difference is physically available and unambiguous.
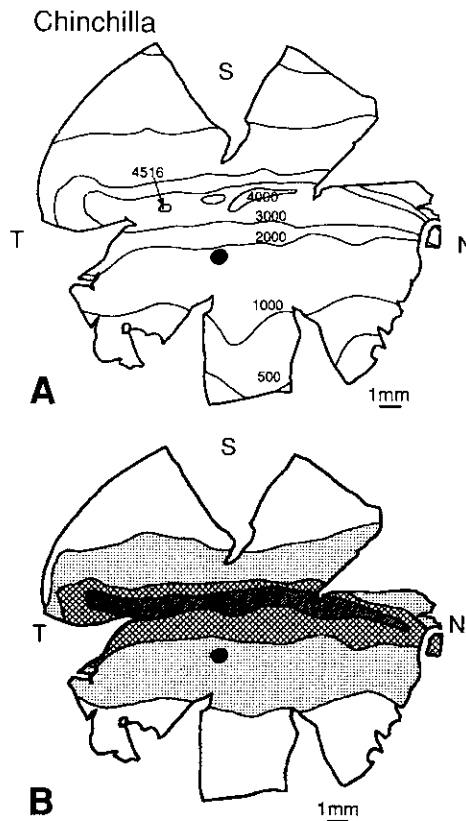
ability to localize pure tones below 5.5 kHz suggests that an animal can use the binaural phase-difference cue and the ability to localize high-frequency pure tones suggests that it can use the binaural intensity-difference cue (Stevens and Newman, 1936).

Fig. 3 illustrates the ability of two chinchillas to localize single pure-tone pips from speakers separated by 60°. As can be seen, the chinchillas were able to localize tones above and below the frequency of ambiguity for phase. Thus, the ability to localize both low and high-frequency tones indicates that chinchillas are probably capable of using both binaural phase- and binaural intensity-difference cues.

However, it should be noted that not all frequencies were localized with equal facility. First, the animals show a decrease in performance in the midrange from 1 to 4 kHz with the lowest performance falling at 2.8 kHz. This suggests that their ability to use binaural phase begins to decline above 500 Hz and may be absent by 2.8 kHz while their ability to use binaural intensity differences does not become maximal until about 4 kHz (cf. Heffner and Heffner, 1987, 1992a). Indeed, the decrease in performance is similar to the decline in phase locking in the eighth nerve of chinchillas which occurs above 400 Hz (dotted line in Fig. 3; Woolf et al., 1981). Second, at frequencies below 250 Hz, performance fell and pure tones of 125 Hz were completely unlocalizable. A decrease in the ability of monkeys to lateralize low-frequency tones has previously been attributed to a decline in phase locking at long wavelengths (Houben and Gourevitch, 1979), and the evidence for a similar low-frequency decline in phase locking for chinchillas, while limited (Fig. 3; Woolf et al., 1981) suggests that this explanation could also apply to chinchillas. Finally, pure tones of 16 and 22.4 kHz were difficult to localize, probably because of the unreliability of interaural intensity differences for high-frequency pure tones (e.g., Harrison and Downey, 1969).

3.3. Retinal ganglion-cell densities

The ganglion cell isodensity contours for the right retina of a chinchilla are illustrated in Fig. 4a. The ganglion cells are arranged in a well differentiated visual streak that is most evident in the region encompassing ganglion cell densities of 2000 cells/mm^2 or greater. As is common, the densest concentration of ganglion cells occurs in the temporal retina (binocular retinal field), however the streak itself extends further nasally than temporally. The maximum density of ganglion cells was 4516 cells/mm^2. Although this maximum density is relatively low compared to many rodents (Heffner and Heffner, 1992b), the large diameter of the retina (20 mm) results in a theoretical maximum visual acuity of 3.84 cycles/deg which is superior to

Chinchilla

Fig. 4. A, retinal ganglion cell isodensity contours in the right retina of a chinchilla; numbers indicate minimum density of ganglion cells per mm^2 within the isodensity contour with 4,516 cells/mm^2 being the maximum observed density. B, ganglion cell density expressed as a proportion of the maximum density: central hatching indicates densities at least 75% of maximum, cross hatching indicates densities at least 50% of maximum, stippling indicates densities at least 25% of maximum, and absence of shading indicates densities less than 25% of maximum. N, nasal; S, superior; T, temporal.

that reported for most rodents (cf, Jacobs et al., 1982; Heffner and Heffner, 1992b).

The retinal ganglion-cell isodensity contours expressed as a percentage of the maximum density are illustrated in Fig. 4b. The 75% contour encompasses what we have operationally defined, for comparative purposes, as the retinal field of best vision (for a detailed discussion of this definition, see Heffner and Heffner, 1992b). This region includes the part of the retina capable of the highest visual resolution as well as acuity within 75% of that maximum. In the chinchilla, this field encompasses 144° of the horizon. As discussed below, the width of the field of best vision is strongly correlated with sound-localization acuity.

4. Discussion

4.1. Localization acuity among mammals

Although the 15.6° threshold of chinchillas is relatively poor when compared with the thresholds of other mammals such as primates and carnivores (Fig. 5), chinchillas are among the more accurate rodents that have been tested. Of the 11 species examined so far, left/right thresholds for brief broadband sounds range from 11.1° for albino Norway rats to 27.8° for groundhogs (Table 1). In addition, there are at least three species (all subterranean rodents) which are unable to localize the brief clicks or 100-ms noise bursts commonly used to assess acuity and instead require sounds of longer duration before demonstrating any ability to localize. Thus, among rodents, chinchillas are
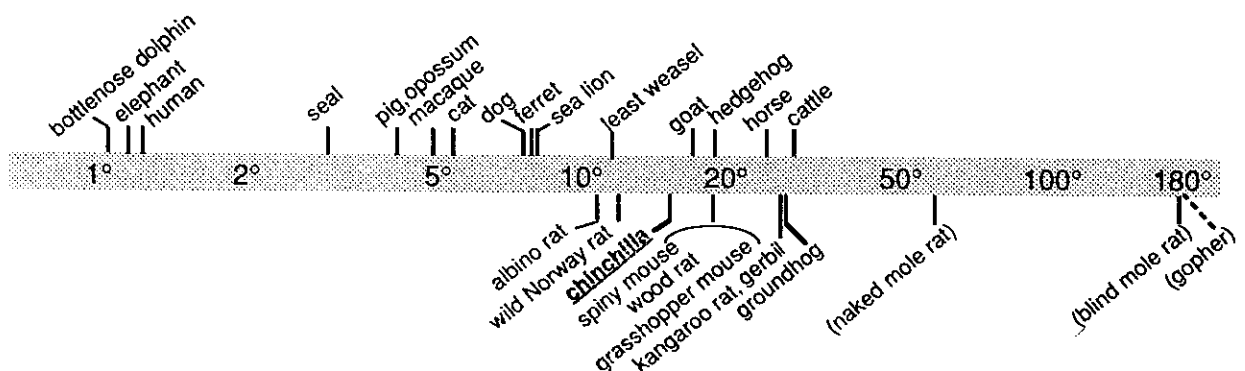
Sound - Localization Thresholds among Mammals

Fig. 5. Sound-localization thresholds among mammals; rodents are placed below the line and non-rodents are placed above the line. Thresholds were obtained using stimuli of 100-ms duration or shorter, with the exception of the three subterranean species (in parentheses) which were tested with 400-ms noise bursts. (Note that the gopher did not achieve threshold performance even at the largest possible angle, 180°). (For references, see Fig. 7)

Table 1
Sound-localization thresholds of eleven species of rodents

Species	Threshold [a]	Source
Surface dwellers		
Norway rat (domestic)	11.1°	Kavanagh and Kelly, 1986; Kelly, 1980
Norway rat (wild)	12.8°	Heffner and Heffner, 1985
Chinchilla	15.6°	Present report
Spiny mouse	19.0°	Mooney, 1992
Wood rat	19.0°	Heffner and Heffner, 1988a
Grasshopper mouse	19.3°	Heffner and Heffner, 1988a
Gerbil	27.0°	Heffner and Heffner, 1988b
Kangaroo rat	27.0°	Heffner and Masterton, 1980
Groundhog	27.8°	Conesa et al., 1992
Subterranean [b]		
Naked mole rat	63.0°	Heffner and Heffner, 1993
Blind mole rat	180.0°	Heffner and Heffner, 1992d
Pocket gopher	—	Heffner and Heffner, 1990a

Threshold was defined as 75% correct for two-choice procedures and 50% detection for conditioned avoidance procedures; thresholds for surface dwelling rodents are based on brief bursts of broadband noise except for the kangaroo rat which is based on 2/s clicks.
[b] Thresholds for the naked mole rat, and blind mole rat were obtained using a single burst of 400-ms noise because these subterranean species cannot reliably localize 100-ms noise bursts even at 80° separation; pocket gophers required an even longer signal to reach 50% detection and no threshold could be obtained with the 100-ms signal.

easily superior to most and second only to Norway rats in their ability to localize sound.

On first analysis, it might seem reasonable to attribute the relatively good localization acuity of chinchillas to the fact that they are larger than most other rodents. As a result, their larger head and pinnae should generate correspondingly larger binaural and monaural (pinna) locus cues. However, the variation in localization acuity in rodents cannot simply be attributed to the availability of locus cues, not only is the acuity of the chinchilla exceeded by that of a smaller rodent, the Norway rat, but the largest rodent tested, the groundhog, has one of the poorest thresholds (cf. Table 1). Indeed, among mammals in general there are additional examples of species, such as horses and cattle, which, despite their large size and correspondingly large heads, have poor sound-localization acuity (Fig. 5).

We have proposed elsewhere that the variation in mammalian sound-localization acuity is not the result of variation in the availability of locus cues, but instead is the result of differences in the degree of accuracy that may be required to direct the visual orienting response (Heffner and Heffner, 1992b). Specifically, sound localization directs the eyes to sound sources and the degree of precision required for this orienting response may be determined by the width of an animal's field of best vision. In the following section we describe how the chinchilla fits this hypothesis.

4.2. Proposed role of vision in mammalian sound-localization acuity

It has been proposed that a major selective pressure influencing the variation in sound-localization acuity among mammals is the need to direct the field of best vision toward a sound source for further scrutiny (Heffner and Heffner, 1992b). Just how accurate sound localization must be to direct the eyes seems to depend on the width of an animal's field of best vision: Animals with narrow fields of best vision, such as humans, require good sound-localization acuity in order to direct their gaze so that the visual image of the sound source falls upon their fovea, whereas animals with broad fields of best vision, such as visual streaks, do not require such acuity. The present information on the sound-localization acuity of chinchillas and the configuration of their field of best vision is consistent with this hypothesis.

Fig. 6 illustrates the relationship between sound localization acuity and the width of the field of best vision (as defined by the horizontal width of the retinal field containing ganglion cell densities of at least 75% of maximum density). As can be seen in this figure, animals with narrow fields of best vision, such as humans, are more accurate localizers than animals with broad fields of best vision such as chinchillas. Among the 16 mammals for which data are available, the correlation between these two factors is high and reliable ($r = 0.864$, $p < 0.001$). Although the sample is yet small, it is representative in that it includes five mammalian orders and fifteen families, nocturnal and diurnal, surface and underground, prey and predatory species. Its major limitation is the lack of aerial and
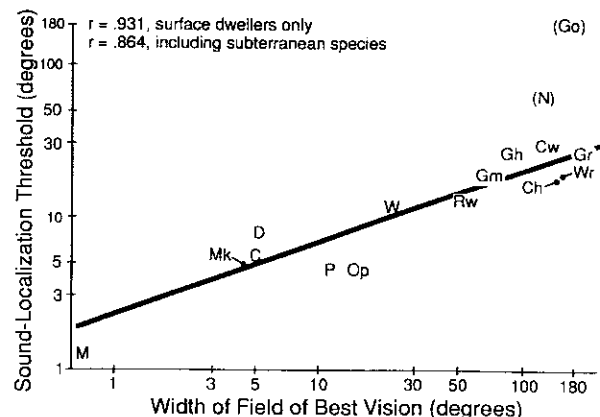

Fig. 6. Relationship between width of the field of best vision (i.e., ganglion cell densities of at least 75% of maximum density) and sound-localization threshold for 16 mammals. Species with a narrow field of best vision have better sound-localization acuity than species with broad fields of best vision. With the exception of the pocket gopher and naked mole rat (in parentheses), all localization thresholds were obtained using a brief 100-ms noise burst or single click. For key to animals see Fig. 7.

aquatic echolocators which may provide major insight into the interpretation of the correlation when their data become available. (For a more complete discussion, see Heffner and Heffner, 1992b.)

It should be noted that the most deviant species in this relationship are the two subterranean rodents, naked mole rats and pocket gophers, animals in which both hearing and vision are vestigial-excluding them from the analysis raises the correlation to r = 0.931. These animals as well as blind mole rats, which have no pattern vision, (Bronchti et al., 1991) represent extreme cases-not only are they adapted to a lightless subterranean environment in which vision is of little value, but their spatial responses are extremely limited by the tunnels which they inhabit. These factors may account for the fact that their sound-localization ability is qualitatively different from that of other mammals in that they have lost entirely the ability to localize brief sounds (cf. Table 1).

The correlation between width of the field of best vision and sound localization is robust and cannot easily be accounted for by other explanatory factors. In analyzing this relationship, we have considered other factors that might plausibly be responsible for the variation in sound-localization acuity. Among the factors were: the magnitude of locus cues available to each species (as estimated by interaural distance), the degree to which a species is a predator or prey, whether the species is primarily nocturnal, diurnal, or arrhythmic, size of the binocular visual field, and visual acuity. However, both simple and multiple regression analyses indicate that the factor correlating most strongly with

localization acuity is the width of the field of best vision (for details of the statistical analysis, see Heffner and Heffner, 1992b).

One surprising result of these analyses was the relatively small amount of the variance in localization acuity accounted for by interaural distance, 20%, as illustrated in Fig. 7. The correlation between sound-localization acuity and interaural distance among the current sample is −0.447 (p = 0.015); mathematically removing the influence of the width of the field of best vision reduces the correlation to −0.163 (p = 0.560) and the variance accounted for to less than 3%. This finding suggests that despite the undeniable fact that interaural distance must place a physical limitation on the availability of binaural locus cues, and thereby on binaural-dependent localization acuity, most species do not seem to reach this limitation. Indeed, as previously mentioned, it is not unknown for large mammals, such as cattle and horses to have poorer localization acuity than smaller mammals such as cats, rats, and even least weasels (cf. Fig. 5).

In summary, sound localization plays an important role in directing the field of best vision toward a sound source for further scrutiny (Pumphrey, 1950) and it does so even more rapidly and accurately than visual stimuli (Whittington et al., 1981). Thus it should come as no surprise that the size of the visual field being directed would exert some selective pressure on the acuity of the directional information provided by the auditory system. The narrower the field of vision being directed (with an extreme being the human fovea), the greater the acuity likely to be demanded of the direc-
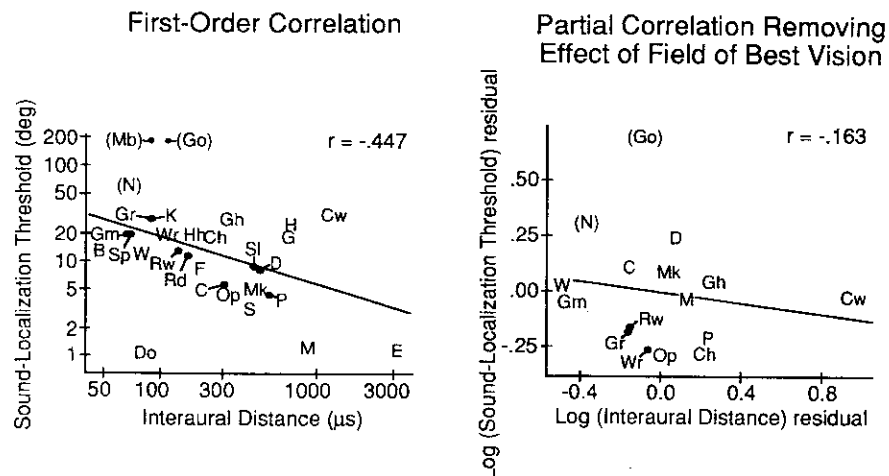

Fig. 7. Relationship between interaural distance and sound-localization acuity among 29 mammals. The significant first order correlation is shown on the left, but removing the influence of the field of best vision, shown on the right, reduces the correlation between interaural distance and localization acuity to insignificance. B, bat (Koay, et al., 1994); C, cat (Heffner and Heffner, 1988c); Ch, chinchilla; Cw, cow (Heffner and Heffner, 1992c); D, dog; Do, dolphin (Renaud and Popper, 1975); E, elephant (Heffner and Heffner, 1982); F, ferret (Kavanagh and Kelly, 1987); Gh, groundhog; G, goat (Heffner and Heffner, 1992c); Gm, grasshopper mouse; (Go), pocket gopher; Gr, gerbil; H, horse; Hh, hedgehog (Chambers, 1971); K, kangaroo rat; M, man; (Mb), blind mole rat; Mk, macaque; (N), naked mole rat; Op, virginia opossum (Ravizza and Masterton, 1972); P, pig (Heffner and Heffner, 1989); Rd, domestic Norway rat; Rw, wild Norway rat; S, seal (Terhune, 1974); Sl, sea lion (Moore, 1975); Sp, spiny mouse; W, least weasel; Wr, wood rat (for remaining citations, see Table 1).

tional information provided by the ears. This emphasis on the close relation between auditory localization and visual orientation may provide insight into the heretofore puzzling correlation between the size of nuclei mediating sound localization and those mediating eye movements (Irving and Harrison, 1967). These results underscore the importance of considering hearing in relation to the other senses in a behaving animal in order to understand the selective pressures influencing its evolution.

4.3. Use of binaural cues

The ability of chinchillas to localize tones both above the frequency at which the interaural phase-difference cue becomes ambiguous as well as below the frequencies that produce interaural intensity differences indicates that, like most mammals, they can use both interaural time- and intensity-difference cues for localization (e.g., Masterton et al., 1975; Heffner and Heffner, 1992a). However, examination of Fig. 3 indicates that chinchillas did not localize all frequencies equally, but rather performance declined at middle frequencies as well as at the highest and lowest frequencies tested.

The calculated frequency above which the phase cue is physically ambiguous for chinchillas at the 60° angle used in these tests was 5.5 kHz. Accordingly, any decline in the ability to use interaural phase differences below 5.5 kHz is probably due to physiological factors such as phase locking in central auditory neurons, which in chinchillas begins its decline at 1 kHz (Woolf et al., 1981). The decline in localization performance in approximately the upper octave of the hearing range is most likely a result of the unreliability of interaural intensity differences for pure tones at high frequencies (Harrison and Downey, 1969). Tests with other species have also reflected this unreliability of pure tones with non-monotonic performance functions and variation between individuals as frequency increases (e.g., Brown et al., 1978; Martin and Webster, 1987; Mills, 1958).

Finally, at 125 Hz and 180 Hz performance also falls even though these frequencies are not near the lower limit of hearing for chinchillas. Although few species have been tested below 250 Hz, a similar reduction in performance has been observed in other species that hear low enough to be tested at these frequencies, including small species such as cats and weasels (Casseday and Neff, 1973; Heffner and Heffner, 1987, 1992a; Houben and Gourevitch, 1979). It is possible that the reduction in performance occurs because at long wavelengths the synchrony of firing in the auditory nerve is reduced resulting in less accurate phase locking. Indeed, phase locking in chinchillas falls from a coefficient of synchronization of greater than 0.9 at 400

Hz to near 0.8 at 200 Hz (Fig. 3; Woolf et al., 1981) and results obtained from guinea pigs suggests that it may fall further as frequency decreases (Palmer and Russell, 1986).

4.4. The role of high frequencies in left / right acuity

It has been argued that the selective advantage of high-frequency hearing in mammals is that it permits sound localization using interaural spectral-difference cues in small species that would be at a disadvantage if forced to rely on the small time cues produced by their small interaural distances (e.g., Masterton et al., 1969; Heffner and Heffner, 1990b). Interaural spectral-difference cues are available to a species as long as it can hear frequencies with a wavelength short enough to be shadowed by its small head and can resolve the spectral shapes thus generated. This view is supported by research that has shown that left/right localization acuity in rats and mice is decreased when high frequencies are removed from the acoustic signal (Heffner, 1989; Heffner and Donnal, 1993; Mooney, 1992).

More recently it has become apparent that not all species require high frequencies for optimum acuity in left/right localization (Heffner and Heffner, 1992a). In humans, frontal acuity is not adversely affected by the removal of high frequencies from an acoustic signal because the time cues extracted from the low-frequency portion provides sufficient resolution (Butler, 1970). Similarly, frontal acuity in horses is not significantly affected by removal of high frequencies and, indeed, both free-field and dichotic studies suggest that horses have given up the use of the binaural spectral difference cue altogether (Heffner and Heffner, 1986, 1988d).

Chinchillas are similar to humans and horses in that their frontal left/right localization acuity is not affected by removal of high frequencies. Fig. 8 summarizes the average sound localization performance for chinchillas localizing a 100-ms burst of 8-kHz high-pass,
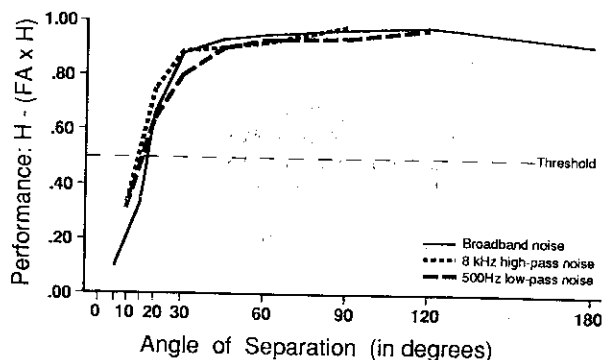

Fig. 8. Average performance of chinchillas localizing three different noise bands. Note that there is no significant difference in either performance or threshold with the three different stimuli.

500-Hz low-pass, and broadband noise. As can be seen, restricting the noise band to either high or low frequencies does not result in any significant change in threshold when compared to broadband noise. However, as seen in the companion papers (Heffner et al., 1995), chinchillas, like humans and horses, do require high frequencies to localize sounds greatly displaced from the midline, and to make front/back and elevation distinctions (Butler, 1975; Heffner and Heffner, 1983; Heffner et al., 1992; Koay et al., 1993).

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