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Functional correlates of characteristic frequency in single cochlear nerve fibers of the Mongolian gerbil

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Summary. Single-unit recordings obtained from the auditory nerve of the Mongolian gerbil, *Meriones unguiculatus*, revealed functional differences in the response properties of neurons tuned to low and high frequencies. The distribution of neural thresholds displayed a distinct rise for auditory nerve fibers with characteristic frequencies (CFs) between 3–5 kHz. This frequency band also marked abrupt changes in both the distribution of spontaneous discharge rates and the shape of the neural tuning curve. For neurons of all CFs, spontaneous firing rates were inversely related to neural threshold but unrelated to sharpness of neural tuning. The range of CF thresholds encountered, even when data from many animals were combined, rarely exceeded 20 dB, suggesting that cochlear nerve responses obtained from this species display little inter-animal variability. These results are compared with similar data from other species and discussed in terms of recent studies on sound communication and cochlear anatomy in gerbils.

Key words: Gerbil – Hearing – Auditory nerve – Physiology

Introduction

For over a decade the Mongolian gerbil, *Meriones unguiculatus*, has been a popular subject for auditory research. This animal offers several advantages for such studies. Unlike other small mammals, such as bats or mice, the gerbil possesses excellent low frequency hearing (Ryan 1976) which makes it a more appropriate model for studies of hearing in humans. In addition, the surgical procedures used to access the auditory nerve in gerbils are much less invasive than those required for cats or chinchillas, thereby reducing the risk of surgical trauma to the cochlea and its neural and vascular supply (Sokolich and Smith 1973). One perceived disadvantage of the gerbil is its fragility in long-term recording experiments, which limits the number of auditory nerve fibers which can be sampled in a single animal. However, as noted by previous workers, the auditory nerve response properties obtained from separate gerbils display a remarkable degree of homogeneity (Schmiedt et al. 1980; Schmiedt 1982a). Several factors may contribute to this. First, the breeding practices employed for this animal have probably resulted in less genetic variation than would be found in domestic cats or even farm-raised chinchillas. For example, the Mongolian gerbils presently used for research in the United States can be ultimately traced to only 5 breeding pairs imported in 1957 (Schwentker 1963). Secondly, these animals are easily raised in large colonies and therefore exposed to similar acoustic environments.

Previous studies of the auditory nerve in adult gerbils have focused on very specific topics such as the effects of noise and drug damage (Schmiedt et al. 1980), adaptation to sound stimuli (Westerman and Smith 1984), or responses to two-tone stimulation (Schmiedt 1982b). It is therefore not surprising that there have been no published studies of certain basic neural features of the gerbil auditory nerve such as the distribution of spontaneous discharge rate (SR) and the relation of SR to tone-evoked response properties.[1] Our information on such topics derives almost exclusively from investigations of the cat auditory nerve by Kiang and his colleagues (Kiang et al. 1965, 1976; Liberman 1978).

The present study provides information on the distribution of SR, the range of single fiber thresholds, and the variety in tuning curve shapes found within the gerbil cochlear nerve. In addition, this study examines the influence of fiber SR and characteristic frequency (CF) on neural threshold and tuning curve morphology. Our findings are compared with available data from other species. A preliminary report of this work has appeared in abstract form (Ohlemiller and Echteler 1987).

Abbreviations: CF characteristic frequency; *SR* spontaneous discharge rate

[1] While this manuscript was undergoing review a paper appeared (Schmiedt 1989) confirming two features of gerbil auditory-nerve fibers reported here: 1) that CF thresholds above 30 dB SPL are exceedingly rare and 2) that SR is inversely related to CF threshold but unrelated to the sharpness of neural tuning

Methods

Animal preparation. Fifty adult gerbils ranging in age from two to 5 months (average life span: 36–48 months) and weighing from 60–80 g were used in this study. All animals were free from middle ear infection. Prior to surgery, each animal was anesthetized via intraperitoneal injection of Nembutal (48 mg/kg) and intramuscular injections of Ketamine (10 mg/kg). Supplemental injections of Nembutal were administered at one-third the original dosage. Our approach to the auditory nerve is patterned after Sokolich and Smith (1973). Briefly, following cannulation of the trachea, the soft tissues and musculature overlying the ventro-posterior surface of the right bulla were removed and the right pinna was transected, exposing the bony external meatus. The bulla was opened with a sharpened pick and forceps to expose the base of the cochlea and the round window niche. A finely sharpened pivot broach was used to make a small hole (50–100 μm) into the dorsal surface of the round window antrum, thereby exposing the auditory nerve (Chamberlain 1977). A Teflon insulated silver ball electrode was placed against the bony rim of the round window to measure gross neural (N1) potentials. Heart rate and rectal temperature were monitored throughout each experiment. Body temperature was maintained at 37–39 °C by means of a thermostatically controlled heating pad.

Following surgery, animals were placed on a vibration-damped table within a double-walled sound-isolation chamber (Industrial Acoustics Corporation). Glass micro-electrodes filled with 3 *M* KCl or 2 *M* NaCl (40–90 MΩ) were advanced through the nerve by a remote-controlled stepping motor (2 μm minimum steps). The amplified signal from the electrode was coupled to a Schmitt trigger interfaced, in turn, with a PDP 11/34 computer.

Sound system. Pure tone and noise stimuli were delivered by a Beyer DT48 earphone. This driver was coupled to the bony external meatus through a 7 mm plastic speculum, which was sealed in place with bone-wax to form a closed acoustic system. This coupler also housed a calibrated, concentrically-placed, probe-tube connected to a Knowles reference microphone for measurement of sound pressure level (SPL) at the tympanic membrane. For each animal, a computer-controlled sound calibration program estimated the maximum SPL available between 0.1–21 kHz. Our sound system produced a flat (deviations of less than 5 dB) maximum signal level of 120 dB SPL, as measured at the tympanum, for frequencies between 0.1 and 4 kHz. SPL rolled off smoothly at 9 dB per octave for frequencies between 4 and 16 kHz. An additional 9 dB loss was observed between 16 and 21 kHz. The search stimulus was a wide-band noise-burst presented 3 times per s. Using audiovisual criteria, the level of this stimulus was at least 25 dB greater than the highest neural thresholds found in this study (37 dB SPL). In earlier experiments, electric shocks (5 ms duration; 3/s) delivered through the recording electrode were also employed to search for low SR units with high neural thresholds. All noise and tone-burst stimuli used in this study were 100 ms in duration, with rise-fall times of 2.5 ms, and a 30% duty cycle. Grason-Stadler logic elements controlled stimulus shaping and the rate of stimulus presentation. Stimulus frequency and intensity were controlled by the computer.

Data collection and analysis. Spontaneous discharge rates, expressed in spikes/s, were determined by averaging the number of spikes occurring within a 5 s period prior to stimulus presentation.

Frequency tuning curve collection was computer-automated. Our algorithm determines, as a function of stimulus frequency, the stimulus intensity required to raise the discharge rate of a unit by a fixed criterion (set by user) above its spontaneous level of discharge. Spike counts were compared during two 50 ms time-windows. The first window opened 10 ms after the start of a 100 ms tone burst; the second began 145 ms after cessation of the stimulus. Unless otherwise noted, threshold was defined as that stimulus intensity which elicited at least 2 more spikes within the first window when compared with the second. In practice, the threshold at the CF recorded by this criterion is within 10 dB of that required to augment spontaneous discharge rate by 40 spikes/s (evaluated by a rate-level function at CF with pseudorandom intensity steps of 2 dB; Ohlemiller, unpublished observations). Stimulus intensity was reduced or increased in 2 dB steps until this criterion was met once and then the stimulus frequency was increased. Threshold was determined once at up to 135 discrete frequencies per tuning curve.

A variety of morphometric measurements were obtained directly from each tuning curve, including threshold at CF, Q_{10}, and Q_{40} (CF/bandwidth at 10 or 40 dB above CF threshold). High-side and low-side slopes of individual tuning curves were measured for segments of the curve extending from 5 to 25 dB above tip threshold.

As previously mentioned, the most extensive studies of auditory nerve responses in mammals are those of Kiang and his colleagues on the domestic cat (Kiang et al. 1970; Liberman 1978). The tuning curve algorithm described above differs considerably from the one employed by Kiang and his coworkers (Kiang et al. 1970). In their paradigm, 4 determinations of threshold are made for each stimulus at a criterion rate increase of 10–20 spikes/s, intensity is adjusted in 2/3 dB steps, and up to 256 frequencies are tested for each tuning curve. In addition, tone bursts are 50 ms in duration, presented at 10/s, and the direction of frequency change is from high to low.

Such differences in paradigm might produce dissimilarites in tuning curve threshold or shape and thereby confound meaningful comparisons between data derived from gerbil and cat. We addressed this issue by comparing the effects of each of these paradigms on the structure of tuning curves obtained from individual gerbil auditory nerve fibers.

Results

Fiber threshold and its relation to characteristic frequency

One hallmark of an auditory nerve fiber is its frequency-specific response to sound. Each neuron can be distinguished by its maximal sensitivity to one characteristic frequency (CF). When many auditory nerve recordings are obtained from one or more animals, neural thresholds are seen to vary for fibers of both similar and different CF. The distribution of thresholds derived from healthy animals, at a specific CF, provides information on the overall range of neural thresholds for a particular species. Comparing the lowest neural thresholds across CF gives a useful indication of the frequency sensitivity of the auditory periphery.

We begin, therefore, by providing a plot of threshold vs. CF for single cochlear nerve fibers in the Mongolian gerbil (Fig. 1). The data represent 361 neural recordings obtained from 50 animals. An examination of this figure reveals 3 important findings. First, the range of auditory nerve fiber thresholds is limited in the gerbil; even when data are pooled from many individuals, 90% of all fibers, at any CF, have thresholds within 20 dB of one another. Moreover, this modest spread in neural thresholds is diminished even further by reducing the sample size from 50 to 2 animals (solid circles). Second, very few units (2%) were encountered with thresholds above 30 dB SPL, regardless of whether electric shocks or acoustic noise-bursts served as the search stimulus. Third, the distribution of CF thresholds appears con-

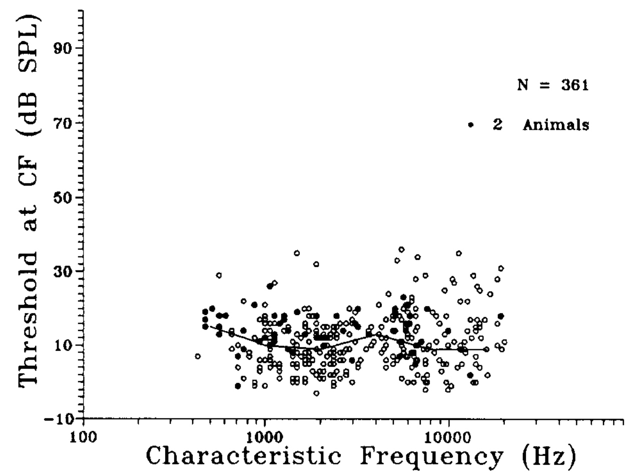

Fig. 1. Distribution of thresholds at the characteristic frequency (CF) for 361 fibers obtained from 50 gerbils. Filled circles represent 83 fibers from 2 animals. Spread of thresholds in these two animals is slightly lower than for the entire group

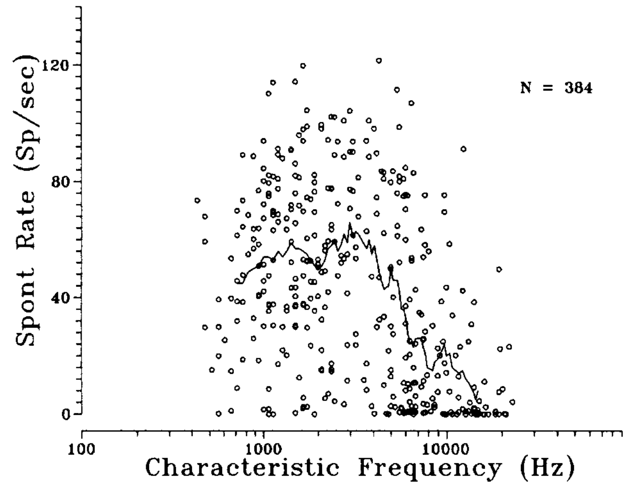

Fig. 2. Distribution of spontaneous firing rates (SR) as a function of fiber CF. The data represent 384 fibers obtained from 50 gerbils. Solid line is a moving average of mean SRs derived as follows: For each frequency an average value was calculated only if more than one fiber had that frequency as its CF. The number of points in this and subsequent curves (Figs. 6, 8) was determined by the spacing of CFs (135 possible in the tuning curve algorithm) meeting this criterion. For each curve this yielded approximately 60 points. The curve was then smoothed using a rectangularly-weighted moving window 7 frequency points wide. As shown by the curve in this figure, average SR is relatively constant up to approximately 4 kHz and decreases for higher frequencies

stricted around 4 kHz. Fewer units are encountered with CFs between 3 and 5 kHz; and those obtained have best neural thresholds which are 4 to 6 dB higher than units tuned to flanking frequencies. The solid line in Fig. 1 depicts mean thresholds calculated in octave bands from 0.5 to 16 kHz.

Spontaneous activity and its neural correlates

Spontaneous firing rate (SR), and its linkage to tuning curve threshold and sharpness, has been a useful way of categorizing auditory nerve fibers in both cats (Kiang et al. 1965, 1976; Liberman 1978) and chinchillas (Salvi et al. 1982). Accordingly, we asked whether such a classification scheme might also be profitably applied to gerbils.

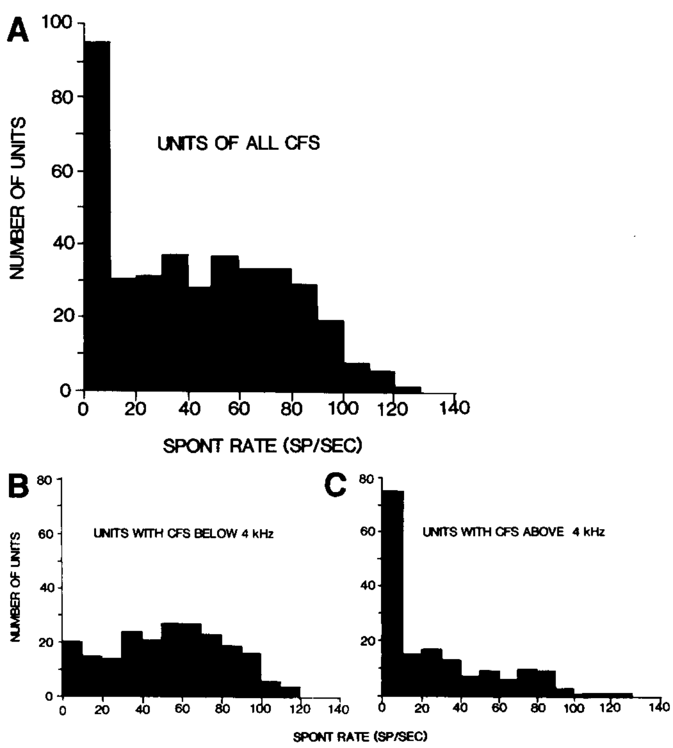

Fig. 3 A–C. Histogram of spontaneous firing rates for fibers of all CFs (**A**), for only those fibers tuned below 4 kHz (**B**), and for only those tuned above 4 kHz (**C**). Bin width 10 spikes/s. The leftmost bin includes fibers with an SR of 0

In Fig. 2 we present a plot of SR distribution as a function of fiber CF. The data are based on 384 auditory nerve recordings obtained from 50 animals. Spontaneous firing rates in gerbil auditory nerve fibers typically range from 0 to 124 spikes/s. The average SR (solid line), however, changes with fiber CF. Above 4 kHz there is a sharp and steady reduction in SR, amounting to a decrease of about 90 spikes/decade. The initial decline in average SR occurs not through a marked compression of higher spontaneous rates but, rather, due to an abrupt increase in the number of low SR neurons encountered. This is even more vividly illustrated when the frequency of occurrence histogram of SR is segregated for fibers with CFs below and above 4 kHz (Fig. 3). The distribution of SR clearly differs for low and high frequency cochlear neurons in the gerbil. Moreover, the transition frequency at which this distribution changes coincides with the center of the notch in the neural threshold distribution (Fig. 1).

The relationship between fiber threshold and SR is provided in Fig. 4. Although the data are pooled from 50 animals, two generalizations appear justified. Average tuning curve thresholds change little for fibers with SRs above 2 spikes/s. Below 2 spikes/s, however, average thresholds rise abruptly by about 10 to 12 dB. We find

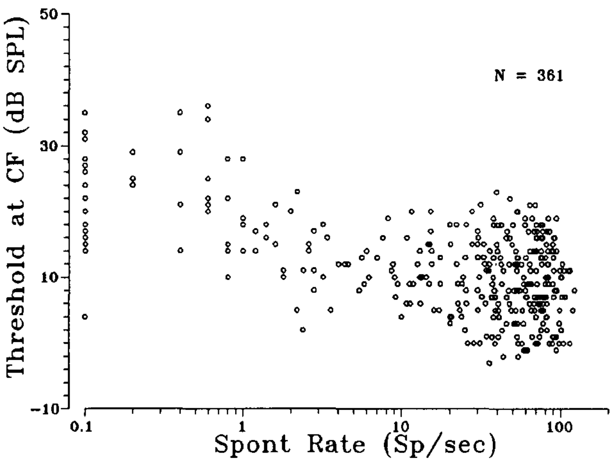

Fig. 4. Relation between CF threshold and SR for the data shown in Fig. 1. SR is determined with a resolution of 0.2 spikes/s. Units with SRs of 0 plotted as 0.1 spikes/s

little evidence, in the gerbil, for distinguishing a third group of 'medium' SR neurons based upon intermediate CF thresholds as has been reported for the cat (Kiang et al. 1976; Liberman 1978).

Tuning curve morphology

A detailed morphometry of tuning curve structure is beyond the scope of this paper. For now, we address the major changes in tuning curve shape which are observed when recording from neurons of different CF in the gerbil auditory nerve. We also examine the relationship between sharpness of tuning and SR.

In Fig. 5 the tuning curve shapes associated with differing CF auditory-nerve fibers are illustrated. Each panel displays a collection of tuning curves with closely matched CFs derived from different animals. Curves have been selected from fibers having SRs greater than 2 spikes/s in order to minimize the vertical shift (at most 8 dB) required to bring them into alignment at CF. This facilitates comparison of tuning curve structure.

Gerbil auditory nerve fibers with closely matched CFs display remarkably similar tuning curve shapes, even when derived from different animals. Below 1 kHz, frequency tuning curves are asymmetrical in gerbils, with the slope of the curve being steeper below than above CF (Fig. 5A). By 1 kHz, tuning curves are generally symmetrical around CF (Fig. 5B). As fiber CF rises above 1 kHz, tuning curve shapes once more become asymmetrical (Fig. 5C). By 4 kHz, a distinct tuning curve 'tail' has emerged at approximately 30–40 dB above tip threshold (Fig. 5D). The distinction between tip and tail segments of the tuning curve becomes increasingly vivid at CFs above 4 kHz, as tail thresholds rise (Fig. 5E–F).

The change in tuning curve shape, as a function of fiber CF, may be better understood by examining quantitative data on tuning curve tip slopes (Fig. 6). Solid lines in each plot represent average slope and solid stars

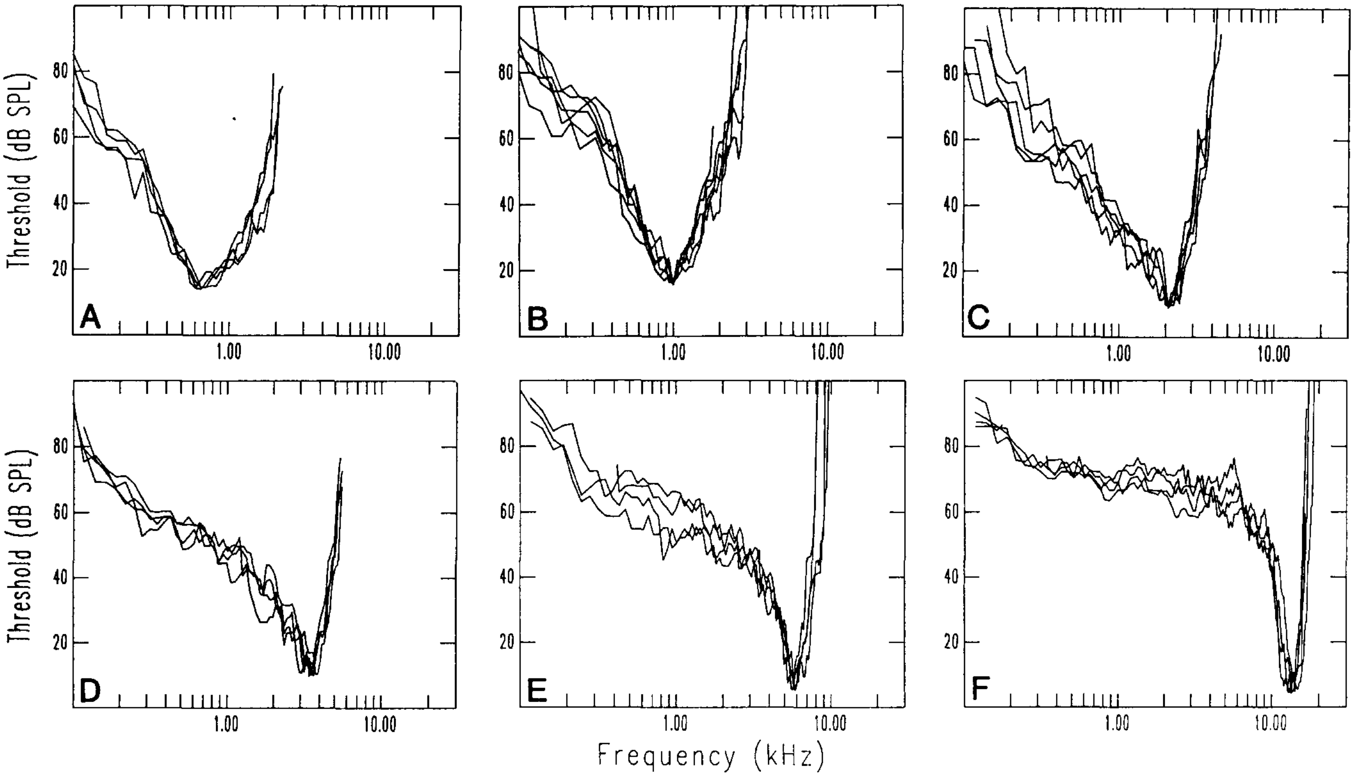

Fig. 5A–F. Tuning curve shape as a function of fiber CF for gerbil auditory nerve fibers. All panels represent curves obtained from 4 or more animals. In each panel curves with a similar CF have been shifted on the ordinate a maximum of 8 dB to facilitate comparison. All tuning curves were derived from fibers having SRs above 2 spikes/s

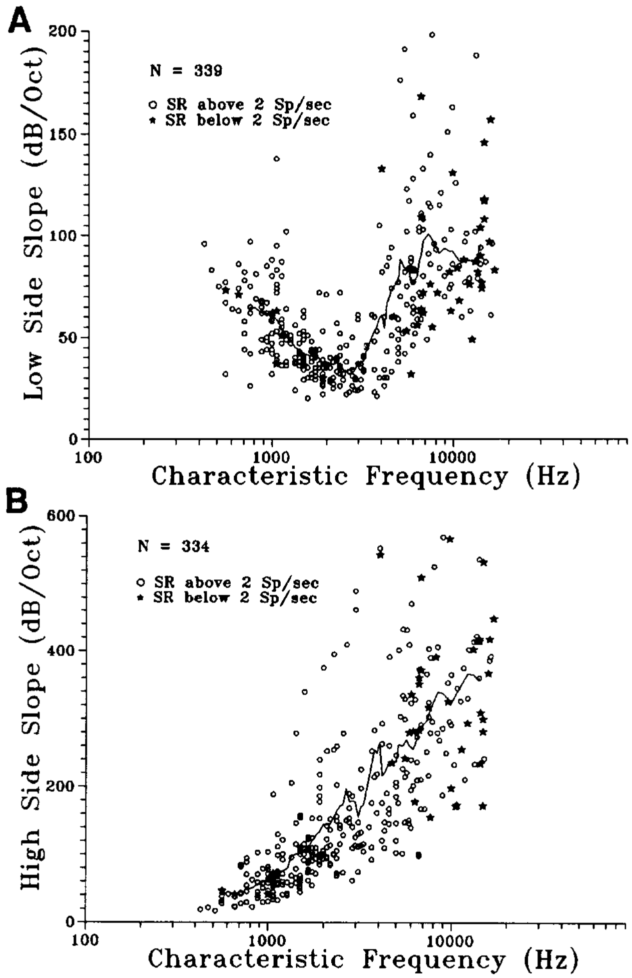

Fig. 6A, B. Low-side slopes (**A**) and high side slopes (**B**) of threshold tuning curves as a function of fiber CF for 339 fibers from 39 animals. Slopes were measured between points 5 and 25 dB above threshold on both sides of the tuning curve. Fibers with spontaneous firing rates below 2 spikes/s indicated by filled stars. The solid line is a moving average derived using the same methods as in Fig. 2

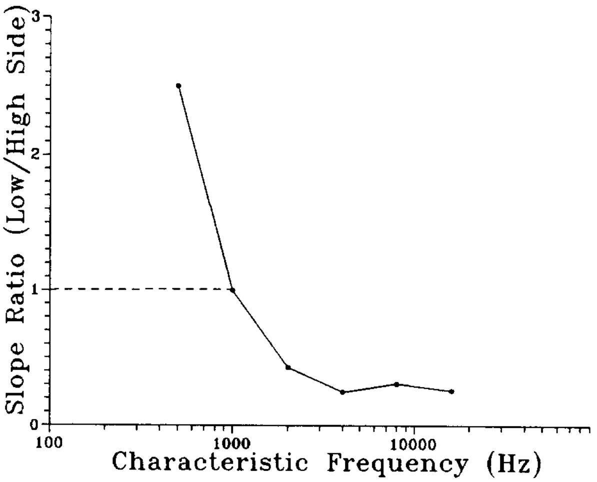

Fig. 7. Ratio of low-side slope to high-side slope of threshold tuning curves. Each point represents the ratio of mean low- and high side slopes of fibers with CFs that fell within 10–25% of the following frequencies: 5 ($N=7$), 1 ($N=28$), 2 ($N=10$), 4 ($N=19$), 8 ($N=7$), and 16 ($N=6$) kHz. The dashed horizontal line denotes perfect symmetry of the tip of the tuning curve. This symmetry is characteristic of fibers with CFs near 1 kHz

denote fibers with SRs below 2 spikes/s. For fibers of very low CF, for example 600 Hz, asymmetries in tuning curve shape arise because high frequency slopes (measured between 5 and 25 dB above CF threshold) range only from 20–50 dB/octave (Fig. 6B), while low frequency slopes can reach 100 dB/octave (Fig. 6A). Additionally, for frequencies below 3 kHz, low frequency slope is inversely proportional to fiber CF (Fig. 6A). As fiber CF approaches 1 kHz, tuning curves become symmetrical since high-side slopes have increased to match those below CF; both now range from 30–100 dB/octave (Fig. 6). At 2 kHz, tuning curves are once more asymmetrical. The asymmetry arises this time, however, because low-side slopes are decreasing as fiber CF increases from 1–2 kHz (Fig. 6A), while high-side slopes continue to climb (Fig. 6B). As fiber CF rises above 2 kHz in the gerbil auditory nerve, tuning curve tip slopes continue to increase above and below CF. The sharpest elevation in low-side slopes occurs at CFs between 3 and 6 kHz, with maximum values occurring between 8 and 10 kHz (Fig. 6A). High-side slopes rise gradually with CF at a rate of 60–80 dB/octave (Fig. 6B).

In Fig. 7 we quantify changes in tuning curve shape, in relation to fiber CF, by forming a ratio of low-side to high-side slopes for individual fibers (see Legend for details). A slope ratio of 1 indicates perfect symmetry of the tuning curve tip. Slope ratios above 1 occur when tuning curve slopes are steepest below CF; values below 1 indicate that tuning curve slopes are steepest above CF. The data suggest that, within the first 25 dB above threshold, tuning curve tip symmetry changes substantially with CF up to about 4 kHz, but little above this frequency.

The relation between fiber CF and sharpness of neural tuning is illustrated in Fig. 8. When tuning curve sharpness is derived from bandwidth measurements made at 10 (Q_{10}) or 40 (Q_{40}) dB above threshold, a gradual increase is observed as fiber CF rises from 0.5–4 kHz. Above 4 kHz, average Q_{10} values (solid line) continue to rise gradually, leveling off at CFs above 6–7 kHz (Fig. 8A); average Q_{40} values, however, rise abruptly between 4 and 6 kHz and continue to increase for CFs above 10 kHz (Fig. 8B). Q_{10} values ranged from 0.4 to 10 in gerbil auditory nerve fibers. Q_{40} values varied from 0.3 to 3.2. It is evident in plots of both Q_{10} and Q_{40}, that the distributions are consistently tighter below 4 kHz (Fig. 8), reflecting the fact that tuning is more homogeneous for low frequency fibers of the same CF in the gerbil.

There appears to be no relation between sharpness of tuning and SR in gerbil auditory nerve fibers. In both Q_{10} and Q_{40} plots, low SR (solid stars) and high SR (open circles) neurons are extensively intermingled throughout the entire range of their distribution (Fig. 8). This is also evident in plots of both low and high fre-

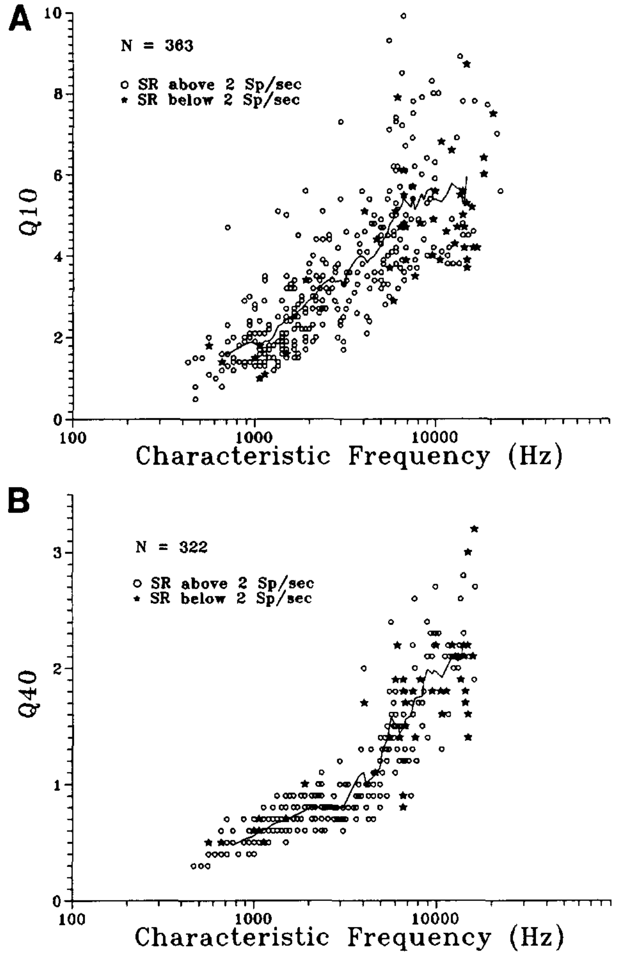

Fig. 8A, B. Q_{10} (**A**) and Q_{40} (**B**) vs. CF for gerbil auditory nerve fibers. Fibers with spontaneous firing rates below 2 spikes/s indicated by filled stars. The solid line in each plot is a moving average derived using the same methods as in Fig. 2

quency slopes (Fig. 6). This finding has been confirmed in recordings from 9 single animals where low and high SR neurons of identical CF were encountered sequentially.

The data presented thus far were derived from tuning curves collected with a detection algorithm different from the one employed by Kiang et al. (1970) in their studies of cat auditory nerve (see Methods). We note in passing that our tuning curves are quite similar in shape to those obtained from gerbils by Schmiedt who did employ the automated tracking procedures described by Kiang (Schmiedt 1982b; Mills and Schmiedt 1983). Nevertheless, if we wish to make direct comparisons with the cat data we must compare the tuning curves produced by each of these algorithms for the same auditory nerve fiber. It is not our intent here to present a complete description of how specific differences in a detection algorithm may influence tuning curve structure. We simply wish to determine whether these two specific paradigms produce tuning curves which are fundamentally alike or different.

We illustrate recordings obtained from low (Fig. 9A), middle (Fig. 9B), and high (Fig. 9C, D) CF

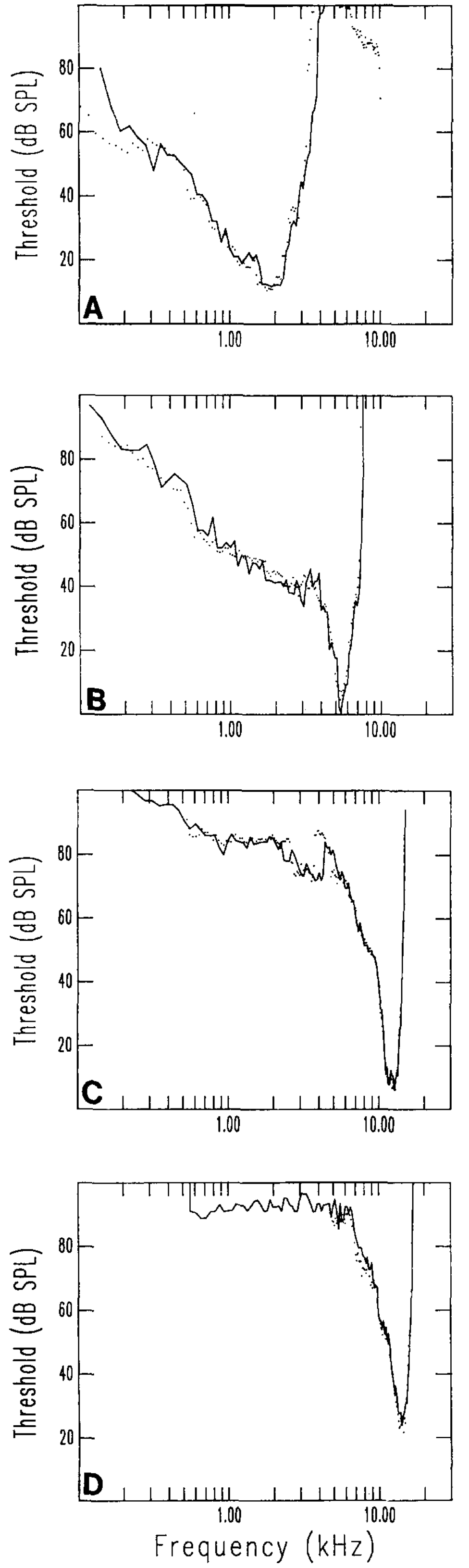

Fig. 9A–D. Comparison of the tuning curve collection algorithm employed in this study (solid lines) with that described by Kiang et al. (1970) (dotted lines) on the shape of neural tuning curves obtained from gerbil auditory nerve fibers of low CF (**A**), medium CF (**B**), and high CF (**C, D**). SRs associated with these fibers were 97.4 spikes/s (**A**), 91.6 spikes/s (**B**), 4.8 spikes/s (**C**) and 0 spike/s (**D**) fibers. Tuning curves derived with our algorithm are plotted as solid lines, those obtained with the Kiang et al. (1970) paradigm are depicted with dotted lines. The SRs associated with these fibers were 97.4 spikes/s (Fig. 9A), 91.6 spikes/s (Fig. 9B), 4.8 spikes/s (Fig. 9C) and 0 spike/s (Fig. 9D). For purposes of clarity we plot only one representative curve obtained with each paradigm. In practice, up to 8 tuning curves were obtained from each auditory nerve fiber and the order in which paradigms were presented was deliberately varied.

Both detection algorithms produce tuning curves which are highly reproducible in morphology from one collection to the next. The one employed by Kiang and colleagues, because of the greater number of frequencies sampled, produces a higher resolution tuning curve. Nevertheless, both paradigms produce tuning curves which are substantially alike in CF threshold and overall shape, regardless of fiber SR (Fig. 9B–D). We note, however, that for neurons of lower CF, the Kiang et al. (1970) algorithm can produce tuning curves with a slightly steeper high side slope if care is not taken to initiate tuning curve collection at a frequency just above CF (Fig. 9A). These slope differences are principally confined to segments of the tuning curve beginning 30 to 40 dB above threshold.

These results demonstrate that our algorithm produces tuning curves which are negligibly different from those derived from the Kiang et al. (1970) paradigm. This might seem surprising considering that our algorithm seeks a single threshold at a driven rate of 40 spikes/s over spontaneous levels whereas the Kiang et al. paradigm determines 4 thresholds at a rate increment of 0–20 spikes/s. Therefore, to further examine this issue we compared CF thresholds derived from our tuning curve algorithm with the sound levels required to augment spike discharge rate by either 20 or 40 spikes/s over spontaneous levels in rate-intensity plots collected at CF. Our sample consisted of 30 fibers ranging in CF from 1 to 20 kHz with SRs between 0 and 102 spikes/s. On average, our tuning curve thresholds were 3 (±3.2) dB lower than those derived from rate level functions at a 40 spikes/s rate criteria, suggesting that our algorithm was more conservative than we had originally anticipated. Moreover, CF thresholds declined only an additional 2 dB when the criterion was reduced from 40 to 20 spikes/s. Presumably, the requirement that success in only a single trial is sufficient for a threshold response effectively reduces the criterion due to the probabilistic nature of an auditory-nerve fiber response near threshold. Thus it is not unexpected that the thresholds determined by one trial and 4 trial algorithms are similar for slightly different driven rate criteria (see also Borg et al. 1988).

Discussion

Fiber threshold as a function of CF

The range of CFs displayed in Fig. 1 is more circumscribed than the hearing range derived for gerbils by behavioral measures (0.1 to 60.0 kHz; Ryan 1976). The lack of CFs above 21 kHz results from our sound calibration program, which only extended to this frequency. However, in subsequent experiments where this calibration has been extended to 30 kHz, we have found few neurons with CFs above 24 kHz. Similarly, although our sound calibration extended below 500 Hz, we encountered very few neurons tuned below this frequency.

Differences in the frequency range of neural and behavioral responses have been previously reported for both gerbils and chinchillas (Dallos et al. 1978). They may also be surmised from existing data for cat (Kiang et al. 1976), guinea pig (Evans 1972) and rabbits (Borg et al. 1988). The reason for these discrepancies is not entirely clear. One possibility is that the more limited range of the neural audiogram may result from a sampling bias in unit recordings due to the decline in innervation densities observed within the extreme apex and base of the mammalian cochlea (Spoendlin 1972; Bohne et al. 1982; Keithley and Schreiber 1987). In the case of the gerbil, it is also conceivable that the relatively constrictive surgical approach to the cochlear nerve through the round window antrum limits the neural population which may be sampled by the experimenter.

The notch in our neural threshold distribution at 4 kHz is less easily explained. Similar notches, centered at 3 kHz, appear in behavioral and neural audiograms obtained from cats (Elliot et al. 1960; Kiang et al. 1965) and may be a common feature of mammalian hearing (Fay 1988). They have been attributed by some to the transmission properties of the middle ear (Dallos 1973; Lynch and Nedzelnitsky 1982). Others have suggested that they result from cochlear pathology arising from environmental noise exposure (Kiang et al. 1976), although similar notches are also found in young cats reared in low-noise chambers (Liberman 1978).

The gerbils used in the present study averaged only 3 months in age but were raised in a conventional animal colony. We therefore cannot exclude the possibility that the local rise in thresholds which we observe from 3 to 5 kHz may result from acoustic trauma. We think this unlikely, however, since tuning curves obtained from neurons with these CFs display none of the typical pathologies associated with noise-induced hearing loss, such as hypersensitivity in the tail region or hyposensitivity of the tuning curve tip (Kiang et al. 1976; Liberman and Kiang 1978; Schmiedt et al. 1980). It is also seems unlikely that this threshold rise can be attributed to selective attenuation of these frequencies by the gerbil middle ear, since the middle ear transfer function for this species shows no prominent inflections within this frequency band (Schmiedt and Zwislocki 1977). Since we do typically encounter fewer neurons with CFs between 3 and 5 kHz it could be argued that we simply missed the low threshold neurons within this frequency band. However, for the data presented in Fig. 1, only 5% fewer neurons are present in the octave band from 3 to 6 kHz as compared with the two adjoining octaves.

The position of the notch within the neural threshold plot is also of interest in view of recent studies on the importance of sound in the behavior of this species. Unlike some small mammals, such as mice or bats, gerbils are very sensitive to low frequency sound (Fay 1988). They are nocturnal animals which dwell in extensive underground burrows within the arid steppes of Northern China, Mongolia, and parts of the Soviet Union (Lay 1972). Their principal predators in the wild are owls and snakes. Spectral analysis of sounds made by these predators, during attack behaviors, reveal mostly low frequencies (ranging up to 2200 Hz) (cited in Lay 1972). Hence the low neural thresholds displayed by low CF auditory nerve fibers in gerbils may reflect a functional specialization required for predator avoidance. While excellent low frequency hearing may be necessary for gerbils to escape predation, well developed high frequency perception is essential for communication with conspecifics (Lay 1972). Vocalizations by Mongolian gerbils consist of short duration (250 ms) frequency-modulated squeeks with a fundamental which sweeps from 6 to 14 kHz and a rich harmonic structure (Plassmann, pers. communication). Examination of Fig. 1 reveals that best neural thresholds decline rapidly between 4 and 6 kHz, thereby providing maximum sensitivity at frequencies which are important for species communication. The notch in the Mongolian gerbil neural threshold plot therefore separates and accentuates frequency bands which are important for species survival.

Distribution of spontaneous activity in the gerbil cochlear nerve

Within the cat auditory nerve the distribution of SR is bimodal due to a curious lack of auditory nerve fibers with SRs between 10 and 40 spikes/s. This feature is consistently observed whether data are pooled from one (Liberman 1978) or many animals (Kiang et al. 1965; Kim and Molnar 1979). The distribution of SR in gerbil auditory nerve fibers is less clearly bimodal since units with SRs between 10 and 40 spikes/s are plentiful at all CFs (Fig. 3). The shape of this SR distribution is, in fact, quite similar to that observed for rabbit auditory nerve fibers (Borg et al. 1988).

It is conceivable that the sampling time over which SR is measured may influence the shape of the SR distribution. This time varied in each of the studies cited above; in our study SR was sampled for 5 s, in rabbits for 10 s (Borg et al. 1988), and in cats for either 10 or 30 s (Kim and Molnar 1979; Liberman 1978). Recently, Teich (1989) has examined the structure of the auditory nerve spike train, as a function of sampling time, in units discharging spontaneously or in response to tonal stimuli. He finds that auditory neural discharge displays a fractal character, such that for counting times above 1 s the variance-to-mean ratio of spike occurrence increases with sampling time (Fig. 4 of cited ref.). This implies that counting times longer than 1 s will not result in a more accurate assessment of SR; further experimentation, however, is required to resolve this issue.

Perhaps the most unexpected finding in this study is that spontaneous firing rates are a function of CF in the gerbil cochlear nerve (Figs. 2, 3). When recording from auditory nerve fibers with CFs above 4 kHz, the likelihood of encountering low SR neurons (2 spikes/s and below) increases substantially. In retrospect, this relationship between SR and fiber CF may be surmised from previously published data from the gerbil auditory nerve (Smith 1977) but until now has received little attention. This relationship differs from findings obtained from the cat auditory nerve, where SR distribution is homogeneous with respect to CF (Kiang et al. 1965; Liberman 1978; Kim and Molnar 1979).

Before concluding that the linkage of SR to CF is species dependent, one must consider changes in SR distribution which might arise from unintentional cochlear injury resulting from acoustic or thermal trauma. For example, when cats are exposed to intense noise a compression of SR is observed in auditory nerve fibers tuned to frequencies within the bandwidth of the stimulus. This compression results in an increase in the proportion of neurons encountered with SRs between 10 and 30 spikes/s and it is accompanied by substantial changes in neural threshold and tuning curve shape (Liberman and Kiang 1978). In our study the decline in average SR observed for auditory nerve fibers with CFs between 4 and 8 kHz (Fig. 2) arises from an increase in the proportion of low SR neurons encountered (Fig. 3). Furthermore, best neural thresholds do not increase within this frequency band, instead they improve substantially (Fig. 1). Since tuning curve structure at these CFs also appears normal we believe it is unlikely that the changes we have observed in SR distribution arise from acoustic trauma.

Compression of SR and elevation in neural threshold have also been observed in 'chamber-raised' and 'routine-normal' cats exposed to reductions in cochlear temperature (Liberman 1978). These effects are limited to fibers of high CF and are minimized when the animal's core temperature is maintained by varying room air temperature (Liberman and Dodds 1984). These results suggest that thermoregulation by heating pad alone may not suffice in species where substantial surgical exposure of the cochlea and its nerve supply are required (Nuttall and La Rouere 1980; Brown et al. 1983). Initially, we maintained normal body temperature only with a heating pad but in subsequent experiments we have incorporated a separate heating source for the gerbil's skull. In recordings from over 100 auditory nerve fibers, where cochlear temperature was measured directly within the basal turn by a micro-thermocouple and maintained at 37°–38 °C, we have observed a similar reduction in SR for fibers with CFs above 4 kHz (Ohlemiller and Siegel, unpublished).

We conclude that the change in SR distribution with CF is most likely an inherent property of the gerbil auditory nerve and does not reflect noise or temperature damage to the cochlea. In this light it is interesting to note that in the cat SR is associated with a particular set of morphological correlates; low and medium SR neurons terminate in small boutons on the modiolar face of the inner hair cell (IHC), whereas high SR neurons have larger terminals placed on the pillar side of the IHC (Liberman 1982). If these structural correlates apply to the gerbil auditory nerve then we would predict, based upon the frequency-place map derived for this species (Schmiedt and Zwislocki 1977), that the size and position of IHC terminal boutons should differ systematically between the basal and more apical turns of the gerbil cochlea.

Spontaneous firing rate and its relation to threshold at CF

An inverse relationship between spontaneous discharge rate and neural threshold at CF is a fundamental characteristic of cat auditory nerve fibers. Although this relationship is best illustrated when data are derived from single animals raised in low-noise chambers (Liberman 1978), it is clearly observable in data pooled from many conventionally-raised animals (Kiang et al. 1976).

This relationship has also been examined in gerbil auditory nerve fibers, but with varying results. In a preliminary study, Schmiedt (1982a), employing an automated tuning curve paradigm, reported that spontaneous firing rate was inversely correlated with threshold at CF; whereas Westerman and Smith (1984), collecting audio-visual tuning curves, found no such relationship.

In the present study, using an automated tuning curve paradigm, we have examined the relationship between SR and threshold at CF in recordings from 361 gerbil auditory nerve fibers. We find that gerbil auditory nerve fibers with SRs below 2 spikes/s generally have CF thresholds which are 10 to 15 dB higher than those found for higher SR fibers (Fig. 4). As in the cat, these neurons display the greatest variability in CF thresholds. Average CF thresholds remain comparatively constant for fibers with SRs above 20 spikes/s; there appears to be little evidence for a distinct group of 'medium' SR fibers based upon homogeneous neural thresholds at CF, as has been reported for cat (Liberman 1978).

In cats relative threshold differences between low and high SR neurons may span 70 dB (Liberman 1978; but see Rhode and Smith 1985 and Geisler et al. 1985). In gerbils raised in our conventional animal colony, thresholds for low and high SR neurons of the same CF differ by only 10–15 dB. Moreover, in agreement with Schmiedt (1982a), we found very few low SR neurons with thresholds above 30 dB SPL, even when electric shocks were used as a search stimulus.

Tuning curve morphology

Tuning curve morphology is profoundly influenced by fiber CF in the gerbil auditory nerve (Figs. 5, 6). In general, the shapes of these tuning curves are quite similar to those reported for guinea pig (Evans 1972), rabbit (Borg et al. 1988), chinchilla (Dallos and Harris 1978; Salvi et al. 1982) and cat (Kiang and Moxon 1974; Liberman and Kiang 1978; Kiang 1984). Thus, a dichotomy in tuning curve structure is apparent for low and high frequency neurons. High frequency tuning curves possess a well defined, sharply-tuned, low-threshold 'tip' around CF and a broadly-tuned, high-threshold 'tail' below CF; in low frequency neurons the tuning curve is more rounded with little or no distinction between tip and tail. Minor differences from the cat which persist regardless of tuning curve paradigm include: 1) the lack of a high frequency 'tail' in fibers tuned below 1 kHz and 2) the absence of a prominent notch separating and accentuating the tip and tail in high CF fibers. Each of these features are also absent from auditory neural tuning curves obtained with automated paradigms from chinchilla (Salvi et al. 1982) and rabbit (Borg et al. 1988). The inverse relationship which we report between CF and low-side tip slopes in units tuned below 3 kHz has not been found in cats (Evans and Wilson 1973), rabbits (Borg et al. 1988), or guinea pigs (Evans 1972).

Regardless of whether we employed our own tuning curve collection algorithm or that of Kiang et al. (1970), we could find no consistent relationship between tuning curve shape and spontaneous firing rate in gerbil auditory nerve fibers, in contrast to previous studies of cats (Kiang et al. 1976; Liberman 1978) and chinchillas (Salvi et al. 1982). The frequency selectivity displayed by low and high SR neurons, of the same CF, was similar whether assessed by bandwidth (Fig. 8) or by steepness of tip slopes (Fig. 6). This is perhaps not surprising considering the relatively minor differences in threshold which we report for fibers of low and high SR. In cats, the sharpest tuning curves are generally observed in low SR neurons with thresholds above 30 dB SPL (Kiang et al. 1976; Liberman 1978). Interestingly, the shapes and thresholds of these tuning curves are highly reminiscent of those derived from high SR fibers using large driven rate criterion (Evans 1975; Borg et al. 1988). One likely explanation for this phenomenon is the lower rate-level curve slope of cat low SR neurons when compared with their high SR counterparts (Sachs and Abbas 1974). For a fixed spike rate criterion, thresholds for low SR fibers will be reached farther out on this curve leading to a vertical shifting of the tuning curve along the intensity axis. At stimulus frequencies above CF, where the rate-level curves of all neurons become more compressed (Sachs and Abbas 1974), these threshold differences will be even more pronounced. One predicted consequence of this would be a steepening of the high-side slopes of tuning curves of low SR fibers relative to those of high SR fibers. In the case of the gerbil, where the threshold differences between low and high SR fibers are relatively modest, sharpening of the tuning curve in the manner described above might not be detected.

In conclusion, it is worth considering that although the shape of frequency tuning curves obtained from different mammals may be similar, the frequency band which marks the transition between neurons displaying 'low' and 'high' frequency tuning curve structures may vary for different species. For example, in guinea pigs tuning curves change in shape most dramatically between 2 and 3 kHz (Evans 1972), in cats between 3 and 4 kHz (Evans and Wilson 1973; Kiang and Moxon 1974; Liberman and Kiang 1978), and in gerbils from 4 to 6 kHz. Undoubtedly, some of this variation arises from differences in tuning curve collection procedures. However, in the gerbil this frequency band also marks abrupt changes in a number of temporal response properties such as SR (this study), the rapid component of adaptation (Westerman and Smith 1984), firing rate saturation and the slopes of rate-level functions (Ohlemiller and Echteler 1988). Taken together, these results suggest that this frequency band may represent an important transition zone in the operation of the gerbil cochlea. Although, at present, the underlying causes for such functional differences are unclear, a recent anatomical study of the gerbil cochlea has identified this same region as the locus for an abrupt change in the thickness of the basilar membrane (Plassman et al. 1987).

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