Threshold tuning curves of chinchilla auditory-nerve fibers. II. Dependence on spontaneous activity and relation to cochlear nonlinearity

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ABSTRACT

Spontaneous activity and frequency-threshold tuning curves were studied in thousands of auditory-nerve fibers in chinchilla. The frequency distribution of spontaneous-activity rates is strongly bimodal for auditory-nerve fibers with characteristic frequency < 3 kHz but only mildly bimodal for the entire sample. Spontaneous activity rates and thresholds at the characteristic frequency are inversely related. The overall shapes of frequency-threshold curves, including tip-to-tail ratio, do not depend on spontaneous activity but fibers with low rates of spontaneous activity have more sharply-tuned tips than fibers with high spontaneous rates. It is shown here that this dependence of tuning on spontaneous rates is consistent with a previously unnoticed non-monotonic dependence on iso-velocity criterion of the frequency tuning of basilar-membrane vibrations.
INTRODUCTION

In cat, frequency-threshold tuning curves (FTCs) are more sharply tuned in auditory-nerve fibers (ANFs) with low spontaneous activity (SR, spontaneous rate) than in high-SR ANFs (Liberman, 1978; Kiang et al., 1976). SRs are associated with specific morphological features of cochlear neurons and their synapses on inner hair cells (Liberman, 1980; Liberman, 1982). Therefore, since ANFs with the same characteristic frequency (CF), regardless of SR, must share the same frequency tuning of inner hair cell receptor potentials (which in turn is determined by the frequency tuning of the organ of Corti) and since organ of Corti vibrations (at least at the base of the cochlea) are more broadly tuned for intense stimulation than at threshold (Robles and Ruggero, 2001), a dependence of ANF frequency tuning on SR must be viewed as somewhat paradoxical.

The finding of a SR dependence of ANF tuning in cat has not been replicated in other species, even though the SR dependence was explicitly sought in studies in gerbil (Schmiedt, 1989; Ohlemiller and Echteler, 1990). The companion paper presents evidence that the SR dependence of frequency tuning also applies to chinchilla ANFs [Fig. 1 of (Temchin et al., 2008)]. The purpose of this paper is to expand on that finding and to show that the seemingly paradoxical dependence of tuning on SR actually reflects a previously unnoticed non-monotonic variation of basilar-membrane tuning as a function of iso-velocity criterion. A preliminary account of this work was published as an abstract (Temchin et al., 1997).
METHODS

All animal procedures, detailed in the companion paper (Temchin et al., 2008), were approved by the Animal Care and Use Committee of Northwestern University. In brief, conventional extracellular microelectrodes were used to record from individual ANFs, via an intracranial approach, in deeply anesthetized chinchillas. [At the end of each experiment, the chinchilla was killed by decapitation while still deeply anesthetized.] White-noise bursts (50-ms duration, presented 3/s) were used as stimuli while attempting to isolate ANFs. Upon isolation of an ANF, a 10-second sample of spontaneous activity was recorded and an FTC was measured using an automated adaptive procedure (Kiang et al., 1970; Liberman, 1978) with threshold criterion equivalent to 20 spikes/s higher than spontaneous rate. Additionally in many cases thresholds were obtained from rate-intensity function for responses to low-frequency (≤1000 Hz) tones.
RESULTS

Here we analyze the relation between spontaneous activity and the frequency tuning of responses to tones recorded in thousands of chinchilla ANFs [see companion paper (Temchin et al., 2008)].

Frequency distribution of spontaneous activity

Spontaneous activity (SR; the average firing rate in the absence of controlled acoustic stimulation) was measured in 4,184 ANFs recorded in 228 chinchillas. Panels A and B of Fig. 1 shows that there is a relative dearth of ANFs with medium and low SRs for CFs lower than 3 kHz. This is quantified in Fig. 1C, which shows that the percentage of SRs <18/s changes abruptly at CFs around 3 kHz, almost doubling between 3 and 4 kHz.

The distribution of SRs for the entire population of ANFs is mildly bimodal (Fig. 2B), exhibiting a large peak for SRs <1 spike/s and a broader, much shallower, peak for higher SRs. However, when SRs for ANFs with CFs lower and higher than 3 kHz are plotted separately (Fig. 2A), it is apparent that the bimodality is confined to the former and absent from the latter. The bimodal frequency distribution of SRs for CFs < 3 kHz justifies the classification of chinchilla ANFs into (only) two SR groups. Nevertheless, for the sake of comparison with other studies, we classified ANFs in three groups: low SR (SR <1 spike/s), middle-SR (SRs 1-18 spikes/s), and high-SR (SRs >18 spikes/s). Those groups comprised 10.9, 23.0, and 66.2 % of the ANF population, respectively.

Relation between SRs and CF thresholds
Figure 3 explores the relationship between SR and CF thresholds in a sample of 144 chinchillas in which 10-μV CAP thresholds were determined using an automated procedure at frequencies separated by 0.5 octave from 0.5 kHz to 16 kHz [see Methods of companion paper (Temchin et al., 2008)]. Data are shown in Fig. 3 only for ANFs with CFs between 0.5 and 12 kHz, a range in which CF thresholds of high-SR ANFs are relatively uniform (Fig. 4). CF thresholds are presented after normalization to CAP thresholds, to attenuate the effects of threshold variations both as a function of CF (in individual animals) and across animals (in any single CF region). In logarithmic coordinates (log SR vs. SPL), data points spread out around a straight line which describes a power function (dashed line). The slopes of regressions calculated separately for low- and medium-SR ANF groups (solid lines) did not differ statistically from the regression for the entire population. On the other hand, a regression for the high-SR group did not differ statistically from a zero-slope line.

Regardless of CF or SR, 85% of all ANFs had thresholds within a 30-dB range. Figure 4 presents CF thresholds, computed separately for high-, medium- and low-SR ANFs, averaged over 2/3-octave CF bands and plotted against CF. Average CF thresholds plus/minus standard deviations (SDs) were 28.2 ± 12.4 dB SPL for low-SR ANFs (n=448), 21.4 ± 12.3 dB SPL for medium-SR ANFs (n=951), and 16.0 ± 11.4 dB SPL (n=2785) for high-SR ANFs. The differences between thresholds for low- and high-SR ANFs were more or less constant across CFs, averaging 13.8 dB in the 0.75-19 kHz CF range. The variance of CF thresholds in any single animal was substantially smaller than in the entire population. The average SD of the mean thresholds in the CF range 0.6-10 kHz, computed in 2/3 octave bands across the entire population of high-SR ANFs (vertical black lines in Fig. 4), was 10.1 dB. The corresponding average SD of CF
thresholds was 8.2 dB after subtracting CAP thresholds individually for each animal, a procedure which tends to remove variance due to inter-animal threshold differences. The average SD was even smaller, 3.9 dB, when computed as the grand average of SDs for individual CF band across animals (red vertical lines in Fig. 4), a procedure that removes both inter-animal variations and the effects of variations as a function of CF in individual animals.

**SRs and FTC shapes**

Figure 5 shows tip-to-tail ratios (circles) for low- and high-SR ANF populations with CF > 3.5 kHz. The ratio differences between the two populations, 4.8 dB SPL ± 2.4 dB on average, were not statistically significant (Student t tests: p > 0.1). In contrast, averaged CF thresholds (squares) measured in the same population of ANFs were significantly higher at all tail frequencies for low-SR ANFs than for high-SR ANFs (p < 0.005). The CF threshold differences averaged 15.1 dB SPL (± 2.7 dB), i.e., the same as for the general population of ANFs (Fig. 4). The similarity of tip-to-tail ratios of low- and high-SR ANFs (circles) contrasts with the results of Fig. 1 of the companion paper (Temchin et al., 2008), as well as Figs. 6, 7 and 8A of the present paper, which show that bandwidths, slopes and Q’s of FTC tips differ between chinchilla ANFs with different SRs.

Figure 6, which shows FTC Q’s as functions of CF for ANFs with low- and high-SRs, extends the findings of Fig. 1D of the companion paper (Temchin et al., 2008), confirming that low-SR ANFs are more sharply tuned than high-SR ANFs, particularly for high CFs. Although the differences in Q’s between low-SR and high-SR ANFs are generally small, in many cases they
are statistically significant (crosses). The largest average differences occur for $Q_{40}$s of ANFs with CF of 4.8 kHz (Fig. 6D), 1.35 vs. 1.79 for high- and low-SR ANFs, respectively, or 32%.

In a companion paper, we showed that the lower and upper limbs of the FTCs and, consequently, the partial bandwidths below and above CF, varied differently as a function of CF [Figs. 1B and 1C of (Temchin et al., 2008)]. Therefore, we enquire here whether the tuning differences between low-SR and high-SR ANFs are linked to either partial bandwidth or to both. We find that the partial bandwidths lower than CF do not differ significantly between low-SR and high-SR ANFs (not shown). On the other hand, as shown in Fig. 7, the partial bandwidths for frequencies above CF for ANFs with CF > 800 Hz are clearly smaller for low-SR than for high-SR ANF. In many cases, the differences in partial bandwidths are statistically significant. Relevant data for lower CFs are scarce but an average partial bandwidth above CF for such CFs (open square in Fig. 7C), computed from the 8 data points with lowest CFs in Fig. 1C of (Temchin et al., 2008), suggests that the difference between partial bandwidths above CF do not apply to CFs < 800 Hz.

**The SR dependence of ANF sharpness of tuning derives from a non-monotonic dependence of BM tuning on response criterion**

The fact that the FTC tips are more sharply tuned in low-SR than in high-SR ANFs [Figs. 6-7 and 8A; also Fig. 1 of companion paper (Temchin et al., 2008)] needs explanation, since SRs are determined at the synapses between ANFs and inner hair cells (Liberman, 1980; Liberman, 1982; Merchan-Perez and Liberman, 1996), presumably devoid of intrinsic frequency tuning, and BM responses are broadly tuned for intense stimuli, i.e., a stimulus-level dependence
seemingly opposite to that of the auditory nerve, in which low-SR ANFs, with higher thresholds, have sharper tuning.

An important clue to the origin of the dependence of tuning on SR is that when FTCs and other iso-rate tuning curves for the same ANF are displaced along the SPL axis, so that their lower limbs overlap, their upper limbs shift systematically to lower frequencies as a function of increasing criterion level. This is illustrated in Fig. 8B, re-drawn from Fig. 3 of (Geisler et al., 1974). On the reasonable assumption that thresholds for any single ANF corresponds to a constant magnitude of BM vibration, the fact that low-SR ANFs have higher thresholds than high-SR ANFs implies that the thresholds of low-SR ANFs correspond to higher magnitudes of BM responses than those of high-SR ANFs. Therefore, average FTCs normalized to CF should have identical lower limbs, regardless of SR, but their upper limbs should shift to lower frequencies as a function of SR. Figure 8A, illustrating synthetic FTCs with CFs of 7.4 kHz constructed from responses of low-SR, mid-SR and high-SR ANFs, shows that the prediction is correct: regardless of SR, FTCs normalized to CF have similar lower limbs but the upper limbs shift to lower frequencies with decreasing SR. As a result, Q’s vary inversely with SR. The FTCs of high-, mid- and low-SR ANFs, respectively, have $Q_{20}$’s of 2.64, 2.80 and 2.90, $Q_{30}$’s of 1.94, 2.15 and 2.27, and $Q_{40}$’s of 1.45, 1.67 and 1.88.

Figure 9 shows iso-velocity tuning curves for BM responses to tones in the cochleae of chinchilla (panels A-C) and gerbil (panel D). To facilitate comparison among the tuning curves obtained with different velocity criteria, the curves in each panel have been normalized to CF. For low response criteria, the iso-velocity curves overlap at most frequencies <CF. In contrast,
the upper limbs of the tuning curves do not overlap. Starting with the lowest criterion velocities, bandwidths first decrease with increasing criterion velocity, until they reach a minimum (solid lines) at which Q’s are maximal. For even higher response criteria (dashed lines), bandwidths increase and Q’s decrease. This non-monotonic behavior of BM tuning as a function of response criterion probably explains why FTCs of low-SR ANFs (Fig. 8A) are more sharply tuned than the FTCs of high-SR ANFs: FTCs of low-SR ANFs reflect BM iso-velocity curves with intermediate criterion velocities, which are more sharply tuned than iso-velocity curves with lower criterion velocities.

The non-monotonic dependence of BM tuning on iso-velocity criterion (Fig. 9) derives not from the compressive growth of BM vibrations per se, but rather from its uneven distribution across frequencies (Ruggero et al., 1997; Rhode and Recio, 2000; Rhode, 2007), at least for high CFs. At (tail) frequencies well below CF, responses are linear. Compression grows as CF is approached and surpassed and is maximal at a frequency higher than CF. For low velocities (e.g., 50-200 μm/s in Fig. 9A), the lower limbs of the BM tuning curves do not change as a function of criterion velocity because responses are linear. In contrast, the upper limbs shift to lower frequencies because the peaks of compression also shift systematically to lower frequencies as a function of increasing criterion velocity. The combined fixed lower limbs and shifting upper limbs result in sharper tuning as a function of increasing velocity for low criterion velocities. For higher criterion velocities (e.g., 400-1600 μm/s), the upper limbs continue shifting to lower frequencies as a function of increasing velocity but so do the lower limbs, at an even faster rate. As a result, BM tuning becomes broader with increasing criterion velocity.
DISCUSSION

**Distribution of SRs in chinchilla and other species**

The range of SRs in the present study (<1 to 140-150 spikes/s) is similar to ranges previously reported for chinchilla (Dallos and Harris, 1978) and other species: cat (Kiang et al., 1965; Liberman, 1978), gerbil (Schmiedt, 1989; Ohlemiller and Echteler, 1990; Müller, 1996), guinea pig (Manley and Robertson, 1976), and rat (el Barbary, 1991a). Categorizing SRs with boundaries at 1 and 18 spikes/s, the percentages of low-, medium-, and high-SR fibers in chinchilla are 11, 23 and 66, respectively. With a similar definition, the percents are 12, 15 and 73 (Tsuji and Liberman, 1997) or 20% for low-SR ANFs in guinea pig (Evans, 1972). With the more commonly used boundaries of 0.5 and 18 spikes/s, low-, medium- and high-SR ANFs constitute 8, 26 and 66% of the population in chinchilla, i.e., very similar to the 11, 23 and 66% reported previously for chinchilla (Salvi et al., 1982). These percents are also similar to those reported for cat [16, 23 and 61 (Liberman, 1978)] and gerbil [10, 30 and 60 (Schmiedt, 1989)].

**SRs as a function of CF in chinchilla and other species**

Contrary to the present results in chinchilla (Fig. 1), some studies of ANFs have found a gradual decline of the upper range of SRs ("SR compression") as a function of increasing CF. Such compression appears to be well established in the case of gerbils [(Schmiedt, 1989; Ohlemiller and Echteler, 1990); see also (Müller, 1996)]. Compression was also described in one study in cats (Liberman, 1978) but not in another (Kim and Molnar, 1979) and seems to be absent in rat [Fig. 3 of (el Barbary, 1991a)]. When it exists, SR compression might reflect basal cochlear dysfunction, either chronic, due to overexposure to intense sounds [since the compression was
not typically found in chamber-raised cats (Liberman, 1978)], or acute, as a result of cochlear cooling after opening of the bulla under anesthesia (Liberman and Dodds, 1984b). However, compression was observed in gerbils even when cochlear temperature was maintained at 37-38 °C (Ohlemiller and Echteler, 1990). In the present study, in which compression was not evident, chinchillas were “routine normals” (with uncertain history of exposure to intense sounds) and no special precautions were taken to avoid cooling of the cochlea. Thus, the absence of SR compression may be one feature in which the chinchilla differs from gerbils (and possibly cats).

In chinchilla the percentage of low-SR fibers is much lower for CF <3 kHz than for higher CFs (Fig. 1C). A scarcity of low-SR ANFs with CF <3 kHz was also reported in gerbil (Schmiedt, 1989; Ohlemiller and Echteler, 1990). In contrast, the distributions of low-SR fibers in cat (Kiang et al., 1965; Liberman, 1978) and rat (el Barbary, 1991b) appear to be uniform across CFs. Computed for the entire ANF population, the frequency distribution of SRs varies widely between species and even among reports for the same species. The distribution is clearly bimodal in cat (Liberman, 1978; Kim and Molnar, 1979]) and guinea pig (Tsuji and Liberman, 1997), only mildly bimodal in chinchilla [Fig. 2B and (Dallos and Harris, 1978)] and rabbit (Borg et al., 1988), but unimodal in rat (el Barbary, 1991a) and mouse (Taberner and Liberman, 2005). For gerbils and macaques, results are mixed; for gerbils, contrast Fig. 5 of (Schmiedt, 1989) with Fig. 3 of (Ohlemiller and Echteler, 1990)]; for macaque monkeys, contrast the results of (Nomoto et al., 1964) and of (Joris et al., 2006).

**SRs and FTC features across species**
SRs and CF thresholds are inversely related in chinchilla [Fig. 3; see also (Salvi et al., 1982)] and in other mammalian species [cat (Liberman, 1978; Liberman and Dodds, 1984a; Kiang et al., 1976; Kiang, 1984), guinea-pig (Winter et al., 1990), Mongolian gerbil (Schmiedt, 1989; Ohlemiller and Echteler, 1990) and, to a lesser extent, in rabbit (Borg et al., 1988)]. The SR dependence of CF thresholds in chinchilla (present work), cat (Liberman, 1978) and guinea pig (Tsuji and Liberman, 1997) can be compared with special confidence because they were obtained using essentially the same tuning curve algorithm. On average, low-SR ANFs in the present chinchilla sample have CF thresholds that are 13.8 dB higher than in high-SR ANFs (Fig. 4). In cat, the CF thresholds of low- and high-SR ANFs differ by 15-30 dB [Fig. 11 of (Liberman, 1978)], a substantially larger amount than in chinchilla (Liberman, 1978). The quantitative difference between the SR dependences in cat and chinchilla may reflect the fact that electric shocks were used as search stimuli in the cat study, thus ensuring the detection of ANFs with nearly-zero SR. Thus, it is possible that the present sample in chinchilla underestimates the numbers of those ANFs, which presumably have especially high thresholds. In guinea pig, low-SR ANFs have CF thresholds about 19 dB higher than high-SR ANFs (Tsuji and Liberman, 1997). In gerbil, low-SR ANFs have CF thresholds between 10 and 20 dB higher than high-SR ANFs.

The tips of FTCs are more sharply tuned in low-SR than in high-SR ANFs in chinchilla [Figs. 6-7 & 8A and Fig. 1 of companion paper (Temchin et al., 2008)] and cat (Kiang et al., 1976; Kiang, 1984; Liberman, 1978). A dependence of sharpness of tuning on SR was sought, but not found, in gerbil (Schmiedt, 1989; Ohlemiller and Echteler, 1990) and has not been reported for any other species. In both chinchilla and cat, the differences of sharpness of tuning between low-
and high-SR ANFs are relatively larger when measured at higher levels (30-40 dB) re CF thresholds. In chinchilla, the largest difference between $Q_{40s}$ occurs for CFs around 5 kHz, with $Q_{40s}$ being 40 % larger in low-SR ANFs than in high-SR ANFs (Fig. 5D). In cat, the differences may be somewhat larger, to judge by Fig. 14 of (Liberman, 1978), which is the only quantitative account of differences of sharpness of tuning between low-SR and high-SR for cat ANFs. On average, for CFs between 800 Hz and 18 kHz, $Q_{40s}$ are about 30 % larger in low-SR than in high-SR ANFs.

The contrasting results regarding a link between SR and sharpness of tuning between studies on chinchilla and cat, on the one hand, and gerbil in the other, may reflect differences between the algorithms used for FTC determination. However, this explanation was disproved by showing that FTCs obtained with different algorithms (one of them the one used for both cat and chinchilla studies) yielded the same sharpness of tuning in low- and high-SR gerbil ANFs (Ohlemiller and Echteler, 1990). Another explanation for the apparent species difference was based on the separations between CF thresholds of low- and high-SR ANFs, judged to be smaller in gerbil than in cat (Ohlemiller and Echteler, 1990). Again, this explanation seems disproved by the present results since the separations between low- and high-SR CF thresholds are similar in chinchilla and gerbil [compare Fig. 4 with Fig. 4 of (Ohlemiller and Echteler, 1990)].

**Conclusions**

1) The properties of spontaneous activity of chinchilla ANFs, including their relation to thresholds at CF, generally resemble those of other mammalian species. However, there are apparent species differences in the salience of the bimodality of the frequency distribution of SR.
2) Even though the overall shapes (including tip-to-tail ratios) of FTCs for high-SR and low-SR chinchilla ANFs are similar, the tips of FTCs are more sharply tuned in low-SR than in high-SR ANFs. This finding is consistent with the (until now, exceptional) reports of SR dependence of ANF FTCs in cat (Liberman, 1978; Kiang et al., 1976).

3) That the tips of FTCs are more sharply tuned in low-SR than in high-SR ANFs is probably explained by the (previously unnoticed) fact that BM tuning curves determined with mid-level iso-velocity criteria are sharper than those measured using lower (or higher) criterion velocities.
ACKNOWLEDGMENTS

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FIGURE LEGENDS

Figure 1. SRs as a function of CF. A) SRs plotted against CF using a linear ordinate. B) SRs plotted against CF with a logarithmic ordinate. SR < 0.1/s plotted as 0.05/s. C) Percentage of SRs <18/s in non-overlapping 1/3-octave CF bands, each representing 28-358 ANFs.

Figure 2. Frequency distribution of SRs. Left ordinates: percent scale. Right ordinates: absolute numbers of ANFs. A: frequency distribution of SRs for ANFs with CF>3 kHz (thick line) and CF<3 kHz (thin line). Binwidth: 5 spikes/s. B: frequency distribution of SRs regardless of CFs. Binwidth: 1 spike/s. Data from 4203 ANFs recorded in 228 chinchillas.

Figure 3. Normalized CF thresholds as a function of SR. To attenuate the effects of inter-animal variability, CF thresholds in each animal were normalized to CAP thresholds measured in the same animal. The black dashed line indicates the trend for the entire population. The red, green and blue lines indicate trends computed separately for the low-, medium- and high-SR ANF populations.

Figure 4. Average CF thresholds for low-, medium- and high-SR ANFs as functions of CF. Average CF thresholds for the entire sample of FTCs were computed separately for low- (blue), medium- (green line) and high-SR (black circles) ANFs within 21 2/3 octave CF bands centered at 1/3 octave intervals. Black vertical lines indicate the corresponding ± SDs for the high-SR ANFs. The red circles and vertical lines indicate the grand averages plus/minus SDs of CF thresholds computed in each band in individual animals. Comparison of the black and red
vertical lines indicates that the variance of CF thresholds of high-SR ANFs is very small in individual animals (average SD = 3.9 dB in the 0.6-10 kHz CF range) and that the relatively large variance across animals (average SD = 10.1 dB in the same CF range) is due to inter-animal variations.

**Figure 5. SR dependence of tip-to-tail ratios and CF thresholds of FTCs with CF ≥ 3.5 kHz.**

Average tip-to-tail ratios (circles), measured as the differences between CF and tail thresholds for low- (open circles) and high-SR (filled circles), are plotted as a function of tail frequency. Average CF thresholds for low- and high-SR ANFs measured in the same chinchillas are indicated by open and filled squares, respectively. Vertical bars are standard errors. 18-116 fibers were averaged in any CF band for high-SR data and 8-20 for low-SR data. Differences in tip-to-tail ratio between low- and high-SR fibers were not statistically significant at any frequency (p>0.05). CF thresholds between low- and high-SR ANFs differed significantly for all frequencies (p<0.005).

**Figure 6. SR dependence of sharpness of tuning of FTCs.** Sharpness of tuning is expressed as $Q_x$ (i.e., CF divided by bandwidth at $x$ dB above CF threshold). $Q_{10\text{dB}}$ (A), $Q_{20\text{dB}}$ (B), $Q_{30\text{dB}}$ (C) and $Q_{40\text{dB}}$ (D) values were averaged separately for low- (open circles) and high-SR (closed circles) within 2/3 octaves bands and plotted as a function of CF. Vertical bars are standard deviations. Numbers of ANFs are indicated in each panel. Only data points for averages from 10 or more ANFs are plotted. Crosses indicate statistically significant differences (p <0.0005) between low- and high-SR ANFs.
**Figure 7. SR dependence of partial bandwidths for FTC frequencies higher than CF.** Partial bandwidths for FTC frequencies $>\text{CF}$ [see Figs. 1B and 1C of companion paper I (Temchin et al., 2008)]. Bandwidths were averaged separately for low- (open circles) and high-SR (closed circles) within 2/3 octaves bands and plotted as a function of CF. Vertical bars are standard deviations. Numbers of ANFs are indicated in each panel. Only data points for averages from 10 or more ANFs are plotted. Crosses indicate statistically significant differences ($p < 0.0005$) between low- and high-SR ANFs.

**Figure 8. SR dependence of sharpness of ANF FTCs and variation of tuning as a function of iso-response criterion.** A) Synthetic FTCs for high-SR (blue), mid-SR (green) and low-SR (red) ANFs, normalized to CF (7.35 kHz) and threshold at CF. B) Iso-rate curves for responses of a single squirrel monkey ANF at the indicated percents of the maximum rate. Data from Fig. 3B of (Geisler et al., 1974).

**Figure 9. The BM origin of the SR dependence of sharpness of tuning in ANF FTCs.** Iso-velocity BM tuning curves, normalized to threshold at CF. Criterion magnitudes are spaced in equal dB steps. A). Chinchilla L208 [Fig. 1A of (Ruggero et al., 2000)]. B). Chinchilla L113 [Fig. 11 of (Ruggero et al., 1997)]. C) Chinchilla N92 [Fig. 1C of (Rhode, 2007)]. D). Gerbil [Fig. 2B of (Ren and Nuttall, 2001)].
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A

Spontaneous Rate (spikes/s)

0 20 40 60 80 100 120 140 160 180 200

B

Characteristic Frequency (Hz)

100 1000 10000

20 30 40 50 in 1/3 oct band

C

% of AFNs (SR<18/s)

228 chinchillas

4184 fibers

228 chinchillas

FIG1 Aug. 7, 2008
Spontaneous Rate (spike/s)

CF re CAP threshold (dB)

n=192 (low SR)
n=407 (med SR)
n=1213 (high SR)

0.5kHz<CF<12kHz
Characteristic Frequency (Hz)

CF threshold (dB SPL)

high SR (n=2785)
medium SR (n=951)
low SR (n=448)
individual high SR (228 chinchillas)
Characteristic Frequency (Hz)

Q10dB

Low SR (n=460)
High SR (n=2643)

Q20dB

Low SR (n=371)
High SR (n=2093)

Q30dB

Low SR (n=226)
High SR (n=1246)

Q40dB

Low SR (n=117)
High SR (n=706)
Figure 7: Aug. 7, 2008

**A** 10dB re CF threshold
- Low SR (n=421)
- High SR (n=2744)

**B** 20dB re CF threshold
- Low SR (n=464)
- High SR (n=2744)

**C** 30dB re CF threshold
- Low SR (n=205)
- High SR (n=1889)

**D** 40dB re CF threshold
- Low SR (n=337)
- High SR (n=2420)
A

CF=7.35kHz

B

Frequency (kHz)

4 5 6 7 8 9

dB re CF threshold

n=124 (low SR)
n=204 (med SR)
n=464 (high SR)

10% 20% 40% 60% 80%

dB

40 50 60 70 80 90 100

FIG8 Aug. 7, 2008