Threshold Tuning Curves of Chinchilla Auditory-Nerve Fibers. I. Dependence on Characteristic Frequency and Relation to the Magnitudes of Cochlear Vibrations

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INTRODUCTION

The frequency tuning of afferent auditory-nerve fibers (ANFs) derives from the frequency tuning of cochlear vibrations, although the exact relationship between neural and mechanical tuning is not fully settled (Robles and Ruggero 2001). In particular, it is unclear whether thresholds correspond to constant magnitudes of basilar-membrane (BM) displacement, velocity, or other quantities or whether such magnitudes are the same throughout the cochlea. Here we seek answers to these questions by studying frequency tuning in ANFs of chinchilla, the species in which BM and/or organ of Corti vibrations are the same throughout the cochlea. Here we seek answers to these questions by studying frequency tuning in ANFs of chinchilla, the species in which BM and/or organ of Corti vibrations are the same throughout the cochlea.

METHODS

All animal procedures were approved by the Animal Care and Use Committee of Northwestern University. Adult chinchillas were initially anesthetized with ketamine hydrochloride (100 mg/kg, injected subcutaneously) and sodium pentobarbital (65 mg/kg) or Dial (diallyl barbituric acid) in urethane (1 g/kg), injected intraperitoneally. Deep anesthesia was maintained with supplemental anesthetic doses to eliminate limb-withdrawal reflexes. (At the end of the experiments, the animal was killed by decapitation while still deeply anesthetized.) Core body temperature was kept near 38°C by means of a servo-controlled electrical heating pad. Tracheotomy and tracheal intubation were performed routinely but forced respiration was used only rarely, as necessitated by apnea or labored breathing. The pinna was resected and part of the bony external ear canal was chipped away to permit for the same normal cochleae (Narayan et al. 1998; Ruggero et al. 2000). Although frequency-threshold curves (FTCs) for chinchilla ANFs have been illustrated in several publications (Dallos and Harris 1978; Ruggero 1992; Salvi et al. 1982; Wang et al. 1997), no account of ANF FTCs in this species is comparable in breadth or detail to accounts available for some other mammalian species (Borg et al. 1988; el Barbary 1991; Ohlemiller and Echelter 1990).

We used two large databases of ANF responses to tones to synthesize representative FTCs throughout the range of characteristic frequencies (CFs) in the chinchilla cochlea. In the present report, the first of a set of two, we show that FTCs undergo a smooth transition in symmetry at CFs around 1 kHz and an abrupt change at CFs of 3–4 kHz. We then compare the synthetic FTCs with existing mechanical-vibration data for chinchilla, including a wealth of newly available BM recordings from several basal cochlear sites (Rhode 2007a,b). At the base of the chinchilla cochlea, ANF FTCs closely match BM isovelocity tuning curves with the same CF. At the cochlear apex, ANF FTCs are more sharply tuned than organ of Corti vibrations in chinchilla. The companion paper in the set (Temchin et al. 2008) addresses the spontaneous rates (SRs) of ANFs, shows that FTCs are more sharply tuned in low-SR ANFs than in high-SR ANFs, and presents evidence that the difference in sharpness of tuning arises from the frequency distribution of cochlear compressive nonlinearity. A preliminary account of this work was published as an abstract (Temchin et al. 1997a).

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visualization of the umbo of the tympanic membrane and insertion of the ear canal. The tendon of the tensor tympani muscle was severed and the stapedius muscle was detached from its anchoring. A silver ball electrode, placed on the round window, was used to record compound action potentials (CAPs). In most experiments, CAP thresholds were measured for stimulus frequencies from 0.5 to 16 kHz with 0.5-octave steps. In the earliest (84) experiments, CAP thresholds were determined by visual inspection of average waveforms. In the more recent (144) experiments, CAP thresholds were determined automatically under software control as the lowest sound pressure level (SPL) at which the magnitude of N1 (averaged over 64 presentations of 10-ms stimuli with 2-ms rise-fall time, random initial phase) exceeded 10 μV. CAP thresholds were generally measured twice, immediately after placement of the round-window electrode and again after intracranial surgery and exposure of the auditory nerve. ANF FTCs were included in the database only if the second set of CAP thresholds did not exceed the first by >6 dB at any frequency. In any single experiment, data collection was terminated as soon as CF thresholds of high-SR ANFs in any given CF region exceeded earlier thresholds by >10 dB. In a sample of 144 chinchillas, 10-μV CAP thresholds were very uniform between 0.7 and 8 kHz, with means of 25.9–30.3 dB SPL and SDs of 0.094 octave (n = 4,155). The discontinuity is 3 kHz in Fig. 1.) The discontinuity is 3 kHz in Fig. 1.

### Results

Here we analyze threshold/frequency pairs for responses to tones of thousands of ANFs recorded over many years in chinchillas (Ruggiero and Rich 1983, 1987; Ruggiero et al. 1996; Temchin et al. 1997b). FTCs were measured using an automated adaptive procedure (see methods) similar to that used by Kiang and Liberman (Kiang et al. 1970; Liberman 1978).

#### Features of individual FTCs as functions of CF and SR

Figure 1 provides an overview of the variation of several FTC features (bandwidths [BW], Q values, and chord slopes) in individual ANFs as functions of CF and SR, focusing on measurements at thresholds 30 dB higher than CF thresholds. In logarithmic coordinates, BWs increase with CF at constant but somewhat different rates at CFs higher and lower than 3–4 kHz, where a clear downward “jog” is evident (Fig. 1A). The origin of the “jog” in Fig. 1A is clarified on computation of partial BWs measured relative to CF (i.e., between CF and the lower or upper 30-dB cutoffs; see insets). These are plotted as functions of CF in Fig. 1, B and C. The lower (<CF) partial BWs (but not the upper partial BWs) exhibit a clear discontinuity at CFs between 3 and 4 kHz (compare red and green trend lines for CFs <3 kHz in Fig. 1B). The discontinuity is also clearly seen in a plot of the lower-limb chord slopes versus CF (Fig. 1E). (The curved “ceiling” for CFs <3 kHz in Fig. 1B and the “floor” for the same CFs in Fig. 1E are artifacts of the 80-Hz limit of FTC frequencies.)

Figure 1 also allows for comparison of the FTC features in high-SR (gray symbols) and low-SR (black symbols) ANFs.
As previously shown for cat (Kiang et al. 1976; Liberman 1978), low-SR ANFs in chinchilla have narrower BWs and higher Q values than those of high-SR ANFs. Differences in frequency tuning between low- and high-SR ANFs are further explored in a companion paper (Temchin et al. 2008).

The near-discontinuity of FTC shapes in the 3- to 4-kHz CF region is dramatically illustrated by plotting measures of “tip-to-tail ratio,” thresholds re CF threshold at frequencies 0.5, 1, and 1.5 octaves lower than CF, against CF (Fig. 2). Except for the transition region (CFs 3–4 kHz), the tip-to-tail ratios vary minimally as a function of CF. For tip-to-tail ratios measured at −1 and −1.5 octaves re CF, slopes jump at the transition region between 20 and 30 dB for CFs >4 kHz.

Synthetic FTCs

Figure 3 illustrates how individual ANF FTCs were averaged within 2/3 octave CF bands (indicated by brackets) and combined with thresholds of input–output functions for responses to low-frequency tones (squares) to produce “synthetic” FTCs (thick traces). The two synthetic FTCs of Fig. 3, centered at CFs of 236 and 9,524 Hz, are representative of those for low- and high-CF ANFs. The thin traces and squares indicate thresholds averaged at fixed frequencies and the circles indicate frequencies averaged at fixed thresholds. At most frequencies the averages produced by the two methods coincide perfectly; however, the averages diverge at the highest frequencies of the FTC upper limbs, at which FTC slopes are steepest: the thin trace curves, resulting from averaging thresholds, have shallower slopes than the loci of the circles—this is an artifact. In general, functions such as FTCs have high-slope segments with well-defined abscissa positions (frequencies) but poorly defined ordinate positions (thresholds). As a result, even small errors in estimating frequencies for individual FTCs will yield FTC averages with slopes smaller than the slopes of the individual FTCs. For this reason, the upper limbs of the synthetic FTCs were obtained by averaging frequencies, as indicated by the coincidence of the thick traces and the circles.

The lower limbs of the synthetic FTCs were principally computed by averaging thresholds at fixed frequencies, as indicated by the full overlap of the thin and thick traces at most frequencies <CF. However, for frequencies ≤1 kHz, thresh-
Thresholds specified from FTCs were complemented by thresholds determined from input–output functions measured for responses to tones (50 and 100 Hz and its multiples, 1,000 Hz). This was convenient because individual FTCs were often incomplete, lacking data for the lowest tail frequencies (note divergence between thin and thick traces at the lowest frequencies). Averages were computed over 2/3-octave CF bands (e.g., brackets in Fig. 3) centered in 21 1/3-octave steps.

Figure 4 shows smoothed FTCs of high-SR ANFs computed for 21 2/3-octave CF bands with CFs centered every 1/3-octave, from 187.5 Hz to 19.05 kHz. In general FTC shapes vary in an orderly manner, with approximately parallel lower and upper FTC limbs around the CFs. However, closer inspection reveals a specially wide separation of the FTC lower limbs in the frequency region 1–2 kHz, corresponding to the 3- to 5-kHz CF region separating ANFs with FTCs with tails from those without tails.

**FIG. 2.** Thresholds at tail frequencies re CF threshold. A: thresholds relative to CF thresholds at frequencies 0.5 octave lower than CF. B: relative thresholds at frequencies 1 octave lower than CF. C: relative thresholds at frequencies 1.5 octave lower than CF. Flat lines indicate averages for CFs 1 kHz and 2 kHz.

**FIG. 3.** Illustration of the method for constructing synthetic FTCs. The brackets indicate the 2/3-octave ranges of CFs included in constructing 2 synthetic FTCs with CFs of 236 and 9,524 Hz. The thin traces indicate frequency-threshold pairs obtained by averaging the thresholds of individual FTCs (measured using the automated adaptive procedure) at fixed frequencies (method A). The open circles indicate frequency-threshold pairs obtained by averaging the frequencies of FTCs at fixed thresholds (method B). The squares indicate average frequency-threshold pairs extracted from a database of rate–intensity functions for single tones (frequencies: 50 Hz and 100–1,000 Hz in steps of 100 Hz) (method C). The thick traces indicate synthetic tuning curves obtained by combining the 3 sets of frequency-threshold pairs. Note that the thin trace for the lower limb of the low-CF FTC is hidden by the thick trace. Methods A and B, respectively, were used to construct the upper limb and the lower limb (except for its lowest frequencies) of the synthetic FTCs. Method C was combined (by weighted averaging) with method A to produce the tail segments of high-CF synthetic FTCs for frequencies 1 kHz. At CF, the synthetic FTCs include data from 91 to 394 ANFs. Each square represents 11–54 ANFs. Each point of the synthetic FTCs represents data from 10–54 ANFs.

**FIG. 4.** Synthetic FTCs for high-SR ANFs. Synthetic FTCs constructed according to the method illustrated in Fig. 3. Curves for CFs 1 kHz were smoothed at frequencies <1 kHz. Values are plotted only for averages including 10 samples. The tip of each synthetic FTC represents responses of 81–486 ANFs.
Bandwidth, sharpness of tuning, and asymmetry of FTCs as functions of CF

The ratios of the partial bandwidths below and above CF (BWb/BWa; see insets of Fig. 1, B and C) provide measures of FTC asymmetry, which are plotted in Fig. 5 against CF. Exact symmetry is indicated by a ratio of 1, at CF \( \approx 900 \) Hz. For CFs \(<900\) Hz, the ratios were \(<1\), i.e., the upper-limb partial FTC BWs were wider than the lower-limb BWs; for CFs \(>900\) Hz, the ratios were \(>1\), i.e., the upper-limb partial FTC BWs were narrower than the lower-limb BWs. The asymmetry ratios grew monotonically with CF up to about 2 kHz. Monotonic growth was interrupted at CFs of 3–5 kHz, where prominent notches are evident. The notches coincide and are consistent with the discontinuities in the growth with CF of the 30-dB BW (Fig. 1A) and, especially, of the partial below-CF BW (Fig. 1B).

Figure 6 summarizes the variation of BWs and Q values, measured from the synthetic FTCs, as functions of CF. Averaged equivalent rectangular bandwidths (ERBs) as well as BWs at 3, 6, 10, 20, 30, and 40 dB are plotted in Fig. 6A. On first observation, BWs appear to increase with CF following power functions with similar slopes. However, closer inspection reveals transitions, consistent with those seen in Fig. 1, in the 3- to 4-kHz CF region. For measurements at 10–40 dB re CF threshold, BWs grew at faster rates for CFs \(>3–4\) kHz \((0.81–0.87 \text{oct/oct})\) than for lower CFs \((0.57–0.74 \text{oct/oct})\). To estimate sharpness of tuning, Q values were computed by dividing CFs by BWs, yielding \(Q_{ERB}\), \(Q_{3dB}\), \(Q_{6dB}\), \(Q_{10dB}\), \(Q_{20dB}\), \(Q_{30dB}\), and \(Q_{40dB}\). These are plotted against CF in Fig. 6B. For CFs \(>4\) kHz, \(Q_{ERB}\), \(Q_{3dB}\), \(Q_{6dB}\), and \(Q_{10dB}\) grew at roughly constant rates as functions of increasing CF. In contrast, curves for \(Q_{20dB}\), \(Q_{30dB}\), and \(Q_{40dB}\) tended to saturate at CFs \(>6\) kHz.

Normalized synthetic FTCs

To facilitate appreciation of the changes of FTC shapes as a function of CF, Fig. 7 shows synthetic FTCs of high-SR ANFs plotted in logarithmic coordinates after normalization to CF threshold and CF. When plotted in this manner, FTCs with CFs \(\geq 6\) kHz are nearly identical (Fig. 7C), regardless of CF, and consist of three segments. A tip segment, within 30–40 dB higher than CF thresholds are plotted as functions of CF. B: Q values (CF divided by BW) are shown for the ERB and for the BWs at levels 3, 6, and 10–40 dB higher than CF thresholds. Data computed from synthetic FTCs of Fig. 4.
the lower limbs of low-CF FTCs grow somewhat steeper as a function of CF, which more than compensates for the (slower) increase of the lower-limb slopes.

The transition between low- and high-CF FTC shapes in the 3- to 4-kHz CF range (Figs. 1 and 2) is also illustrated in Fig. 7B: the shapes of the lower limbs of the FTCs change drastically and the distinction between tip and tail becomes increasingly evident. The salient features of the variation of FTCs with CF (Figs. 1, 2, 5, and 7) suggest that the chinchilla cochlea consists of distinct segments extending apically and basally from the region with CF 3–4 kHz. The dependence on CF of other aspects of ANF properties also suggests physiological differences between the apical and basal segments of the cochlea (see DISCUSSION).

Absence of high-frequency plateaus in ANF FTCs

High-frequency amplitude plateaus (arrows in Fig. 8, A and B), at which vibrations are linear, are routinely observed in BM vibrations at the base of the cochlea at levels as low as 70–80 dB SPL (e.g., Figs. 8, 9, and 11 of Ruggero et al. 1997 and middle panel of Fig. 2 of Cooper and Rhode 1997; see also Cooper and Rhode 1992; Narayan et al. 1998; Ruggero et al. 1990; Wilson 1992). Narayan et al. (1998) recorded from BM sites and ANFs in the same two chinchilla cochleae with open scalae tympani (see Ruggero et al. 2000) and showed that BM responses, but not ANF FTCs, exhibited high-frequency amplitude plateaus. In the present series of experiments, FTCs were measured for 56 ANFs (CFs: 1–11 kHz) from two cochleae in which the otic capsule was also perforated (as for recording BM vibrations) without causing any elevation of CAP thresholds. High-frequency plateaus were never found, even when (occasionally) stimuli exceeded CF threshold by 90 dB, confirming that the high-frequency plateaus in BM recordings are not artifacts associated with opening the otic capsule (Narayan et al. 1998; Ruggero et al. 2000).

Relationship between frequency tuning in ANFs and BM vibrations at the base of the cochlea

The tips of tuning curves of ANFs and BM responses at the base of the cochlea are nearly identical in chinchilla (Rhode 2007a; Robles et al. 1986; Ruggero et al. 1990, 1997) and probably also guinea pig (Sellick et al. 1982). It is not yet certain whether ANF FTCs more closely match isodisplacement or isovelocity BM tuning curves or some combination thereof (e.g., Rhode 2007a). Comparisons of ANF and BM data obtained both in individual chinchillas (Narayan et al. 1998) and in different groups of animals suggest that ANF FTCs match BM isoresponse values intermediate between constant velocity and constant displacement but closer to constant velocity (Ruggero et al. 1990, 2000). Figure 8C updates the group comparisons using a synthetic ANF FTC with CF = 8.35 kHz (solid line in Fig. 8C), constructed in the same manner as the ANF FTCs of Fig. 4. Again, the average ANF FTC falls close to the BM isovelocity curve.

Previous comparisons of mechanical and neural tuning in the chinchilla cochlea were carried out for CFs in the 8- to 10-kHz range. Rhode and Recio have published a treasure trove of high-quality BM data from several additional basal sites of chinchilla cochleae (Rhode 2007a,b; Rhode and Recio 2000) that now permit comparing BM and ANF tuning for CFs as low as 6.4 kHz and as high as 12 kHz. Figure 8, A, B, and D shows
comparisons of isoresponse curves from those cochleae with synthetic ANF FTCs constructed in the same manner as the ANF FTCs of Fig. 4, with CFs chosen to match the BM CFs. In every case, the tips of the ANF FTCs and of the BM isoresponse curves are identical. When the comparisons are carried out over sufficiently wide frequency ranges, the ANF FTCs match the BM isovelocity curves either nearly perfectly (Fig. 4A) or much more closely than the isodisplacement curves (Fig. 4B). In other words, high-pass filtering with slopes approaching 6 dB/octave occurs between BM displacement and spike generation in ANFs.

Relationship between frequency tuning in ANFs and BM vibrations at the apex of the cochlea

Figure 9 compares the frequency tuning of neural responses and mechanical vibrations for apical sites of the chinchilla cochlea with nominal CFs of 500 and 600 Hz (see Table 1 of Rhode and Cooper 1996). The solid lines indicate isovelocity curves (30 and 5 μm/s) for two chinchilla cochleae (computed from isodisplacement curves in Fig. 12 of Rhode and Cooper 1996). The dashed lines indicate synthetic ANF FTCs, constructed in the same manner as those of Fig. 4, for CFs comparable to those of the BM responses. The lower and upper limbs of the neural and mechanical tuning curves have similar slopes. However, the similarity of the lower limbs is probably partly an artifact: since the mechanical data were obtained in unsealed cochleae, the mechanical lower-limb slope is spuriously enhanced at a rate of ~6 dB/octave (Dong and Cooper 2006). ANF FTCs have well-defined, moderately sharp tips, whereas the mechanical tuning curves have ill-defined and blunt tips. The BWs at 10 dB above the minimum are 50% larger for the mechanical tuning curves (523 and 686 Hz) than for the ANF FTCs (309 and 457 Hz). The ANF FTCs have Q₁₀ values of 1.37 and 1.46, whereas the mechanical tuning curves have Q₁₀ values of 0.77 (CH35) and 0.97 (CH33), computed on the basis of the nominal CFs, 500 and 600 Hz.

DISCUSSION

CF dependence of FTC shapes: differences for CFs higher and lower than 3–4 kHz

In chinchilla, ANF FTC shapes undergo abrupt changes in the 3- to 4-kHz CF region: 1) when normalized to CF, FTCs with higher CFs are nearly identical, regardless of CF (Fig. 7C), whereas FTCs with CF <3–4 kHz change systematically with CF, particularly in their upper limbs (Fig. 7A); 2) the slopes of the lower limbs of the FTCs change abruptly, roughly from about ~25 dB/octave for CFs <3–4 kHz to ~70 dB/octave for higher CFs (Figs. 1E and 7). Abrupt changes in the lower limb of FTCs were previously described for gerbil in the same CF region (Ohlemiller and Echteler 1990; Schmiedt 1989) and, as noted by Schmiedt (1989), probably also exist in cat (see Fig. 14 of Liberman 1978 and Fig. 3 of Javel 1994).
FIG. 9. Comparison of ANF and BM frequency tuning at apical sites of the chinchilla cochlea. Solid lines: isovelocity tuning curves for vibrations at apical sites in 2 chinchilla cochleae. Dashed lines: synthetic chinchilla ANF FTCs constructed in the same manner as the FTCs of Fig. 4 for CFs comparable to the nominal CFs of the mechanical responses (see Table 1 of Rhode and Cooper 1996). Thick lines: 500-Hz CF; thin lines: 600-Hz CF. The isovelocity curves have been computed on the basis of 1-nm tuning curves in Fig. 12 of Rhode and Cooper (1996): BM vibrations in ch33 (500-Hz CF; 5 μm/s criterion) and tectorial-membrane vibrations in ch35 (600-Hz CF; 30 μm/s criterion). Numbers of ANFs averaged at frequencies near CF: 139 (500 Hz) and 187 (600 Hz).

To the extent that FTCs reflect BM vibrations and recalling that each octave of CF subtends an approximately fixed distance on the BM (Eldredge et al. 1981; Greenwood 1990; Müller et al. 2008), the similarity of FTCs at the base of the chinchilla cochlea (Fig. 7C) implies that the envelopes of the BM traveling wave are identical and that the number of wavelengths in the traveling waves are the same, regardless of frequency. The existence of this property of cochlear mechanics—“scaling symmetry”—was apparently first conjectured by Zweig (1976) on the basis of Rhode’s earliest BM data for squirrel monkey (Rhode 1971). In chinchilla, scaling symmetry applies to CFs >4 kHz, corresponding to the basal third of the cochlea (Eldredge et al. 1981; Müller et al. 2008) but does not apply to the remainder, i.e., the apical 2/3 of the cochlea (Fig. 7, A and B).

Other differences between cochlear responses for CFs higher and lower than 3–4 kHz

Systemic administration of furosemide alters FTC shapes differently across the 3- to 4-kHz CF boundary (Sewell 1984): tip-to-tail ratios are much reduced for FTCs of ANFs with CFs >4 kHz but less so or not at all for lower CFs. The CF-specific effect of furosemide on high-CF ANFs is due to a corresponding effect on BM vibrations at the base of the cochlea (Ruggiero and Rich 1991): furosemide temporarily abolishes the active process, reducing sensitivity and compressive nonlinearity at CF. The lesser effect of furosemide on FTCs of ANFs with CF <3 kHz suggests that amplification and CF-specific compression play lesser roles in apical regions than in basal regions of the cochlea.

Differences in the strength and CF specificity of BM compressive nonlinearity across the 3- to 4-kHz CF boundary probably explain why putative “BM” input–output functions derived from responses of ANFs are less compressive for CFs <4 kHz than for higher CFs (Cooper and Yates 1994), may account for the weaker modulation of ANF CF responses by low-frequency tones in low-CF ANFs than in high-CF ANFs (see Fig. 8 in Temchin et al. 1997b), and may help to explain why the increases of CF thresholds induced by cochlear cooling are larger in high-CF ANFs than in low-CF ANFs (Ohlemiller and Siegel 1994). In addition to differences in frequency tuning and its lability across the 3- to 4-kHz CF boundary, the timing of ANF responses also changes abruptly around the same CF region: the phases of responses to low-frequency tones (<600 Hz) undergo a shift amounting to nearly π radians (Ruggiero and Rich 1983, 1987; Ruggiero et al. 1996) and the onset delays of “impulse responses” measured using Wiener kernels jump by 0.3–0.5 ms (see Fig. 15A of Recio-Spinoso et al. 2005).

Implication for low-frequency suppression of the near-velocity sensitivity of excitation in high-CF ANFs

Because suppression of BM responses to CF tones by low-frequency tones requires suppressor displacement magnitudes at least as large as the responses to the CF tones (Geisler and Nuttall 1997), the existence of neural suppression of CF tones by nonexcitatory low-frequency tones (Cai and Geisler 1996; Fahey and Allen 1985; Temchin et al. 1997b) has led to questioning whether this neural phenomenon has a BM correlate (Rhode 2007b), or to postulating the existence of “synaptic suppression” in low-SR ANFs (Cai and Geisler 1996). In fact, 4–6 dB/octave high-pass filters interleaved between BM vibrations and the receptor potentials of inner hair cells can fully account for neural suppression of CF tones by nonexcitatory low-frequency tones, especially in the case of low-SR ANFs [see companion paper (Temchin et al. 2008)], that are relatively insensitive (see Cheatham 2008; Temchin et al. 1997b).

Tuning, compressive nonlinearity, and amplification at low-CF sites of the chinchilla cochlea

The tuning discrepancies between mechanical and neural responses at low-CF sites (Fig. 9) may indicate the existence of an apical “second filter” interposed between organ of Corti vibrations and neural excitation. Evidence for such a “second filter” comes principally from recordings in well-sealed guinea pig cochleae, where the magnitudes of apical vibration are essentially low-pass (rather than band-pass) in nature (Dong and Cooper 2006). Another possibility is that the apparent broad tuning of apical mechanical vibrations is partly due to abnormally weak amplification caused by surgical trauma. At apical sites of the chinchilla cochlea, compression extends over the entire frequency range of responses, so that tuning hardly changes as a function of stimulus level (Rhode and Cooper 1996). Therefore it is appropriate to measure amplification as the difference between the peak magnitudes of responses to low- and high-level stimuli (see Robles and Ruggiero 2001). Using this definition, amplification at basal sites of the chinchilla cochlea with CF of 9–10 kHz amounts to, at most, 46 dB (see Table 1 of Robles and Ruggiero 2001). At apical sites of
the chinchilla cochlea, amplification has been reported as 14–18 dB (Rhode and Cooper 1996), although an independent estimate based on Fig. 2 of Rhode and Cooper (1997) indicates amplification of about 30 dB. Therefore it is possible that in normal chinchilla cochleae amplification at the apex is weaker than that at the base by only 16 dB (i.e., 46 minus 30) or less.

**ANF FTCs in different species**

To a first approximation, the shapes of the FTCs of ANFs and their dependence on CF in chinchilla are similar to the patterns found in other species. In chinchilla and cat, thresholds converge at low frequencies (see Figs. 4 and 8 of Kiang 1984). In most species, high-CF ANF FTCs have distinct tip segments around CF, with relatively steep slopes, and tail segments at low frequencies, with relatively flat slopes. However, tails may be lacking in ANF FTCs of macaque monkey (Joris et al. 2006). The transition between tail and tip is smooth and monotonic in chinchilla (Figs. 4 and 7), gerbil (Ohlemiller and Echteler 1990; Schmiedt 1989), guinea pig (Evans 1972; Robertson and Johnstone 1979), rat (el Barbary 1991), mouse (Taberner and Liberman 2005), and rabbit (Borg et al. 1988), but includes a notch in cat FTCs (see Figs. 2, 3, 7, and 8 in Kiang and Moxon 1974; and Figs. 5 and 12 in Javel 1994). Javel (1994) described a break in the upper limb of high-CF ANFs of cat at 20–35 dB re CF threshold, which seems to coincide in level with the inflections of the upper limbs of chinchilla FTCs (Fig. 7). The upper limbs of low-CF ANF FTCs of cat often include “shoulders” marking the transition between the tip and “high-frequency tails” (Javel 1994; Kiang 1984). Such shoulders are not seen in FTCs of low-CF chinchilla ANFs.

Regardless of overall FTC shape, the Q₁₀ values of the FTC tips increase systematically with increasing CF in all mammalian species (e.g., Fig. 6). Taberner and Liberman (2005) showed that the Q₁₀ values of ANF FTCs measured with identical automated procedures in mouse, gerbil, guinea pig, chinchilla, and cat are similar over the CF range 0.7–20 kHz (Fig. 11 of Taberner and Liberman 2005). Ruggero and Temchin (2005) argued that such similarity may also extend to squirrel monkey and humans in spite of striking differences in cochlear lengths (Fig. 6 of Ruggero and Temchin 2005). Nevertheless, their Fig. 6A does show differences between the Q₁₀ values for chinchilla and other species, particularly for high CFs (Ruggero and Temchin 2005). Specifically, in the 10-kHz region Q₁₀ values ranged from 4.6 for chinchilla to 6.3 for squirrel monkey (a New-World primate). An even larger difference may exist between chinchillas and macaques (Old-World monkeys). Our analysis (not shown) of a plot of Q₁₀ versus CF for *Macaca irus* and *Macaca mulatta* (Fig. 1 of Nomoto 1980) yields an average Q₁₀ of 9.7 at CFs of about 10 kHz (albeit with large variance: SD = 5.3). Although it is uncertain whether those findings in macaque (based on FTCs measured using “audiovisual” criteria) are fully comparable with findings in other species (based on FTCs obtained with automated procedures), they are consistent with a recent abstract reporting that Q₁₀ and Q₄₀ values in macaque are larger than those in cat (Joris et al. 2006). Enhanced frequency tuning in primates, especially those native to the Old World, is of interest in the context of the unresolved controversy on whether humans (Old-World primates) have exceptionally sharp cochlear tuning (Ruggero and Temchin 2005; Shera et al. 2002).

**Summary and conclusions**

1) FTCs flip their asymmetry gradually at a CF of about 1 kHz (Figs. 5 and 7A) and their shapes change abruptly in the 3- to 4-kHz CF region (Figs. 1, 2, 4, 5, and 7B). The 3- to 4-kHz CF boundary coincides with the boundary at which several other aspects of cochlear physiology, including the phases of ANF responses to low-frequency tones (Ruggero and Rich 1987; Ruggero et al. 1996) and the lability of FTC shapes (Sewell 1984), also change substantially. Such changes suggest that BM vibrations and/or their translation into neural excitation differ substantially between apical and basal segments of the cochlea.

2) At the base of the chinchilla cochlea, ANF FTCs more closely resemble BM isovelocity tuning curves than isodisplacement curves. The near correspondence of ANF thresholds to constant BM velocity helps explain suppression of near-CF ANF responses by nonexcitatory low-frequency tones (Cheatham 2008; Temchin et al. 1997b).

3) FTCs of low-CF ANFs are sharper than published isoreponse tuning curves for apical vibrations in chinchilla cochleae. This implies that existing mechanical recordings are not representative of fully normal chinchilla cochleae and/or that a “second filter” is interposed between vibrations and spike generation.

4) The CF-dependent features of chinchilla FTCs, including their shape transitions at CFs of 1 and 3–4 kHz, resemble those of other mammalian species. However, high-CF ANF FTCs may be less sharply frequency tuned in chinchilla than in monkeys.

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