Shapes and Level Tolerances of Frequency Tuning Curves in Primary Auditory Cortex: Quantitative Measures and Population Codes

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Sutter, Mitchell L. Shapes and level tolerances of frequency tuning curves in primary auditory cortex: quantitative measures and population codes. J Neurophysiol 84: 1012–1025, 2000. The shape and level tolerance of the excitatory frequency/intensity tuning curves (eFTCs) of 160 cat primary auditory cortical (A1) neurons were investigated. Overall, A1 cells were characterized by tremendous variety in eFTC shapes and symmetries; eFTCs were U-shaped (~20%), V-shaped (~15%), upper-tail-lower-sharp (~10%), lower-tail-upper-sharp (~10%), V-shaped (~10%), lower-tail-upper-sharp (~10%), upper-tail-lower-sharp (~10%), slant-lower (~10%), slant-upper (<3%), multipeaked (~10%), and circumscribed (~20%). Quantitative analysis suggests that eFTCs are best thought of as forming a continuum of shapes, rather than falling into discrete categories. A1 eFTCs tended to be more level tolerant than eFTCs from earlier stations in the ascending auditory system as inferred from other studies. While individual peaks of multipeaked eFTCs were similar to single peaked eFTCs, the overall eFTC of multipeaked neurons (spanning the range of all peaks) tended to have high-frequency tails. Measurements of shape and symmetry indicate that A1 eFTCs, on average, tended to have greater area on the low-frequency side of characteristic frequency (CF) than on the high-frequency side. A1 cells showed a relationship between CF and the inverse slope of low-frequency edges of eFTCs, but not for high-frequency edges. These data demonstrate that frequency tuning, particularly along the eFTC low-frequency border, sharpens along thelemniscal pathway to A1. The results are consistent with studies in mustached bats (Suga 1997) and support the idea that spectral decomposition along the ascending lemniscal pathway up to A1 is a general organizing principle of mammalian auditory systems. Altogether, these data suggest that A1 neurons’ eFTCs are shaped by complex patterns of inhibition and excitation accumulating along the auditory pathways, implying that central rather than peripheral filtering properties are responsible for certain psychophysical phenomena.

INTRODUCTION

To understand one of the most fundamental receptive field properties of auditory neurons, frequency tuning, it is essential to understand how frequency tuning varies with intensity. Many auditory perceptual phenomena, such as sound localization, complex spectral processing, and critical band processing vary little with changing intensity (Comalli and Altschuler 1976; Fletcher 1940; Seaton 1979). Suga and colleagues (Suga 1994, 1995, 1997; Suga and Tsuzuki 1985) elegantly reason that constancy in frequency selectivity across intensity (called “level tolerance”) is essential for information processing in echolocating mustached bats. Despite the importance of intensity invariant processing in auditory perception, very little is known about the neurophysiology underlying it. Therefore investigating the intensity dependence of auditory neurons’ frequency receptive field properties is critical if we are to understand auditory perception and behavior.

Although frequency tuning traditionally has been measured at a single intensity (e.g., Calford et al. 1983), this approach cannot reveal level tolerance (Suga 1997). To quantify level tolerance one must characterize excitatory frequency tuning curve (eFTC) “shape,” i.e., how frequency tuning varies with intensity. Characterizing eFTC shapes has provided insight into population codes of sound. For example, the prevalence of extended low-frequency tails, and sharp high-frequency cutoffs in auditory nerve (AN) fiber eFTCs (e.g., Kiang et al. 1967) indicate that more AN fibers will respond to a loud low-frequency sound than a loud high-frequency sound. This type of population code cannot simply be determined by sharpness measures, such as bandwidths or quality (Q) factors, but rather requires quantifying how low- and high-frequency edges of eFTCs vary with intensity.

An additional advantage of quantifying eFTC shapes is that it facilitates correlation between eFTCs and other physiological or anatomical properties. Neurons are frequently categorized based on their qualitative eFTC shapes to demonstrate different properties between groups of neurons. Usually, these analyses show multiple differences between cells having U-shaped, V-shaped, multi-peaked, circumscribed, and tailed eFTCs (e.g., Calford and Semple 1995; Casseday and Covey 1992; Sutter and Schreiner 1991). Unfortunately, these subjective descriptive measures can differ between investigators. In fact, the lack of a quantitative framework to classify cells results in categorization that is subjective and somewhat arbitrary. Furthermore, whether these classifications are truly based on discrete classes of neurons, or rather on arbitrary sub-divisions along a continuum, remains unanswered. Therefore to make meaningful comparisons across laboratories and different brain areas, standard reliable quantitative measures of shape are required.
While shape measures have been made on AN fiber eFTCs (Brugge et al. 1981; Javel 1994; Kiang and Moxon 1974), quantification of central neurons’ eFTC shapes are uncommon (e.g., Salvi et al. 1994; Sams-Dodd and Capranica 1994; Wang et al. 1996).

In this paper, the coarse shape of A1 neurons’ eFTCs are characterized by quantitatively analyzing the level dependence of their low- and high-frequency eFTC borders. With this analysis both eFTC shape and frequency tuning can be addressed in more detail than one obtains with bandwidth measures alone. The results indicate that most A1 eFTCs in cats are slightly shifted toward lower frequencies and are quite level tolerant.

**METHODS**

**Surgical preparation**

Surgical preparation, stimulus delivery, and recording procedures have been described previously (Sutter and Schreiner 1991; Sutter et al. 1999) and are summarized below. Single units were recorded from the right hemisphere of 23 cats and the left hemisphere of 3 cats. After venous cannulation, an initial dose of pentobarbital sodium (30 mg/kg) was administered. Animals were maintained at a surgical level of anesthesia with continuous infusion of pentobarbital sodium (2 mg·kg\(^{-1}\)·h\(^{-1}\)) in lactated Ringer solution (infusion volume: 3.5 ml/h) and, if necessary, with supplementary intravenous injections of pentobarbital. The cats were also given dexamethasone sodium phosphate (0.14 mg/kg im) to prevent brain edema and atropine sulfate (1 mg im) to reduce salivation. The animals’ rectal temperature was maintained at 37.5°C.

After 72–120 h of recording, animals were deeply anesthetized and perfused transcardially with saline followed by Formalin so brain tissue could be processed for histology. Cresyl-violet and fiber staining was used to reconstruct electrode positions from serial frontal 50-μm sections. Electrode positions were marked with electrolytic lesions (5–15 μA for 5–15 s) at the final few recording sites.

**Stimulus generation and delivery**

Experiments were conducted in double-walled sound-shielded rooms (IAC). Calibrated insert speakers (STAX 54) enclosed in small chambers that were connected to sound delivery tubes sealed into the acoustic meati of the contralateral ear (Sokolich 1981, U.S. Patent 4251686) were used. This sound delivery system was calibrated with a sound level meter (Bruel and Kjaer), and distortions were measured either with waveform analyzers (General Radio) or a computer acquisition system (TDT). The frequency response of the system was essentially flat up to 14 kHz and did not have major resonance deviating more than ±6 dB from the average level. Above 14 kHz, the output rolled off at a rate of 10 dB/octave. The presented intensity values were not corrected for the fluctuation in the transfer function; however, for cells that responded to tones above 14 kHz, we accounted for the roll-off and adjusted intensity values appropriately in the data analysis. Harmonic distortion was better than 35 dB below the primary.

**Recording procedure**

Parylene-coated tungsten microelectrodes (Microprobe, impedance 1–8.5 MΩ at 1 kHz) were inserted into A1 with a hydraulic microdrive. Penetrations were approximately orthogonal to the brain surface. Recordings were made at depths from 600 to 1,000 μm below the cortical surface, as determined by the microdrive. Dimpling of the cortical surface was usually <100 μm, and thus not a major factor in determining electrode depth. Histological verification from several animals indicated that the recording sites were from cortical layers 3 and 4. Electrical signals from the electrode were amplified, and action potentials from individual neurons were isolated with a window discriminator.

**Single-tone frequency response areas**

Frequency response areas (FRAs) were obtained for 160 single neurons. Six-hundred seventy-five tone bursts (50 ms long, 3-ms linear rise/fall time, and 400- to 1,200-ms interstimulus interval) were presented in a pseudo-random sequence of different frequency-intensity combinations selected from 15 intensities and 45 frequencies. Intensities were spaced 5 dB apart for a total range of 75 dB. The frequencies were logarithmically spaced with ranges between 2 and 5 octaves, depending on the estimated frequency tuning curve (FTC) width. Logarithmic spacing was chosen because of the nearly logarithmic spacing of frequency in the periphery, and because of the logarithmic nature of auditory filters (Moore 1995). Typically a 3-octave range, centered on the cells best (most sensitive) excitatory frequency (BEF) was used, providing 0.067-octave resolution.

The time constraints of single-unit recording necessitated characterizing FRAs on as few stimulus repetitions as possible. If a response was evoked for more than approximately 50% of the stimuli inside of each excitatory band, the FRA was deemed well-defined. In A1, this criterion corresponds roughly to the mean spikes-per-presentation minus 1 SD. If after one presentation per frequency-intensity combination the resulting FRA was not well-defined, the process was repeated with and the resulting responses were added. If necessary, the FRA recording procedure was repeated up to five times.

**Single-tone eFTC construction**

Excitatory FTCs (the borders of the excitatory spectral receptive fields), were constructed from the FRAs based on the estimated spontaneous rate plus 20% of the peak rate (examples of eFTCs derived from FRAs can be seen in Sutter et al. 1991, 1999). This criterion was applied after a weighted response averaging with the eight frequency-intensity neighbors was applied to each FRA coordinate. This smoothing increased the effective number of presentations!

![FIG. 1. Schematized representation of methods for analyzing inverse-slopes (ISs). A: measuring the IS by comparing edges of the frequency tuning curve at 5 and 25 dB below threshold (IS\(_{5-25}\)), and calculating the rolloff in octaves. Although not shown in this figure, the ISs between 5 and 25 dB above threshold (IS\(_{5-25}\)) were also measured. B: measuring the IS of the lower and upper edges using regression. This analysis was performed by drawing a regression line through the excitatory frequency/intensity tuning curve (eFTC) edges (points) starting at 15 dB above threshold and going to the highest intensity tested (IS\(_{15}\)). The same technique was also applied starting at 10 dB above threshold (IS\(_{10}\)). C: demonstration of how slope varies dramatically around vertical eFTC edges. The top edge with a solid line has a slope of +4,000 dB/octave, whereas the top edge with a dashed line has a slope of −4,000 dB/octave. This difference is very large compared with the small differences in these eFTCs. The ISs (0.01 octaves/40 dB and −0.01 octaves/60 dB) more appropriately reflect the small differences.](http://jn.physiology.org/content/1013/3/1013.full)
per frequency-intensity combination by a factor of 2.5 at the expense of frequency resolution. This method was robust, yielding comparable results across repeated measurements (see Table 3 of Sutter and Schreiner 1991). The first step of eFTC analysis was to identify each excitatory band. Then, the upper and lower frequency bounds of each excitatory band as well as of the bounds of the entire eFTC were calculated at all intensities.

**Measures of steepness of eFTC edges: inverse-slopes and edge regressions**

To quantify the level dependence of eFTCs, the inverse-slopes (IS) of their low- and high-frequency borders were calculated. Generally IS provides robust characterizations of eFTC borders by measuring the frequency difference in octaves at two different intensities along an eFTC edge. Figure 1A demonstrates this calculation for both the lower and upper edge at 15 and 50 dB above threshold. In this schematized example, the IS for the low-frequency border, IS\(_{15–50, \text{lower}}\), is ~0.25 octaves (per 35 dB). Negative numbers denote slopes toward lower frequencies at higher intensities. For the high-frequency border, IS\(_{15–50, \text{upper}}\) was 0.10 octaves (per 35 dB). IS\(_{5–25}\), IS\(_{5–45}\), IS\(_{5–65}\), and IS\(_{30–60}\) were also measured, comparing the frequency of the edges of eFTCs at 5 and 25 dB, 5 and 45 dB, 5 and 65 dB, and 30 and 60 dB above threshold, respectively.

In addition to measuring the ISs by sampling two-points along the eFTC edge, the ISs of eFTC edges were also measured by fitting a regression line through each border of the eFTC (Fig. 1B). The spacing for the data points for the regression was identical to that used for FRA collection: i.e., 5 dB. The regression was started at 15 dB above threshold to eliminate any effects near the tip of the eFTC. Regressions were also made starting at 10 dB above threshold.

The IS measure was used, rather than more traditional slope measurements, because of an instability of slope measurements around...
vertical eFTC edges. For example, a cell with an upper edge IS of 0.01 octaves/40 dB has a slope of 4,000 dB/octave (Fig. 1C, --), while a cell that slightly slants toward lower frequencies with a upper IS of −0.01 octaves/40 dB (Fig. 1C, ---) has a slope of −4,000 dB/ octave. So, although the eFTC edges differ by only 0.02 octaves per 40 dB, the slope measures differed by 8,000 dB/octave. Accordingly, at 40 dB above threshold, the high-frequency borders of the first and second cells’ eFTCs look very similar but have very different slope measurements because of the instability around infinite slope. Using inverse slopes circumvents this problem.

Determining strength of intensity tuning

The monotonicity ratio (the number of spikes elicited at the highest intensity tested divided by the number of spikes elicited at the maximum of the spike count versus intensity function) was used to quantify the strength of intensity tuning (Sutter and Schreiner 1995). For each intensity of the spike count versus intensity function, the number of spikes from a 1/4 octave bin around the unit’s BEF and a 15-dB wide intensity bin were summed. One-quarter octave usually comprised 4 different frequencies and 15 dB covered three intensities, providing a minimum of 12 different stimulus presentations per data point in the spike count versus intensity functions. Therefore a cell that fired maximally at the highest tested intensity had a monotonicity ratio of 1; a cell that was completely inhibited at the highest tested intensity had a monotonicity ratio of 0. Only units that were recorded from a minimum of 45 dB above threshold were analyzed for monotonicity ratio.

RESULTS

General shape of excitatory bands

In general, there was tremendous variety in the shapes and symmetries of eFTCs for the 160 neurons recorded from primary auditory cortex (A1). To characterize eFTC shape, the most commonly employed method of classification was used; eFTCs were classified based on visual inspection of their general appearance. Figure 2 schematically depicts the percentages of different eFTC types. The frequency tuning of U-shaped eFTCs does not depend on intensity and therefore is sometimes called level-tolerant. The frequency tuning of U-shaped eFTCs becomes broader on the low- and high-frequency sides of their eFTCs with increasing intensity. Lower-tail-upper-sharp (LTUS) eFTCs have large “tails” on their low-frequency edges, but have sharp, relatively vertical high-frequency edges. Slant-lower eFTCs have high-frequency edges slanting to lower frequencies. Multipeaked eFTCs have more than one distinct excitatory region separated by a non- excitatory region. Sharp multipeaked eFTCs have two or more level tolerant excitatory areas. Mixed multipeaked or “high heel” eFTCs resemble a high heel shoe and tend to have very broad lower excitatory bands and sharp upper excitatory bands. Circumscribed eFTCs are completely enclosed.

Although many of these eFTC classes have been reported in the auditory cortex of several species, the proportions of these classes have not been extensively examined. Of the recorded neurons that were classifiable, 22.4% (33/147) had U-shaped eFTCs. This characterization of U- or V-shaped depends more on the shape of the eFTC at higher intensities than near the low-intensity threshold (eFTC “tip”) and therefore what this paper refers to as “U-shaped” can include cells that others call “pencil shaped” (e.g., Suga 1995). The criteria employed herein would also classify cells with rounded eFTC tips, but rapidly increasing bandwidth at higher intensities, as V-shaped. U-shaped curves (e.g., Fig. 3, A and B) had a range of bandwidths and were sometimes intensity-tuned (also called non-monotonic). A large percentage of cells were classified as having V-shaped eFTCs (19.0%, 28/147). V-shaped eFTCs (Fig. 3, C and D) could be narrow at the tip and expand only at higher intensities or could be relatively broad at most intensities. V-shaped eFTCs could be intensity-tuned and could have complex response profiles within their eFTC. The cell whose FRA is shown in (Fig. 3D), for example, preferred intensities between 15 and 30 dB, had a strongly responsive area from 17–21 kHz, and had weaker responding upper and lower tails making a V-shaped curve. Circumscribed eFTCs (Fig. 3E) were also common (20.4%, 30/147) and by definition were intensity tuned. Circumscribed eFTCs tended to be sharp, although there was some variability in frequency tuning. Only 13.6% (20/147) of the cells had LTUS eFTCs (Fig. 3F), which is the most common class of eFTCs in AN fibers (Kiang and Moxon 1974). However, the present classification is not identical to that used in the AN because there was large variation in the slope of tails, which probably included shallower tails than are observed in the AN. Surprisingly, 10.2% (15/147) of the cells possessed eFTCs that slanted toward lower frequencies (Fig. 3, G and H). Most of these cells were intensity-tuned, and some resembled circumscribed cells with low-frequency remnants (Fig. 3G). The degree of slant was variable. Cells with eFTCs slanting toward higher frequencies were unusual (2.7%, 4/147). Cells with multiple excitatory frequency bands were also found where the bands were narrow (7.5%, Fig. 3I) or broad (2.7%, Fig. 3J).

The results suggest that the eFTC types form a continuum

FIG. 4. Distribution of inverse-slopes of eFTC edges for different intensity ranges. IS<sub>5-25</sub> measures the change in bandwidth between 5 and 25 dB above threshold for each edge; IS<sub>5-45</sub> measures the change in bandwidth between 5 and 45 dB above threshold for each edge, etc. Note that each panel had different IS units so that numbers correspond to the total number of octaves spanned over the intensity range used. For example for IS<sub>5-25</sub> the units are in octaves/20 dB because there is a 20-dB range between 5 and 25 dB. In Table 1, all measures are converted into units of octaves/40 dB.
being robust for eFTCs with near vertical edges (see METHODS), slope. IS has the advantage over traditional slope measures of as a function of intensity and is the reciprocal of eFTC edge steeply the frequency of an eFTC edge changes or “rolls off” every eFTC were calculated. Generally, IS measures how borders of eFTCs

Analysis of shape: slopes of upper and lower frequency borders of eFTCs

It is advantageous to visually inspect and subjectively score eFTCs because one can assess the entire eFTC, analyze data rapidly, and present qualitatively intuitive data analysis. However, hand-scoring forces one to subjectively determine class boundaries. Therefore to obtain a quantitative measure of eFTC shape, the ISs of the low- and high-frequency borders of every eFTC were calculated. Generally, IS measures how steeply the frequency of an eFTC edge changes or “rolls off” as a function of intensity and is the reciprocal of eFTC edge slope. IS has the advantage over traditional slope measures of being robust for eFTCs with near vertical edges (see METHODS, Measures of steepness of eFTC edges: inverse slopes and edge regressions).

In general, A1 eFTCs were relatively sharp and level tolerant. Distributions for upper and lower ISs are shown in Fig. 4, which compares the magnitude of change of the edges at three successively higher intensities. Many eFTC edges had ISs near zero, confirming that near vertical eFTC edges were common. Notice how the distributions get flatter with larger mean magnitudes as one progresses from ISs to ISs, indicating that the eFTC edges on average are broadening with increasing intensity. The IS measurements are converted to units of octaves/40 dB in Table 1 to compare ISs for different intensity excursions and to allow comparisons to the common bandwidth measure 40 dB above threshold. The mean and median ISs for lower borders were approximately and for upper borders were approximately 0.19 and 0.10 octaves/40 dB, respectively. The more negative inverse-slope of the mean was because the distributions were skewed by large negative ISs. The mean and median ISs for upper borders were approximately 0.19 and 0.10 octaves/40 dB, respectively. It is noteworthy that the median values of the lower ISs were more constant across intensity, whereas upper inverse-slopes were larger for measures near the tip of eFTCs and smaller for measures at higher intensities (Table 1). This indicates that low-frequency borders had a relatively constant slope across intensity, but high-frequency eFTC borders had broader tips near threshold and sharper tips at higher intensities.

TABLE 1. Inverse-slopes normalized to units of octaves/40 dB

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<tr>
<th></th>
<th>Lower Border</th>
<th>Upper Border</th>
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<tr>
<td></td>
<td>25th %</td>
<td>Median</td>
</tr>
<tr>
<td>ISs, 25</td>
<td>-0.40</td>
<td>-0.22</td>
</tr>
<tr>
<td>ISs, 45</td>
<td>-0.36</td>
<td>-0.20</td>
</tr>
<tr>
<td>ISs, 65</td>
<td>-0.44</td>
<td>-0.21</td>
</tr>
<tr>
<td>ISs, 50</td>
<td>-0.39</td>
<td>-0.22</td>
</tr>
<tr>
<td>ISs, 60</td>
<td>-0.55</td>
<td>-0.28</td>
</tr>
<tr>
<td>ISs, 75</td>
<td>-0.43</td>
<td>-0.22</td>
</tr>
</tbody>
</table>

Values in Mean are means ± SD. IS, inverse-slope.

rather than falling into discrete classes. For example, if some broad multipeaked units did not have separation between their excitatory bands, they would look like upper-tail-low-sharp (UTLS) units. Furthermore, some U-shaped eFTCs were close to being V-shaped (Fig. 3K), circumscribed (Fig. 3B), or slanted, while some V-shaped eFTCs were close to upper or lower tail (Fig. 3L).

Inverse-slopes, as measured by regression fits (Table 1), were similar to other IS measures, although the regression fit, on average, yielded larger tails. The regression measure, however, was not as closely linked to hand scoring as other IS measures (see Analysis of shape: comparisons of hand-scoring to objective measures).

Analysis of shape: comparing upper and lower edges within cells

It is common to read in the literature that cells in a certain part of the auditory system have mainly U- or V-shaped eFTCs, or that eFTCs are “level-tolerant,” or “have a low-frequency tail and a sharp high-frequency rolloff.” Such classifications hinge on comparing both eFTC edges. Distributions on a two-dimensional IS space are needed to determine whether these properties fall into obvious categories, and if they do not, the degree to which eFTCs are shaped differently. From Fig. 5 it can be seen that for most cells both eFTC edges are sharply tuned. The individual lower and upper IS histograms show skewed tails toward more broadly tuned edges and do not indicate a clear dividing line between eFTC categories. The two-dimensional IS space shares the properties of the single histograms, except the points appear to fall along a diagonally oriented distribution. This was confirmed by finding a relationship between lower and upper edge IS (slope of lower tail) and a sharp high-frequency rolloff. Such classifications hinge on comparing both eFTC edges. Distributions on a two-dimensional IS space are needed to determine whether these properties fall into obvious categories, and if they do not, the degree to which eFTCs are shaped differently. From Fig. 5 it can be seen that for most cells both eFTC edges are sharply tuned. The individual lower and upper IS histograms show skewed tails toward more broadly tuned edges and do not indicate a clear dividing line between eFTC categories. The two-dimensional IS space shares the properties of the single histograms, except the points appear to fall along a diagonally oriented distribution. This was confirmed by finding a relationship between lower and upper edge IS (slope = −0.25, Pslope < 0.01). These data indicate that if one wishes to formally categorize eFTC types, one must proceed with further analysis. So the next logical question is: How does hand-scoring subdivide this space?

Analysis of shape: comparisons of hand-scoring to objective measures

Quantitatively derived distributions of cell types were similar to those obtained by hand-scoring. The quantitative measures (of ISs, ISs, etc.) most closely approximating subjective classification were determined to facilitate comparisons of hand-scoring to the two-dimensional IS space. To categorize edges objectively, an “optimal” cutoff criterion in the two-dimensional IS space was determined for each measure by minimizing the error between subjective and quantitative categorization (see APPENDIX 1).

Edges with IS absolute values greater than the criterion were classified as broad tails, whereas edges with IS absolute values less than the criterion were classified as sharp. ISs (with a cutoff of 0.23 octaves/40 dB, Table 2) most closely approximated the percentages of different eFTC types as calculated by...
hand scoring. Other measures, including those derived by fitting regression lines (10 slope, 15 slope) to eFTC edges, were not as closely linked to hand scoring (Table 3).

Analysis was also done on a cell-by-cell basis to determine whether the objective criteria was related to hand scoring. Once again, IS15–50 most closely resembled hand-scoring.

Eighty percent of eFTCs were classified the same by hand-scoring and IS15–50 with a cutoff criterion of 0.30 octaves/40 dB (Fig. 6; Table 3). The average cutoff from the population and cell-by-cell optimization was used to divide the two-dimensional IS space into categories in Fig. 7 (zzz). Cells with different hand-scored classification are represented by different symbols. The diagonal line beginning at the origin and continuing in the lower right quadrant with a slope of 2 marks perfect symmetry that would be characteristic of U- and V-shaped eFTCs. Any point falling along this line would represent a perfectly symmetric eFTC. Points further from that line represent neurons with less symmetric eFTCs. Points above and to the right of the diagonal line roughly represent eFTCs possessing a larger response area on the high-frequency side of the BEF. Points below and to the left of the line (the majority of points) represent neurons with eFTCs possessing a larger response area on the low-frequency side of the BEF. As would be predicted from Fig. 5, it is particularly difficult to distinguish where categorical boundaries should be drawn without the help of the hand-categorization and fiduciary lines. Because the drawing of shape boundaries appears relatively arbitrary, it might be better to think of eFTCs shapes as forming a continuum, rather than falling into discrete categories. Nevertheless, this figure displays the rough correspondence between hand-scoring and classification using IS15–50. By demonstrating that categorization using IS15–50 closely parallel the results obtained by hand-scoring, it is not meant to imply that this is the best shape measure or that categories exist, but rather to

TABLE 2. Comparison of subjective and objective classification of eFTCs

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<tr>
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<th>IS15–50</th>
<th>Handscored</th>
<th>Objective</th>
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<tbody>
<tr>
<td>Circumscribed</td>
<td>*</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>Multipeaked</td>
<td>*</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>“U”</td>
<td>24.4%</td>
<td>26.0%</td>
<td></td>
</tr>
<tr>
<td>“V”</td>
<td>17.9%</td>
<td>17.9%</td>
<td></td>
</tr>
<tr>
<td>Slant lower</td>
<td>9.0%</td>
<td>4.9%</td>
<td></td>
</tr>
<tr>
<td>Slant upper</td>
<td>2.4%</td>
<td>0.8%</td>
<td></td>
</tr>
<tr>
<td>Low-tail, up-sharp</td>
<td>14.6%</td>
<td>19.5%</td>
<td></td>
</tr>
<tr>
<td>Low-sharp, up-tail</td>
<td>1.6%</td>
<td>0.8%</td>
<td></td>
</tr>
<tr>
<td>Minimum RMS error</td>
<td></td>
<td>1.1%</td>
<td></td>
</tr>
<tr>
<td>Best cutoff, octaves/40 dB</td>
<td></td>
<td>0.23</td>
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<tr>
<td>$N_{sub}$†</td>
<td>86</td>
<td>86</td>
<td></td>
</tr>
<tr>
<td>$N_{all}$‡</td>
<td>123</td>
<td>123</td>
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RMS, root mean square. * Circumscribed and multipeaked excitatory frequency/intensity tuning curves (eFTCs) were not scored for slopes because they could not be categorized solely using the 2-dimensional IS space. † All hand-scored cells for which the given IS measure could be made and which were not multipeaked or circumscribed by hand-scoring. ‡ Adjusted $N$ to assume that 30% of the cells are multipeaked or circumscribed. The formula is $N_{all} = 0.3 \times N_{all}/0.7$. 
demonstrate a relationship between subjective and objective classification using inverse slopes.

Multi-peaked eFTCs

In the above analysis, inverse-slopes of entire eFTCs were calculated. Thus for multipeaked eFTCs, IS measurements were only applied to the largest possible eFTC interpretation covering all peaks. Under these conditions, multipeaked FTCs (in Fig. 7) tended to have upper tails. Cells with multipeaked eFTCs had a median IS of 0.25 octaves/40 dB compared with 0.06 octaves/40 dB for other cells. These differences were confirmed statistically (Table 4).

Each peak within multipeaked eFTCs was also analyzed separately, and the ISs of individual peaks were compared with single-peaked eFTCs. The lower and upper edges of individual peaks of multipeaked eFTCs did not vary significantly from those of single-peaked eFTCs (Table 4).

Relationship of intensity tuning to eFTC shape

Intensity-tuning and eFTC shape were related (Fig. 8). After circumscribed cells, slant lower cells were the next most intensity-tuned class. For many of these cells, the slanting of the upper edge caused cells to respond weakly to loud tones at BEF (e.g., Fig. 3, G and H), thereby creating intensity tuning for BEF tones. Multipeaked eFTCs were the next most intensity tuned, possibly due to inhibition in the center of their eFTCs (Sutter et al. 1999). U-shaped eFTCs were less intensity tuned, followed by tailed and V-shaped eFTCs. If one thinks of U-shaped eFTCs as requiring the most inhibition abutting the excitatory eFTC, and V-shaped the least, the results are consistent with a relationship between intensity tuning and on-BF or surround inhibition.

Symmetry and shape measures

So far, shape classification has been based on a two-dimensional distribution of eFTC low- and high-frequency ISs. However for comparative purposes, collapsing the two-dimensional IS space into one measure would be advantageous. Accordingly, symmetry and shape measures were derived. U- and V-shaped eFTCs are symmetric because they have near equal bandwidth above and below BEF, whereas slanted, LTUS and UTLS eFTCs are nonsymmetric (Fig. 9). Symmetry was defined as the excess bandwidth, (in octaves) to one side of the eFTC.

<table>
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<th>Table 3. Results of optimization</th>
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<td>RMS</td>
</tr>
<tr>
<td>Criteria, octaves/40 dB</td>
</tr>
<tr>
<td>N&lt;sup&gt;*&lt;/sup&gt;</td>
</tr>
<tr>
<td>% matched†</td>
</tr>
<tr>
<td>Criteria, octaves/40 dB</td>
</tr>
<tr>
<td>N&lt;sup&gt;‡&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

RMS, root mean square. * Adjusted to assume 30% of the cells are either circumscribed or multi-peaked by the formula N<sup>+</sup> = 0.3 N<sup>‡</sup>/0.7. † Percentage of cells for which hand-scoring and quantitative methods classified the eFTC the same. ‡ Excluding all circumscribed and multipeaked cells.

FIG. 6. Optimization of calibrating several objective measurements to hand-scoring. Different cutoff criteria for inverse-slopes (x-axis) were applied and then eFTCs classified based on this cutoff. The plots show 0.1 octaves/40 dB resolution to emphasize the different symbols for the 3 curves, although the analysis used 0.0025 octaves/40 dB increments. Left: root mean square (RMS) error was obtained by subtracting the percentages of shapes determined objectively from the hand-scored derived percentages and squaring the difference. All the differences were then added, and the mean of the square root of this sum was calculated (Table 3). Not all curves used the same number of cells. For IS<sub>15–50</sub> and IS<sub>5–45</sub>, all cells for which data were collected to at least 50 dB above threshold were used (n = 86, excluding multipeaked and circumscribed eFTCs). For IS<sub>5–45</sub> and IS<sub>15–50</sub>, n = 123 after adjustment to make 30% of cells intensity tuned or multipeaked. The optimization was then made comparing the objective scoring to the hand scoring with the same 86 cells. For IS<sub>5–45</sub>, all cells with at least 45 dB of recorded range above threshold were used (n = 95, excluding multipeaked and circumscribed eFTCs). The optimization for IS<sub>5–45</sub> was then made comparing the objective scoring to the hand scoring with the same 91 cells. Right: optimization of the percentage of cells where objective classification yields the same result as hand-scoring. IS<sub>5–45</sub> showed the closest correspondence to hand scoring where 80% of the cells were classified correctly for a cutoff criterion of 0.3 octaves/40 dB. The cutoff for this within-cell optimization tended to be larger than the optimal cutoff for capturing the population statistics.
Symmetry values near 0 indicate U- or V-shaped eFTCs, whereas large negative or positive values indicate excess bandwidth on the low- or high-frequency side of BEF, respectively. The average and median A1 neuron had 0.11 ± 0.38 (mean ± SD) and 0.09 octaves more bandwidth on the low-frequency side of BEF than on the high-frequency side as measured by Symmetry15–50 (Fig. 10).

**TABLE 4.** Inverse-slopes in octaves/40 dB of multipeaked and circumscribed eFTCs

<table>
<thead>
<tr>
<th></th>
<th>Multipeaked</th>
<th>Non-Multipeaked</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Median lower IS15–50 (outer slopes*)</td>
<td>-0.14</td>
<td>-0.22</td>
<td></td>
</tr>
<tr>
<td>Median upper IS15–50 (outer slopes*)</td>
<td>0.25</td>
<td>0.06</td>
<td>&lt;0.01†</td>
</tr>
<tr>
<td>Median lower IS15–50 (individual peaks†)</td>
<td>-0.13</td>
<td>-0.18</td>
<td></td>
</tr>
<tr>
<td>Median upper IS15–50 (individual peaks‡)</td>
<td>0.01</td>
<td>0.06</td>
<td></td>
</tr>
</tbody>
</table>

For abbreviations, see Tables 1 and 2. * For outer slopes we measured the slopes of the outline of the entire eFTC, ignoring what was in the middle. † Mann-Whitney \( U \). ‡ For individual peaks we calculate the ISs of the individual peaks of multipeaked eFTCs.

**FIG. 7.** Scatter plot comparing objective and subjective eFTC classification. Each point’s symbol-color combination corresponds to its hand-scored classification (see bottom right-hand legend). For example, purple crosses correspond to neurons whose eFTCs were hand-scored as Lower-tail-upper-sharp (LTUS). Schematized eFTCs for each hand-scored class are shown as insets whose color matches the corresponding symbols. The diagonal line represents eFTCs with equivalent magnitude inverse-slopes for the low- and high-frequency edges of their eFTCs, i.e., neurons with mirror symmetric eFTCs around the frequency axis. Dotted lines demarcate boundaries of different eFTC categories using the optimal criterion for comparing IS15–50 to subjective scoring. The optimal criterion was determined by averaging the optimum RMS and % matched criteria (Table 3).

**FIG. 8.** Intensity tuning for different classes of cells. The mean monotonicity ratio is plotted for each cell type. Note that the mean monotonicity ratio for circumscribed cells is >0. Three reasons contribute to this. First, the criterion for defining eFTC edges is spontaneous rate plus 20% of the peak, and therefore areas outside of the eFTC still might have responses below this level. Second, for calculating the response at the highest intensity smoothing across \( \frac{1}{4} \) octave and 10 dB was used, and therefore in some eFTCs this might have overlapped the responsive area. Third, firing rate was not adjusted for spontaneous in calculating monotonicity ratio.
Symmetry\(_{15–50}\) has the advantage of quantifying the degree of eFTC asymmetry in octaves, but the disadvantage of being bandwidth-dependent and, therefore not measuring normalized shape. For example, negative Symmetry\(_{15–50}\) values can result from either LTUS or Slant-lower eFTCs. To derive a metric that could distinguish these two possibilities (and the corresponding possibilities for UTLS and Slant-upper) a measure of shape was derived, which is the symmetry measure normalized for bandwidth

\[
\text{Shape}_{15–50} = \frac{(a + b)}{(a - b)}
\]

Where \(a\) is the excess bandwidth on the high-frequency side of the center frequency and \(b\) is the excess bandwidth on the low-frequency side of the center frequency (Fig. 11, A–C) (see APPENDIX 2).

Like Symmetry\(_{15–50}\), if the extent of the eFTC is predominantly below or above the center frequency, Shape\(_{15–50}\) is negative or positive respectively. Unlike Symmetry\(_{15–50}\) Shape\(_{15–50}\) can also distinguish slanted from tailed eFTCs. If Shape\(_{15–50}\) of an eFTC is more than 1 or less than \(-1\), the eFTC can be classified as “slant-upper” slant lower, respectively (Fig. 9, F and G). Shape\(_{15–50}\) values close to 0 indicate a symmetric eFTC (Fig. 9, D and E). LTUS eFTCs have shape values more than or equal to \(-1\) and less than 0. UTLS eFTCs have values less than or equal to +1 and more than 0 (Fig. 9C). For the eFTCs of A1 neurons, Shape\(_{15–50}\) indicates on average, asymmetric tuning, slightly shifted toward low frequencies (mean Shape\(_{15–50}\) = \(-0.26 \pm 0.63\); median, \(-0.17\), Fig. 10).

Level tolerance of the bandwidth of A1 cells

Suga et al. (1997) defined neurons as level-tolerant when their eFTC bandwidth (in kHz) at 70 dB above threshold was less than four times the bandwidth 10 dB above threshold. Because eFTCs were not generally characterized over a 70-dB range, a modified metric was created: Bandwidth level intolerance (BLI) = (BW\(_{50}\)/BW\(_{10}\)), where BW\(_{50}\) is the bandwidth of the cell, in kHz, 50 dB above threshold. Adjusting the criterion for the smaller intensity range used in this study, a cell was defined as level-tolerant if its eFTC bandwidth (in kHz) at 50 dB above threshold is <3 times the bandwidth at 10 dB supra-threshold. The median BLI value is 2.23 with 25\(^{th}\) and 75\(^{th}\) percentile values of 1.13 and 3.82 (Fig. 10), and 60.6% of A1 cells were characterized as level-tolerant.

BLI is not normally distributed because of a large percentage of highly level-tolerant cells with low BLI values (including circumscribed eFTCs for which BLI = 0), and a long tail caused by cells with high BLI values because of narrow tuning at 10 dB above threshold (Fig. 10). This highly skewed distribution is unsuitable for many statistical analyses, including regression. Therefore another level tolerance measure was defined: Bandwidth level dependency (BWLD) = BW\(_{50}\) – BW\(_{10}\), where the bandwidths are measured in octaves. By using subtraction rather than division, the problem of the unstable nature of dividing by small numbers that creates the tail in the BLI distribution is ameliorated (see APPENDIX 3). Also, by using octaves, small differences in the bandwidth 50 dB above threshold are more uniformly distributed, reducing the compression near zero in the BLI distribution. Because the resulting BWLD distribution is less skewed and more normal, BWLD is easier to work with quantitatively.

Frequency dependency of eFTC shape

The IS of the low-, but not high-, frequency edge of eFTCs seemed to depend on characteristic frequency (CF). IS\(_{15–50,\text{Low}1}\) had a regression slope of 0.085 octaves/40 dB of IS per octave of CF (\(P < 0.05\)), indicating that the eFTC edges are sharper in higher CF cells (Fig. 12A). The ISs of the high-frequency eFTCs edge did not show a significant dependence of CF. One should be cautious about the generality of these results because of a bias against recording cells with lower CFs. It is therefore worth noting that in the inferior colliculus of chinchillas, eFTC shapes are dramatically different for neurons with very low CFs than for cells from the middle of the animal’s frequency hearing range (Nuding et al. 1999).

Level tolerance had a weak nonsignificant dependence on CF (Fig. 12). Low CF cells tended to be less level tolerant than high CF neurons. Although not significantly different from zero (\(P = 0.052\)), the slope was \(-0.111\) octaves of BWLD per 40 dB.
A variety of eFTC shapes were found in A1, with most neurons having larger response areas on the low-frequency side of CF than on the high-frequency side. Robust quantitative eFTC shape and level tolerance measures were introduced because more established metrics were not always suitable for A1 cells. Quantitative eFTC measures yielded results comparable to subjective hand-scoring; however, they suggest that eFTC shape forms a continuum. There was a strong relationship between eFTC shape and intensity tuning, but a weaker one between CF and eFTC shape.

Choosing the correct metrics to quantify and compare tuning curves

Historically, choice of metric has a major impact on the interpretation of neurophysiological data. For example, whether one sees sharpening of frequency tuning as the lenticular auditory system is ascended depends critically on one’s definition of tuning (Suga 1995). Therefore it is important to discuss the appropriateness of the metrics used in this study. A major advantage of these metrics is that they provide convenient indexes of shape properties such as slanted and tailed eFTCs, which traditional bandwidth values cannot disambiguate. Whereas Q values quantify neuronal bandwidth, IS provides additional information about how bandwidth is distributed, and shape and symmetry measures transform this information into one number.

The metrics herein also circumvent problems that ratio metrics often encounter when the denominator can have small values. For example, the more traditional measure of slope in dB/octave (Borg et al. 1988; Goldberg and Brownell 1973) presents problems for many cortical neurons because of its nonlinear behavior for very sharp edges (see METHODS). Also, Q (CF/Bandwidth), the most used bandwidth measure in the auditory system, is inappropriate for intensity-tuned neurons that have zero bandwidth at high intensities, and thus infinite Q values. For both Q and slope, performing statistical analyses such as regression against CF is impossible because of A1 neurons with infinite values. The BLI (BW50/BW10) measure suffers from a similar problem. Cells with very narrow eFTC tips have excessively large BLI values because one must divide by the bandwidth 10 dB above threshold. This creates very skewed distributions necessitating clipping the very high BLI values. BLI therefore is far from ideal for statistical analysis, whereas BWLD (BW10–BW50 in octaves) seems better. Accordingly, the newer metrics have the flexibility to be applied to make meaningful comparisons across the wide range of eFTC shapes encountered across brain areas and species.

However, one must not forget that these metrics have limitations. First, the shape measure is a ratio, which like Q, needs modification for circumscribed eFTCs. Also, choosing just two intensities can affect classification. For example the eFTC in Fig. 3C was classified as V-shaped by hand-scoring and LTUS by classification using IS15–50. This difference most likely results from the broadening of the eFTC more than 50 dB above threshold. Another disadvantage is that like any threshold metric, those used herein only quantify the limits of the frequencies to which a cell is sensitive; however, important frequency information is also carried by gradations of responses within a neuron’s eFTC. Finally, it should be noted that the metrics derived in this paper are still simple and can only capture gross aspects of eFTC shape and not fine detail that the eye can often see. In conclusion, the measures used in this paper represent a step toward better understanding eFTC shape by providing an incremental improvement over previous approaches.
Comparisons of eFTC level tolerance and shape in A1 of bats and cats

Responses of A1 neurons have arguably been most extensively studied in cats and the Doppler-shifted constant frequency (DSCF) area of mustached bat A1. Distributions of quantitative level tolerance measures have not been reported for A1 neurons; however, Q10 and Q50 values for mustached bat DSCF neurons have been (Suga and Manabe 1982), and potentially provide an estimate of level tolerance. The results of dividing the mean Q50 value by the mean Q10 value suggests that bat DSCF neurons (Q50/Q10 = 1.28), on average, are more level tolerant than cat A1 neurons (Q50/Q10 = 2.70). The greater level tolerance in mustached bats indicates that DSCF neurons in mustached bats are not simply scaled down, more sharply tuned versions of A1 cells in other animals, but rather, are disproportionately sharper at higher intensities than low.

Unfortunately, quantitative data on the level tolerance of A1 neurons with CFs outside of the 60-kHz DSCF area are not available. However, A1 cells outside of the DSCF area in mustached bat are more broadly tuned than DSCF neurons (e.g., Suga and Tsuzuki 1985). Therefore neurons tuned to frequencies other than 60 kHz in bats might have comparable level tolerances to cat A1 cells. Similarly eFTCs in little and big brown bat A1 tend to be more broadly tuned than for DSCF mustached bat neurons (Dear et al. 1993; Shen et al. 1997). This leaves open the intriguing possibility that, outside of the DSCF area, level tolerance might be similar across A1 of many species.

The proportions of slanted eFTCs in cat and bat A1 further support the notion that there are some common organizational principles responsible for creating central eFTCs across species. The percentages of slant-lower eFTCs are similar in bats (Kanwal et al. 1999) to those report here in cats. Slant-upper eFTCs are also uncommon in both species, implying that the slant-lower eFTC shape is either functionally or mechanistically advantageous to have in the auditory system, and that there might be common organizational principles responsible for creation this eFTC type.

Quantitative measures and comparisons of inverse slopes within the ascending auditory system

The results of this study indicate that A1 neurons are sharper and more level tolerant than cells at earlier stations in the auditory system, and that much of this is probably due to sharpening of the low-frequency border of eFTCs by inhibition. There are a few quantitative studies of slopes of eFTCs.
The slopes of the edges of AN (Borg et al. 1988) and cochlear nucleus (CN) (Goldberg and Brownell 1973) eFTCs strongly vary as a function of CF. The anterior ventral cochlear nucleus (AVCN) slope distribution (Goldberg and Brownell 1973) appears bimodal, possibly reflecting the convergence of only a few auditory nerve fibers onto AVCN neurons. The slopes of the edges of AN and CN neurons appear to be broader and more dependent on CF than A1 neurons, although a sharpening of the low-frequency edge as a function of CF was found in A1. Part of this discrepancy might be due to the present study’s use of a more limited CF range than both the Goldberg and Brownell and the Borg et al. studies. For cells above 2 kHz in these earlier studies, there is no apparent relationship between CF and upper edge eFTC slopes, and the relationship between CF and lower edge slopes is weaker than across all CFs (e.g., Fig. 1, Goldberg and Brownell 1973).

The results of the present study were compared with those from the AN (Javel 1994; Kiang and Moxon 1974; Kiang et al. 1967) and CN (Goldberg and Brownell 1973) of anesthetized cats, using only cells in the 5- to 15-kHz range to mitigate CF dependencies. This was achieved by measuring slopes directly from the published eFTCs. Lower edges sharpen substantially from a median IS15–50_lower of approximately $-2.10$ to $-1.70$ to $-0.20$ octaves/40 dB in the AN, CN, and A1, respectively. Sharpening of eFTC upper edges was less obvious, going from 0.25 to 0.22 to 0.09 from AN to CN to A1. This suggests a sharpening of both sides of eFTCs in the ascending auditory system with more pronounced sharpening of the low-frequency edge.

Hierarchical degradation of eFTC classes

Cortical eFTCs are shaped from convergence and integration of excitatory and inhibitory inputs. Many brain structures contribute to this shaping in what appears to be a gradual change with ascension in the auditory system. This is well exemplified with intensity-tuned and circumscribed eFTCs. Within several auditory stations some neurons have intensity tuning that is sharpened by GABAergic or glycnergic inhibition (e.g., Evans and Zhao 1993; Grothe 1994; Pollak and Park 1993; Suga et al. 1997; Yang et al. 1992). Additionally, higher threshold excitatory inputs might be added to eFTCs to overcome the effects of earlier intensity tuning (Pollak and Park 1993). Thus each neuron’s intensity tuning results from a differing number of inhibitory sharpening and excitatory integrating stages.

These arguments can be reasonably extended to sharpening of frequency tuning. One can hypothesize that eFTC shapes are also progressively formed along the ascending auditory system. This gradual re-shaping of eFTC properties would be consistent with creating the appearance of shape continua. For example, “discrete” classes, such as multi-peaked eFTCs, could fall along continua related to spectral integration. There are at least two ways in which a continuous change in one variable can produce a gradual change from single- to multi-peaked properties. One way is to vary the frequency spacing of convergent excitatory input. When the integrated excitatory bands are closely spaced in frequency, single-peaked eFTCs are created; however, when the frequency spacing between overlaid excitation increases, multipeaked frequency tuning begins to emerge. Alternatively, multiple eFTCs could be produced if inhibition were placed within an eFTC. Classification of multipeaked eFTCs would result when the strength of inhibition is sufficient to bring the middle of the eFTC below the isoresponse criteria used to judge eFTC edges. This would occur even if the strength of the central inhibition were continuously graded.

Inhibition continuously graded in strength and bandwidth also could create continua in which many eFTC “classes” fall. If inhibition with a CF within the eFTC were broad toward high frequencies, the entire high-frequency side of the tuning curve would be chopped off creating a slant-lower unit. On the other hand, if the inhibition were weak, it will likely produce an intensity tuned unit that is U- or V-shaped (e.g., Fig. 4C). Thus by continuously varying the properties of inhibition and spectral integration, multiple continuous dimensions can emerge that encompass many eFTC classes.

Under the above scenario, as excitatory and inhibitory spectral properties are hierarchically integrated in the ascending auditory system, divisions between classes continue to blur. Auditory nerve fiber eFTCs have a characteristic LTUS shape with a moderately sharp tip (~$\frac{1}{2}$ octaves) that melds into a broad low-frequency tail 40–60 dB above threshold (e.g., Javel 1994; Kiang and Moxon 1974). Arguments have been made that CN eFTCs fall into several categories that are related to cell morphology, and specific patterns of ascending, descending, and internal connections (e.g., Evans and Nelson 1973; Joris 1998; Young and Brownell 1976; Zhang and Ortel 1994). Type I–III CN eFTCs are similar to AN eFTCs but are sharpened by inhibitory domains within and abutting the eFTC (Evans and Nelson 1973; Goldberg and Brownell 1973; Spirou et al. 1999). Type IV and V eFTCs have more complex inhibition, with a large variation in the location of within-eFTC inhibition (Spirou and Young 1991; Young and Brownell 1976). However, in the dorsal cochlear nucleus (DCN), the complexity and variance in integration, and the variety of inputs begin to blur the physiological distinction between classes (e.g., Joris 1998; Spirou et al. 1999). In the IC, further transformations occur, and although categorization has been made based on physiological responses and hypothesized segregated inputs from the brain stem (Ramachandran et al. 1999), it is difficult to discern whether these categories correspond to clusters in a physiological parameter space. Qualitative inspection IC central nucleus (ICc) neurons [based on eFTCs from Ehret and Merzenich (1988) and Yang et al. (1992)] suggests that their eFTCs have properties somewhere between CN and A1 neurons. In particular, ICc neurons, on average, look more symmetric, sharper, and more level tolerant than AN neurons, but less symmetric, broader, and less level tolerant than A1 neurons (Ehret and Schreiner 1997). The little evidence that is available from the medial geniculate body (MGB) indicates that its neurons might fall in the middle of this trend (based on eFTCs from Imig et al. 1997). Therefore unlike in the visual system, where dramatic qualitative receptive field changes can occur between hierarchical stations, in the auditory system the changes appear to be more gradual, resulting in populations at successive stations that overlap substantially in their eFTC properties.
Relationship of average eFTC shape to population codes

Our results indicate that labeled-line population codes of frequency become more refined as one ascends the auditory system. At low intensities, every AN fiber responds to a narrow range of frequencies, and therefore can be assigned as representing a particular frequency (Javel 1994). However, for high-intensity tones one would expect activity in fibers with CFs up to approximately 2 octaves above the frequency of the presented tone because of their broad low-frequency tails (Kim and Molnar 1979). In A1 cells, the low-frequency tail--induced asymmetry should be much less pronounced than in the AN. At 50 dB above threshold, one would expect activity in A1 neurons with CFs up to approximately 1/2 octave above the frequency of the presented tone. This frequency range is remarkably similar to many critical band phenomena and, when combined with the level tolerance of A1 neurons and other physiological critical band experiments (e.g., Ehret and Schreiner 1997), suggests that sharpening of frequency tuning in the central auditory system contributes to perceptual critical band phenomena.

APPENDIX 1

To optimize IS cutoff criteria for the population statistics, IS criteria (x-axis in Fig. 6A) were varied for different IS measurements (different lines in Fig. 6A). Within an optimization run, the criteria for defining an edge as a broad tail or as sharp was the same for lower and upper eFTC edges. Multipeaked and circumscribed eFTCs were not used because they could not be categorized based on the two-dimensional IS space. Root mean square (RMS) error was determined by subtracting the percentages determined by objective scoring from hand-scoring for each of U-, slant-lower, slant-upper, LTUS, and UTLS shaped eFTC. These differences were summed and the square root of the sum was taken and divided by six shapes. Using Table 2, the RMS error for IS15–50 with a cutoff criteria of 0.23 octaves/40 dB would be calculated by RMS = \[\frac{[(24.4 - 26.0)^2 + (17.9 - 17.9)^2 + (9.0 - 4.9)^2 + (2.4 - 0.8)^2 + (14.6 - 19.5)^2 + (1.6 - 0.8)^2]^{1/2}}{6}\] = 1.1. With the optimum criterion of 0.23 octaves/40 dB for IS15–50, a V-shaped eFTC was defined as having IS15–50_upper > 0.23 octaves/40 dB and IS15–50_lower < -0.23 octaves/40 dB. A U-shaped eFTC was defined as having 0.00 > IS15–50_upper > 0.23 octaves/40 dB, and -0.23 < IS15–50_lower < 0.00 octaves/40 dB. Furthermore, with this criteria, a slant-lower eFTC was defined as having IS15–50_upper and IS15–50_lower < 0.00 octaves/40 dB. An LTUS eFTC with this criteria was defined as having its upper edge IS between 0.00 and 0.23 octaves/40 dB and its lower edge having an IS more negative than -0.23 octaves/40 dB, etc.

APPENDIX 2

The detailed formula for shape measurement is

\[
\text{Shape}_{15-50} = \frac{[\log_2(F_{UE50}) - \log_2(CF_{15})] + [\log_2(F_{LE50}) - \log_2(CF_{15})]}{[\log_2(F_{UE50}) - \log_2(CF_{15})] - [\log_2(F_{LE50}) - \log_2(CF_{15})]}
\]

where CF_{15} is the center frequency on a logarithmic scale at 15 dB above the neuron’s threshold, F_{UE50} is the frequency of the upper edge at 50 dB above threshold, and F_{LE50} is the frequency of the lower edge at 50 dB above threshold. If the absolute value of the above calculation is >1, then the Shape_{15-50} is 1 + log of the absolute value of the above calculation. This adjustment prevented the number from getting excessively large for narrowly tuned slanted cells. For shape_{15-50} the center frequency 15 dB above threshold was always used as a reference point (Fig. 11A and C) rather than the IS of each edge (Fig. 11B) to calculate shape because using the IS of each edge could inadvertently cause a slant-lower cell to be classified as a slant-upper or vice versa. In Fig. 11, B and C, the same slant-lower eFTC is shown. Unlike a typical slant-lower eFTC where the lower edge has a more negative IS than the upper edge (Fig. 11D), in Fig. 11, B and C, the upper edge’s IS is more negative than the lower edge’s (i.e., if extrapolated the edges would intersect at a higher intensity). In Fig. 11C the metric defined above was used. In Fig. 11B the IS of each edge was used to calculate shape’ (i.e., shape’ = (IS\_upper + IS\_lower)/ (IS\_upper - IS\_lower)). When shape was calculated using the IS of each edge (Fig. 11B), its value was greater than one which would misleadingly indicate a slant-lower cell. However, by using the center frequency measure of (Fig. 11C) the shape value was less than -1 as expected. The eFTC in Fig. 3G provides an example of a neuron whose upper edge IS is more negative than its lower edge IS. If the lower edge had a more negative IS, using the center frequency also correctly results in negative Shape_{15-50} values (Fig. 11D). However, using the center frequency might cause a slight underestimation of slanted eFTCs when the slanting edge does not cross the center frequency. When this happens, however, the shape values will be near the correct value, so a slant-lower cell, could result in a value close to but slightly greater than -1. Therefore using the center frequency stabilizes the measure and prevents hypersensitivity to changes in slope for spindle-shaped cells, but tends to underestimate the number of slanted cells.

APPENDIX 3

One cannot just take the log of BLI and get BLWD. Taking the log of BLI one gets

\[
\log(bLI) = \log(F_{UE10} - F_{LE10}) - \log(F_{UE50} - F_{LE50})
\]

which is different from BWLD

\[
\text{BWLD} = \log(F_{UE50}) - \log(F_{LE50}) - [\log(F_{UE10}) - \log(F_{LE10})]
\]

For BWLD one takes the log of frequency, which can never be 0; however, for log (BLI) one takes logs of differences in frequency that can be zero and therefore could yield an undefined value.

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REFERENCES


SHAPES OF FREQUENCY TUNING CURVES IN A1


