

Frequency selectivity of single cochlear-nerve fibers based on the temporal response pattern to two-tone signals

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The physiological basis of auditory frequency selectivity was investigated by recording the temporal response patterns of single cochlear-nerve fibers in the cat. The characteristic frequency and sharpness of tuning was determined for low-frequency cochlear-nerve fibers with two-tone signals whose frequency components were of equal amplitude and starting phase. The measures were compared with those obtained with sinusoidal signals. The two-tone characteristic frequency (2TCF) is defined as the arithmetic-center frequency at which the fiber is synchronized to both signal frequencies in equal measure. The 2TCF closely corresponds to the characteristic frequency as determined by the frequency threshold curve. Moreover, the 2TCF changes relatively little (2%–12%) over a 60-dB intensity range. The 2TCF generally shifts upward with increasing intensity for cochlear-nerve fibers tuned to frequencies below 1 kHz and shifts downward as a function of intensity for units with characteristic frequencies (CF's) above 1 kHz. The shifts in the 2TCF are considerably smaller than those observed with sinusoidal signals. Filter functions were derived from the synchronization pattern to the two-tone signal by varying the frequency of one of the components over the fiber's response area while maintaining the other component at the 2TCF. The frequency selectivity of the two-tone filter function was determined by dividing the vector strength to the variable frequency signal by the vector strength to the CF tone. The filter function was measured 10 dB down from the peak ($2T Q_{10 \text{ dB}}$) and compared with the $Q_{10 \text{ dB}}$ of the frequency threshold curve. The correlation between the two measures of frequency selectivity was 0.72. The $2T Q_{10 \text{ dB}}$ does change as a function of intensity. The magnitude and direction of the change is dependent on the sharpness of tuning at low and moderate sound-pressure levels (SPL's). The selectivity of the more sharply tuned fibers ($2T Q_{10 \text{ dB}} > 3$) diminishes at intensities above 60 dB SPL. However, the broadening of selectivity is relatively small in comparison to discharge rate-based measures of selectivity. The selectivity of the more broadly tuned units remains unchanged or improves slightly at similar intensity levels. The present data indicate that the frequency selectivity and tuning of low-frequency cochlear-nerve fibers are relatively stable over a 60-dB range of SPL's when measured in terms of their temporal discharge properties.

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INTRODUCTION

Auditory frequency selectivity, which underlies the ability to comprehend speech and appreciate music, changes relatively little over an enormous range of intensities (Scharf and Meiselman, 1977). Only at high-intensity levels (> 70 dB SPL) does the auditory system's ability to analyze concurrently presented frequencies diminish (Pick, 1980). And even at these levels, the deterioration in human performance is relatively small.

The physiological basis of this auditory frequency selectivity is unknown. The discharge rate of most single cochlear-nerve fibers saturates 20 to 30 dB above (rate) threshold. As a consequence, the ability of cochlear-nerve fibers to represent the spectrum of complex sounds, such as speech, in terms of the spatial distribution of rate information, is seriously compromised at moderate-to-high intensities (Sachs and Young, 1979).

An alternative means of encoding spectral information in the cochlear nerve is in terms of the timing pattern of

single fiber discharge. Cochlear-nerve fibers synchronize their discharge activity to frequencies as high as 4 to 5 kHz (Rose *et al.*, 1967; Johnson, 1980). At moderate-to-high sound-pressure levels many features of the speech spectrum are preserved in the temporal discharge pattern (Young and Sachs, 1979; Sinex and Geisler, 1983; Delgutte and Kiang, 1984), thus raising the possibility that, for frequencies in the lower portion of the speech range (< 5 kHz), frequency selectivity is based on the timing pattern of peripheral auditory neurons.

Consistent with this hypothesis are the results of studies which have determined the frequency selectivity of low-frequency cochlear fibers using reverse correlation (de Boer and Kuyper, 1968; Evans, 1977). In this technique, the fiber's impulse response is computed by averaging the signal (a broadband noise) preceding each action potential. The input filter function¹ of the fiber is estimated by computing the Fourier transform of the impulse response. Evans (1977) has shown that the frequency selectivity of single

cochlear-nerve fibers, as inferred from reverse correlation, changes relatively little over a wide range of sound-pressure levels. Similar results have been obtained based on the response of cochlear fibers to click trains (Evans, 1983). These results contrast with the extensive broadening of the response areas of cochlear-nerve fibers observed in response to sinusoidal stimulation (e.g., Rose *et al.*, 1971). The disparity suggests that the cochlear response to complex signals may be of a kind that preserves the frequency selectivity which, by all standard measures (i.e., using sinusoidal signals), has considerably broadened at moderate-to-high sound-pressure levels.

The present study sought to explore the synchrony-based frequency selectivity of single cochlear-nerve fibers using two-tone signals whose frequency components were of equal amplitude and starting phase. Such signals were chosen because they encapsulate certain features of more complex signals, while retaining a degree of analytical simplicity which facilitates analysis of the timing patterns.

The first objective was to determine the characteristic frequency based on the synchronization pattern to the two-tone signal (two-tone CF) over a range of sound-pressure levels and to compare it with the estimate of CF based on the frequency threshold curve (FTC). Because of the possibility that the two measures of CF may differ for any given fiber, the determination of the two-tone CF was also required for the second phase of the study in which the filter function for low-frequency cochlear-nerve fibers was determined, based on their synchronization patterns to two-component signals. This measure of frequency selectivity was obtained over a range of signal sound-pressure levels and compared to the filter function derived from the frequency threshold curve using sinusoidal signals.

I. EXPERIMENTAL METHODS

A. Surgical procedure

Experiments were performed on healthy, adult cats manifesting no sign of middle or external ear pathology. The experimental animal, weighing between 2.5 and 4.5 kg, was anesthetized with sodium pentobarbital (40 mg/kg) and was maintained in an areflexive state on this barbiturate during the course of the experiment. A small dose of atropine methyl nitrate (0.05 mg/kg) was administered before surgery in order to minimize fluid accumulation in the trachea.

A tracheotomy was performed and a glass or plastic cannula was inserted into the cat's trachea. The animal's body temperature was maintained at 37 °C during the experiment with a thermostatically controlled heating pad.

The animal's scalp and left pinna were removed and the musculature overlying the posterior portion of the cranium reflected back. The tip of a 80-mm-long 0.76-mm-i.d. plastic tube was inserted into the bulla to relieve the buildup of middle-ear pressure during the course of the experiment. The head was mounted into a headholder and a hole (approximately 10 mm × 5 mm) was made immediately posterior to the bony tentorium to expose the dura overlying the left dorsal surface of the cerebellum. After careful dissection and reflection of the dura, the two most superficial cerebellar folia were aspirated. The remaining cerebellar tissue was re-

flected with small cotton pledgets soaked in warm saline in order to expose the cochlear nerve at its emergence from the internal auditory meatus.

A Davies-type plastic chamber was cemented onto the skull and positioned over the cochlear nerve. The evacuated space was filled with warm mineral oil and the microelectrode assembly attached to the top of the chamber in such a fashion as to form a tight hydraulic seal.

B. Sound delivery system and acoustic calibration

A calibrated probe tube was inserted into the remaining portion of the external meatus and its tip positioned with the aid of an otoscope so as to be within a few mm of the eardrum. The other end of the probe tube was connected to a 1/2-in. Bruel and Kjaer (B & K 4134) microphone whose output was amplified with a gain of 100 and sampled by a Harris/5 computer. The acoustic system was calibrated in 20-Hz steps between 0.06 and 30 kHz and a sound-pressure level correction table was computed based on the output of the calibration. The SPL correction table was used to adjust the attenuator settings so as to compensate for any inhomogeneities in the frequency response of the two Telex headphones. In the frequency region of greatest interest (0.1–4 kHz) the *uncorrected* response curves rarely deviated from the mean by more than 5 dB. The Telex phones were each mounted in a shielded metal enclosure and connected to the sound speculum with a plastic-coupled "Y" tube. This arrangement permitted each frequency of the two-component signal to be delivered by a separate acoustic transducer and thus served to minimize any intermodulation distortion which might arise. Total harmonic distortion for each channel was –80 dB or less.²

Sinusoidal signals were generated by a digital stimulus system (DSS) controlled by the Harris computer. The DSS permitted each sinusoid to be specified independently in terms of frequency, phase, duration, and amplitude (Rhode, 1976). Stimuli were either single or two- (equiamplitude) component signals.

C. Data acquisition

Action potentials of single cochlear-nerve fibers were recorded with glass micropipettes filled with 3M KCl. An electrode, of 20- to 40-M Ω impedance, was inserted into the cochlear nerve under direct visual control with a hydraulic motorized microdrive (Trent Wells). The action potentials were amplified with a gain of either 10 or 100 and routed to an oscilloscope which served as a triggering device with which to discriminate the neural spikes. The pulse triggered by each action potential was sampled by a unit-event timer which recorded the timing of each spike with a precision of 2 μ s. The times of spike occurrence could then be used to compute interval, post-stimulus time, and period histograms as well as other measures of the fiber's timing pattern such as the vector strength and autocorrelation function.

Cochlear-nerve fibers were contacted by advancing the electrode in small steps (3–5 μ m) during presentation of a broadband (0.6–30 kHz) swept-tone signal of moderate intensity (60–70 dB SPL). Care was taken to record only from first-order units as determined by the monopolar shape of

the action potentials and from the unit response latencies to clicks (Kiang *et al.*, 1965).

D. Frequency threshold curve

Upon isolation of an acoustically driven unit, the fiber's FTC was determined using a digitally controlled sequential tracking algorithm as described in Kochhar (1981) and Geisler *et al.* (1985). The procedure tracked the threshold of a given fiber by varying the frequency and intensity of a 250-ms tone required to evoke a spike count one greater than the sum of the fiber's mean spontaneous discharge rate and its standard deviation. The thresholds, spontaneous rates, and frequency selectivity ($Q_{10\text{ dB}}$) of fibers, as determined by their FTC's, fell within the normal range for feline cochlear-nerve fibers (Kiang *et al.*, 1965; Evans, 1975).

II. RESULTS

A. Two-tone characteristic frequency

The fiber's two-tone CF was determined for 93 low-frequency units (CF's < 3.5 kHz) by repeated presentation of an equi-amplitude two-component signal whose center frequency varied in small steps (1%–2% of the CF) so as to span the unit's response area. The component frequency separation ($F_H - F_L$) was fixed between 15%–25% of the FTC CF. The sound-pressure level of the signal was 15–35 dB above the fiber's discharge rate threshold. In most instances, the stimulation intensity caused the fiber to discharge at or close to its rate-saturation level. Signals were 250 ms in duration (with a linear rise/decay function of 15.6 ms) and were presented once every 500 ms, a total of five times for each frequency condition.

The basic experimental paradigm is illustrated in Fig. 1(a). Shown is the frequency threshold curve for fiber 83045-10 along with a schematic drawing of the two-component signal being stepped through the fiber's response area. In the current example, the two-tone signal is presented at an intensity of 30-dB SPL/component, 24 dB above the fiber's rate threshold at CF. The signal center frequency was varied in 20-Hz steps from 1100 to 1440 Hz. The component frequency separation ($F_H - F_L$) was 200 Hz at all center frequencies. For clarity of illustration, only two signals, one centered at 1100 Hz, the other at 1400 Hz, are shown.

The vector strength, a measure of the fiber's synchronization (Goldberg and Brown, 1969), is plotted for each center frequency condition in Fig. 1(b). Dashed lines indicate the vector strengths corresponding to the two stimulus conditions illustrated. The vector strength is plotted for both the upper (F_H) and lower components (F_L). When the frequency of both components was lower than the fiber CF, the temporal discharge pattern was dominated by F_H because of the filtering properties of the cochlea. The fiber's timing pattern was dominated by F_L when both components were above the CF for the same reason. The significant stimulus condition is the one in which the vector strength to F_L is equal to that of F_H , as indicated by the arrow labeled "2TCF." It is at this point that the two components were driving the fiber's temporal discharge pattern with equal force and are therefore presumed to have been arithmetically

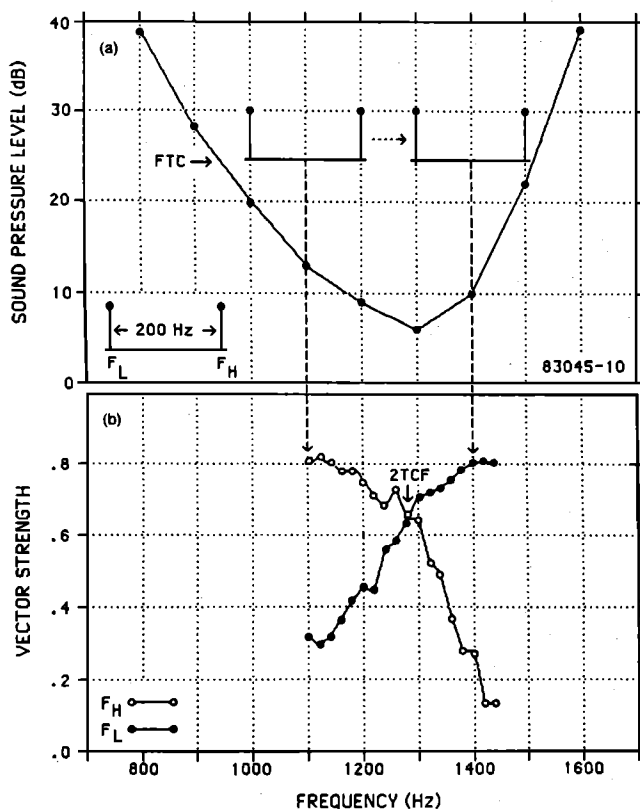


FIG. 1. (a) The experimental paradigm for determination of a cochlear fiber's characteristic frequency. A two-component signal (30-dB SPL/component) is stepped through unit 83045-10's response area in 20-Hz increments. The signal's difference frequency ($F_H - F_L$) is fixed at 200 Hz. (b) The computation of the two-tone CF (2TCF). The vector strength of the fiber's response to both the lower (F_L) and upper (F_H) components is shown for each step. The vector strengths are plotted at the arithmetic mean of the signal component frequencies. The 2TCF is defined as the point where the vector strength of F_H is equal to that of F_L .

centered around the peak of the fiber's filter function. Although the general filter function is usually symmetric only for fibers with CF's around 1 kHz, the FTC tip region of most low-frequency units is roughly symmetrical (on a linear scale). Thus, for the frequency separations used, it can be assumed that the signal frequencies lie at roughly equivalent points on the filter curve when the vector strengths for both components are equal.

Notice in the bottom portion of Fig. 1, at the cross-over point, when the signal is arithmetically centered around the two-tone CF (2TCF), the vector strength to either component is smaller than that when the component dominates the timing pattern. This reduction in vector strength does not necessarily imply suppression but may merely be the result of half-wave rectification of the input signal induced by inner hair cell excitation. Simulation of passing two-tone signals through a simple rectifier has indeed shown similar vector-strength reductions (Greenwood, 1985).

The FTC is an iso-output measure (i.e., a constant discharge-rate criterion is used) of a fiber's frequency selectivity and the two-tone measure of CF used in the present study is an iso-input measure (i.e., constant amplitude input signals are used) of the fiber's filter function. The FTC is based on the average-rate threshold evoked by sinusoidal signals

while the latter measure is derived from the fiber's temporal discharge pattern to two-component signals presented at suprathreshold intensities. The two methods would, in theory, yield equivalent results if the transduction responsible for the filtering is linear.³ Because the peripheral auditory system contains such nonlinear transduction properties as intensity-dependent frequency tuning (Rhode, 1980) and discharge-rate saturation, it is of interest to determine how closely the two measures of frequency selectivity actually do correspond.

In Fig. 2, the FTC characteristic frequency is plotted as a function of the two-tone CF for 93 cochlear-nerve fibers. Only those fibers which could be classified unambiguously as "normal" are included in the sample. They had thresholds less than 35 dB SPL (excepting fibers with CF's below 400 Hz), and their spontaneous discharge rates were less than 10 or greater than 25 spikes per second. Fibers whose FTC's did not conform to the patterns for healthy units illustrated in Liberman and Kiang (1978) were also excluded. Among this latter number are those in which the tip of the FTC is spuriously elongated, occasioned by an error in the automated threshold-tracking procedure. Due to the deterioration of neural synchronization at higher frequencies, only fibers with CF's below 3200 Hz are included in the present sample. This upper frequency limit was necessary to insure that the vector strength pattern was reliable and not contaminated unduly by neural "noise." In no instance was the vector strength less than 0.4 for the dominant frequency component.

Figure 2 illustrates the correlation between the FTC CF and 2TCF when the two-tone signal was presented at a level between 15 and 35 dB above discharge rate threshold. At the lowest levels, the response of cochlear-nerve fibers is considered to be roughly linear (Littlefield, 1973). At the higher end of the intensity range, certain response nonlinearities, such as saturation of average discharge rate, operate but do not conspire to reduce the correlation between the FTC CF and the 2TCF.

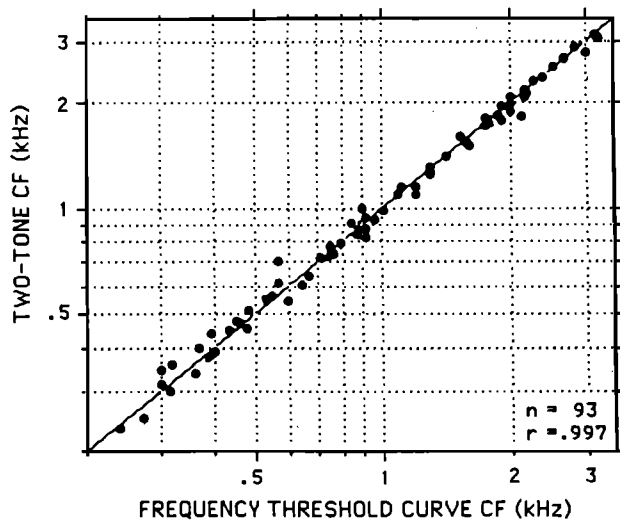


FIG. 2. Correlation of the frequency threshold curve CF with the CF determined by the procedure illustrated in Fig. 1 (2TCF) for 93 "normal" cochlear-nerve fibers. The solid diagonal line represents a slope of one. The correlation coefficient (r) is 0.997.

The correlation coefficient between the two measures of characteristic frequency shown in Fig. 2 is 0.997 ($p < 0.001$). The correlation coefficient does not provide a precise estimate of the average disparity between the FTC CF and the 2TCF. Such an estimate is complicated by the fact that the step size of the FTC (usually 6 to 12 steps per octave) was three to five times larger than that of the two-tone procedure. Occasionally, the FTC frequency steps were linear, being approximately 5% of the FTC CF. The two-tone step size was always linear, typically being 1% to 2% of the FTC CF. The correspondence between the two different measures of CF can, therefore, be most accurately assessed in terms of the FTC step size. In this respect, the correlation between the FTC CF and 2TCF is even more striking, as the disparity between the two was less than one-half of the FTC step size in two-thirds of the fibers. In only three instances did the disparity exceed more than a single step interval, and in no instance did the disparity exceed 1.25-FTC steps.

In general, the difference frequency, $F_H - F_L$, was approximately 15% to 20% of the estimated CF. For 12 fibers, the difference frequency was increased in steps spanning, in some instances, an octave range. The 2TCF changed relatively little as a consequence of broadening the frequency separation between the two components. The average shift was 3% per octave change in the difference frequency. The direction of the shift was independent of the unit CF.

In Fig. 3 the FTC is illustrated for fiber 83026-6, along with the 2TCF estimated at seven different sound-pressure levels over a 60-dB range of intensities. On the right-hand side are the vector strength curves obtained at four different amplitude levels. For this fiber, the estimate of the 2TCF changes only about 10 Hz over the entire 60-dB range, and this change is not in a consistent direction.

However, the 2TCF's of most other cochlear fibers do change in a consistent direction as a function of sound-pressure level (Fig. 4). Ten of the 16 fibers tuned to frequencies below 1 kHz show an upwards shift in the 2TCF with increasing intensity, while 8 of 11 fibers with CF's above 1 kHz exhibit a downwards shift in the 2TCF at higher levels. The magnitude of these frequency shifts is small, usually being between 2% and 5%. In no instance did the 2TCF shift by more than 12%. It is interesting to note that the pattern of these shifts is the same as that observed in the iso-intensity response curves induced by sinusoidal stimulation for fibers of comparable CF (Rose *et al.*, 1971), although the shifts observed in the latter study were of considerably greater magnitude than those seen in the present work. Characteristic frequency can also be estimated from the frequency response curves obtained with reverse correlation. In one such study (Evans, 1977), it was found that the estimated CF of 1-kHz fiber changed hardly at all over an 80-dB range of intensities, while the apparent CF of fibers tuned to higher frequencies changed a great deal over a similar range of intensities.

B. Shape of the two-tone filter function and the two-tone $Q_{10\text{ dB}}$

The characteristic frequency provides only a single point on a fiber's frequency selectivity curve. Of special im-

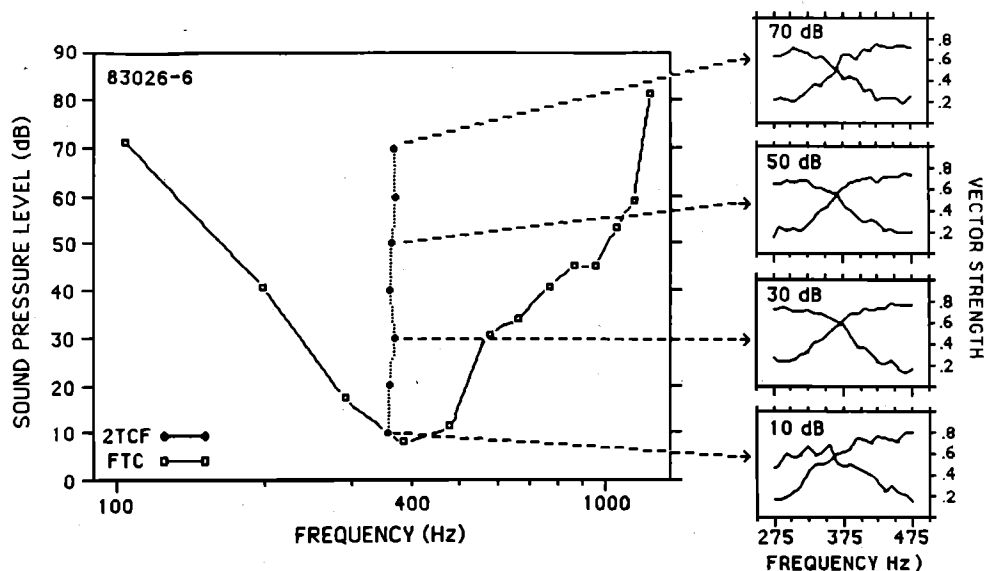


FIG. 3. Two-tone CF determined for unit 83026-6 over a 60-dB range. The two-tone CF is indicated for each of seven sound-pressure levels. The associated vector strength patterns are illustrated for four different intensity levels. The vector strength curves are derived from data collected at 10-Hz steps. The two-component frequency separation was fixed at 50 Hz. The frequency coordinates refer to the center frequency of the two-tone signal. The two-tone CF's are shown within the frequency threshold curve of the cochlear-nerve fiber. The sound-pressure levels indicated refer to the amplitude of each component. Unit 83026-6's rate threshold was 8 dB SPL. Its spontaneous rate was 59.2 and its $Q_{10 \text{ dB}}$ was 1.7.

portance is its sharpness of tuning and the general shape of its filter function. These two measures of frequency selectivity were derived from a second set of two-tone stimulus conditions in which the frequency of one component (F_{cf}) was set at the 2TCF, while the other component (F_v) varied in frequency from approximately two-thirds of an octave below to about three-quarters of an octave above F_{cf} . As in the 2TCF condition, the signal component amplitudes were equal. Signals were 1050 ms in duration (with 15.6-ms rise/decay functions), presented once every 2 s a total of ten times at each frequency condition. The frequency steps for F_v were large (approximately 10%–20%) when it was well above or below F_{cf} and gradually decreased in size to about 1%–2% of 2TCF as it approached F_{cf} . Signal intensity was almost always near or above the rate saturation level. This is clearly observed in the two-tone rate functions where there is little change in the discharge rate as a function of the interval between F_v and F_{cf} for almost all fibers.

The basic experimental paradigm is illustrated in Fig. 5(a) for fiber 83140-4. Shown in the figure is the fiber's FTC

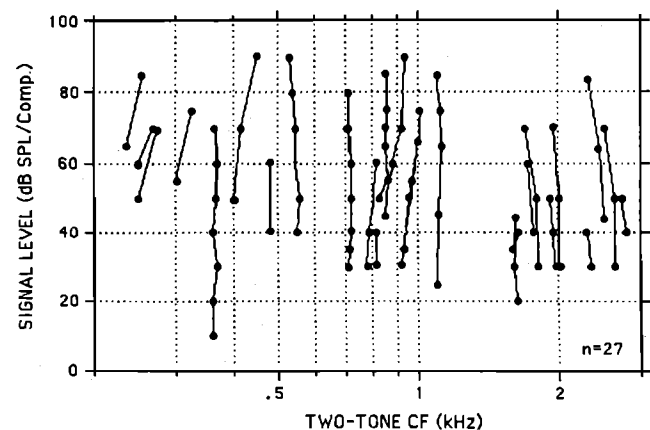


FIG. 4. The two-tone CF measured for each of 27 cochlear fibers as a function of sound-pressure level per component. The lowest two-tone CF for each fiber was determined between 10- and 20-dB/component above the fiber rate threshold.

and a schematic illustration of two stimulus conditions. One component, F_{cf} , is always set at the 2TCF while the second component, F_v , is varied in unequal steps both below and above (not shown) F_{cf} . The smallest separation between F_{cf} and F_v was typically 5% of the 2TCF. The signal frequencies, F_{cf} and F_v , were usually successive odd harmonics of a common fundamental in order to preclude the possibility of a rectification distortion product of F_{cf} affecting the estimated vector strength magnitude of F_v . Stimulus intensity for these data was 60-dB SPL/component, 22 dB above the discharge rate threshold of the fiber.

The two-tone filter function derived from the stimulus conditions shown in Fig. 5(a) is illustrated in Fig. 5(b). Because of our interest in determining the relative effectiveness of the two components, we chose to represent the output by means of a ratio, the vector strength for F_v divided by that of F_{cf} . The resultant coefficient R_v/R_{cf} is a measure of the fiber's ability to represent each of the two frequencies on the basis of its timing pattern. When F_v is distant from F_{cf} , the latter component dominates the fiber's temporal discharge pattern and consequently R_v/R_{cf} is small. As F_v moves closer to F_{cf} , more of its energy will pass through the fiber's filter and, hence, the unit will synchronize more closely to the complex waveform formed by the summation of the two components. When the separation between the two components is less than approximately 10% of F_{cf} , the fiber synchronizes to the frequencies in roughly equal measure (i.e., R_v/R_{cf} approaches 1). At this point, the fiber represents each component equally well on the basis of synchrony and has, in some sense, reached a limit on its frequency resolving power. However, the fiber's ability to represent only one component has begun to diminish at considerably larger frequency separations. The vector strength for F_v in this two-tone paradigm is less than that produced by the same F_v when presented by itself.

As seen in Fig. 5, the functional dynamic range of the two-tone filter function computed on the basis of the vector strength ratio is approximately tenfold. This is due to inherent limitations on the ability to reliably measure the degree

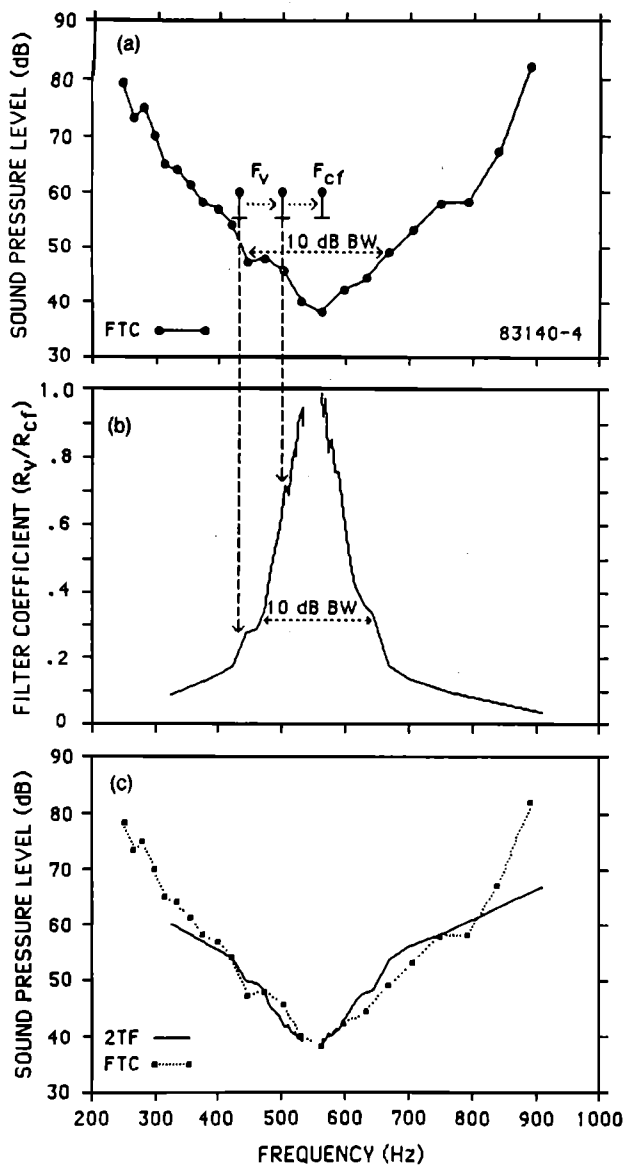


FIG. 5. Experimental paradigm for determination of the two-tone filter function [Fig. 5(a)]. The frequency of one component (F_{cf}) is held constant at the two-tone CF (545 Hz), while the other component (F_v) is varied in frequency from approximately two-thirds of an octave below to about three-quarters of an octave above F_{cf} . The sound-pressure level of both components is equal to 60 dB SPL. The dashed lines are drawn to indicate the corresponding place on the two-tone filter function [Fig. 5(b)]. The sharpness of tuning is computed for the FTC 10 dB above rate threshold (FTC $Q_{10\text{ dB}}$) and for the analogous level of the two-tone filter function (2T $Q_{10\text{ dB}}$). The two-tone filter function is transformed into logarithmic coordinates, multiplied by 20, inverted, and plotted over the tip region of the FTC [Fig. 5(c)]. The FTC $Q_{10\text{ dB}}$ of fiber 83140-4 is 2.6. Its 2T $Q_{10\text{ dB}}$ is 2.9. The FTC CF is 561 Hz. The fiber's rate threshold was 38 dB SPL. Its spontaneous discharge rate was 90 spikes/s.

of synchronization at low-synchronization levels. When R_v/R_{cf} is small (< 0.1), the vector strength for F_v (R_v) is necessarily small as well. Small absolute changes in the magnitude of R_v will result in large changes in the filter coefficient R_v/R_{cf} . Thus the flanks of the filter function, where R_v/R_{cf} is small, should be interpreted with caution.

The ratio R_v/R_{cf} primarily reflects the magnitude of R_v as it changes over a much larger range than R_{cf} . Thus R_v increases from approximately 0.05 at the flank of the filter

function to 0.5 when within 5% of the 2TCF. On the other hand, R_{cf} decreases at a much more leisurely pace, as F_v advances into the fiber's response area. It declines from a high of approximately 0.75 when F_v is on the filter's flank to about 0.53 when F_v is close to the fiber CF. Much of the decline in R_{cf} may be due to the half-wave rectification of the input signal (Greenwood, 1985).

To facilitate comparison of the tip region of the FTC with the two-tone filter function, the latter was transformed into analogous units by multiplying the logarithm of the filter coefficient R_v/R_{cf} by 20. The transformed filter function was inverted and its tip aligned vertically with that of the FTC [Fig. 5(c)]. For this fiber, the correlation between the FTC and the two-tone filter function is high for the uppermost 20 dB of the filter functions. Beyond this range there is a large disparity between the two, probably the result of the restricted dynamic range of the two-tone filter function.

The two-tone frequency selectivity may be quantitatively compared with that of the FTC by computing the bandwidth of the filter function at 10 dB down from the peak [Fig. 5(b)] and dividing the CF by this bandwidth ($2T Q_{10\text{ dB}}$). The relevant level is the one where R_v/R_{cf} is equal to 0.316 as illustrated in Fig. 5(b). In this instance, the FTC $Q_{10\text{ dB}}$ of 2.6 corresponds closely to the $2T Q_{10\text{ dB}}$ of 2.9.

A similar comparison is made for 31 cochlear-nerve fibers in Fig. 6 where the FTC $Q_{10\text{ dB}}$ is plotted as a function of the two-tone $Q_{10\text{ dB}}$. Signal levels were between 15- and 35-dB/component above the fiber's discharge rate threshold at CF. The solid line represents a slope of unity. The correlation between the two measures is high ($0.72, p < 0.05$). Sixteen of the 31 points fall close to the unity-slope line. For the remainder, most of the data points fall below the line indicating that the two-tone $Q_{10\text{ dB}}$ tends to be smaller than the FTC $Q_{10\text{ dB}}$. This is particularly so for those fibers where the FTC $Q_{10\text{ dB}}$ is greater than 3. Most of these fibers have CF's

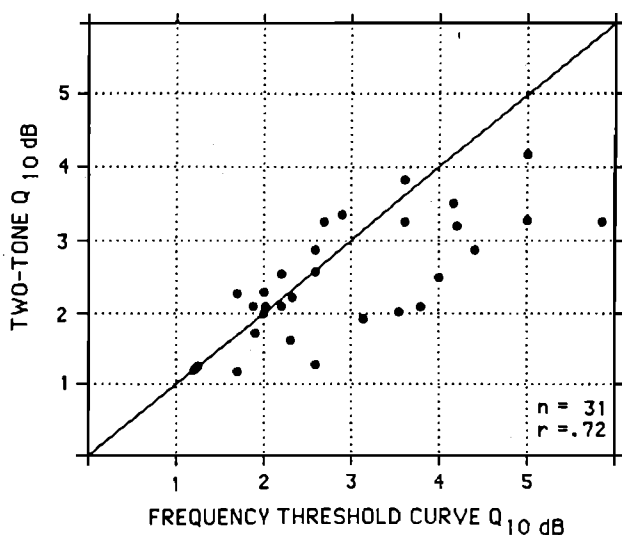


FIG. 6. The correlation between the FTC $Q_{10\text{ dB}}$ and the 2T $Q_{10\text{ dB}}$ for 31 cochlear-nerve fibers. The correlation coefficient (r) is 0.72. The solid diagonal line represents a slope of one. Note that most of the data points fall below the unity slope line, indicating that there is a trend towards the FTC $Q_{10\text{ dB}}$ being higher than the 2T $Q_{10\text{ dB}}$.

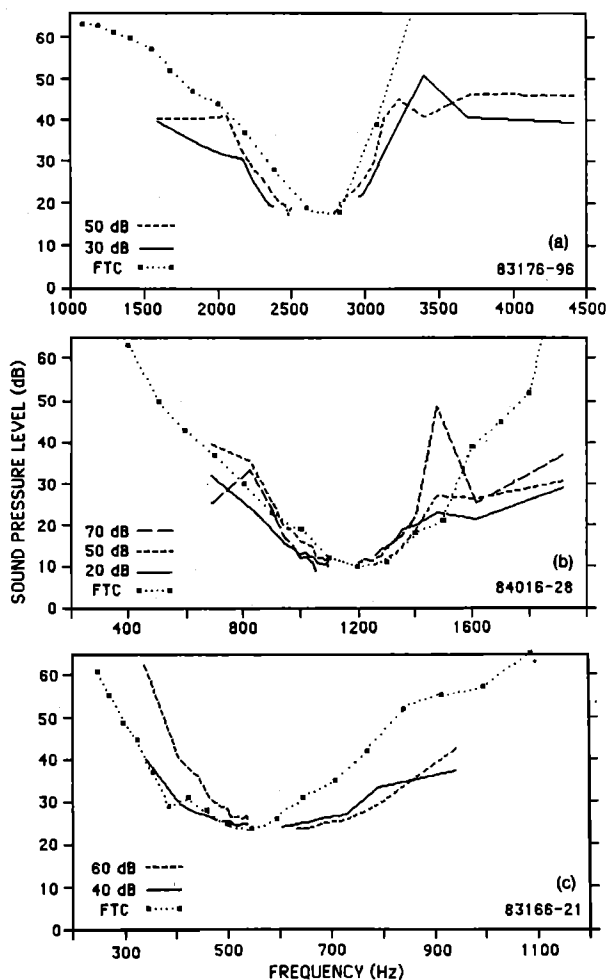


FIG. 7. A comparison of the tip region of the FTC with the two-tone filter functions obtained over a range of intensities for three separate fibers. The two-tone filter functions are inverted in order to facilitate comparison. (a) The FTC and two-tone filter functions for fiber 83176-96 whose FTC CF was 2828 Hz and whose two-tone CF was 2650 Hz. Unit rate threshold was 18 dB SPL. Spontaneous discharge rate was 78.8 spikes/s. The FTC $Q_{10\text{ dB}}$ was 5. The $2T Q_{10\text{ dB}}$ was 3.26 at 30 dB and was 2.93 at 50 dB. (b) The FTC and two-tone filter functions for fiber 84016-28. Note that the filter functions span a 50-dB range. The FTC CF was 1200 Hz and the two-tone CF was 1150 Hz. The FTC $Q_{10\text{ dB}}$ was 3.8. The two-tone $Q_{10\text{ dB}}$ was 2.09 at 20 dB, 2.38 at 50 dB, and 2.41 at 70 dB. Rate threshold was 11 dB SPL. Spontaneous rate was 3.2 spikes/s. (c) The FTC and two-tone filter functions for fiber 83166-21. The FTC CF was 545 Hz and the two-tone CF was 565 Hz. The change in the two-tone filter slopes with increasing level is consistent with an upward shift in the two-tone CF. Rate threshold was 24 dB SPL. Spontaneous rate was 1.6 spikes/s. The FTC $Q_{10\text{ dB}}$ was 1.7. The $2T Q_{10\text{ dB}}$ was 1.18 at 40 dB and was 1.2 at 60 dB.

above 2 kHz. Eight out of nine units with a CF greater than 2 kHz fall well below the unity-slope line.

Many measures of frequency selectivity indicate that the tuning of cochlear-nerve fibers becomes less sharp at moderate-to-high intensities, presumably due to the compressive nonlinear discharge-intensity function. Two-tone filter functions were computed over a range of intensities for eleven cochlear fibers. The FTC and corresponding two-tone filter functions for three of them are shown in Fig. 7.

The data for fiber 83176-96 are illustrated in Fig. 7(a). The 2TCF of the unit is 2650 Hz, near the upper limit of reliable synchronization. The two-tone filter functions were

obtained at 12- and 32-dB/component above the fiber's rate threshold of 18 dB SPL. Although the general shape of the filter functions parallels that of the tip region of the FTC, the two-tone selectivity is, in this instance, somewhat broader than that of the FTC. Over this relatively small range of intensities there is hardly any change in the two-tone selectivity ($2T Q_{10\text{ dB}}$ is 2.93 at 30 dB SPL and 3.24 at 50 dB SPL). As expected, the correspondence between the two-tone filter functions and the FTC diminishes considerably for that portion of the filter function greater than 20 dB from the tip.

Figure 7(b) shows the FTC and two-tone filter functions for fiber 84016-28 ($2TCF = 1150$ Hz). The two-tone filter functions cover a 50-dB range of intensities, from 10 to 60 dB above the fiber's rate threshold (10 dB SPL). The two-tone filter functions are slightly broader than the FTC ($2T Q_{10\text{ dB}} = 2.1 - 2.4$, $FTC Q_{10\text{ dB}} = 3.8$). Yet the two-tone curves parallel the FTC tip region fairly closely up to 15-20 dB from the tip. Moreover, there is relatively little change in the filter functions over the 50-dB range. The large deviation of the upper frequency branch of the filter obtained at 70-dB SPL/component is due to the relatively small values of the vector strength for F_v ($R_v < 0.2$).

Figure 7(c) illustrates the correspondence between the FTC and the two-tone filter function for the low-frequency fiber 83166-21 ($2TCF = 545$ Hz). The fit between the two measures is not very good, except for the lower frequency branch of the filter obtained at 40-dB SPL/component. The lack of a close fit between the FTC and two-tone filter function is atypical. Notice that the lower frequency branch of the 60-dB filter function shifts upward in frequency.

The two-tone $Q_{10\text{ dB}}$ is shown as a function of sound-pressure level for eleven cochlear fibers in Fig. 8. The $2T Q_{10\text{ dB}}$ of most of the more sharply tuned fibers decreases somewhat with increasing intensity, while the $2T Q_{10\text{ dB}}$ of the more broadly tuned fibers increases at higher sound-pressure levels. The boundary between the two patterns is approximately a $2T Q_{10\text{ dB}}$ of 2.5. Within this

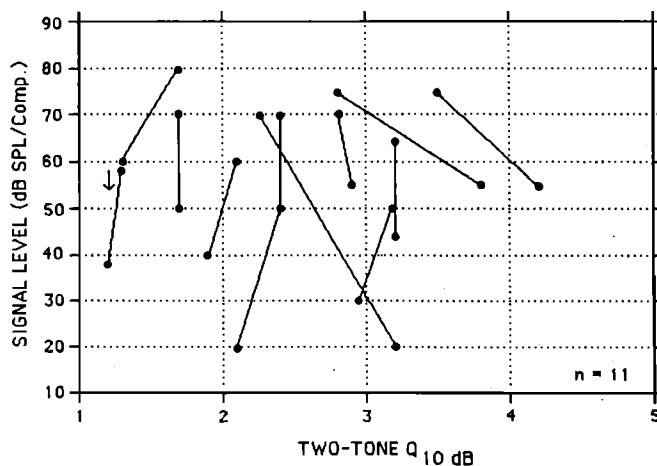


FIG. 8. The two-tone $Q_{10\text{ dB}}$ as a function of sound-pressure level for 11 cochlear-nerve fibers. The lowest amplitude data point for each unit was computed from responses to a signal between 10 and 20 dB above rate threshold. Stimulus levels for the lowest- Q fiber (arrow) are slightly offset for clarity of illustration.

sample there is no significant correlation between the fiber CF and the magnitude of the $2T Q_{10\text{ dB}}$.

III. DISCUSSION

The results of the present study indicate that the frequency selectivity of low-frequency, cochlear-nerve fibers is preserved over a large range of intensities when measured in terms of fiber vector strength ratios.

The characteristic frequency determined with a two-component signal within 30 dB of rate threshold is virtually the same as the CF determined by the frequency threshold curve. At higher intensity levels, there is an upwards shift of approximately 2% to 10% in the two-tone CF for fibers tuned to frequencies below 1 kHz and a downwards shift of comparable magnitude for units tuned to frequencies above 1 kHz. This shift in the CF at moderate-to-high intensities is roughly consistent with the data of Møller (1977, 1978, 1983) who derived cochlear-nerve fiber filter functions by Fourier transformation of the cross correlation of the temporal discharge pattern with a broadband noise stimulus.

The shape of the input filter function derived from the cochlear-fiber temporal response pattern to two-component signals is, under most circumstances, very similar to that derived from the frequency threshold curve. This result is hardly surprising when the input signal level is within 20–30 dB of the fiber's discharge rate threshold. However, there is still a fairly high degree of correlation between the two measures at levels up to 60 dB above rate threshold.

The two-tone $Q_{10\text{ dB}}$ of most highly tuned fibers, as measured with a two-tone signal, does diminish somewhat with increasing sound-pressure level. However, the drop in the two-tone $Q_{10\text{ dB}}$ is relatively small. In no instance did the $2T Q_{10\text{ dB}}$ of these fibers fall below 2. Interestingly, the $2T Q_{10\text{ dB}}$ of less sharply tuned fibers does not decline at high levels. In fact, the selectivity of some of these units *increased* slightly at high sound-pressure levels. The significance of this pattern is not clear. However, there is an implication that the frequency selectivity of cochlear-nerve fibers may be less heterogeneous at moderate-to-high intensities, at least as represented in fiber timing patterns.

These data are not entirely consistent with those reported by Møller (1978) who found that the $Q_{10\text{ dB}}$ diminished at higher intensities regardless of the fiber's sharpness of tuning. Harrison and Evans (1982) also reported that the $Q_{10\text{ dB}}$ declined at higher intensities for all fibers. However, the $Q_{10\text{ dB}}$ of the more sharply tuned fibers tends to diminish more appreciably than that of the more broadly tuned units at high sound-pressure levels. Thus there is a reduction of the $Q_{10\text{ dB}}$ range at moderate-to-high levels in their data as well as in ours. Possible reasons for the discrepancy between the data of Møller (1978) and those presently reported include the difference in experimental species (rat versus cat) and analysis techniques.

Although there are changes in both the two-tone CF and two-tone filter functions, the magnitude of change is relatively small for most cochlear fibers over a wide intensity range. The $2TCF$ changes by less than 5% for the majority of fibers over a 20- to 60-dB range. The $2T Q_{10\text{ dB}}$ declines by a greater amount for some sharply tuned fibers, but the deter-

ioration is never so much as to seriously degrade the frequency analyzing ability of the fibers.

Nevertheless, the fit between the two-tone and FTC measures of frequency selectivity is imperfect, particularly for that part of the two-tone filter function more than 20 dB down from the peak. This is probably due to a limitation on the ability of synchrony information to linearly encode frequency information where the effective amplitude ratio of the signal components exceeds ten. For ratios greater than ten, the vector strength for the variable frequency component is too low for reliable measures to be made.

It is of interest to consider the consequences of the preservation of frequency selectivity in the fiber timing patterns to complex signals in view of the saturation of *both* discharge rate and vector strength at moderate intensities in response to *sinusoidal* signals. There is no frequency-specific information contained in the magnitude of average discharge rate. Information concerning the signal spectrum can only be inferred from the topographic distribution of discharge rate information across a population of cochlear fibers. If most fibers are discharging at saturation level, then it will be difficult to infer the location of spectral prominences on the basis of the spatial pattern of rate activity. Saturation does not affect the frequency-encoding capabilities of timing information in the same way because the timing pattern of discharge activity conveys frequency-specific information which is preserved even at suprasaturation intensities. Thus neural synchronization is one means by which spectral information is preserved across a wide range of intensities in the presence of saturating and compressive nonlinearities.

In the present study, attention has been focused on signals for which the amplitudes of the two components are equal and the frequency of one or both components is varied systematically. Under these conditions, changes in the synchronization pattern are observed that bear a certain similarity to those discussed by Hind *et al.* (1967), Brugge *et al.* (1969), Javel *et al.* (1978), Javel (1981), among others, for experimental conditions in which the frequencies are held constant and the amplitude of one or both components is varied. Sometimes, under these conditions, the synchronized response to one component is reduced upon introduction of a second component of sufficient intensity (e.g., Javel, 1981). These reductions have been cited as instances of "two-tone suppression."

Because the variable frequency component, in our experiment, would, under most conditions, evoke a vigorous synchronized response from the fiber were it presented by itself, the two-tone filter functions involve some form of "synchrony suppression." Yet, this suppression operates in such a manner that the shapes of the two-tone filter functions obtained at different intensities are similar to that of the fiber's FTC. Thus the relative amplitudes of the principal response components can be predicted over a wide range of intensities by using the corresponding amplitude ratios observed in the FTC (i.e., by linear analysis). In other words, the ratios of the component amplitudes in the timing pattern of the neural responses are like those produced by a linear filter (cf. de Boer and de Jongh, 1978; Møller, 1983). The conditions over which this linear analysis applies have not

been established. However, it does not appear to apply when there are large differences in the amplitude spectrum such as would be the case in many speech sounds (Sinex and Geisler, 1984).

Despite the fact that many of the present data satisfy the formal definition of suppression, our paradigm differs from the conventional one used in studies of two-tone suppression. Most investigations of two-tone suppression have analyzed the suppression from the perspective of the frequency component closest to the fiber CF (e.g., Sachs and Kiang, 1968; Abbas and Sachs, 1976; Young and Sachs, 1979). Typically, the amplitude of the so-called "suppressor" tone required to significantly alter the synchrony of the discharge pattern of the near-CF component is determined for signals spanning a range of frequencies and intensities. In the present study, the filter function largely reflects the growth in the fiber's synchronization to F_v as it moves into the center of the response area, rather than a decline in the synchronization to F_{cf} . Although there is a decrease in R_{cf} as F_v becomes closer to F_{cf} , the decline is small (typically from 0.8 to 0.6). Much of this decrease in vector strength may be attributable to rectification distortion (Greenwood, 1985). Presumably, this reduction in vector strength affects the representation of F_v and F_{cf} to relatively equal degrees and can therefore be compensated for, as has been done in the present study, by measuring the ratio of R_v to R_{cf} . However, this compensation for rectification must be regarded as only approximate.

Although the present data do not directly address the question as to whether synchrony suppression, in general, is a necessary consequence of the rectification distortion (as suggested by Greenwood, 1985), they suggest that at least part of the suppression observed in the studies of Javel *et al.* (1978, 1981), Young and Sachs (1979), Sinex and Geisler (1984), among others, may be the consequence of rectification (and some form of a compressive nonlinearity) acting in concert with the frequency selectivity of the cochlea.

The present study has shown that the frequency selectivity of the cochlea, as manifested in the FTC, is preserved, to a large degree, at moderate-to-high intensities, in one property of the timing pattern of single cochlear-nerve fibers (namely, R_v/R_{cf}). However, this preservation of frequency selectivity need not imply that the ability to resolve individual components is actually based on such a measure. The physiological basis of frequency selectivity may actually be derived from other properties of the neural discharge pattern, related, in some way, to R_v/R_{cf} , but which operate over a larger frequency range than the present measure. The nature of such an alternative means of frequency representation is a topic worthy of future study.

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¹For a linear system, the frequency selectivity can be derived from the impulse response, and vice versa (Oppenheim *et al.*, 1983). For a nonlinear system such as the cochlea, such transformations must be regarded as only first-order approximations.

²The harmonic distortion was measured on a single channel acoustic system.

³In a linear system, the "amplitude-gain function," defined by the outputs to iso-amplitude inputs, is the same (on a decibel scale) as the "frequency threshold curve" defined by a constant-output criterion. Consider the hypothetical case of two sinusoids of equal amplitude (iso-input condition) that produce outputs differing in amplitude by 20 dB (i.e., $R_1 = R_2 + 20$ dB). If now, A_2 , the amplitude of the less effective signal, is increased by 20 dB, then R_2 will also increase by 20 dB and become equal to R_1 . Thus, in this iso-input condition, $A_{2dB} = A_{1dB} + 20$ dB. By either measure sinusoid 1 is 20 dB more effective than sinusoid 2.

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