Hearing Research, 49 (1990) 225–246
Elsevier

HEARES 01444

Two-tone rate suppression in auditory-nerve fibers: Dependence on suppressor frequency and level

Bertrand Delgutte

Research Laboratory of Electronics, Massachusetts Institute of Technology, Cambridge, Massachusetts, Department of Otolaryngology, Harvard Medical School, and Eaton-Peabody Laboratory, Massachusetts Eye and Ear Infirmary, Boston, Massachusetts, U.S.A.

(Received 16 October 1989; accepted 25 April 1990)

The growth of two-tone rate suppression with suppressor level was studied for auditory-nerve fibers in anesthetized cats. The level of a tone at the characteristic frequency (CF) was adjusted by an adaptive procedure (PEST) so that, when presented with a suppressor tone, the CF tone would produce a criterion discharge rate. Suppression (in dB) was defined as the CF-tone level that met criterion in the presence of a suppressor minus the level that met criterion in quiet. The growth of suppression with suppressor level was well characterized by a straight line whose slope (in dB-excitor/dB-suppressor) varied with suppressor frequency by as much as a factor of 10 in the same fiber. These slope differences were systematically related to the position of the suppressor frequency relative to the fiber CF: for below-CF suppressors, slopes ranged from 1 to 3 dB/dB, while, for above-CF suppressors, they were between 0.15 and 0.7 dB/dB. Slopes decreased rapidly with increasing suppressor frequency near the CF, but, for frequencies well below the CF, the slope reached a maximum that increased gradually with CF. These results resemble psychophysical data on the growth of masking and psychophysical suppression, and pose difficulties for existing models of two-tone suppression.

Auditory nerve; Two-tone suppression; Cochlear nonlinearities; Masking; Peripheral auditory models

Introduction

The work of Kiang and his colleagues on nonlinear response properties of auditory-nerve fibers has been influential in both physiology and psychophysics (Kiang et al., 1965, 1986; Sachs and Kiang, 1968; Goldstein and Kiang, 1968; Kiang and Moxon, 1972, 1974; Liberman and Kiang, 1984). Among these nonlinear phenomena, two-tone suppression, which was systematically studied by Sachs and Kiang (1968), has important functional implications and is key for testing models of nonlinear cochlear processing. The suppression of a signal by a masking stimulus contributes to the masking of the signal (Dallos and Cheatham, 1977; Pickles, 1984; Delgutte, 1990a). On the other hand, the unmasking of a signal when new components are added to a nonsimultaneous masker may be due to suppression among components of the masker (Houtgast, 1974; Shannon, 1976; Duifhuis, 1980). Suppression seems to play a role in the coding of speech and other complex stimuli (Javel, 1980; Schalk and Sachs, 1980; Sachs and Young, 1980; Carney and Geisler, 1986; Deng et al., 1987), and in the detection of acoustic signals in background noise (Geisler and Sinex, 1980; Costalupes et al., 1984). Further experimental data on suppression are needed for developing and testing peripheral auditory models that predict psychophysical performance and responses to speech over a wide range of stimulus conditions.

One key issue for modeling is the dependence of suppression on suppressor frequency (Duifhuis, 1980; Kim, 1986; Goldstein, 1988, 1989). Sachs and Kiang (1968) showed that suppression thresholds were lower for suppressor frequencies above the characteristic frequency (CF) of auditory-nerve fibers than for below-CF suppressors. This observation was confirmed for auditory-nerve

---

Correspondence to: Bertrand Delgutte, Eaton-Peabody Laboratory, Massachusetts Eye and Ear Infirmary, 243 Charles Street, Boston, MA 02114, U.S.A.

0378-5955/90/$03.50

fibers in several mammalian species (Harris, 1979; Schmiedt, 1982; Prijs, 1989). On the other hand, there is considerable evidence that suppression grows faster with suppressor level for below-CF suppressors than for above-CF suppressors (Kiang and Moxon, 1974; Abbas and Sachs, 1976; Sachs et al., 1980; Javel et al., 1983; Fahey and Allen, 1985; Costalupes et al., 1987) so that the amount of suppression may actually be greater below the CF than above the CF for stimulus levels encountered in conversational speech. This paper reports systematic data on the growth of suppression with suppressor level and how this rate of growth depends on suppressor frequency. Results show that this dependence is more complex than was previously thought.

In auditory-nerve fibers, suppression can be measured for either the average rates of discharge or the synchronization of discharges to the excitatory stimulus. Systematic data are available on the growth of synchrony suppression (Javel et al., 1983), but comparable data for rate suppression are more limited (Abbas and Sachs, 1976; Costalupes et al., 1987). It has long been known that synchrony suppression is predicted by certain classes of models that do not produce rate suppression (Johnson, 1974; Hall, 1979; Geisler, 1985). This point has recently been emphasized by Greenwood (1986), who argued that certain forms of synchrony suppression might be an artifact due to the use of the synchronization index to measure suppression. This paper provides data on rate suppression which can be compared with synchrony suppression data in order to determine whether these difficulties are important in practice.

Sachs and his colleagues (Sachs, 1969; Abbas and Sachs, 1976) measured rate suppression by means of the fractional response, which is the ratio of the response to a CF tone in the presence of a suppressor to the response to the CF tone alone. This measure has a limited dynamic range because the discharge rates of auditory-nerve fibers grow with intensity over only 20–30 dB (Kiang et al., 1965; Sachs and Abbas, 1974). Javel et al. (1978) showed that a fixed suppressor shifted the rate-level function for a tone at the CF by an approximately constant amount over a broad range of CF-tone levels. This horizontal shift (in decibels) provides a measure of suppression that is not limited by the narrow dynamic range of auditory-nerve fibers. This paper introduces an adaptive procedure for efficiently measuring this shift, making it possible to measure suppression growth for many different frequencies in a single fiber. A preliminary report of these findings has been presented (Delgutte, 1986a).

Methods

Animal preparation

Surgical techniques for dorsally accessing the auditory nerve in cats anesthetized with Dial in urethane were as described by Kiang et al. (1965) and Liberman (1978). After surgery, the animal was placed in a sound-proof, electrically-shielded chamber, and an acoustic cavity containing a Brüel and Kjær 1-in condenser microphone and a calibrated probe microphone was sealed into the auditory meatus. Glass micropipettes filled with 2 M-KCl were inserted into the auditory nerve. For each fiber, the characteristic frequency (CF) and threshold at CF were estimated from a tuning curve measured by a tracking algorithm (Kiang et al., 1970; Liberman, 1978). The spontaneous discharge rate (SR) was measured for a duration of 20 s in order to classify fibers into three groups depending on whether SR is below 0.5 spikes/s, between 0.5 and 18 spikes/s, or above 18 spikes/s (Liberman, 1978). The stability of the preparation was assessed by monitoring both the pattern of fiber thresholds against CF (Liberman, 1978) and the threshold of the click-evoked compound action potentials (CAP). Only fibers whose thresholds were within the normal range (Liberman and Kiang, 1978) are included in this report.

Stimuli

Two-tone stimuli were generated by two unsynchronized oscillators (Wavetek Model 157 and Krohn-Hite Model 4031R). The output of each oscillator was gated by an electronic switch, producing a 50-ms tone burst with a 2.5-ms rise-fall time. Measurements of harmonic and intermodulation distortion for these oscillators and for the acoustic output of the condenser microphone have been reported (Delgutte, 1990a).

Suppression tuning curves

Suppression tuning curves (Sachs and Kiang, 1968; Frezza, 1978; Schmiedt, 1982; Prijs, 1989) were measured for all auditory-nerve fibers in order to rapidly determine frequency-intensity regions in which suppression occurred. The method for measuring suppression tuning curves was adapted from that of Schmiedt (1982): Suppression thresholds were measured first for suppressors above the CF in descending frequency steps of 0.01 decade, then for suppressors below the CF in ascending frequency steps. For each suppressor frequency, two 50-ms stimuli were presented in alternation at a rate of 10/s. One stimulus consisted of a fixed tone at the CF and a variable suppressor tone, while the other one was the CF tone alone. The CF-tone level was chosen so that it would produce a discharge rate corresponding to about 67% of the maximum driven rate estimated from a rate-level function for 50-ms tone bursts at the CF. The suppressor level was adjusted by a tracking procedure (Kiang et al., 1970; Liberman, 1978) so that there would be one fewer spike during the interval containing the suppressor than during the CF-tone interval. Thus, the suppression threshold is the suppressor level that decreases the response to the CF tone by 10 spikes/s (Liberman, 1978).

Suppression growth functions

Suppression growth functions were measured for one to six suppressor frequencies in each auditory-nerve fiber, as time permitted. These functions describe how the amount of suppression (in decibels) increases with suppressor level. The top panel of Fig. 1 shows the rationale behind the method for measuring suppression growth. Each trace shows an idealized rate-level function for a CF tone in the presence of a fixed suppressor, with suppressor level differing for each trace. If, as suggested by the literature (Javel et al., 1978; Abbas, 1978; Javel, 1981; Costalupes at al., 1987), the effect of a suppressor is to shift the entire rate-level function horizontally, then there is no need to measure complete rate-level functions in order to characterize this shift: It is more efficient to measure the level of the CF tone for which discharge rate reaches a certain criterion, and define suppression as the difference in levels for which the criterion is crossed with and without a suppressor.

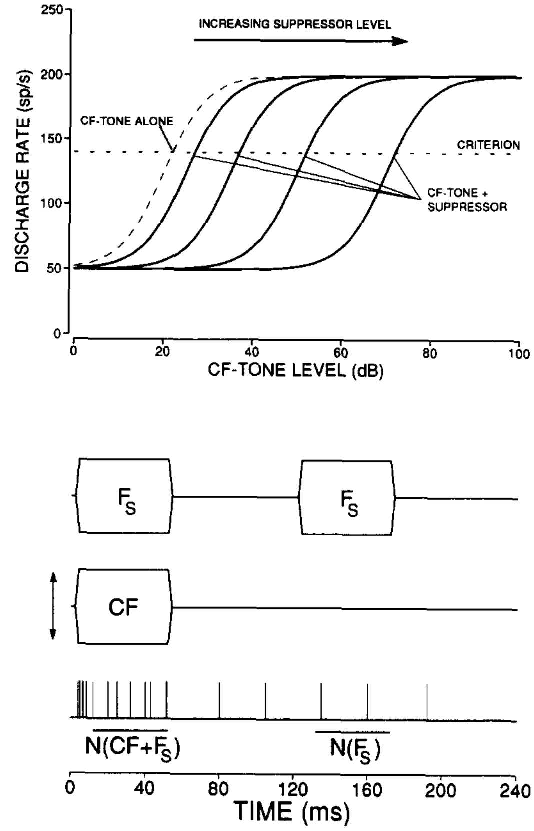

Fig. 1. (Top) Discharge rate as a function of stimulus level for a tone at the CF, alone (thin, dashed line) and in the presence of suppressing stimuli with increasing intensities (thick lines). The horizontal dashed line shows the rate criterion used in measuring horizontal shifts between the rate-level functions. (Bottom) Stimulus paradigm for measuring the effect of a suppressor on the level at which the discharge rate for a CF tone reaches the criterion. The top two traces show the waveform envelopes for the suppressor F_S and the CF tone. The sum of these two waveforms is delivered to the ear on each stimulus presentation. The bottom trace shows the spike times recorded from an auditory-nerve fiber in response to the stimulus.

The bottom panel of Fig. 1 shows how this idea was implemented. Pairs of 50-ms stimuli were presented at intervals of 240 ms. The first stimulus in each pair consisted of a fixed suppressor plus a variable tone at the CF, while the second one was the suppressor alone. The number of spikes $N(CF + F_S)$ in a 40-ms interval starting 12 ms after the onset of the CF tone plus suppressor was counted, and the CF-tone level adjusted by an adaptive procedure so that the spike count would reach a certain criterion, usually 67% of the maximum driven rate. The number of spikes $N(F_S)$ in a second 40-ms interval starting 12 ms after the onset of the suppressor alone was also counted in order to measure the discharge rate for the suppressor. Thus, the excitation and the suppression produced by the same tone were measured simultaneously.

The adaptive procedure used for bringing discharge rate to criterion was a modified PEST (Taylor and Creelman, 1967). For each CF-tone level, a count of the number of spikes in response to all stimulus presentations was accumulated, and, for each trial, this cumulative count was compared to the count that would be expected if discharge rate were equal to criterion. When the difference between actual and expected counts exceeded a certain value, the CF-tone level was changed according to the rules of PEST. Each adjustment was started with level increments of 4 dB, and stopped when the increment reached 0.25 dB. Adjustments were first made for a suppressor level well below the suppression tuning curve, then for increasing suppressor levels in 5-dB steps, until any one of three events occurred: (1) The suppressor level reached a maximum value of about 95 dB SPL, (2) the CF-tone level reached maximum during an adjustment, or (3) the response to the suppressor became so large that the criterion was always exceeded regardless of CF-tone level.

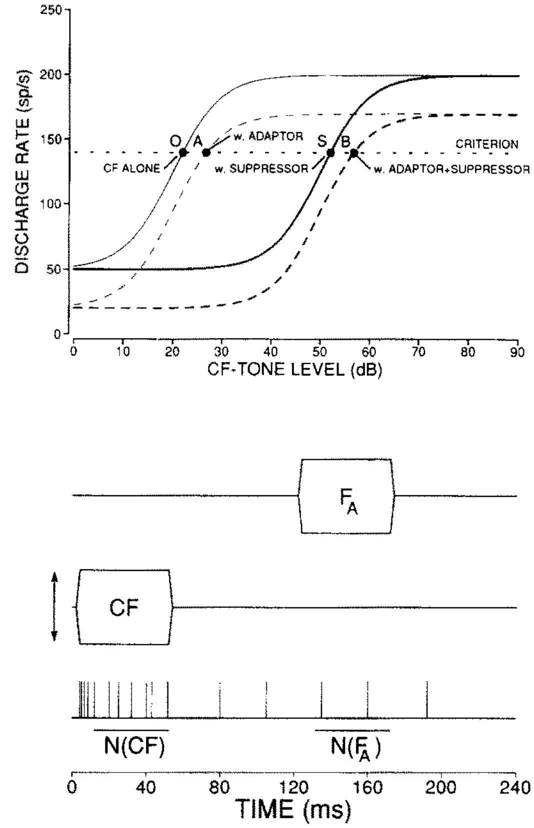

Fig. 2. (Top) Discharge rate as a function of level for a tone at the CF, alone (thin continuous line), and in the presence of a suppressor (thick continuous line), an adaptor (thin dashed line) and both an adaptor and a suppressor (thick dashed line). The horizontal dotted line shows the criterion used in measuring shifts between the various curves. (Bottom) Stimulus paradigm for measuring the effect of an adaptor F_A on the level at which the rate for the CF tone reaches criterion.

Correction for adaptation

The second stimulus in Fig. 1 is used only for measuring the discharge rate in response to the suppressor and is not involved in adjusting the CF-tone level. In order to discuss the effects of this tone on suppression measurements, it helps to call it an 'adaptor', even though it is the same as the 'suppressor' in the first interval. So long as the discharge rate in response to the adaptor is low, the presence of the adaptor should not greatly affect the level of the CF tone that meets criterion, and measurements of suppression should be accurate. However, if the response to the adaptor is large, the response of the auditory-nerve fiber might show adaptation produced by preceding presentations of the adaptor, so that the measurement of suppression would be biased.

The top panel of Fig. 2 shows the principle of a method for correcting suppression measurements for effects of adaptation. Idealized rate-level functions are shown for the CF tone, alone, and in the presence of an adaptor, a suppressor, and both a suppressor and an adaptor. Suppression is defined as the horizontal distance OS between the function for the CF tone alone and that with a suppressor. The paradigm shown in Fig. 1 overestimates the amount of suppression because it actually measures the distance OB to the function with both an adaptor and a suppressor. However, if the shift in rate-level functions produced by the adaptor is the same with and without a suppressor (i.e. if OA = SB), then suppression can also be measured from the distance AB between the rate-level function with an adaptor and that with both an adaptor and a suppressor. The proposition that OA = SB is supported by the following argument: The adaptor is the same whether or not a suppressor is present, so that, ceteris paribus, it should produce the same discharge rate for both conditions. The discharge rate during the interval that contains the CF tone should also be nearly the same for both conditions because it is maintained near criterion by the adaptive procedure. According to experimental results (Smith 1977, 1979; Harris and Dallos, 1980), adaptation depends only on the discharge rate produced by an adapting stimulus regardless of its intensity or spectral content. Thus, because all discharge rates are approximately the same with and without a suppressor, adaptation should be the same for both conditions.

The bottom panel of Fig. 2 shows how effects of an adaptor on the level of a CF tone that meets criterion were measured. All stimulus parameters, adaptive procedures, and threshold criteria are the same as in Fig. 1, except that the suppressor is absent from the first interval. The resulting adaptation growth function (plot of the CF-tone level that meets criterion against adaptor level) was subtracted point-by-point from the suppression growth function for the same adaptor frequency in order to correct for effects of adaptation on the growth of suppression. In practice, adaptation growth functions were always measured after the corresponding suppression growth functions, so that the correction could not be applied when contact with the fiber was lost prematurely.

Data analysis

Suppression growth functions typically consisted of two segments separated by a brief transition (Figs. 3–6): A low-level segment in which the CF-tone level is approximately constant, and a high-level segment in which CF-tone level grows approximately linearly with suppressor level. In order to quantitatively estimate this rate of growth, a 4-parameter function was fitted to the data by a nonlinear, least-squares algorithm (Press et al., 1988; pp. 540–547). This function, which is a slight elaboration of the attenuation factor 'g' in the Sachs and Abbas (1976) model of suppression, is defined by the equation

$$L_{CF} = L_0 + \alpha W \log_{10}[1 + 10^{(L_S - \theta)/W}] \qquad (1)$$

The independent variable is the suppressor level L_S in dB SPL, while L_{CF} is the CF-tone level that meets criterion, in dB SPL. Fitted parameters are (1) the CF-tone level L_0 for low suppressor levels, (2) the asymptotic rate of growth of suppression α for high suppressor levels, (3) the width W of the transition from the low-level segment to the high-level, linearly-increasing segment, and (4) the suppressor level θ where the transition occurs. The Sachs and Abbas (1976) 'g' function corresponds to a special case of (1) when W is equal to 10 dB. Fitted values of W ranged from less than 1 dB to over 20 dB. The root-mean-square deviation between the measured data and the fitted curve was typically 0.8–1.8 dB. This fitting procedure was applied either to suppression growth data that were corrected for effects of adaptation or, when adaptation could not be measured, to uncorrected data. In the following, emphasis is placed on the rate of growth of suppression (in dB-excitor/dB-suppressor) measured by the parameter α.

For many fibers, adaptation growth functions were measured for only one adaptor frequency, while suppression growth functions were obtained for several frequencies. Even in these cases, suppression growth functions could be corrected for effects of adaptation using adaptation data for a different frequency by assuming that two tones with different frequencies have the same adapting effects if they produce the same discharge rate (Smith 1977, 1979; Harris and Dallos, 1980). Fig. 3 shows the method for this cross-frequency correction. Circles in the top left panel show the uncorrected suppression growth function for a 0.4-kHz suppressor. This function was corrected using the adaptation growth data for a 1-kHz adaptor shown in the top right panel. For each suppressor level L_S, the first step was to find the level L_A of the 1-kHz adaptor that produced the same discharge rate as the 0.4-kHz tone at L_S. For this purpose, the function proposed by Sachs and Abbas (1974) was fitted by the least-squares method to the rate-level functions for both 1-kHz and 0.4-kHz tones, and the fitted functions were used for interpolating between the data points (bottom panels). The second step was to find the CF-tone level A that met criterion in the presence of the 1-kHz adaptor at level L_A. This was done by interpolating the 1-kHz adaptation growth function using Equation (I) (top right). Finally, this correction A was subtracted from the CF-tone level S that met criterion in the presence of the 0.4-kHz suppressor at level L_S to yield the corrected suppression S-A. An obvious effect of correction is to shift the suppression growth function down to the 0-dB line at low levels. This is to be expected because, when there is no adaptation and no suppression, the CF-tone level that meets criterion should be the same in the left and right panels, so that S-A should be zero.

Results

Single-fiber data

Suppression growth functions were measured for 256 auditory-nerve fibers in 18 cats. The top panel of Fig. 4 shows both excitatory and suppression tuning curves for a low-CF (0.54-kHz) fiber. The suppression area above CF is well defined, but suppression thresholds could not be measured below the CF. This result, which is not uncommon for fibers with CFs below 1–2 kHz, means either that suppression was smaller than the 10 spikes/s criterion that defines suppression threshold, or that the intensity range over which suppression exceeded 10 spikes/s was too narrow for the tuning curve algorithm to function reliably. The center panel shows suppression growth functions for 4 suppressor frequencies and for the ranges of sup-

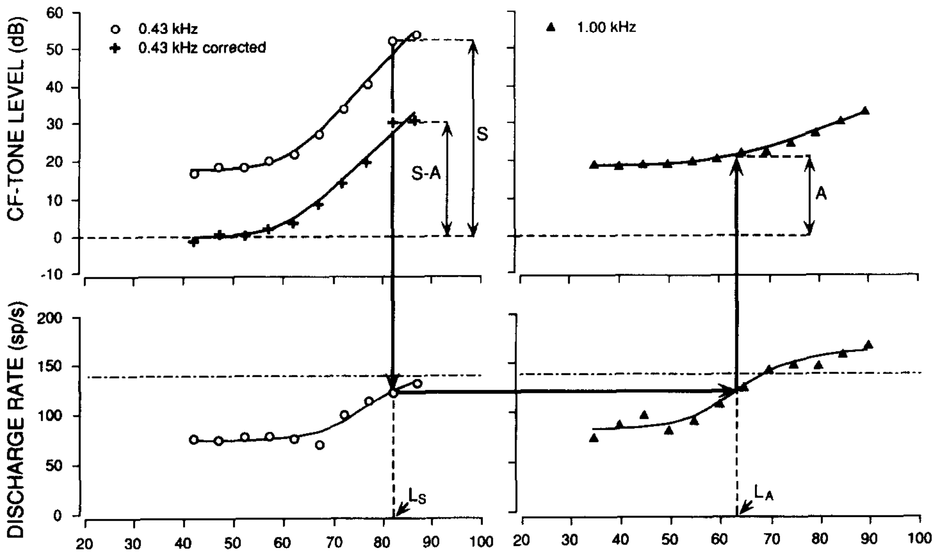

Fig. 3. Correction for effects of adaptation when the adaptor frequency differs from the suppressor frequency. The top left panel shows both uncorrected (circles) and corrected (plusses) suppression growth functions for a 0.43-kHz suppressor. The continuous curves are least-squares fits of Equation (1) to the data. The bottom left panel shows the rate-level function for the 0.43-kHz tone (circles) and a least-squares fit of the Sachs and Abbas (1974) model to the data. The bottom right panel shows the rate-level function of the same auditory-nerve fiber for a 1-kHz tone. The top right panel shows the adaptation growth function for the 1-kHz adapting tone. Connected arrows show how the correction for effects of adaptation is determined for one suppressor level L_S: The CF-tone level A at the end of the last arrow is subtracted from the level S at the origin of the first arrow to give the corrected suppression S-A.

pressor levels shown by arrows in the top panel. For the 0.33-kHz suppressor (circles), the CF-tone level that met criterion was approximately constant for low suppressor levels, meaning that there was no suppression. When the suppressor level exceeded 35 dB SPL, suppression began to occur, in the sense that the level of the CF tone had to be increased in order to maintain the discharge rate at criterion. The growth of suppression was well characterized by a straight line with a slope of 1 dB/dB for suppressor levels above 50 dB SPL. Shifts in CF-tone level exceeding 30 dB could be obtained for this suppressor frequency, even though the tuning-curve algorithm failed to measure a suppression threshold. A possible explanation is that discharge rate grew very slowly near the CF-tone level used in measuring suppression tuning curves, so that even large horizontal shifts of the rate-level function produced only small rate decrements that failed to reliably exceed the 10-spikes/s criterion of the tuning-curve algorithm.

Results were qualitatively similar for the other 3 suppressor frequencies, except that the range of suppressor levels investigated with the 1.05-kHz suppressor was too restricted for the low-level, constant portion of the suppression growth function to be apparent. Rates of growth of suppression decreased monotonically with increasing suppressor frequency, from a maximum of 1.4 dB/dB for the 0.2l-kHz suppressor, to a minimum of 0.38 dB/dB for the 1.05-kHz suppressor. Thus, for this low-CF fiber, growth rates varied by more than a factor of 3 depending on suppressor frequency. As a result of these differences in growth rates, suppression reached a maximum of 30–35 dB for frequencies below the CF, but did not exceed 15–20 dB for above-CF suppressors, even though

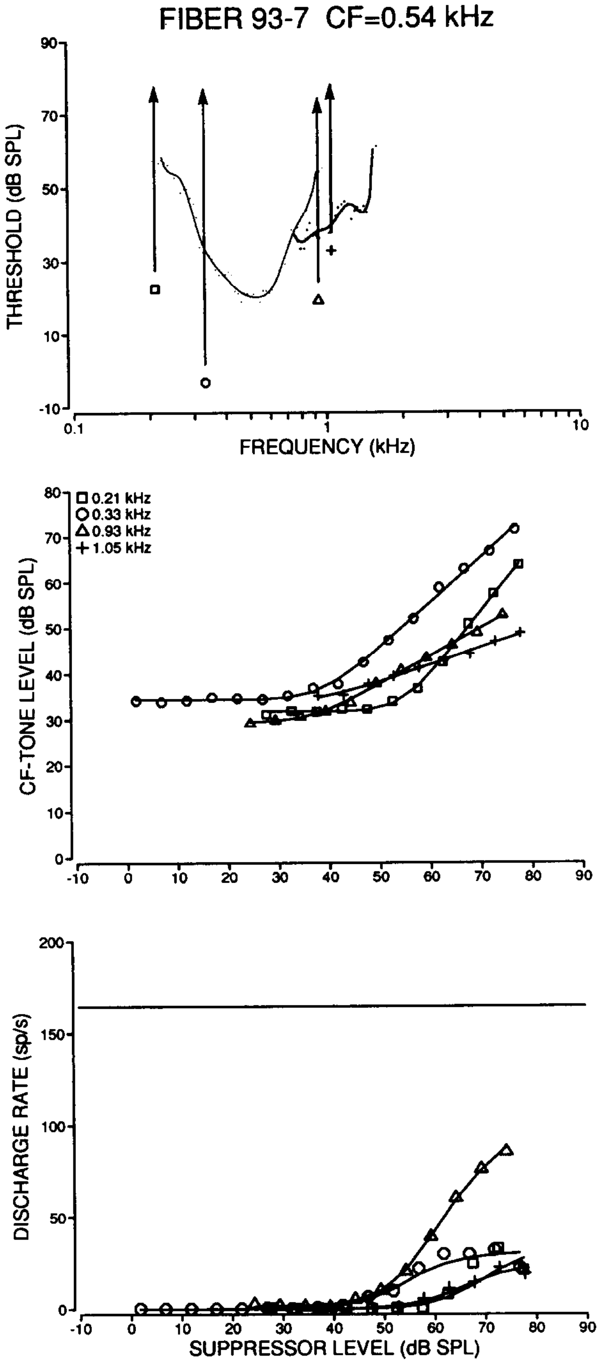

Fig. 4. (Top) Threshold tuning curve (thin line) and suppression tuning curve (thick line) for a medium-SR auditory-nerve fiber with a CF of 0.54 kHz. These lines are cubic splines that were fitted to the data (dots) by the least-squares method. Arrows show the ranges of intensities over which suppression growth functions were measured for 4 different frequencies. (Center) Suppression growth functions for 4 different frequencies for the same fiber as on top. Symbols show the data points for each suppressor frequency, while the curves are least-squares fits of Equation (1) to the data. (Bottom) Discharge rate for the suppressor alone as a function of level for the same frequencies as on top. The continuous lines are least-squares fits of the Sachs and Abbas (1974) model of rate-level functions to the data. The horizontal line shows the rate criterion used in measuring suppression growth functions.

suppression thresholds were lower for the latter. The low-level plateau in the fitted curves varied by about 5 dB for different suppressor frequencies. Because, in principle, this plateau represents the CF tone level that meets criterion in the absence of a suppressor, these variations provide a measure of the repeatability of the PEST procedure over intervals of many minutes.

The bottom panel of Fig. 4 shows discharge rate as a function of the intensity of the suppressor alone for the same 4 frequencies as in the middle panel. The difference between the level where discharge rate begins to increase over spontaneous and the level where suppression begins to occur varies from less than 5 dB for the 0.21-kHz suppressor to over 25 dB for the 1.05-kHz suppressor. Thus, there appears to be no simple relation between excitation and suppression thresholds.

Fig. 5 shows similar data for an auditory-nerve fiber with a CF of 8.6 kHz. In this case, the suppression tuning curve was successfully measured both below and above the CF, which was typical for fibers with CFs between 2 and 20 kHz. Suppression growth functions were measured for 6 different frequencies. These data were well fitted by the functional description, and, again, there were obvious differences in the rates of growth of suppression depending on suppressor frequency. Rates of growth ranged from 0.26 dB/dB for the highest-frequency (13-kHz) suppressor to 2.3 dB/dB for the 1-kHz suppressor. Growth rates for below-CF suppressors were about twice as great for this fiber as for the low-CF fiber of Fig. 4, so that maximum suppression exceeded 50 dB in some cases. The bottom panel shows that discharge rates in response to the suppressors remained near spontaneous rate for all frequencies with the exception of the 4.8 kHz suppressor. Thus, a tone that produces virtually no increase in rate over spontaneous can suppress a CF tone by 40–50 dB.

Fig. 6 shows suppression growth data for a high-CF (21 kHz) fiber. The suppression tuning curve could be measured for frequencies below the CF, but not for frequencies above the CF. This result was not uncommon for fibers with CFs above 20 kHz. Nevertheless, crosses in the middle panel show that the 26-kHz tone, which was above the CF, could suppress the response to the CF tone by over 20 dB, confirming that the tuning curve algorithm is not the most sensitive way to

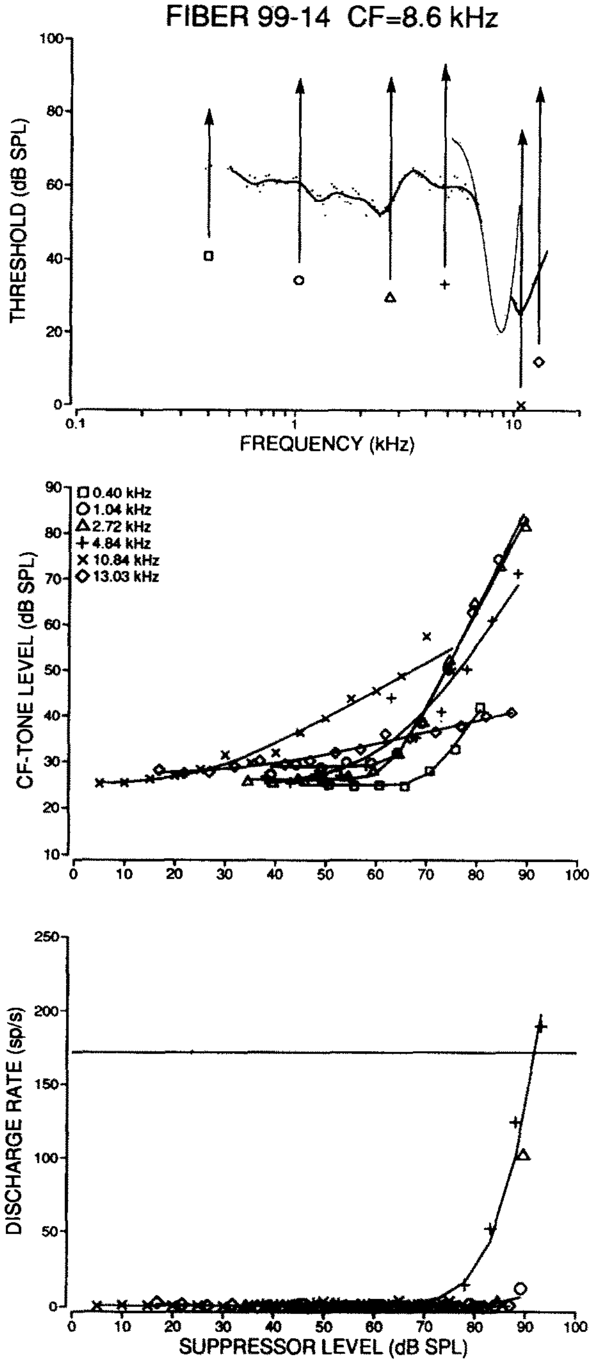

Fig. 5. Same as Fig. 4 for a medium-SR fiber with a CF of 7.9 kHz.

detect suppression. Both the rates of growth of suppression (ranging from 0.58 dB/dB for the 26-kHz tone to 3 dB/dB for the low-frequency suppressors) and the suppression magnitudes were similar to those for the 8.6-kHz fiber in Fig. 5. Comparison of the middle and bottom panels shows that the 16-kHz tone (plusses) and the 4.3-kHz tone (triangles) produced similar amounts of suppression, even though discharge rate was much greater for the former than for the latter. Thus, the excitatory and suppressive effects of a tone do not appear to be related simply.

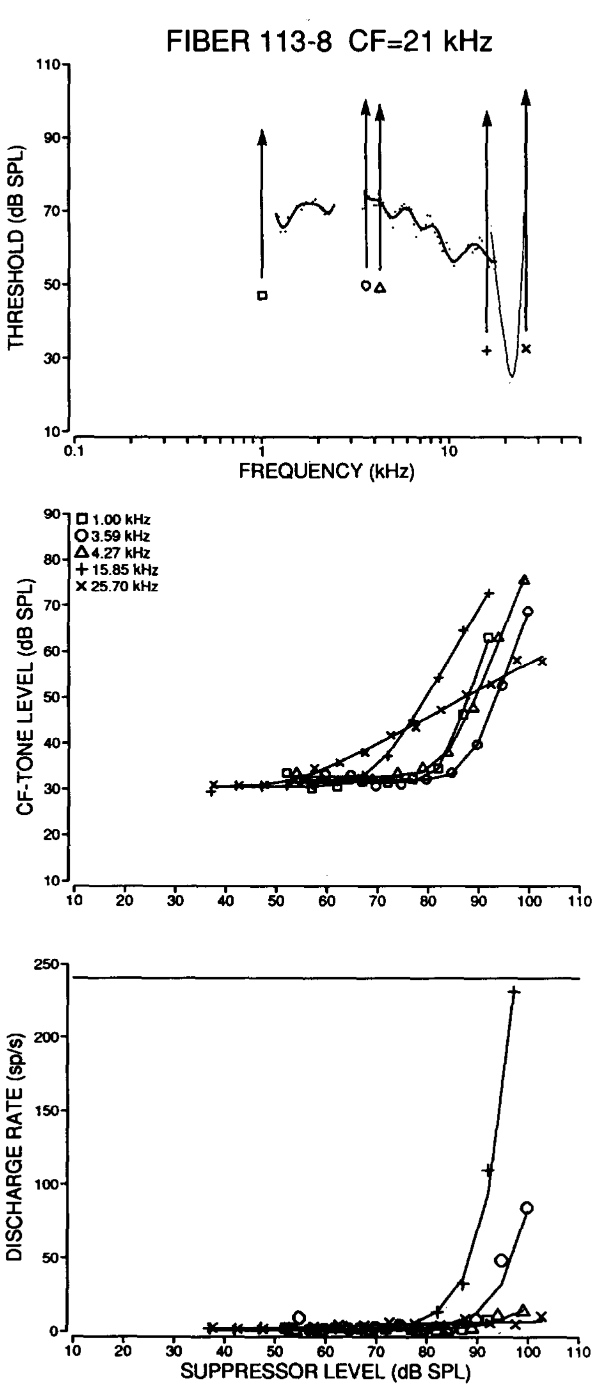

Fig. 6. Same as Fig. 4 for a medium-SR fiber with a CF of 21 kHz.

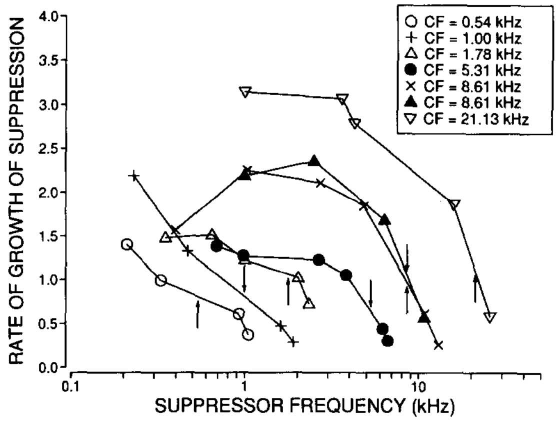

Fig. 7. Rate of growth of suppression as a function of suppressor frequency for 7 auditory-nerve fibers with different CFs. Data from the same fiber are connected by solid lines. Arrows point to the position of the fiber CF along the frequency axis.

Fig. 7 shows the rate of growth of suppression as a function of suppressor frequency for 7 auditory-nerve fibers for which suppression growth data were available for at least 4 frequencies. This sample includes the three fibers shown in Figs. 4–6. Arrows indicate the position of the CF for each fiber. Nearly all rates of growth are greater than 1 dB/dB for below-CF suppressors, and smaller than 1 dB/dB for above-CF suppressors. For each fiber, the rate of growth decreases monotonically with increasing suppressor frequency, with few exceptions such as the lowest frequency for the 8.6-kHz fiber (crosses). This particular estimate of the rate of growth was based on only a few data points (squares in Fig. 5). The decrease in rate of growth with suppressor frequency is always rapid near the CF but, for fibers with CFs above 1–2 kHz, there seems to be a low-frequency region in which the rate of growth is approximately constant. The growth rate in this plateau region increases with CF.

Effect of rate criterion

Our method for measuring suppression growth relies on the assumption that suppressors shift the rate-level function for a CF tone by the same amount regardless of the rate criterion at which shift is measured (Javel et al., 1978; Abbas, 1978; Costalupes et al., 1987). In order to examine the validity of this assumption, suppression growth functions were measured in two cats with a criterion of 33% of the maximum driven rate in addition to the usual 67% criterion. With the low criterion, the range of suppressor levels over which suppression could be measured was restricted because the PEST procedure failed as soon as the discharge rate for the suppressor approached criterion. In 25 auditory-nerve fibers for which suppression growth functions could be measured over a sufficient range of levels, rates of growth estimated with the low criterion were on the average 25% lower than those for the high criterion. These results are consistent with the observation by Costalupes et al. (1987) that rate-level functions for CF tones are made shallower by intense suppressors in addition to being horizontally shifted. Thus, our measurements of suppression growth are not completely criterion-independent, although the effects of criterion on rates of growth are small relative to those of suppressor frequency.

Correction for adaptation

The suppression growth data shown in Figs. 4–7 were not corrected for effects of adaptation, and therefore might somewhat overestimate the growth of suppression. For about 100 fibers, contact was long enough to provide adaptation growth data used for correcting the suppression growth functions. Figure 8 shows both corrected and uncorrected suppression growth functions for a 0.53-kHz auditory-nerve fiber in which effects of the correction were particularly clear. The general trend in the data is similar for corrected and uncorrected data, and the data are well fitted by Equation (1) in both cases. There are however some differences between corrected and uncorrected functions. For the 1-kHz suppressor (plusses), which evoked only low discharge rates (bottom panel), correction did not change the rate of growth of suppression very much. For the 0.19-kHz (squares) and 0.88-kHz (triangles) suppres-

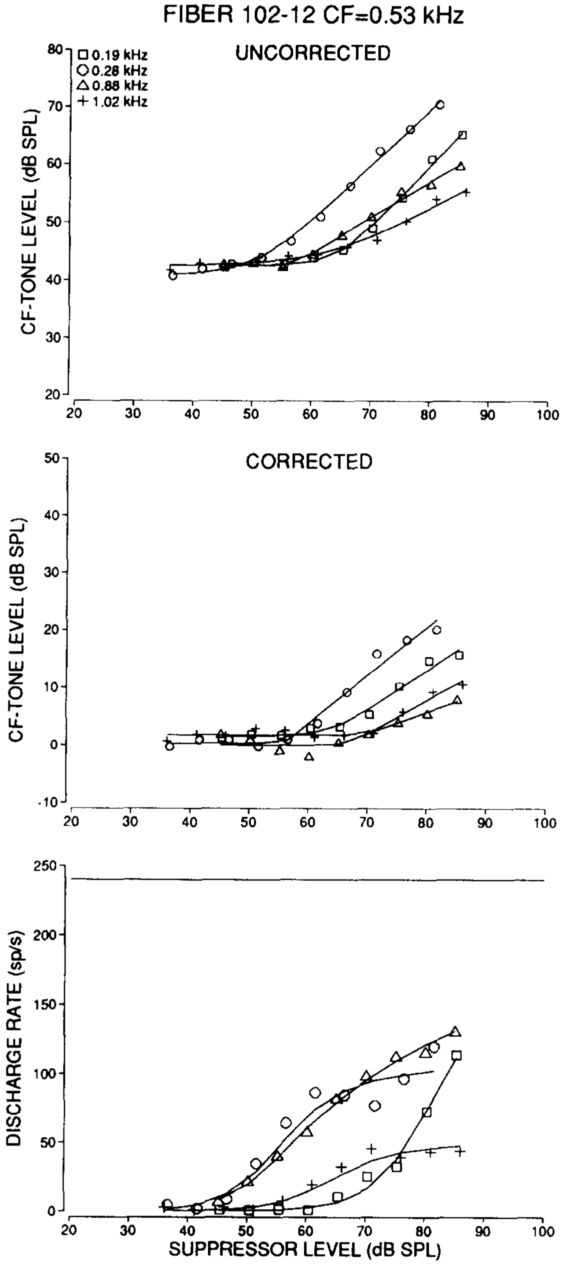

Fig. 8. (Top) Uncorrected suppression growth functions for a low-SR fiber with a CF of 0.53 kHz. Plotting conventions are as in Fig. 4. (Center) Same suppression growth functions as on top after correction for effects of adaptation by means of the adaptation growth function for a 0.88 kHz adaptor, using the method of Fig. 3. (Bottom) Rate-level functions for the same suppressor frequencies as on top.

sors, which produced large discharge rates, correction markedly decreased the rates of growth of suppression as well as the suppression magnitudes. For the 0.28-kHz suppressor (circles), which also produced large discharge rates, correction did not change the rate of growth, but raised the suppression threshold, also resulting in decreased suppression magnitudes. Thus, as expected, correction seems to have large effects only when the discharge rate in response to the suppressor is appreciably above spontaneous rate.

In order to systematically assess the effects of correction on the rates of growth of suppression, the difference between corrected and uncorrected growth rates was examined as a function of the maximum discharge rate produced by the suppressor. So long as the discharge rate for the suppressor was less than 40% of the criterion used in measuring suppression growth functions, corrected and uncorrected growth rates differed by no more than a few percent. When the response to the suppressor exceeded 40% of criterion, differences in growth rates of as much as 30–50% were sometimes found. The remainder of this report (Figs. 9–13) shows growth rate data based either on corrected suppression growth functions, or on uncorrected functions for which the response to the suppressor was less than 40% of criterion.

Population data

The single-fiber data of Fig. 7 suggest that, for a given CF, the rate of growth of suppression decreases with increasing suppressor frequency. One way to express this trend for a population of auditory-nerve fibers with different CFs is to normalize the suppressor frequency with respect to the CF. Fig. 9 shows the rate of growth of suppression as a function of normalized suppressor frequency for all auditory-nerve fibers. Auditory-nerve fibers were split into two groups depending on whether CF is below or above 2 kHz because single-fiber data such as those of Fig. 7 suggested that the frequency dependence of the rate of growth of suppression differs for the two groups. Indeed, the data for low-CF fibers can be fitted by a single straight line, whereas, for high-CF fibers, a better fit is obtained with two separate lines below and above the CF. Table I shows that the slopes of the regressions of rate of growth on the logarithm of normalized frequency were significantly smaller than zero for all three frequency ranges (CF < 2 kHz, CF > 2 kHz and F_S < CF, and CF > 2 kHz and F_S > CF). Thus, normalized suppressor frequency is a key variable for predicting rates of growth of suppression.

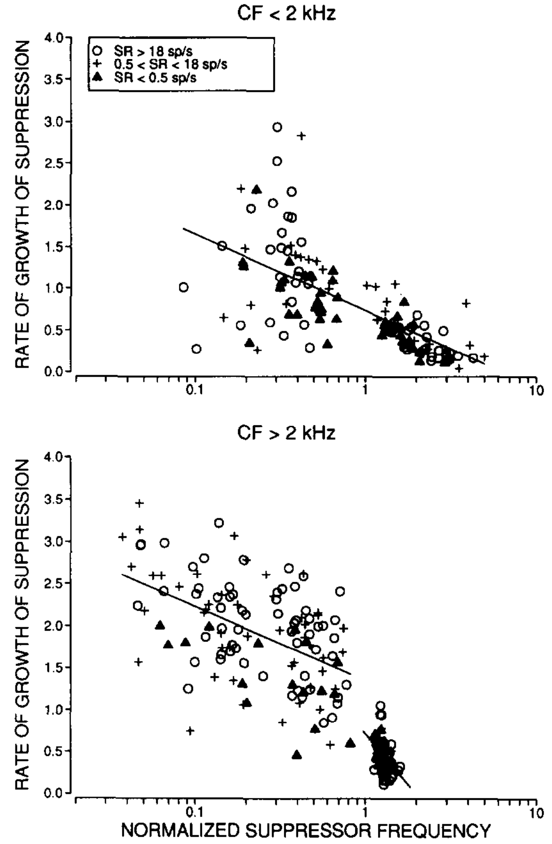

Fig. 9. Rate of growth of suppression as a function of normalized suppressor frequency for all auditory-nerve fibers with CFs below (top) and above (bottom) 2 kHz. Normalized frequency is the ratio of the suppressor frequency to the CF. Each point represents the rate of growth for one auditory-nerve fiber, estimated either from a corrected suppression growth function, or from an uncorrected function for which the response to the suppressor was less than 40% of criterion. Symbols refer to the three groups of fibers defined on the basis of spontaneous discharge rate. The straight lines were fitted to the data by the least-squares method. In the bottom panel, two lines were fitted separately for above-CF and below-CF suppressors.

In Fig. 9, there is considerable overlap in rates of growth of suppression for the three groups of fibers defined on the basis of spontaneous dis-

TABLE I

REGRESSIONS OF THE RATE OF GROWTH OF SUPPRESSION ON THE LOGARITHM OF NORMALIZED FREQUENCY F_S/CF. SIGNIFICANCE AND 't' REFER TO A STATISTICAL TEST OF THE NULL HYPOTHESIS THAT THE SLOPE IS ZERO

Range	N	Intercept	Slope	Correlation	t	Significance
CF < 2 kHz	127	0.74	−0.91	0.654	9.68	$P < 0.001$
CF > 2 kHz, F_S < CF	125	1.35	−0.88	0.509	6.56	$P < 0.001$
CF > 2 kHz, F_S > CF	81	0.72	−2.39	0.438	4.33	$P < 0.001$
$F_S = 1$ kHz	63	0.84	−1.48	0.909	16.99	$P < 0.001$

charge rate, although low-SR fibers seem to have somewhat lower rates of growth than the other two groups for below-CF suppressors and CFs above 2 kHz. In order to systematically examine these differences, analyses of covariance were carried out with the logarithm of normalized frequency as the control variable, and SR group as the categorical variable. In effect, this technique factors out the effect of frequency before testing for differences in rates of growth among the 3 SR groups. Separate analyses were conducted for each of the three ranges of frequencies over which different regression lines were fitted in Fig. 9. No significant effect of SR group on rate of growth was found for either CFs below 2 kHz (F[2,123] = 1.701, $P = 0.37$), or for above-CF suppressors and CFs above 2 kHz (F[2,77] = 0.26, $P = 0.46$). For CFs above 2 kHz, a significant effect was found for below-CF suppressors (F[2,121] = 7.57, $P < 0.002$). Overall, this analysis confirms the visual impression given by Fig. 9 that spontaneous rate is not a major factor in predicting rates of growth, although it does have some effect for high-CF fibers and suppressors below the CF. Of course, suppression magnitudes are greater for low-SR and medium-SR fibers than for high-SR fibers because the range of levels over which suppression grows is larger for the former than for the latter (Schmiedt, 1982).

The large variability in Fig. 9 may be partly due to pooling data from many cats. Fig. 10 shows the rate of growth of suppression as a function of normalized suppressor frequency for fibers with CF's below 2 kHz for each of the 3 cats from which the most data were available. The general downward trend in the frequency dependence of the rate of growth is similar for all 3 cats. How-

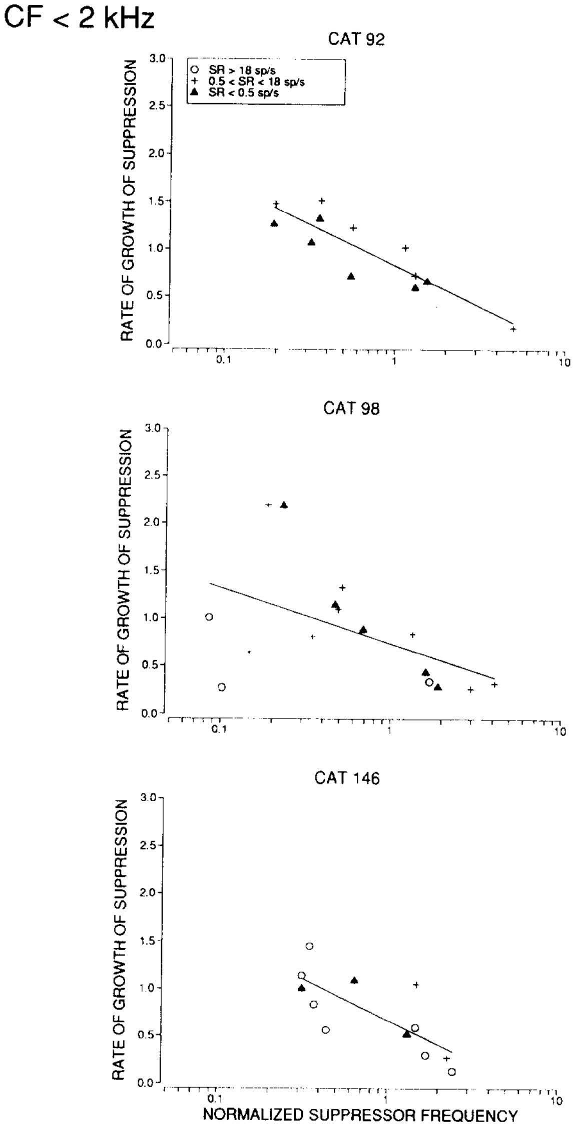

Fig. 10. Rate of growth of suppression of fibers with CFs below 2 kHz as a function of normalized suppressor frequency for 3 cats. Plotting conventions are as in Fig. 9.

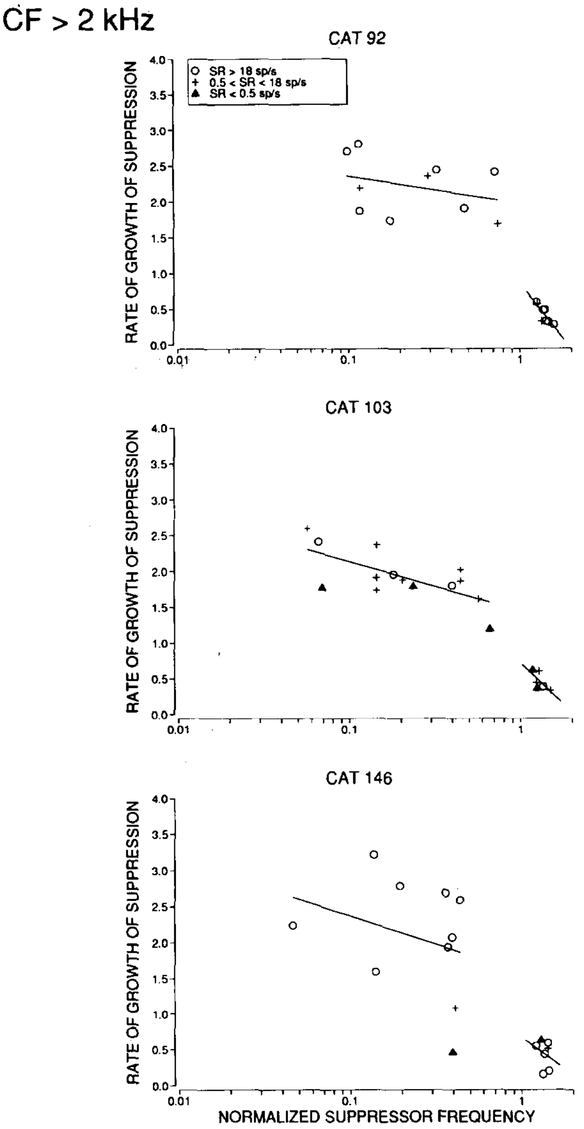

Fig. 11. Same as Fig. 10 for fibers with CF's above 2 kHz. Two of the cats (92 and 146) are the same as in Fig. 10. This could not be done for the third cat (103) due to a lack of data.

ever, the variability in the data differs for the three cats, being smaller than that of the pooled data of Fig. 9 for Cats 92 and 146, and about comparable to that of the pooled data for Cat 98. Fig. 11 shows similar data from individual cats for fibers with CF's above 2 kHz. Again, the mean trends are similar for all 3 cats, and the data show large differences in variability. Variability is small for Cats 92 and 103, and large for Cat 146. An analysis of covariance was carried out for rate of growth of suppression, with the logarithm of normalized frequency as the control variable and cat number as the categorical variable. Separate analyses were conducted for each of the three frequency ranges over which different regression lines were fitted in Fig. 9. No significant effects of cat number were found for either fibers with CFs below 2 kHz (F[24,101] = 1.62, $P = 0.10$), or for above-CF suppressors and CFs above 2 kHz (F[22,57] = 1.14, $P = 0.67$). A significant effect was found for below-CF suppressors and CFs above 2 kHz (F[22,101] = 2.01, $P = 0.021$). However, the statistical significance of the effect could be drastically altered by eliminating a few data points that appeared to be 'outliers'. Overall, this analysis suggests that between-cat variability in suppression growth is not the major cause for the scatter seen in Fig. 9, although it may contribute somewhat for below-CF suppressors in fibers with CFs above 2 kHz.

The variability seen in Fig. 9 may also be due, in part, to pooling data from fibers with widely different CFs. Indeed, the single-fiber data of Fig. 7 suggest that the rate of growth of suppression for suppressors well below the CF may increase with CF. The top panel of Fig. 12 shows the rate of growth of suppression for 1-kHz suppressors as a function of CF for many auditory-nerve fibers. This suppressor frequency is the one for which most data were available. The rate of growth clearly increases with CF, an observation which is confirmed by the slope of the regression line being significantly greater than zero (Table I). This analysis does not separate the effects of CF and suppressor frequency on the rates of growth because, if the suppressor frequency F_S is fixed at 1 kHz, the normalized frequency F_S/CF varies inversely with the CF. However, the fact that the slope of the regression on the logarithm of the CF (1.48) is appreciably greater than that of the regression on the logarithm of normalized frequency in Fig. 9 (0.88) suggests that there may be an effect of CF independent from that of normalized frequency.

One way to test this hypothesis is to examine how the maximum rate of growth of suppression depends on CF for suppressors well below the CF. In practice, the maximum rate of growth among below-CF suppressors was computed for all fibers

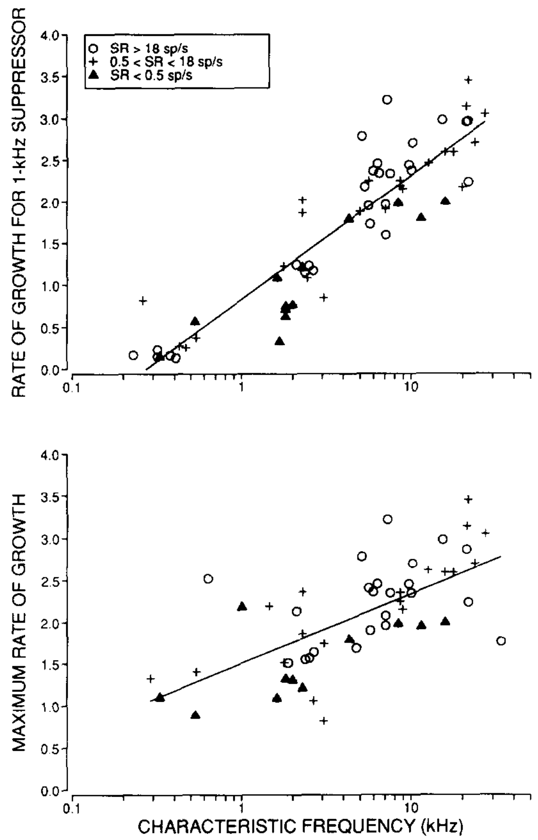

Fig. 12. (Top) Rate of growth of suppression as a function of CF for 1-kHz suppressors. (Bottom) Maximum rate of growth of suppression as a function of CF for all auditory-nerve fibers in which suppression growth measurements were available for at least two frequencies below the CF. In both panels, solid lines are least-squares fits to the data points.

in which suppression growth functions were available for at least two frequencies below the CF. The bottom panel of Fig. 12 shows that this maximum rate of growth slowly increases with CF. Again, the slope of the regression line (0.83) is significantly greater than zero ($t[51] = 6.45$, $P < 0.001$), confirming that the rate of growth of suppression increases with CF for low-frequency suppressors.

Quantitative description

In order to summarize the effects of CF and suppressor frequency on rates of growth of suppression, a 5-parameter model was fitted to the suppression growth data. This model expresses the rate of growth of suppression α as a function of CF and suppressor frequency F_S, both in kHz, by means of the equation:

$$\alpha = 1.44 + 0.81 \log_{10} CF - (1.46 + 1.43 \log_{10} CF) \times g(F_S/CF), \qquad (2)$$

where

$$g(F_S/CF) = \begin{bmatrix} \log_{10}(F_S/CF) & \text{if } F_S/CF > 0.32 \\ 0 & \text{otherwise} \end{bmatrix} \qquad (3)$$

The top panel of Fig. 13 shows the rate of growth predicted by the model as a function of suppressor frequency for 5 different CFs (shown by arrows). At each CF, the rate of growth increases with decreasing suppressor frequency for frequencies near the CF, reaching a plateau at 1.6 octave below the CF. Both the height of the low-frequency plateau, and the steepness of the dependence of the rate of growth on frequency near the CF increase with increasing CF. These model predictions resemble the single-fiber data of Fig. 7.

The bottom panel of Fig. 13 replots the data of Fig. 9 as a function of normalized suppressor frequency after the dependence on CF predicted by the model was subtracted out for each data point. Examination of Equation (2) shows that, after elimination of the CF dependence, model predictions for the corrected rate of growth α_c as a function of normalized suppressor frequency are given by the expression:

$$\alpha_C = 1.44 - 1.46 g(F_S/CF) \qquad (4)$$

Equation (4) is plotted in Fig. 13 as the solid line superimposed on the data points. Although there is considerable scatter, the model captures the main trends in the corrected rates of growth. In particular, the corrected rates of growth do seem to plateau for low suppressor frequencies, as do the single-fiber data of Fig. 7. Thus, the lack of a low-frequency plateau in Fig. 9 can be attributed to pooling data from fibers with different CF's.

The 5-parameter model predicted 75% of the variance among the 330 measurements of rates of growth of suppression. The data were also fitted

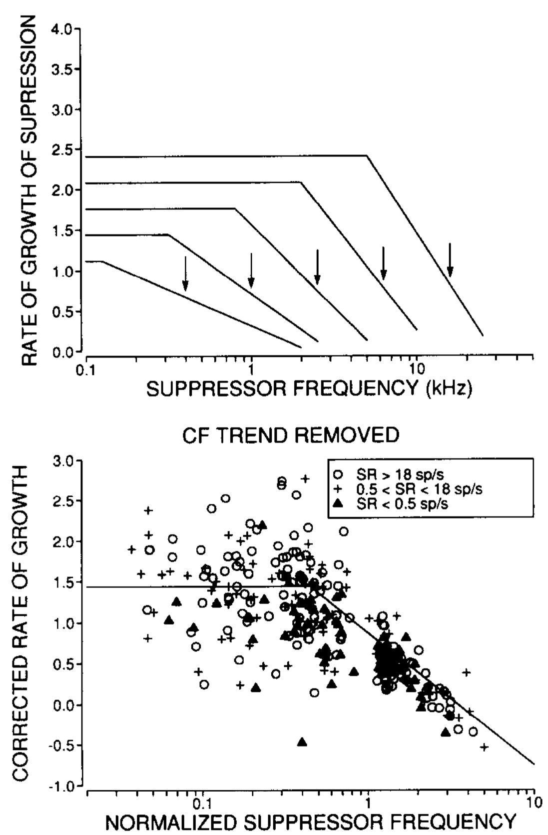

Fig. 13. (Top) Model predictions for rate of growth of suppression as a function of suppressor frequency for 5 different CFs (0.4, 1.0, 2.5, 6.3 and 16 kHz). Arrows point to the position of each CF along the frequency axis. (Bottom) Corrected rate of growth of suppression as a function of normalized suppressor frequency for all auditory-nerve fibers. Corrected rates of growth were derived by subtracting out from each data point in Fig. 9 the dependence on CF predicted by the model, i.e. the expression $(0.81-1.43\ g(F_S/CF))\log_{10}$ CF in Equation (2). The solid lines show model predictions for the dependence of the corrected rate of growth on normalized frequency, as defined by Equation (4).

with simpler models in which there was no low-frequency plateau, or the height of the plateau was the same for all CFs, or the slope of the dependence of rate of growth on normalized frequency did not vary with CF. Statistical analyses showed that these 4-parameter models provided significantly poorer fits to the data than the 5-parameter model ($F[326,327] > 1.34$, $P < 0.006$). On the other hand, a more complex model that included a smooth transition between the low-frequency-plateau and the high-frequency, falling line failed to improve the fit. Thus, the 5-parameter model represents a reasonable compromise between complexity and goodness of fit.

To summarize the data shown in Fig. 9–13, rates of growth of suppression depend on both CF and the frequency separation between the suppressor and the CF. For suppressors near the CF, the rate of growth decreases markedly with increasing suppressor frequency. However, the rate of growth reaches a plateau for suppressor frequencies well below the CF. The rate of growth in this plateau region increases slowly with increasing CF, as does the steepness of the dependence of rate of growth on suppressor frequency near the CF. Rates of growth of suppression do not appear to vary strongly either among cats or with spontaneous discharge rate although small effects were found for high-CF fibers and below-CF suppressors.

Discussion

Comparison with other physiological studies of suppression

Since Sachs and Kiang (1968) reported finding two-tone rate suppression for all the auditory-nerve fibers that they studied in the cat, there has been some controversy as to whether suppression might be lacking for certain CF regions in some mammals (Arthur et al., 1971; Harris, 1979; Fahey and Allen, 1985; Costalupes et al., 1987; Prijs, 1989). For example, Harris (1979) reported that only a small fraction of fibers with CF's below 3 kHz showed suppression for below-CF tones in the chinchilla, while Costalupes et al. (1987) found below-CF suppression for all the fibers that they studied in the same species. Figs. 4 and 6 show instances in which a suppression threshold could not be measured by an automatic tracking procedure (Kiang et al., 1970), while tones at the same frequency shifted the rate-level function for a CF tone by more than 30 dB. Thus, statements concerning the nonexistence of suppression should be scrutinized for measurement methods and suppression criteria. Our results do show clearly that suppression magnitudes vary strongly with CF and suppressor frequency. Suppression was strongest for tones below the CF of fibers with CF's above 2 kHz: Under these conditions, suppression magnitudes of 40–50 dB were routinely observed. For above-CF suppressors in any CF region, and for suppressors below the CF of low-CF fibers, suppression magnitudes rarely exceeded 20–30 dB, and were often smaller than 10 dB. These results are consistent with the observations of Fahey and Allen (1985) that CF tones 10 dB above threshold could always be suppressed to spontaneous rate by suppressors below the CF of high-CF fibers, but not by above-CF suppressors or for low-CF fibers. There may in addition be species differences in the relative prominence of below-CF and above-CF suppression (Prijs, 1989). For example, Costalupes et al. (1987) rarely found suppression magnitudes of over 30 dB in the chinchilla, even below the CF. Studies in which the same techniques are used to measure suppression in different species are needed to resolve these issues.

Our results on the growth of two-tone rate suppression with suppressor level confirm and extend those of previous physiological studies. Abbas and Sachs (1976), using the fractional response to measure suppression, showed that suppression grows more rapidly with suppressor level for below-CF suppressors than for above-CF suppressors. Consistent with our results, they further found that the rate of growth of suppression decreases with increasing suppressor frequency above the CF. However, they failed to find such a frequency dependence for below-CF suppressors, in contradiction to the results of Fig. 9 and 13. Perhaps most of their data were from the low-frequency plateau region in which rates of growth of suppression do not vary greatly with frequency (Fig. 13), or differences in rates of growth were obscured by the limited dynamic range of the fractional response. Fahey and Allen (1985), using the shift in the threshold for a tone at CF to measure suppression, found rates of growth of suppression of 1–3 dB/dB for suppressors below the CF. This range fits well with that of Fig. 9 for the same stimulus condition. Costalupes et al. (1987), using shifts in normalized rate-level functions for tones at the CF to measure suppression in the chinchilla, also found ranges of rates of growth of suppression that were similar to ours both below and above the CF. However, their results differ from ours in that they found no obvious variation in rates of growth with frequency for either below-CF or above-CF suppressors (their Fig. 6). While species differences cannot, of course, be ruled out, it is also possible that their pooling data from fibers with many different CFs, as well as the large variability in their measurements obscure trends that might be detected in a larger set of data. Both the single-fiber data of Fig. 7 and the statistical analyses of the pooled data of Fig. 9 and 13 show conclusively that, in the cat, the rate of growth of suppression decreases with increasing suppressor frequency both above and below the CF. In addition, these results show that the growth of rate suppression depends on CF, an effect which has not been reported before. This effect is consistent with the view that nonlinear tuning mechanisms might differ for different parts of the cochlea.

The view that a suppressor produces an approximately constant shift in the rate-level function for a CF tone is widely accepted based on evidence presented in the literature (Javel et al., 1978; Sachs and Abbas, 1976; Abbas, 1978). However, recent reports from auditory-nerve fibers have suggested that this property might not strictly hold, particularly for low-SR fibers (Sokolowski et al., 1989), and when the suppressor produces a large excitatory response (Costalupes et al., 1987). Our observation that rates of growth of suppression depend somewhat on the rate criterion used in the PEST procedure supports the notion that rate-level functions for CF tones are not completely parallel in the presence of suppressors with different intensities. Our finding that, in certain conditions, rates of growth of suppression are lower for the low-SR group than for the other groups is also consistent with the view that suppression is smaller for high CF tone levels than for low levels (Sokolowski et al., 1989). These observations add to a growing body of evidence from auditory-nerve fibers (Frezza, 1978; Deng and Geisler, 1985), hair-cell receptor potentials (Cheatham and Dallos, 1989), and basilar membrane motion (Robles et al., 1986, 1989) that suppression does not act like a simple attenuation of the excitatory tone.

Our data on the rate of growth of two-tone rate suppression resemble the synchrony suppression data of Javel et al. (1983) in many respects (Fig. 9 and their Fig. 5). Both studies show that the rates of growth of suppression are greater for below-CF suppressors than for above-CF suppressors, that rates of growth decrease with increasing frequency for both below-CF and above-CF suppressors, and that this frequency dependence differs for low-CF and high-CF fibers. These similarities suggest that the physiological mechanisms that underlie the frequency dependence in the growth of suppression may be the same for rate and synchrony suppression. There are however clear differences between rate and synchrony suppression. Javel et al. (1983) pointed out the similarity between the frequency dependence of synchrony suppression thresholds and that of single-tone synchrony thresholds, suggesting that the ability of a tone to suppress is closely related to its ability to produce phase-locked discharges. The present study shows that tones can produce over 40–50 dB of suppression without increasing discharge rate over spontaneous (Fig. 5), and that two tones that produce the same suppression can differ greatly in their discharge-rate response (Fig. 6). These results, which are consistent with previous observations (Sachs and Kiang, 1968; Schmiedt, 1982; Fahey and Allen, 1985) suggest that there exists a frequency selective stage of processing between the nonlinearities that produce rate suppression and the responses of auditory-nerve fibers (Pfeiffer, 1970; Duifhuis, 1976; Hall, 1977). Thus, it may be useful to think of suppression in auditory-nerve fibers as resulting from two types of nonlinearities: Nonlinearities involving cochlear mechanical events (Robles et al., 1986, 1989) which produce both rate and synchrony suppression and have a complex frequency dependence, and nonlinearities involving hair-cell saturation and/or synaptic gain-control mechanisms (Johnson, 1974; Geisler, 1985) which produce only synchrony suppression and do not depend strongly on frequency. The first type of suppression dominates for suppressors that are far from the CF in normal animals, while the second one dominates near the CF and in damaged cochleas.

Comparison with psychophysics

It is well known that the psychophysical masked threshold for a tone signal in the presence of a low-frequency masker grows by more than 1 dB when the masker level is increased by 1 dB (Wegel and Lane, 1924; Egan and Hake, 1950; Maiwald, 1967). This 'upward spread of masking' resembles our observation that the rate of growth of suppression is greater than 1 dB/dB for below-CF suppressors if masking is assumed to be due to the masker suppressing the response to the signal in fibers tuned to the signal frequency. Similarly, when the signal is lower in frequency than the masker, masking grows slower than 1 dB/dB, consistent with our observations for above-CF suppressors. However, masking cannot always be due to two-tone rate suppression because it is maximum when the masker and the signal are close in frequency, whereas rate suppression does not occur for suppressors near the CF. In this condition, masking may be excitatory, in the sense that the fibers tuned to the signal frequency respond to the masker rather than to the signal. A recent study (Delgutte, 1990a) in which masked thresholds of auditory-nerve fibers were compared for simultaneous and nonsimultaneous techniques in order to separate excitatory and suppressive masking concluded that, for a 1-kHz tone masker, the contribution of suppression to masking is largest for signal frequencies well above the masker and for high masker levels. This stimulus condition is one in which particularly large suppression magnitudes were found in the present study. However, the complex dependence of the rate of growth of suppression on both CF and suppressor frequency suggests that the contribution of suppression to masking may show a somewhat different pattern for maskers with different frequencies. A model that simulates the dependence of suppression growth on CF and frequency is necessary to make detailed predictions of masking on the basis of physiological data (Delgutte, 1989, 1990b).

Under certain nonsimultaneous masking conditions, the psychophysical masked threshold of a tone signal can be lower for a two-tone masker than for one of its two components (Houtgast, 1974; Shannon, 1976). This unmasking phenomenon is thought to be due to the suppression of one component of the masker by the other (Houtgast, 1974). Duifhuis (1980) used the pulsation threshold technique to measure the growth of unmasking with the intensity of the 'suppressor' component of the masker. The 'excitor' component of the masker and the tone signal were always at the same frequency. This situation is analogous to our physiological suppression experiments if the signal is assumed to probe the activity of the auditory-nerve fibers that are tuned to its frequency. With this interpretation, the general pattern of Duifhuis's results resembles our results. Specifically, rates of growth of unmasking were greater than 1 dB/dB for suppressors below the excitor, and smaller than 1 dB/dB for suppressors above the excitor. For the latter condition rates of growth of unmasking decreased with increasing suppressor frequency. However, Duifhuis' results differ from ours in that such a frequency dependence was not found for suppressors below the excitor, in contrast to our results for below-CF suppressors. Thus, despite the general similarity between our results and those of Duifhuis (1980), close examination reveals some discrepancies. These discrepancies might be due to species differences, or to central contributions to unmasking (e.g. lateral inhibition), or to changes in the population of fibers that are involved in psychophysical signal detection depending on stimulus conditions. Again, an accurate model of suppression would help in studying some of these possibilities.

Models of suppression

One of the earliest models of two-tone rate suppression was the bandpass nonlinearity (BPNL) model proposed by Pfeiffer (1970), and studied by Duifhuis (1976). This model consists of a compressive, memoryless nonlinearity 'sandwiched' between two linear, bandpass filters. As pointed out by Sachs and Abbas (1976), this model is inconsistent with physiological data because it predicts no frequency dependence in the rate of growth of suppression. Goldstein (1988, 1989) added a second, parallel channel to the BPNL model in order to simulate the strong suppression for below-CF suppressors. His multiple bandpass nonlinear (MBPNL) model does predict the differences in rates of growth of suppression between below-CF and above-CF suppressors. To some extent, it also simulates the gradual decrease in rates of growth with suppressor frequency that was observed both below and above the CF, but has difficulties for suppressor frequencies well above the CF, where the predicted rates of growth are too large. In order to further test the MBPNL model, two independent estimates of the compression factor v of the nonlinearity were obtained for each auditory nerve fiber from suppression growth functions for below-CF and above-CF suppressors. There was only a very weak correlation (0.147) between below-CF compression and above-CF compression for a sample of 145 auditory-nerve fibers. This means that the MBPNL model's notion that rates of growth of suppression for below-CF and above-CF suppressors originate in a single nonlinearity accounts only for a small fraction of the variance in rates of growth. Thus, while the MBPNL model qualitatively predicts a wide variety of nonlinear phenomena in auditory-nerve responses, it fails to account for certain features of the present suppression data.

The phenomenological model of Sachs and Abbas (1976) is not tested by the present series of experiments because both the model and our experimental design are based on the assumption that suppressors produce criterion-independent shifts in rate-level functions for CF tones. In fact, our measurements of rates of growth of suppression can be considered as estimates of the frequency-dependent growth parameter α in the Sachs and Abbas model. An obvious defect of this model is that it does not explicitly make predictions for stimuli with more than two frequency components. A generalization of the Sachs and Abbas model to stimuli with arbitrary spectra that is consistent with the present results has been presented recently (Delgutte, 1990b).

Another class of models that have been successful in predicting two-tone rate suppression are nonlinear models of basilar-membrane motion (Kim et al., 1973; Hall, 1977, 1979; Jau and Geisler, 1983; Zwicker, 1986; see Kim, 1986 for a review). The Hall (1977) model is a transmission line analog of the cochlea with nonlinear damping elements that increase with basilar-membrane velocity. By itself, this transmission line failed to predict two-tone rate suppression below the CF because low-frequency tones that were sufficiently intense to suppress the response to a CF tone always produced a greater response than that to the CF tone (Hall, 1977). Hall (1977) solved this problem by introducing a second filter that reduced the response to the suppressor at the place of the excitor. Thus, the Hall model is similar to the BPNL model, except that the first filter and the nonlinearity are combined into a nonlinear transmission line (Kim, 1986). This model does simulate the differences between below-CF suppressors and above-CF suppressors that were observed by Abbas and Sachs (1976). It is further apparent from Hall's (1979) Fig. 5 that the rate of growth of suppression gradually decreases with suppressor frequency both below and above the CF, consistent with the present physiological results. However, rates of growth do not appear to vary with frequency by more than a factor of two in the Hall model, in contrast with the variations by a factor greater than five for many of our fibers (Fig. 7). Furthermore, suppression magnitudes do not exceed 20 dB in the Hall model, well below the 40–50 dB magnitudes that are routinely observed for below-CF suppressors. Thus, while the Hall model makes qualitatively correct predictions about many aspects of two-tone suppression, it severely underestimates the magnitudes of certain effects. It would be interesting to establish whether adjustments of either the frequency selective elements or the form of the nonlinearity in the Hall model might yield better predictions.

Jau and Geisler (1983) used a nonlinear transmission line analog of the cochlea in which damping increased with basilar membrane velocity integrated over a longitudinal portion of the cochlea rather than at a single place. With such longitudinal coupling, they were able to obtain two-tone rate suppression below the CF without introducing a second filter. However, the suppression magnitudes were very small (less than 5 dB), and the rates of growth of suppression were much smaller than 1 dB/dB, in contradiction to our data. Zwicker (1986) replaced the nonlinear damping in the Hall model by an active, nonlinear feedback circuit intended to simulate the action of the outer hair cells. In this model, intense, off-CF tones turn off the enhancement that the active feedback produces in the responses to CF tones, resulting in a form of synchrony suppression which Zwicker called 'de-enhancement'. However, it is obvious from Zwicker's (1986) Figs. 3 and 4 that, for suppressors below the CF, the response to the suppressor must be larger than the response to the CF tone in order to obtain suppression, so that the model does not produce rate suppression. Thus, neither Jau and Geisler's (1983) longitudinal coupling, nor Zwicker's (1986) active feedback seem to overcome the difficulties that nonlinear cochlear models have with two-tone rate suppression for below-CF suppressors. Despite recent progress in understanding cochlear mechanisms, it may be some time before physically-motivated models can accurately simulate even the limited set of phenomena presented in this paper.

Placing these models into the broader context of predicting other nonlinear auditory phenomena besides suppression, both the Hall (1977) model and the Zwicker (1986) model qualitatively simulate combination tones, level-dependent changes in tuning, and, with minor modifications in the case of the Hall model (Furst and Lapid, 1988), otoacoustic emissions. Thus, given the difficulties that the Zwicker model has with rate suppression, the type of model that best simulates a wide range of nonlinear phenomena remains the nonlinear cochlear models with second filters such as Hall's (1977, 1979). However, none of the cochlear models predicts the rapid changes in discharge rates and phase shifts that occur in the responses of auditory-nerve fibers to single tones at high intensities (Liberman and Kiang, 1984). These properties are predicted by Goldstein's (1989) MBPNL model, which, on the other hand, has difficulties with propagated combination tones, otoacoustic emissions, and certain aspects of two-tone suppression. Thus, no existing model is able to simulate even qualitatively all these functionally-important nonlinear auditory phenomena.

In recent years, there has been a great deal of interest in peripheral auditory models for speech processing (e.g. Dolmazon et al., 1982; Allen, 1985; Delgutte, 1986b; Deng and Geisler, 1987; Shamma, 1988; Seneff, 1988). One motivation for these models is to serve as front-ends to speech recognition systems in the hope of improving the performance and robustness of these systems (Ghitza, 1988). Although most of these models predict a form of synchrony suppression, none of them, with the possible exception of Deng and Geisler (1987), is able to produce rate suppression. The present results vividly show that rate suppression is a large effect that depends in a complex manner on stimulus and fiber parameters. In particular, the prominence of below-CF suppression suggests that the first formant of speech may considerably suppress the responses of auditory-nerve fibers tuned to the second and third formant frequencies (Sachs and Young, 1980). In fact, if synchrony information were not used by the central processor for frequencies above a few hundred Hz, it would be more important for speech-processing models to simulate rate suppression rather than the form of synchrony suppression available in existing models. Until these phenomena are accurately simulated by future generations of models for speech processing, any conclusion as to the possible contribution of peripheral auditory models to automatic speech recognition is premature.

Acknowledgements

I thank M.F. Bourgeois, L.W. Dodds, S. Pierce and P. Riley for surgical assistance, B.E. Norris for help with the figures, and M. Furst, J. Goldstein, N.Y.S. Kiang, M.C. Liberman, and T.F. Weiss for critically reading the manuscript. This research was supported by NIH grant NS13126.

References

Abbas, P.J. (1978) Effects of stimulus frequency on two-tone suppression: A comparison of physiological and psychological results. J. Acoust. Soc. Am. 63, 1878–1886.

Abbas, P.J. and Sachs, M.B. (1976) Two-tone suppression in auditory-nerve fibers: Extension of a stimulus-response relationship. J. Acoust. Soc. Am. 59, 112–122.

Allen, J. (1985) Cochlear modeling. IEEE-ASSP Magazine 2, 3–29.

Arthur, R.M., Pfeiffer, R.R. and Suga, N. (1971) Properties of 'two-tone inhibition' in primary auditory neurones. J. Physiol. 212, 593–609.

Carney, L.H. and Geisler, C.D. (1986) A temporal analysis of auditory-nerve fiber responses to spoken consonant-vowel syllables. J. Acoust. Soc. Am. 79, 1896–1914.

Cheatham, M.A. and Dallos, P. (1989) Two-tone suppression in inner hair cell responses. Hearing Res. 40, 187–196.

Costalupes, J.A., Rich, N.C. and Ruggero, M.A. (1987) Effects of excitatory and nonexcitatory suppressor tones on two-tone rate suppression in auditory-nerve fibers. Hear. Res. 26, 155–164.

Costalupes, J.A., Young, E.D. and Gibson, D.J. (1984) Effects of continuous noise backgrounds on rate response of auditory-nerve fibers in cat. J. Neurophysiol. 51, 1326–1344.

Dallos, P. and Cheatham, M.A. (1977) Analog of two-tone suppression in whole nerve responses. J. Acoust. Soc. Am. 62, 1048–1051.

Delgutte, B. (1986a) Two-tone rate suppression in auditory-nerve fibers: Variations with suppressor level and frequency. Abstr. Assoc. Res. Otolaryngol., Clearwater, FL.

Delgutte, B. (1986b) Analysis of French stop consonants using a model of the peripheral auditory system. In: J.S. Perkell and D.H. Klatt (Eds.), Invariance and Variability in Speech Processes, Erlbaum, Hillsdale, NJ, pp. 163–177.

Delgutte, B. (1989) Physiological mechanism of masking and intensity discrimination. In: C.W. Turner (Ed.), Collected papers from the special session on 'Interactions between Neurophysiology and Psychoacoustics', 117th Meet. Acoust. Soc. Am., Syracuse, NY, pp 81–101.

Delgutte, B. (1990a) Physiological mechanisms of psychophysical masking: Observations from auditory-nerve fibers. J. Acoust. Soc. Am. 87, 791–809.

Delgutte, B. (1990b) Two-tone suppression in auditory-nerve fibers: A model and its psychophysical implications. Abtr.. Assoc. Res. Otolaryngol., St. Petersburg Beach, FL., p 192.

Deng, L. and Geisler, C.D. (1985) Changes in the phase of excitor-tone responses in cat auditory nerve fibers by suppressor tones and fatigue. J. Acoust. Soc. Am. 78, 1633–1643.

Deng, L. and Geisler, C.D. (1987) A composite auditory model for processing speech sounds. J. Acoust. Soc. Am. 82, 2001–2012.

Deng, L., Geisler, C.D. and Greenberg, S. (1987) Responses of auditory-nerve fibers to multiple-tone complexes. J. Acoust. Soc. Am. 82, 1989–2000.

Dolmazon (1982) Representation of speech-like sounds in the peripheral auditory system in light of a model. In: R. Carlson and B. Granstrom (Eds.), The Representation of Speech in the Peripheral Auditory System, Elsevier, Amsterdam, pp. 151–163.

Duifhuis, H. (1976) Cochlear nonlinearity and second filter: Possible mechanism and implications. J. Acoust. Soc. Am. 59, 408–423.

Duifhuis, H. (1980) Level effects in psychophysical two-tone suppression. J. Acoust. Soc. Am. 67, 914–927.

Egan, J.P. and Hake, H.W. (1950) On the masking pattern of a simple auditory stimulus. J. Acoust. Soc. Am. 22, 622–630.

Fahey, P.F. and Allen, J.B. (1985) Nonlinear phenomena as observed in the ear canal and at the auditory nerve. J. Acoust. Soc. Am. 77, 599–612.

Frezza, W.A. (1978) The effect of two-tone acoustic stimulation on the discharge rate of single auditory-nerve fibers. S.M. Thesis, Dept. of Electrical Engineering, Massachusetts Institute of Technology, Cambridge, MA.

Furst, M. and Lapid, M. (1988) A cochlear model for acoustic emissions. J. Acoust. Soc. Am. 84, 222–2220.

Geisler, C.D. (1985) Effects of a compressive nonlinearity in a cochlear model. J. Acoust. Soc. Am. 78, 257–260.

Geisler, C.D. and Sinex, D.G. (1980) Responses of primary auditory fibers to combined noise and tonal stimuli. Hear. Res. 3, 317–334.

Ghitza, O. (1988) Temporal non-place information in the auditory-nerve firing patterns as a front-end for speech recognition in a noisy environment. J. Phonetics 16, 109–123.

Goldstein, J.L. (1988) A model for active nonlinear frequency analysis. Abstr. Assoc. Res. Otolaryngol., p. 19.

Goldstein, J.L. (1990) Modeling rapid waveform compression in the basilar membrane as multiple-bandpass nonlinearity filtering. Hear. Res. 49, 39–60.

Goldstein, J.L. and Kiang, N.Y.S. (1968) Neural correlates of the aural combination tone $2f_1-f_2$. Proc. IEEE 56, 981–992.

Greenwood, D.D. (1986) What is 'synchrony suppression'? J. Acoust. Soc. Am. 79, 1857–1872.

Hall, J.L. (1977) Two-tone suppression in a nonlinear model of the basilar membrane. J. Acoust. Soc. Am. 61, 802–810.

Hall, J.L. (1979) Cochlear models: Two-tone suppression and the second filter. J. Acoust. Soc. Am. 67, 1722–1728.

Harris, D.M. (1979) Action potential suppression, tuning curves and thresholds: Comparison with single fiber data. Hear. Res. 1, 133–154.

Harris, D.M. and Dallos, P. (1980) Forward masking of auditory nerve fiber responses. J. Neurophysiol. 42, 1083–1107.

Houtgast, T. (1974) Lateral Suppression in Hearing. Academische Pers, Amsterdam.

Jau, Y.C. and Geisler, C.D. (1983) Results from a cochlear model utilizing longitudinal coupling. In: E. De Boer and M.A. Viergever (Eds.), Mechanics of Hearing, Martinus Nijhof, The Hague, pp. 169–176.

Javel, E. (1980) Coding of AM tones in the chinchilla auditory nerve: Implications for the pitch of complex tones. J. Acoust. Soc. Am. 68, 133–146.

Javel, E. (1981) Suppression of auditory-nerve responses I: Temporal analysis, intensity effects and suppression contours. J. Acoust. Soc. Am. 69, 1735–1745.

Javel, E., Geisler, C.D. and Ravindran, A. (1978) Two-tone suppression in auditory nerve of the cat: Rate-intensity and temporal analyses. J. Acoust. Soc. Am. 63, 1093–1104.

Javel, E., McGee, J., Walsh, E.J., Farley, G.R. and Gorga, M.P. (1983) Suppression of auditory-nerve responses II. Suppression threshold and growth, isosuppression contours. J. Acoust. Soc. Am. 74, 801–813.

Johnson, D.H. (1974) The response of single auditory-nerve fibers in the cat to single tones: Synchrony and average discharge rate. Doctoral Dissertation, Massachusetts Institute of Technology, Cambridge, MA.

Kiang, N.Y.S., Liberman, M.C., Sewell, W.F. and Guinan, J.J. (1986) Single unit clues to cochlear mechanisms. Hear. Res. 22, 171–182.

Kiang, N.Y.S. and Moxon, E.C. (1972) Physiological considerations in artificial stimulation of the inner ear. Ann. Otol. Rhinol. Laryngol. 81, 1–17.

Kiang, N.Y.S. and Moxon, E.C. (1974) Tails of tuning curves of auditory-nerve fibers. J. Acoust. Soc. Am. 55, 620–630.

Kiang, N.Y.S., Moxon, E.C. and Levine, R.A. (1970) Auditory-nerve activity in cats with normal and abnormal cochleas. In: G.E. Wolstenholme and J. Knight (Eds.), Sensorineural Hearing Loss, Churchill, UK, pp. 241–273.

Kiang, N.Y.S., Watanabe, T., Thomas, E.C. and Clark, L.F. (1965) Discharge patterns of single fibers in the cat's auditory nerve. Research Monograph No. 35, MIT Press, Cambridge, MA.

Kim, D.O. (1986) A review of nonlinear and active cochlear models. In: J.B. Allen, J.L. Hall, A. Hubbard, S.T. Neely and A. Tubis (Eds.), Peripheral Auditory Mechanisms, Springer Verlag, Berlin, pp. 239–247.

Kim, D.O., Molnar, C.E. and Pfeiffer, R.R. (1973) A system of nonlinear differential equations modeling basilar-membrane motion. J. Acoust. Soc. Am. 54, 1517–1529.

Liberman, M.C. (1978) Auditory-nerve response from cats raised in a low-noise chamber. J. Acoust. Soc. Am. 63, 442–455.

Liberman, M.C. and Kiang, N.Y.S. (1978) Acoustic trauma in cats: Cochlear pathology and auditorynerve activity. Acta Otolaryngol. Suppl 358, 1–63.

Liberman, M.C. and Kiang, N.Y.S. (1984) Single-neuron labeling and chronic cochlear pathology. IV. Stereocilia damage and alterations in rate- and phase-level functions. Hear. Res. 16, 55–74.

Maiwald, D. (1967) Beziehung zwischen Schallspektrum, Mithorschwelle und der Erregung des Gehors. Acustica 18, 69–80.

Pfeiffer, R.R. (1970) A model for two-tone inhibition in single cochlear-nerve fibers. J. Acoust. Soc. Am. 48, 1373–1378.

Pickles, J.O. (1984) Frequency threshold curves and simultaneous masking functions in single fibres of the guinea pig auditory nerve. Hear. Res. 14, 245–256.

Press, W.H., Flannery, B.P., Teukolsky, S.A. and Vetterling, W.T. (1988). Numerical Recipes in C, (Cambridge University Press, Cambridge).

Prijs, V.F. (1989) Lower boundaries of two-tone suppression regions in the guinea pig. Hear. Res. 42, 73–82.

Robles, L., Ruggero, M.A. and Rich, N.C. (1986) Mössbauer measurements of the mechanical response to single-tone and two-tone stimuli at the base of the chinchilla cochlea. In: J.B. Allen, J.L. Hall, A. Hubbard, S.T. Neely and A. Tubis (Eds.), Peripheral Auditory Mechanisms, Springer Verlag, Berlin, pp. 121–128.

Robles, L., Ruggero, M.A. and Rich, N.C. (1989) Nonlinear interactions in the mechanical response of the cochlea to two-tone stimuli. In: J.P. Wilson and D.T. Kemp (Eds.), Cochlear Mechanisms, Plenum, pp. 369–375.

Sachs, M.B. (1969) Stimulus-response relation for auditory-nerve fibers: Two-tone stimuli. J. Acoust. Soc. Am. 45, 1025–1036.

Sachs, M.B. and Abbas, P.J. (1974) Rate versus level functions for auditory-nerve fiber in cats: tone burst stimuli. J. Acoust. Soc. Am. 56, 1835–1847.

Sachs, M.B. and Abbas, P.J. (1976) Phenomenological model for two-tone suppression. J. Acoust. Soc. Am. 60, 1157–1163.

Sachs, M.B. and Kiang, N.Y.S. (1968) Two-tone inhibition in auditory-nerve fibers. J. Acoust. Soc. Am. 43, 1120–1128.

Sachs, M.B. and Young, E.D. (1980) Effects of nonlinearities on speech encoding in the auditory nerve. J. Acoust. Soc. Am. 68,858–875.

Sachs, M.B., Young, E.D. and Bernardin, C.P. (1980) Suppression effects in the responses of auditory-nerve fibers to broadband stimuli. In: G. Van den Brink and F.A. Bilsen (Eds.), Psychophysical, Physiological and Behavioral Studies in Hearing, Delft U.P., Delft, pp. 284–291.

Schalk, T. and Sachs, M.B. (1980) Nonlinearities in auditory-nerve fiber response to bandlimited noise. J. Acoust. Soc. Am. 67, 903–913.

Schmiedt, R.A. (1982) Boundaries of two-tone rate suppression of cochlear-nerve activity. Hear. Res. 7, 335–351.

Seneff, S. (1988) A joint synchrony/mean-rate model of auditory speech processing. J. Phonetics 16, 55–76.

Shamma, S. (1988) The acoustic features of speech sounds in a model of auditory processing: vowels and voiceless fricatives. J. Phonetics 16, 77–91.

Shannon, R.V. (1976) Two-tone unmasking and suppression in a forward-masking situation. J. Acoust. Soc. Am. 59, 1460–1470.

Smith, R.L. (1977) Short-term adaptation in single auditory-nerve fibers: Some poststimulatory effects. J. Neurophysiol. 40, 1098–1112.

Smith, R.L. (1979) Adaptation, saturation and physiological masking in single auditory-nerve fibers. J. Acoust. Soc. Am. 65, 166–178.

Sokolowski, B.H.A., Sachs, M.B. and Goldstein, J.L. (1989) Auditory-nerve rate-level functions for two-tone stimuli: Possible relation to basilar-membrane nonlinearity. Hear. Res. 41, 115–124.

Taylor, M.M. and Creeman, C.D. (1967) PEST: Efficient estimates of probability functions. J. Acoust. Soc. Am. 41, 782–787.

Wegel, R.L. and Lane, C.E. (1924) The auditory masking of one pure tone by another and its possible relation to the dynamics of the inner ear. Physics Rev. 23, 266–285.

Zwicker, E. (1986) Suppression and $2f_1-f_2$ difference tones in a nonlinear cochlear preprocessing model. J. Acoust. Soc. Am. 80, 163–176.