XIV. COMMUNICATIONS BIOPHYSICS*

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A. AUDITORY NERVE FIBER RESPONSES TO TWO-TONE STIMULI

[This report gives a brief summary of a Ph.D. thesis of the same title, submitted to the Department of Electrical Engineering, M.I.T., August 1966. Further details and results may be found in the thesis itself.]

Electrophysiological investigations of auditory nerve fiber responses thus far have been limited largely to what have been called "simple" acoustic stimuli: clicks, tones, and tone bursts. Some recent findings[1,2] have revealed rather complicated interactions in the responses to more complex stimuli and have indicated that extension of results from simple to complex stimuli may not be straightforward. There have been few

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quantitative data relating to these interactions, however. In this study we have attempted to describe quantitatively the responses of auditory nerve fibers to somewhat more complex stimuli, sums of two tones. We have chosen to describe the fiber responses by a single variable, rate of spike discharge.

We have used a sweep-frequency technique[3] to construct iso-rate contours for responses to one- and two-tone stimuli. An iso-rate contour is the locus of points in the frequency-level plane corresponding to stimuli that evoke a specified rate of response from a fiber. Such contours provide a convenient means for illustrating general characteristics of the dependence of rate on stimulus frequency and level. When measuring rate as a function of the frequency of one of two tones, we presented that tone as a sweep-frequency signal. If a second tone was present, it was presented as a continuous tone at the fiber's characteristic frequency (CTCF). Figure XIV-1 shows iso-rate contours for a typical fiber for both one- and two-tone stimuli. In this figure we have specified stimulus levels in terms of peak-to-peak stapes displacement. In doing so, we hope to isolate effects produced by the cochlea from effects produced by the frequency dependence of the middle-ear transmission.[4]

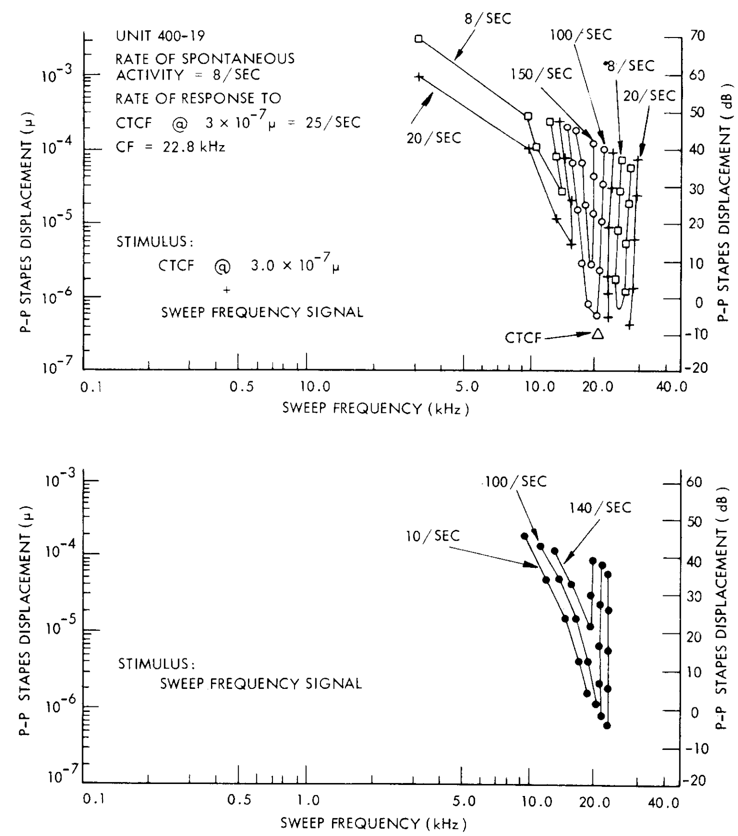

Fig. XIV-1. Iso-rate contours.

For one-tone stimuli (lower portion of Fig. XIV-1) we find a limited region in the stimulus plane within which a fiber's rate of discharge is increased above its spontaneous level. For each fiber the "excitatory response area" is defined to be that area in the stimulus plane bounded below by the iso-rate contour corresponding to a rate 20 per cent greater than the spontaneous rate. From Fig. XIV-1 it is evident that all stimuli lying within a fiber's excitatory response area evoke a rate of response at least 20 per cent above the spontaneous rate.

In the two-tone stimulus situation (CTCF plus sweep-frequency signal — upper section of Fig. XIV-1) the fiber exhibits a region in the sweep-frequency stimulus plane in which the effect of the sweep-frequency signal is to increase the rate of discharge above its value for the CTCF presented alone. To the right and left of this region are regions in which the effect of the sweep-frequency signal is to reduce the rate below its value for the CTCF alone. For any CTCF level, we define the "inhibitory response area" to be the region in the sweep-frequency stimulus plane bounded below by the iso-rate contours corresponding to a rate equal to 80 per cent of the rate to the CTCF alone. Any tone with stimulus parameters within the inhibitory response area causes a reduction in the rate of response to the CTCF of at least 20 per cent. We call the reduction in the

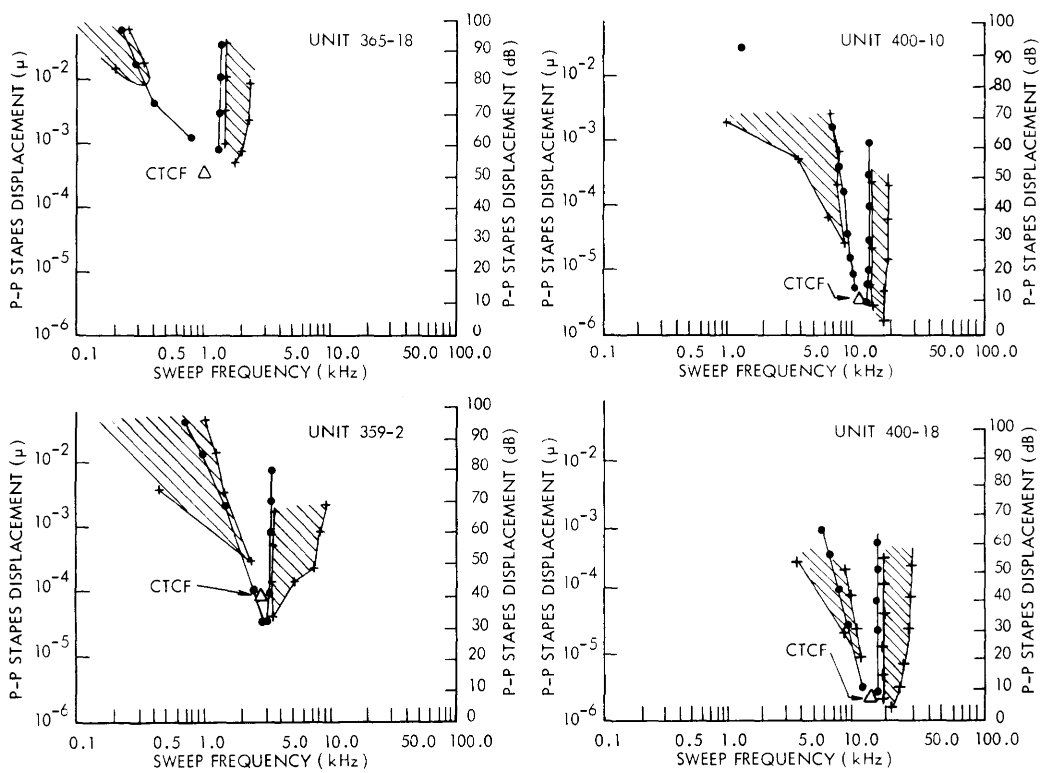

Fig. XIV-2. Excitatory and inhibitory response areas for four fibers.

fiber's rate of discharge to a CTCF by the presentation of a second tone "two-tone inhibition." All second tones with stimulus parameters within the inhibitory response area produce two-tone inhibition. We have observed two-tone inhibition for more than 300 fibers; we have never failed to find two-tone inhibition for any fiber when we were able to look for it systematically.

Figure XIV-2 shows excitatory and inhibitory response areas for four fibers covering a broad range of characteristic frequencies. These areas are typical of more than 200 fibers. The fibers all have inhibitory areas on both sides of their excitatory response areas. We have found that the extent of the inhibitory areas depends on the level of CTCF employed. An increase in CTCF level causes an upward shift in the boundaries of the inhibitory areas in the sweep-frequency stimulus plane. As is illustrated by Unit 359-2 (Fig. XIV-2), if the level of the CTCF is low enough, the inhibitory area above the CF extends down to levels very close to the tip of the excitatory response area. Higher levels are needed, however, to produce two-tone inhibition at frequencies below fiber CF. The minimum levels necessary to reduce rate by a given amount at frequencies below the CF are at least 20 dB greater than the minimum levels of stapes displacement needed at frequencies above the CF.

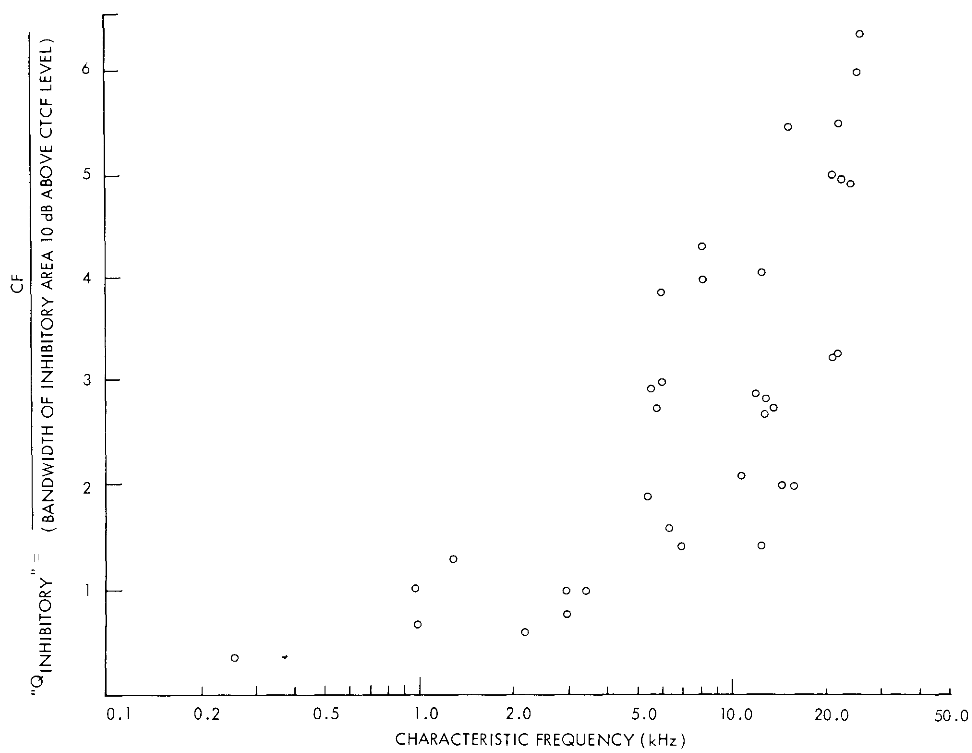

Fig. XIV-3. "Q_{INH}" as a function of CF.

An appropriately defined "Q" can be taken as a measure of the extent of the inhibitory areas in the sweep-frequency stimulus frequency dimension. We have adopted the following definition of the "Q" of an inhibitory area: Q_{INH} = CF/bandwidth of the inhibitory area 10 dB above the CTCF level. Figure XIV-3 shows a scatter plot of Q_{INH} versus fiber CF for 35 fibers. The dependence of these inhibitory Q's on CF is similar to the dependence of the tuning curve Q's given by Kiang,[1] in that both the tuning curve Q's and inhibitory Q's are roughly constant for CF below 2 kHz, and for higher frequencies both Q's increase with increasing CF.

In order to collect data with which we could test mathematical descriptions of the two-responses, we used tone-burst stimuli and measured the discharge rate after the transient at the tone-burst onset. Using this method, we developed the following expression to describe the relationship between discharge rate and the stimulus parameters of the two-tones. (Our data are restricted to the case in which one tone is at fiber CF.)

$$r(P_{CF}, f_C, P_2, f_2) = R_{SP} + R(P_{CF}, f_C)\, g\left(\frac{P_2}{P_{CF}}, f_C, f_2\right) + R(P_2, f_2)\, g\left(\frac{P_{CF}}{P_2}, f_2, f_C\right),$$

where

$r(P_{CF}, f_C, P_2, f_2)$ = spike discharge rate as a function of the two-tone stimulus parameters

P_{CF} = sound-pressure level of the tone at the characteristic frequency

f_C = characteristic frequency

P_2 = sound-pressure level of the second tone

f_2 = frequency of the second tone

$R_{SP} = r(0, f_C, 0, f_2)$ = spontaneous discharge rate

$R(P_{CF}, f_C) = r(P_{CF}, f_C, 0, f_2) - R_{SP}$ = "driven part" of the rate to one tone alone

$g\left(\frac{P_2}{P_{CF}}, f_C, f_2\right)$ = "inhibitory multiplier."

The function R(P, f) is a monotone nondecreasing function of P. The inhibitory multiplier $g\left(\frac{P_2}{P_{CF}}, f_C, f_2\right)$ is 1 for a small value of P_2/P_{CF} and is a monotone decreasing function of P_2/P_{CF}. This mathematical form has been adequate to "fit" all data that we have obtained, although we lack sufficient data for certain conditions. We have suggested how this result might be extended to more general two-tone stimuli (neither tone at the CF) and to the sum of an arbitrary number of tones.

M. B. Sachs

References

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