

Thresholds for primary auditory fibers using statistically defined criteria

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The discharge behavior of auditory-nerve fibers near "threshold" was investigated in anesthetized cats using low-intensity sinusoidal stimuli presented at the respective characteristic frequencies. Particular attention was paid to fibers with "low" and "medium" rates. Estimates of threshold derived from statistically significant increases in discharge rate indicate that the average threshold values for low-spontaneous fibers are only slightly higher (ca. 5 dB) than the averages for the corresponding high-spontaneous fibers, with the medium-spontaneous fibers having intermediate averages. The difference between these average values is considerably less than the more than 20-dB difference obtained using threshold criteria based on an absolute increment in discharge rate [e.g., M. C. Liberman, *J. Acoust. Soc. Am.* **63**, 442-455 (1978)]. The main reason for the difference between the results of the two techniques is the fact that the slopes of the rate-intensity functions for the high-spontaneous fibers are considerably steeper near "threshold" than those for fibers of the other two classes. The results are taken as supportive of a recent model of primary-fiber discharge [C. D. Geisler, *Brain Res.* **212**, 198-201 (1981)].

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INTRODUCTION

It has been known for many years that the spontaneous discharge rates of primary auditory neurons are not evenly distributed but occur in a bimodal distribution (Kiang *et al.*, 1965). Using threshold criteria, Liberman (1978) divided the group containing the lower mode in two and defined three categories: "low" (0-0.5 discharges/s), "medium" (0.5-18/s), and "high" (above 18 discharges/s). For purposes of discussion, we will use these same three divisions throughout this paper. Recent work indicates that some physiological properties of the primary neurons are correlated with their spontaneous discharge rates. For one, the "intensity thresholds" were found to be inversely correlated with spontaneous rate. In the most careful study of these properties, Liberman (1978) found that the thresholds of the low-spontaneous fibers were, on average, at least 20 dB higher than the thresholds of high-spontaneous fibers at any particular characteristic frequency.

Despite the generality of these observations (Kiang *et al.*, 1965, 1970; Geisler *et al.*, 1974), caution in interpreting these data is suggested by a model of the primary fibers' discharge properties (Geisler, 1981). In the model, any changes in stimulus amplitude (expressed in terms of vesicle-release rates) at low intensities caused *percentage* changes in discharge rate for the low- and medium-spontaneous fibers that were approximately twice as large as those of the high-spontaneous fibers. Yet the *absolute* magnitude of the changes in rate were so much less for the model's low- and medium-spontaneous fibers than for the high-spontaneous ones that the rate-change criteria usually used to define threshold would set considerably lower thresholds for the high-spontaneous fibers.

Motivated by this finding, we have studied the discharge properties of primary auditory fibers, particularly those with low- and medium-spontaneous rates, at low stimulus intensities. We found, using three different criteria, that the thresholds of low-spontaneous fibers do not differ, on the average, by more than about 5 dB from those of the high-spontaneous fibers.

I. METHODS

Discharges of single auditory-nerve fibers were recorded from anesthetized adult cats having no signs of middle-ear pathology, using methods previously described in detail (Geisler and Sinex, 1982). Briefly, this procedure involved inserting under visual control a glass pipette, filled with 3M KCl, into the auditory nerve, which had been exposed by a posterior-fossa approach that involved aspiration (combined in later experiments with reflection) of the overlying cerebellum. The middle ear was vented by a long narrow tube in order to avoid changes in middle-ear pressure (Guinan and Peake, 1967). The pipette was advanced by a hydraulic microdrive (Trent-Wells) using a moderately intense sweep-tone search stimulus. Electrical stimulating pulses were not used. All fibers used in this study satisfied the traditional criteria for primary fibers: monopolar positive potentials whose click latencies, when frequently checked, were comparable to those reported by Kiang *et al.* (1965). Because the present data were collected in the context of experiments exploring the temporal-encoding properties of primary fibers, most fibers had characteristic frequencies of less than 4 kHz. Sinusoidal stimuli were generated by a custom-designed stimulus system (Rhode, 1976) and presented to the animal by electromagnetic earphones in a closed, individual-

ly calibrated arrangement. A Harris/5 computer was used to control the experiments and to record the data.

During the experiments, threshold-tuning curves for all fibers encountered were determined by means of a sequential tracking program (Kochhar, 1981). For each fiber, the program first sampled the spontaneous activity for 20 stimulus-length periods (usually 250 ms each). The mean and standard deviation of these 20 samples were determined, and a threshold criterion C (thr) of one count greater than the sum of the mean and standard deviation was set. This criterion level was then compared with the spike count obtained during each stimulus presentation. If the count was greater than C (thr), the SPL was reduced by 2 dB. If the count was less than C (thr), the SPL was increased by 2 dB. This incrementing process was continued until a SPL, call it L 1, was found at which the count crossed the criterion level. To minimize variability, an "up-down" process was then instituted. First, the stimulus intensity was changed back to its immediately preceding level. If the spike count also reversed sign relative to C (thr), then the intensity was changed back to L 1. If the sign reversed yet again, the threshold criterion was considered satisfied and the program went on to the next frequency, starting its search at an intensity derived from the immediately preceding five threshold points. Occasionally there were fibers for which a threshold determination was difficult at some frequencies. Since convergence is not guaranteed by this process, a limit of 20 presentations was instituted for any one frequency. If "threshold" had not been determined by then, the program marked it as a missing point and went on. The program determined thresholds over a range of frequencies typically spanning 3–6 oct in 6 or 8 equally spaced (on a logarithmic scale) steps per oct. From the threshold-response curve so generated, the computer determined the characteristic frequency (CF) and the threshold (hereafter called the *tracking threshold*) at that frequency. Our experience with the program was favorable. Threshold-response curves took between 2–5 min to run, and repeated determinations were very similar to each other in the large majority of cases. Different determinations of CF usually differed by at most a few percent and different "tracking thresholds" by only a few dB. The averaged values of any such repeated determinations were used in our analyses. Very occasionally, a clearly errant point or series of points (e.g., as judged by abnormally high Q_{10} s) was generated by the program. Such data were discarded.

Next, rate-intensity curves were obtained at the CF, generally using a single-tone burst with a duration of 20–60 s. Occasionally, bursts of shorter duration were used. Stimulus intensities usually ranged from 9 dB below the tracking threshold to approximately 6 dB above it, in 2- or 3-dB steps (with three exceptions: 5-dB steps were used with two fibers and 6-dB steps with another). The resulting rate-intensity curves were analyzed off-line in several different ways. First, the slope of each curve was determined at the tracking-threshold point. Because initial attempts to obtain these slopes from the raw data produced variable results, the slope was obtained from a second- or third-order polynomial fitted to the curve (using the lowest-order polynomial that gave a good fit to the eye). In a few cases, some points at intensities

well below the tracking threshold were deleted to provide better fits. Next, for each of the fibers giving a sufficiently large number of discharges to provide reliable statistics (those with spontaneous rates greater than about 0.7/s), a 3σ threshold was calculated in the following manner. From the spontaneously occurring spikes, the mean spontaneous interval and the standard deviation of spontaneous intervals were calculated. The average interval at "3 σ threshold" was defined as the mean spontaneous interval less three standard deviations of the mean spontaneous interval (three standard deviations of spontaneous intervals/ \sqrt{n}). The corresponding stimulus intensity was read from the rate-intensity curve. Third, for each rate-intensity curve whose higher-intensity portion was essentially monotonically increasing,¹ a threshold based on shape was also computed. This *shape threshold* was defined as the intensity of the midpoint of the lowest segment of the essentially monotonically increasing part of the curve which showed an appreciable increase and which yielded a discharge rate that was greater than the mean spontaneous rate and all of the subthreshold data points.

Data from eight experiments, all those with fiber thresholds near normal (Liberman, 1978), are presented here. With the following exceptions, all neurons whose action potentials rose very clearly and unambiguously above the background noise and thus provided essentially errorless triggering were included in our results. Threshold values for the last ten fibers of one experiment and the last five of another were abnormally high compared to the ones obtained earlier in the respective animal and so were discarded as representing deteriorating cochleas. Each summary curve contains data from all fibers that met the stated criteria.

II. RESULTS

Representative rate-intensity curves are shown in Fig. 1 for two fibers from the same auditory nerve having comparable characteristic frequencies but differing spontaneous rates. The curve for the high-spontaneous fiber, shown in Fig. 1(a), begins its essentially monotonically rising segment (with a single point of exception at 4 dB SPL) at -5 dB SPL, so a "shape threshold" of -3.5 dB SPL was assigned to it. By contrast, the "tracking threshold" for this fiber was found to be 1 dB SPL. The rate-intensity curve for the low-spontaneous fiber is shown in Fig. 1(b). Notice that while it also has a monotonically rising shape similar to the high-spontaneous curve, the ordinate scale has more than three times the resolution of that used in Fig. 1(a). Even at 17 SPL, 13.5 dB above the shape threshold of 3.5 dB SPL, the discharge rate has not yet reached 10/s. With more data, the shape threshold might possibly have been extended even below 3.5 dB. This fiber had a tracking threshold of 11.5 dB SPL.

Two important characteristics of the rate-intensity curves are apparent from an examination of the data in Fig. 1. First, the slope of the low-spontaneous curve near the operationally defined thresholds is much smaller than that of the high-spontaneous curve. Second, the differences in discharge rate between the spontaneous level and the thresh-

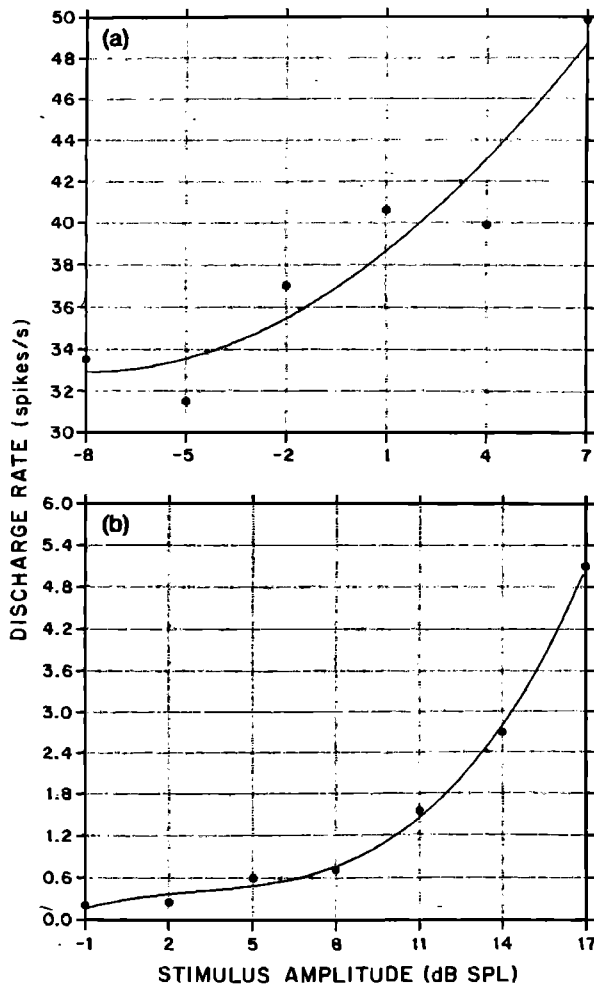


FIG. 1. Discharge rate (in spikes/s) versus intensity (in dB SPL) for two auditory-nerve fibers from cat 83-095. (a) Fiber 94, CF = 7.07 kHz, spontaneous rate = 27/s, tracking threshold = 1 dB SPL, stimulus was one 10-s tone. (b) Fiber 74, CF = 8.03 kHz (average of 2 determinations, 8.0 and 8.06 kHz, respectively), spontaneous rate = 0.1/s, tracking threshold = 11.5 dB SPL (average of 2 determinations, 11 and 12 dB SPL, respectively), stimulus was one 60-s tone.

olds are considerably greater for the high-spontaneous fiber. These characteristics prove to be true for auditory-nerve fibers in general. Figure 2 shows the slopes of the rate-intensity curves at tracking threshold for 63 of the 64-member set of fibers whose rate-intensity functions have an essentially monotonically increasing high-intensity limb. The correlation ($r = 0.69$) with spontaneous rate is unmistakable. The average slope for the high-spontaneous fibers is 2.7 spikes/s/dB, while for the low-spontaneous fibers it is 0.5. The slopes for the medium-spontaneous fibers are intermediate, averaging 1.2 spikes/s/dB.

The data in Fig. 2 are important for understanding the behavior of operationally defined thresholds, but, because of sampling variability, they may not represent the slopes near more accurately determined thresholds. It might be, for example, that more data and longer time samples would have extended the monotonically increasing portion of the point in Fig. 1(a) far to the left of -8.0 dB SPL, producing a slope at shape threshold equal to or less than the slope at the comparable point of the curve for the fiber of Fig. 1(b). Thus, until this possibility is further explored, the theoretical im-

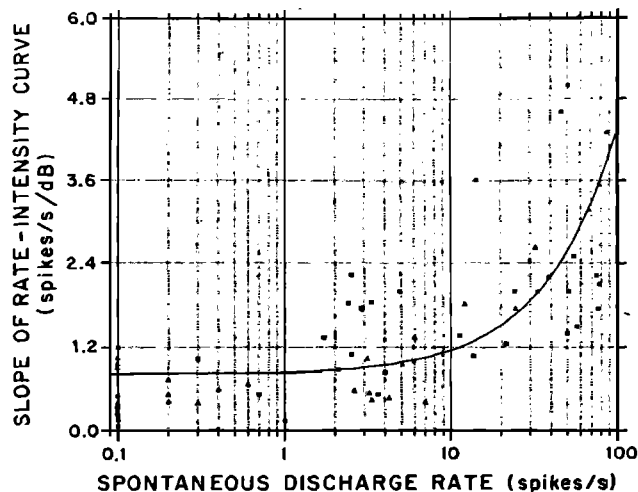


FIG. 2. Slope of the CF rate-intensity curve at the tracking-threshold point for 63 of the 64 fibers which had an essentially monotonically increasing curve¹ at the higher intensities (one of these fibers had a tracking threshold invalidated by one errant point). Smoothing for the curve of each fiber was accomplished by fitting a second- or third-order polynomial to the data points, using least-mean-square criteria. In this and in Figs. 4-6, the points indicated by the open triangle (Δ) are all from one of our most stable preparations, 83-095. For purposes of display only, fibers with spontaneous rates below 0.1/s were here and in Fig. 4 assigned rates of 0.1/s. The best linear fit (on a least-mean-square basis) to the data (on linear scales) is also shown ($r = 0.69$).

portance of the data in Fig. 2 must be interpreted with caution.

Another and perhaps more revealing way of displaying the rate-intensity data is to use log-log coordinates as in Fig. 3. Notice that the data points in each panel of that figure are closely fitted by a straight line ($R > 0.94$), indicating equal percentage changes per dB of stimulus amplitude. Such a straight-line fit was determined for each of the 64 rate-intensity curves in our sample. The slopes of these lines, shown in Fig. 4, decrease with increasing spontaneous rate, going from an average of 2.5 dB/dB for the low-spontaneous fibers to 0.35 dB/dB for the high spontaneous.

Another measure of possible interest is the difference between the spontaneous discharge rate and the rate at the shape-threshold point of the rate-intensity curve. Data points for each fiber of the full 64-member set are shown in Fig. 5. Here again the trends are unmistakable. For the high-spontaneous fibers, shape threshold averaged 9.2 spikes/s more than the spontaneous activity, while a corresponding increment of only 0.5 spikes/s was observed for low-spontaneous fibers. As with other measures, the medium-spontaneous fibers behaved in an intermediate fashion, with shape thresholds occurring at rates that averaged 2.1 spikes/s more than the mean spontaneous rate. An analysis of the differences between the rate at tracking threshold and the spontaneous rate for these same fibers yielded very similar results, except with greater increments, averaging 17.0 spikes/s for the high-spontaneous, 6.1 for the medium-spontaneous, and 1.7 for the low-spontaneous fibers.

The values of threshold determined by the tracking-threshold program proved to be very consistently related to the shape thresholds, which we have designated our standards. As seen in Fig. 6(a), the tracking threshold was an

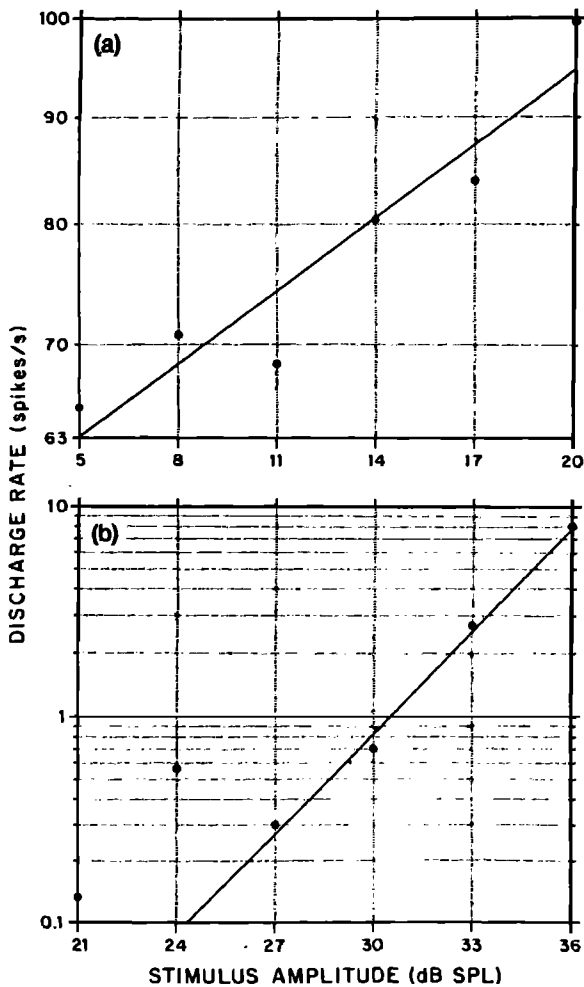


FIG. 3. Discharge rate (in spikes/s) plotted on a log scale versus intensity (in dB SPL) for two auditory nerve fibers from cat 83-016. (a) Fiber 28, CF = 12.5 kHz, spontaneous rate = 55/s, shape threshold = 12.5 dB SPL, tracking threshold = 16 dB SPL, stimulus was one 30-s tone. (b) Fiber 46, CF = 15.2 kHz, spontaneous rate = 0.3/s, tracking threshold was 33 dB SPL, shape threshold = 28.5 SPL, stimulus was one 30-s tone. The best linear fit to the data points in each panel is also shown [the left-most two points in panel (b) were omitted in the fitting procedure].

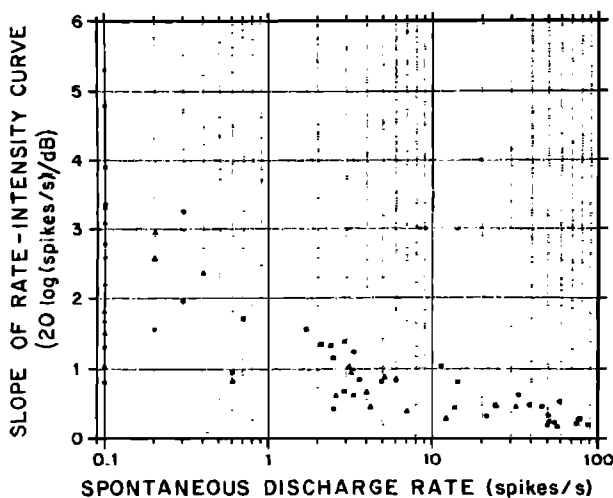


FIG. 4. Slope [in $20 \log(\text{spikes/s}/\text{dB})$] of the best linear fit to the essentially monotonically increasing portion of the CF rate-intensity curve plotted on log-log coordinates for each of the 64 fibers in our shape-threshold set.

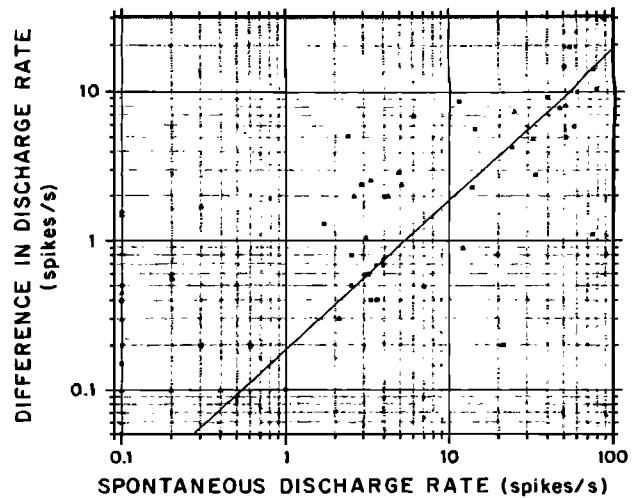


FIG. 5. The difference between discharge rate at shape threshold and the mean spontaneous rate for each of the 64 fibers (cf. Fig. 2). Also shown is the best fit to the data (on linear scales) of a straight line with an intercept of (0,0). One fiber with a difference in discharge rates of zero was assigned, for display purposes only, a difference rate of 0.05 spikes/s.

average of 5.1 dB higher than the shape threshold. The scatter of points was relatively restricted, with 55 of the 63 fibers having tracking thresholds that fell within 5 dB of that average offset. Moreover, the statistical variation in the difference between the tracking threshold and the shape threshold is almost independent of spontaneous rate (with a correlation $r = 0.14$).

Our method for determining shape threshold is non-standard. In order to apply a more conventional method, we also calculated the statistically well-defined 3σ thresholds

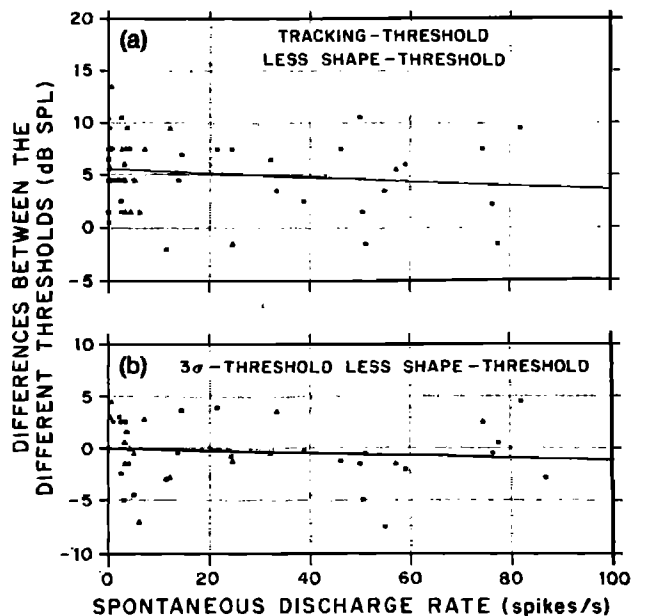


FIG. 6. Differences in the values of the different threshold determinations. (a) The value of the tracking threshold less that of the shape threshold for 63 of 64 fibers (cf. Fig. 2). Also shown is the best linear fit (on at least-mean-squares basis) to the data ($r = 0.18$). (b) The value of the 3σ threshold less that of the shape threshold for each of 40 fibers (all those of the 64 for which confident estimates of spontaneous-rate standard deviation could be made). Also shown is the best linear fit (on a least-mean squares basis) to the data ($r = 0.09$).

for the 40 fibers for which we have sufficient spike counts to provide reasonable numbers. The differences in threshold obtained by the two methods, both of which use the rate-intensity curves, are shown in Fig. 6(b). For any one fiber, the differences seldom exceeded 5 dB (average was -0.3 dB), and there was very low correlation ($r = 0.10$) between it and the spontaneous discharge rate. Therefore, the shape-threshold and 3σ -threshold methods provide, on average, very similar results.

Tracking thresholds for all of the 256 fibers studied in our eight experiments (156 points are from our three most stable experiments) are shown in Fig. 7(a), while thresholds for the individual spontaneous-rate classes are displayed in Figs. 7(b)–(d). In many respects the data are like those obtained by Liberman (1978). The most sensitive of the high-spontaneous fibers provided points that are near 0 dB SPL for frequencies between 0.7 and 10 kHz (cf. Liberman's "best-threshold curve"), and most of the thresholds at any one CF occur within a range of about 20 dB [Fig. 7(b)]. Moreover, the percentage of fibers in the different spontaneous-rate classes (58%, 25%, and 17%, from high- to low-spontaneous, respectively) are very similar to those found by Liberman (61%, 23%, and 16%, respectively). Furthermore, 19% of the fibers had spontaneous rates between 10–

40/s, a figure which is close to that obtained for "routine" cats by Liberman. There is, however, one big difference between the data in Fig. 7 and that reported by others: the threshold distributions for the three classes of fibers virtually overlap. The low-spontaneous points [Fig. 7(d)] are distributed throughout nearly the same range as the medium-spontaneous [Fig. 7(c)] and high-spontaneous points [Fig. 7(b)]. Moreover, the smoothed lines drawn through the points in the three plots are not greatly different from each other in either shape or values. For comparison purposes, the threshold of each of the fibers with CFs below 10 kHz was normalized to the average value of comparable high-spontaneous fibers. (Our small sample size of high-spontaneous fibers with CFs greater than 10 kHz and their wide range of threshold values prevented the calculation of reliable averages at high frequencies.) The reference values were calculated by averaging the tracking thresholds of the high-spontaneous fibers in each of 40 bins (equispaced on a logarithmic scale) between 100 Hz and 10 kHz (cf. Liberman, 1978), smoothing the averages, and linearly interpolating between points. The average relative threshold of the low-spontaneous fibers was 4.1 dB, for the medium-spontaneous fibers it was 0.8 dB, and for the high spontaneous it was -0.4 dB. When similar calculations were done on the 151 fibers with CFs below 10

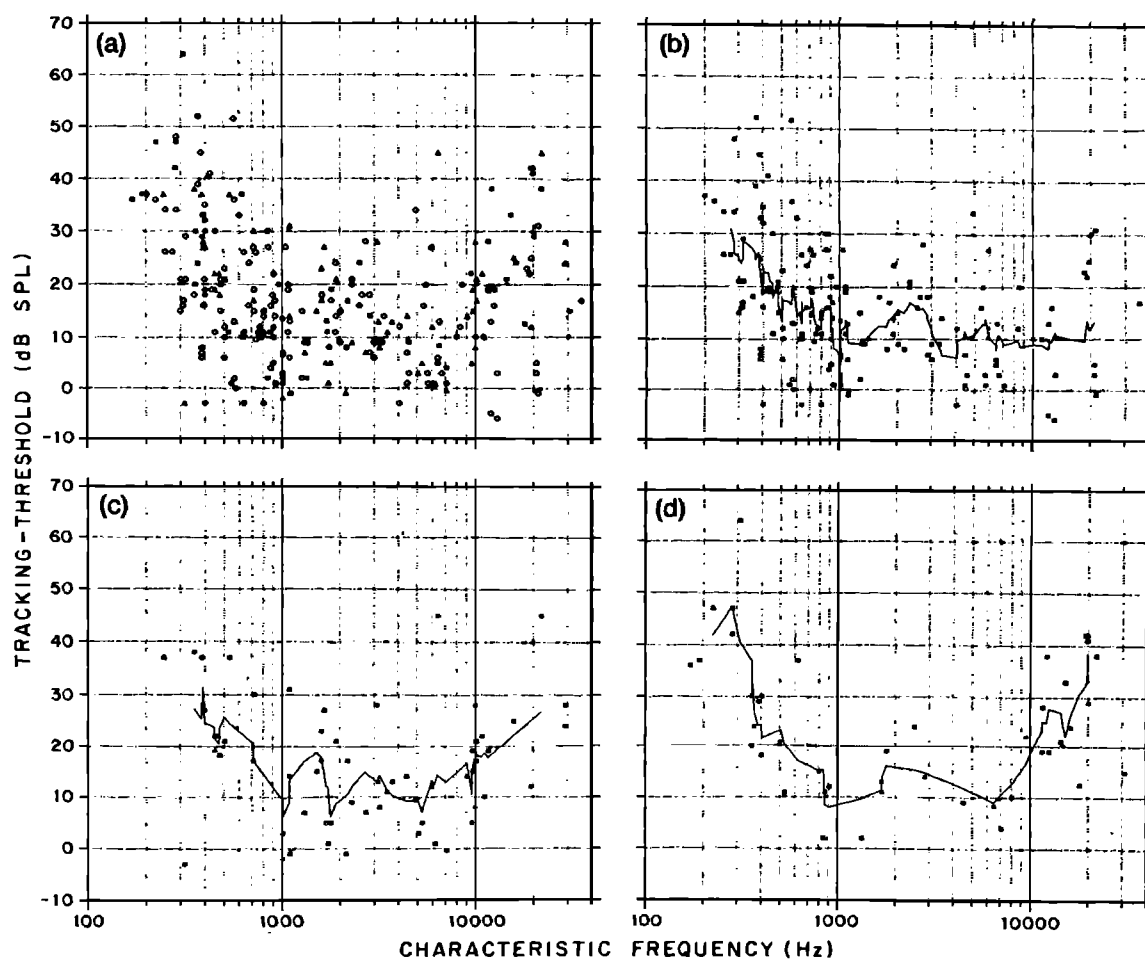


FIG. 7. The value of tracking threshold (in dB SPL) (at CF). (a) For each of the 256 fibers in our set. In this panel, and in Fig. 8, high-spontaneous fibers are indicated by open circles (O), medium-spontaneous fibers by open triangles (Δ), and low-spontaneous fibers by asterisks (*). (b) For each fiber of the high-spontaneous subset (149/256). A nine-point smoothed average line (with endpoints deleted) is also shown. (c) For each fiber of the medium-spontaneous subset (63/256), with a five-point smoothed-average line. (d) For each fiber of the low-spontaneous subset (44/256), with a five-point smoothed-average line.

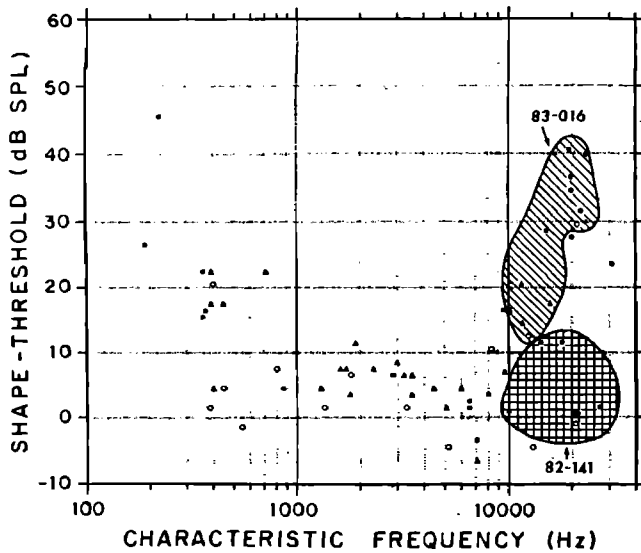


FIG. 8. The value of the shape threshold (in dB SPL) at CF for each of the 64 fibers in our set. Numbers of high-spontaneous, medium-spontaneous, and low-spontaneous points are 17, 25, and 22, respectively. Data from the high-frequency fibers of cat 82-141 are indicated by the checkered area, and of cat 83-016 by the diagonally striped area.

kHz encountered in the three most stable experiments, average relative thresholds of 5.4 dB (low spontaneous), 1.2 dB (medium spontaneous), and -0.1 dB (high spontaneous) were obtained.

Identical conclusions are reached upon examination of the shape thresholds, which are shown in Fig. 8. Notice that here again the thresholds for the fibers of all classes are intermingled. This near independence of thresholds from spontaneous rates holds for the data from each animal, as well as for that of all animals together, as can be seen quite clearly for the points with CFs above 10 kHz. Thresholds in that region from animal 83-016 (in the diagonally striped area) are all uniformly high, including those of the two high-spontaneous fibers and the four medium-spontaneous ones. Points from animal 82-141 (in the checkered area) are all uniformly low, including those of the three low-spontaneous fibers and the single medium-spontaneous one. Relative thresholds for each of the shape thresholds were calculated using the same procedure as described above for the tracking thresholds except that the full CF range was used. To account for the great variability among animals which occurs in the high-frequency region (cf. Liberman, 1978), two different standards were used for CFs above 10 kHz. The standard threshold for each high-frequency fiber (i.e., CF above 10 kHz) was calculated from the corresponding high-spontaneous, high-frequency points of either cat 83-016 or 82-141, whichever had closer data points. Relative threshold for the three classes of fibers, from high- to low-spontaneous categories, were -0.7 , 3.5 , and 5.0 dB, respectively.

The separation of auditory-nerve fibers into different classes according to their spontaneous discharge rates raises the question as to whether common or different mechanisms govern the generation of their respective discharges. In the process of gathering data from fibers with lower spontaneous rates, we gathered long samples of spontaneous activity for comparison, on a statistical basis, with that of high-spon-

taneous fibers (Kiang *et al.*, 1965; Walsh *et al.*, 1972; Manley and Robertson, 1976). We attempted to determine the modes of the interval distributions from these data. However, even with our 60-s samples, the number of discharges obtained was usually too small to obtain good modal estimates: values differed considerably from one sample to the next. Thus interval statistics were calculated instead. Means and standard deviations of intervals are shown in Fig. 9. Apart from the slight displacement towards the right at the low mean intervals (rapid discharge rates), all of the data points cluster about the 45° line.

III. DISCUSSION

The primary finding of this study is the close correspondence between the threshold distributions of the three different categories of auditory-nerve fibers. The average threshold values for fibers of the three spontaneous-activity categories were separated by approximately 5 dB in our tracking-threshold data (cf. Fig. 7), as well as in our shape-threshold data (Fig. 8). By contrast, Liberman (1978) found that the thresholds for the three groups were much more widely spaced, both in his "chamber-rised" and "routine-normal" cats. His high-spontaneous fibers had thresholds that were at least 20 dB lower, on average, than those for the low-spontaneous fibers. In our opinion, the major reason for the difference in findings of the two studies is the difference among the threshold criteria used. The criterion used in the Liberman study (1978) involved a fixed increment in discharge rate (e.g., 0 or 1 over the immediately preceding non-stimulus period). It resulted in identifying a stimulus intensity that caused an increase, on the average, of about 10 spikes/s over the spontaneous discharge rate, regardless of what that rate was. The values obtained by the method would correspond to comparable points on the rate-intensity curves for the fibers of all spontaneous classes, if the rate-intensity curves for all fibers had the same shape near threshold. However, our data (Fig. 2) show that the slopes of the rate-intensity curves near tracking thresholds are considerably lower for the low-spontaneous fibers than for the high-

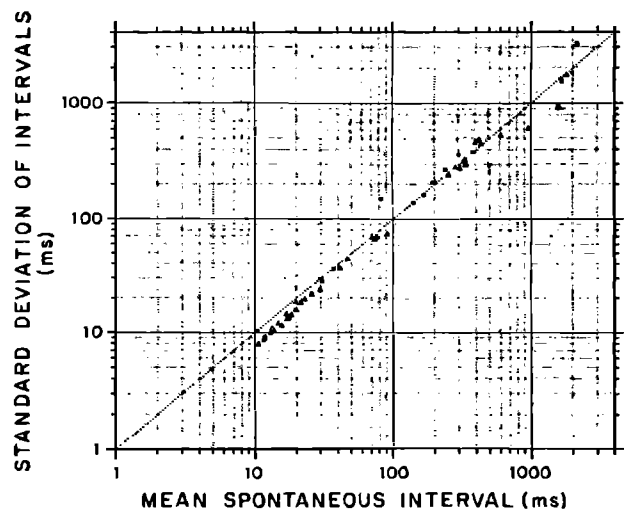


FIG. 9. Mean interval versus standard deviation of intervals for spontaneous activity for each of 58 fibers. A linear line with unity slope is also shown.

spontaneous ones. Thus the threshold values estimated by the constant-increment method will be relatively further out on the rate-intensity curves, and hence higher up, for the low-spontaneous fibers than for the high-spontaneous. By contrast, all three of the criteria that we employed are functions of the statistics of the individual fiber's spontaneous activity. Hence, the increments used were highest for the high-spontaneous fibers and lower for the others. These methods yielded threshold intensities for the low-spontaneous fibers that corresponded to much less than 10/s increments in discharge rates (Fig. 5). Not using the same threshold-tracking program as Liberman, we do not know the exact thresholds which that program would have determined for our fibers. We did, however, calculate comparable thresholds for as many as possible of the 64 fibers in our shape-threshold population by determining what stimulus intensity corresponded to a spike rate that was 10/s higher than the mean spontaneous rate. The average relative threshold of the low-spontaneous fibers determined in this way was greater than 21 dB [our intensities did not go high enough to get a full 10/s increase for most of these fibers, e.g., Fig. 1(b)], while for the high-spontaneous it was -0.4 dB. The medium-spontaneous fibers had an average relative threshold of 10.4 dB. These figures are comparable to those found by Liberman (1978).

Stimulus duration also plays a role in the value assigned to threshold. If the fixed-increment method were to be used with 250-ms stimuli (instead of the 50-ms pulses used by Liberman), the results obtained by the two methods would be more nearly equal. Another factor that may have contributed to the difference in the two studies was the use of electrical exciting shocks in the Liberman study. That technique enabled him to locate fibers with low spontaneous rates and high audio-visual thresholds that we might have missed with our strictly acoustical stimuli. However, the near equality of the percentages of low spontaneous encountered in the two studies suggests that the number of any such fibers that we missed was quite small.

From a practical point of view, the differences in the thresholds determined by the two tracking methods are probably of minor importance. After all, information is not being sent very rapidly at discharge rates below 10/s. Which type of tracking-threshold program to use is therefore more a matter of individual judgment than anything else. The constant-increment method is quite rapid and maintains a continual check on the spontaneous discharge behavior of the fiber, but it tends to overestimate statistically defined thresholds for low-spontaneous fibers. That drawback could be reduced by using sample times larger than 50 ms. By contrast, the method using statistically determined increments gives thresholds that, apart from a bias of approximately 5 dB, are rather accurate reflections of the thresholds determined from long-duration rate-intensity curves. However, our procedure is a little lengthy, and its failure to keep track of changing discharge characteristics occasionally yields erroneous results.

There are several important implications that arise from our finding that the statistically defined thresholds of auditory-nerve fibers have similar distributions, at least to

within 5 dB, regardless of spontaneous activity level. First of all, it suggests that all type I primary afferent auditory fibers (cf. Liberman, 1982), or at least those excitable by the acoustic-search stimuli that we used, have stimulus thresholds that are statistically similar. The variation in relative thresholds among different fibers is still greater than 20 dB in any one animal, but the similar averages for the different categories of fibers suggest that similar excitation mechanisms are at work in all fibers near threshold. Other mechanisms that are similar for all fibers are suggested by the characteristics of the two-tone rate suppression caused by tones whose frequencies are below CF (Schmiedt, 1982). In that study, the absolute values of large segments of the lower "suppression boundaries" agreed with each other, to within about 10 dB, regardless of fiber spontaneous rate, at least for fibers with CF thresholds no more than 25 dB above the most sensitive ones. Also, Schmiedt found, in agreement with our findings, not much difference in the CF thresholds between fibers in the different spontaneous-rate classes. The relatively small variability produced by these various types of effects suggests that at least some of the mechanisms involved act in common on many hair cells.

The data presented here are also relevant for the testing of the model which inspired the study, whereby the only differences between the fibers of the different spontaneous classes are the magnitudes, relative to fiber threshold, of the "unitary" excitatory potentials produced by single quanta of neurotransmitter (Geisler, 1981). The low- and medium-spontaneous fibers in this model are approximately twice as sensitive as the high-spontaneous fibers, in terms of the percentage changes in spike rate that are caused by the same changes in quantal-release rates (say from 25–50/s). In our data (Fig. 4), the medium-spontaneous fibers are, in general agreement with the model, about 2.5 times more sensitive, on a percentage basis, than the high-spontaneous fibers. The average percentage sensitivity of the low-spontaneous fibers is approximately 7 times that of the high-spontaneous, however, larger than that expected from the model, although the model's output has not yet been calculated for rates below 0.1/s. This approximate agreement between the model predictions and our experimental data, at least for the medium- and high-spontaneous fibers, lends further support for the model. Recent research on auditory-nerve fibers (Liberman, 1982) even suggests a mechanism whereby the distinction between the high-spontaneous fibers and the others (the model, and our data, provide no grounds for further subdividing the fibers) might be achieved. The high-spontaneous fibers have the thickest unmyelinated portions (average diameter about $0.9 \mu\text{m}$), and therefore would provide longer space constants for excitatory potentials generated by the hair-cell neurotransmitter. This long space constant could result in a suprathreshold potential produced at the first node of Ranvier, the presumed trigger zone, by a single "unitary" EPSP. The other fibers have thinner diameters (average about $0.55 \mu\text{m}$) and so are expected to have shorter space constants. "Unitary" EPSPs therefore could be so attenuated along the unmyelinated portions of these fibers that they would produce subthreshold potentials at the trigger zones. Variations in the diameters of the fibers would produce var-

iations in attenuating characteristics and hence variations in discharge behavior. Further predictions of the model are being studied.

Previous reports on the statistical characteristics of the spontaneous activity of auditory-nerve fibers have had few data points for fibers with spontaneous discharge rates less than 10/s (Kiang *et al.*, 1965; Walsh *et al.*, 1972; Manley and Robertson, 1976). Our data (Fig. 9) show that the mean of the spontaneous-interval distribution for each primary fiber is, regardless of spontaneous rate (at least down to 0.5 spikes/s), nearly equal to the standard deviation of its intervals. Thus, as with the high-spontaneous primary fibers, the pattern of spontaneous discharges by medium-spontaneous fibers is consistent with their generation by Poisson processes (which would yield points of equal mean interval and standard deviation), modified with brief refractory effects (Gray, 1967). More data, from extremely long sampling periods, would be necessary in order to form reliable estimates of other interval statistics, such as the mode, which could be used to test further the modified Poisson-process hypothesis in mammalian fibers with low spontaneous rates and to provide comparisons with spontaneous-discharge data obtained from comparable primary auditory fibers in other types of vertebrates (e.g., Eatock *et al.*, 1981, reporting on the Tokay Gecko).

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¹For 55 fibers out of our 64-fiber set, the higher-intensity portion of the rate-intensity curve was strictly monotonic [e.g., Fig. 1(b)]. For the other nine fibers, the rising portions of the rate-intensity curve had a single point, well above threshold, that violated monotonicity to a small extent [e.g., point at 4 dB SPL in Fig. 1(a)].

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