# Auditory-nerve response from cats raised in a low-noise chamber

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A litter of four cats, born and raised in a soundproofed chamber, was studied in an attempt to determine which, if any, features of the auditory-nerve response from routinely available cats might be due to the chronic effects of noise exposure. Two features of routine-normal response were especially suspect in this regard: (1) a "notch" in the distribution of single-unit thresholds centered at characteristic frequencies (CF's) near 3 kHz and (2) a compression of the distribution of rates of spontaneous discharge for units with CF above 10 kHz. A third feature of response in routine animals was the presence of a small number (roughly 10%) of units with virtually no spontaneous discharge and very high thresholds, sometimes 80 dB less sensitive than high-spontaneous units of similar CF. In the data from chamber-raised animals, the high-spontaneous units showed exceptionally low thresholds at all CF regions, however, there were signs of the midfrequency notch in the threshold distribution of at least two of these animals. The compression of the spontaneous rate distribution was not seen in any of the three most sensitive animals. The data suggest that there is a significant amount of "normal pathology" in the high-CF units from routine animals. Low-spontaneous, high-threshold units were present in all four chamber-raised ears with the same characteristics as in routine animals (exceptionally narrow tuning curves and exceptionally low maximum discharge rates) and at roughly the same percentage of the unit sample. A class of units with medium spontaneous rates and intermediate thresholds could also be identified. The possible significance of a classification of auditory-nerve units according to spontaneous rate is discussed.

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## INTRODUCTION

The present report grew out of an ongoing study of the chronic effects of high-intensity sound on the response properties of auditory-nerve fibers. To evaluate the nature and degree of the noise-induced abnormalities, there is a need for a well-defined standard of auditory-nerve response. This standard is not so easily obtained. The population of cats which is routinely available as experimental animals shows a wide range of sensitivity at the single-unit level. In some cases, thresholds are so high that there is little trouble in deciding that the data should not be considered "normal." In other cases, the decision is more difficult. Even the most sensitive ears show, in some subset of the single-unit population, response properties that resemble clearly abnormal behavior seen in noise-exposed ears. Since, for the most part, our experimental animals were obtained as adults, it seemed possible that each had been exposed to significant environmental noise at some time in its life.

These observations suggested that there might be significant differences between the "normal" single-unit activity, i.e., that which is commonly seen, and activity that would represent the characteristics of an undamaged peripheral auditory system. As a first step toward establishing a baseline for the evaluation of auditory-nerve response, a litter of four cats was raised from birth in a soundproofed chamber. This report summarizes the response characteristics of the more than 1000 auditory-nerve units obtained in these four animals and the differences between these responses and those seen in routinely obtained animals.

## I. METHODS

The cats used as experimental animals in this study included four (two male and two female) which were born and raised in a soundproofed chamber. When the chambers are empty, the ambient noise is below the threshold of hearing at all frequencies (Vér, Brown, and Kiang, 1975). However, these animals were not sound deprived since they could move and vocalize. In addition, animal caretakers had to enter the room periodically. Nevertheless, the most intense acoustic stimuli which these cats would hear prior to the experiment were probably their own vocalizations; thus, we hoped that their ears would be virtually free of noise-induced pathologies. The experimentation on these animals was carried out when they were between five and six months of age. The routine-normal animals were of unknown age but selected to be near 2 kg in body weight. One animal (MCL85) was purchased from a facility which breeds and raises laboratory animals; the rest were chosen from among those which are routinely available to us from local animal suppliers. The acoustic traumatization of animals was carried out as described in a previous publication (Kiang, Liberman, and Levine, 1976).

The surgical preparation, presentation of acoustic stimuli, recording of single-unit activity and processing of responses were basically as has been described previously (Kiang *et al.*, 1965), except that electric shocks (5-ms duration, delivered at 10/s) were used as a search stimulus while the microelectrode was advanced through the nerve. These shocks were passed directly through the recording electrode and served to locate those units with low rates of spontaneous discharge and high thresh-

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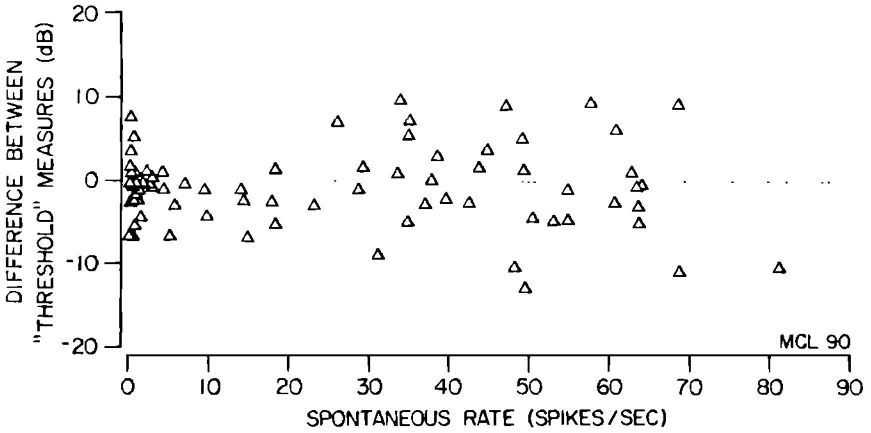

FIG. 1. Effect of spontaneous rate on the performance of the tuning-curve algorithm. The data are from one routine-normal animal in which the tuning curves were determined with a "criterion" of 0. Each point represents data from a different unit. The abscissa represents the difference between the "threshold" at CF as determined by the algorithm and the intensity required (as determined from the rate-level function) to increase the unit's firing rate by 10 spikes/s. A positive value of the abscissa indicates that the algorithm registered a threshold level which was higher than that required to produce the predicted rate increase. In this and all subsequent figures, the spontaneous rate represents the average rate as determined over a 30-s sample.

olds to acoustic stimuli. The acoustic stimuli used in this study were 50-ms tone bursts with a 2.5-ms rise-fall time and a 50% duty cycle. The frequency and intensity of these tone bursts could be varied under computer control to determine the rate-level functions and threshold-tuning characteristics of the auditory-nerve fibers.

The pure-tone level sweeps (run to measure response rate as a function of stimulus level) were performed in the following way. The computer-controlled oscillator was set at the characteristic frequency (CF) of the unit, and the level of the tone bursts was raised systematically in 2-dB steps from a level roughly 25 dB below the unit's threshold to approximately 55 dB above threshold. (However, in no case was the stimulus allowed to exceed 85 dB SPL.) Ten tone bursts were presented at each stimulus level. The responses to each level of the stimulus were gated in such a way that only those occurring during the tone bursts were counted. (Actually, the timing of the spike gate was delayed by 1.25 ms with respect to the onset of the electric stimulus to the earphone to compensate for the accumulated delay in the auditory-nerve response.)

The "threshold tuning curve" is determined by an automated procedure briefly described previously (Kiang, Moxon, and Levine, 1970). Since the thresholds as measured by this method are of central importance to this study, the procedure will be more fully described here. The automated tuning curve procedure was designed to determine, as a function of frequency, the stimulus level required to cause the unit to fire at a given rate above its spontaneous rate of discharge. This level is determined in the following way. A 50-ms tone burst of a given frequency and level is presented. The LINC computer subtracts the number of spikes occurring in the 50 ms subsequent to the tone burst from the number of spikes which occurred in the 50 ms when the tone burst was on. This difference is then compared to a "criterion" value (set by the user, typically at 0 or 1). If the spike difference is less than or equal to the criterion, the tone level is raised by two steps ($\frac{4}{3}$ dB). If the spike difference is greater than criterion, the tone level is lowered by one step ($\frac{2}{3}$ dB). At any given frequency the tone bursts are presented at a rate of 10/s, and the tone level is raised or lowered according to the comparison between the criterion and the spike difference. A "threshold" value is registered at a given frequency only after two conditions have been met: (1) that the tone level at the current trial is the same as that three trials previously; and (2) that the current level was reached by lowering the tone level by one step. After the registration of a threshold value, the frequency is lowered by one step, and the process is repeated. The frequency resolution is 32 points/octave in the eight octaves between 0.16 and 40.96 kHz.

With a criterion of 0, the tuning-curve algorithm should theoretically seek out those tone levels eliciting a firing-rate increase of 0–20 spikes/s since (1) the tone level is lowered only if there is at least one more spike during the 50-ms tone burst than during the subsequent 50-ms period, and (2) a spike difference of 1 spike/50 ms corresponds to a rate increase of 20 spikes/s. In practice, the "threshold" at CF registered by the paradigm at criterion 0 is within 10 dB of the tone level required to elicit a firing-rate increase of 10 spikes/s (as evaluated in a tone-level sweep) regardless of the unit's rate of spontaneous discharge (Fig. 1).

## II. RESULTS

### A. Threshold at the characteristic frequency

A fundamental property of any auditory-nerve fiber is its characteristic frequency or CF. The CF of a unit is that frequency to which it is maximally sensitive. The distribution of thresholds at CF for all the units obtained in any given animal can give a useful picture of the overall sensitivity of the peripheral auditory system. In Fig. 2, the distributions of CF thresholds for three animals are compared: One was raised in a soundproofed room (MCL96); the others were not. The data from

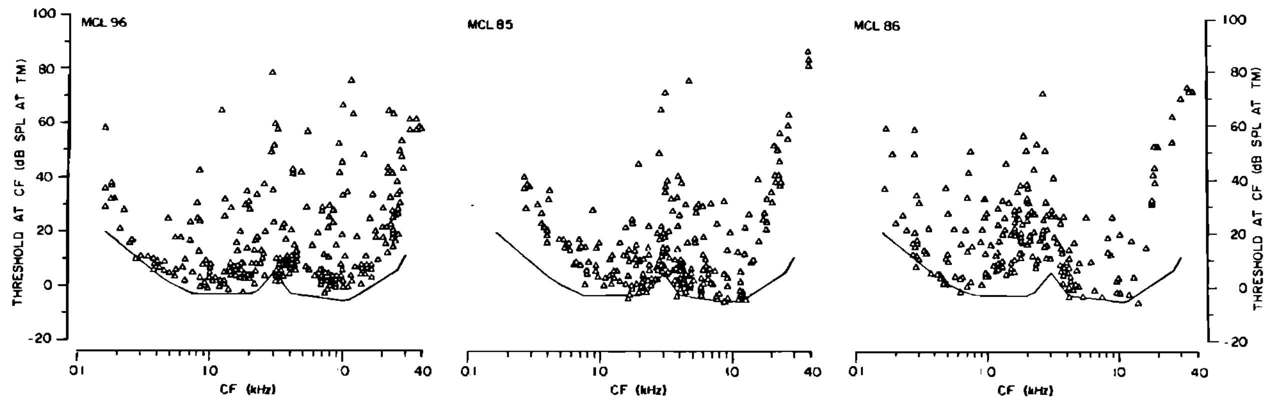

FIG. 2. Distribution of thresholds at CF obtained in three different cats. Each panel plots the threshold at the CF for each of the units encountered in one animal. For each unit, the "threshold" is that value obtained by the automated tuning-curve paradigm with a criterion of 1. The case in the left panel (MCL96) was one of the animals raised in the soundproofed room. The other two cases were cats from the population routinely available to us as experimental animals. Superimposed on the data from each animal is the "best-threshold curve," or BTC (see text). Since the BTC has been smoothed, some of the data points in MCL85 and 86 fall a few decibels below the curve. In this and all subsequent figures the sound pressure levels are expressed in decibels *re* 0.0002 dyn/cm$^2$, as measured near the tympanic membrane (TM).

each ear are compared to the best-threshold curve (BTC) which represents, as a function of CF, the lowest threshold at CF seen among more than 4500 units from 43 routine-normal animals.

MCL85 and MCL86 (Fig. 2) were among the most sensitive of cats *not* raised in the low-noise environment. The portion of the BTC from 2 to 12 kHz was defined by the data from MCL85; much of the BTC below 1 kHz was defined by MCL86. It should be noted that both these animals were purposely selected at the time because we thought they might have had a low level of environmental noise exposure: MCL85 was bought from a facility which breeds cats for laboratory use; MCL86 had been born and raised on a farm.

As was the case with virtually all the routine-normal animals, MCL85 and MCL86 showed a notch in the threshold distribution near the 3-kHz CF region. The notches in these ears were quite small. In other ears, notches of 20 dB were not uncommon, and notches as deep as 40–50 dB have been seen. MCL86 and MCL85 also showed thresholds in the high-CF region that deviated significantly from the BTC. In general, the routine-normal animals showed a great deal of threshold variability in the high-CF region. Only rarely were high-CF units seen with thresholds near the BTC.

As can be seen in Fig. 2, the minimum thresholds in the chamber-raised animal MCL96 were within 10–15 dB of the BTC throughout the entire CF range from 0.1 to over 30 kHz. Such a statement cannot be made for any of the routine-normal animals we have examined. In the CF region near 3 kHz, the units from this chamber-raised animal showed lower threshold at CF than in any routine normal. There was, however, a slight threshold notch in this ear, centered near 4 kHz.

The distributions of CF threshold for the other three chamber-raised animals are shown in Fig. 3. In each case there is some sign of the midfrequency notch, at most some 10 dB in depth. In two cases, MCL93 and MCL94, the overall sensitivity is exceptional, especially at the high CF: Minimum thresholds are again within 10–15 dB of the BTC at all CF regions. In MCL95, however, the high-CF sensitivity is markedly worse

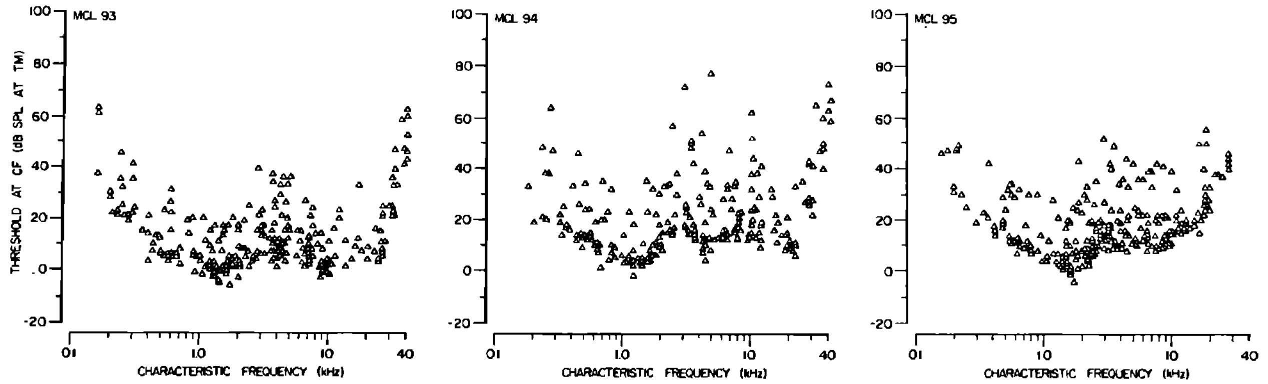

FIG. 3. Distribution of thresholds at CF seen in three of the chamber-raised cats. Since the thresholds in these three cases were determined by the automated tuning-curve paradigm at criterion 0, the BTC from Fig. 2 cannot be directly compared to these data.

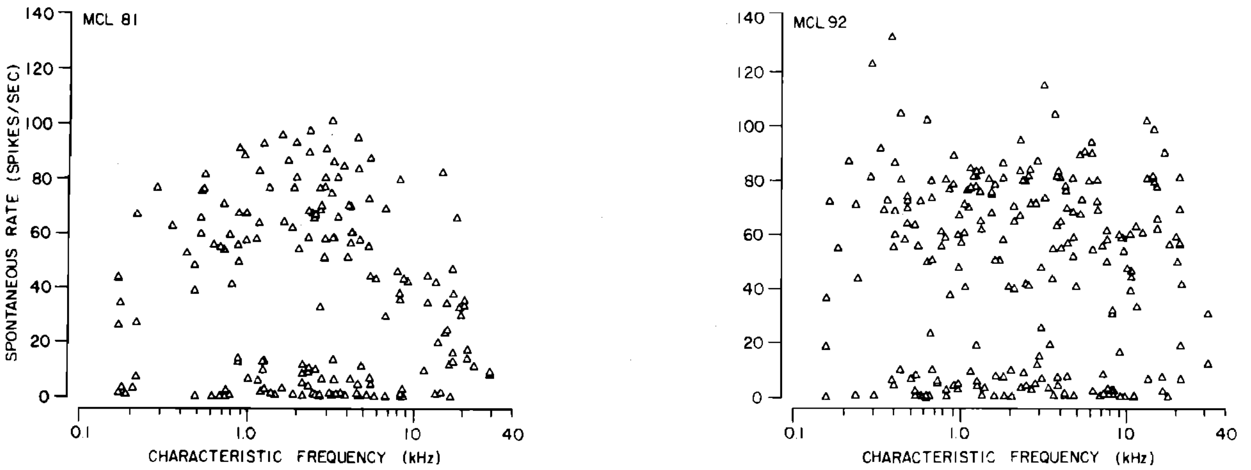

FIG. 4. Distribution of spontaneous rates as a function of CF in each of two routine-normal animals. Each point represents data from a different single unit. Each panel displays all the data obtained from each animal.

than in the other three ears. This cat was *not* the last of the litter to be sacrificed: The experiment on MCL96 was performed four weeks later.

### B. Distribution of spontaneous rates

In the absence of controlled acoustic stimulation, single units in the auditory nerve discharge spontaneously. Several fundamental features of the spontaneous activity (spont) in the auditory nerve of the cat were described by Kiang *et al.* (1965). They observed: (1) that the rates of spont can range from near zero to over 100 spikes/s, (2) that the distribution of rates of spont appears essentially bimodal, and (3) that there is no clear difference in the distribution of spont in different CF regions. These observations were based on single-unit data pooled across many animals.

When it became possible to gather data from large numbers of units in the same animal, it became clear that there was significant variability between "normal" individuals with respect to the distribution of spont (Fig. 4). In some cases, as shown in the right panel of Fig. 4, the spont distribution is similar to that seen in the earlier pooled data. The distribution of rates appears bimodal: one cluster of units with rates of 40–90 spikes/s, another cluster with rates below 10 spikes/s, and a paucity of units with rates near 20 spikes/s. However, in other cases the spont distribution is clearly nonuniform across CF (left panel, Fig. 4). For CF above 10 kHz the distribution of rates can appear compressed, showing very few units with rates greater than 40 spikes/s and an inordinately large proportion of units with rates near 20 spikes/s.

A similar compression of the spont rate distribution has been seen in the mid-CF region of ears experimentally exposed to midfrequency noise (Fig. 5). This finding, as well as the observation that among routine animals the high-CF thresholds were often very high *re* the BTC (Fig. 2), led us to suspect that the compression of the spont rate distribution was an acquired characteristic and might be related to the animal's history of noise

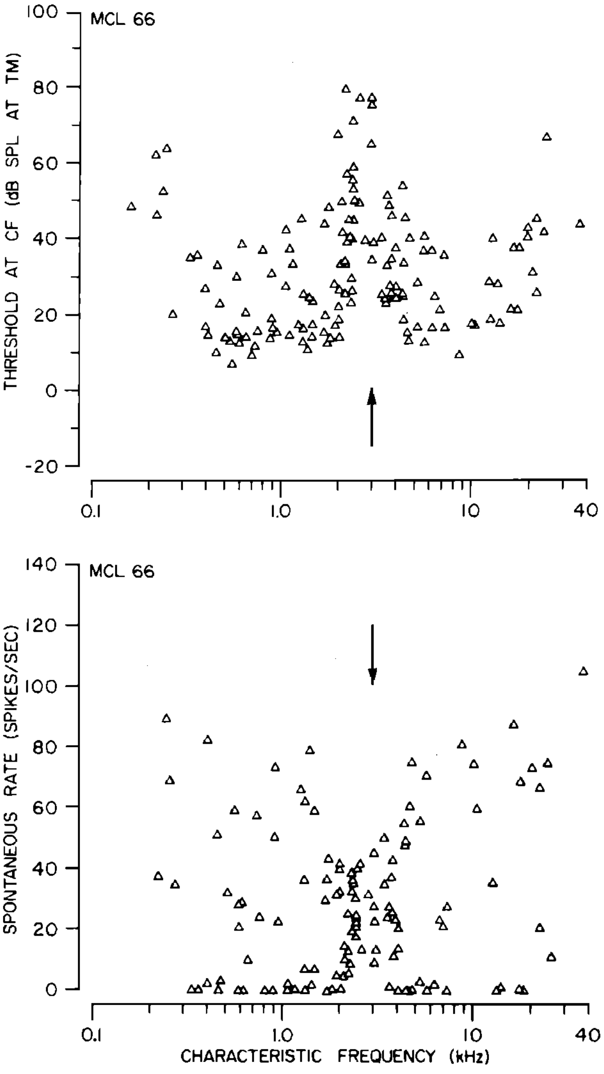

FIG. 5. Comparison of spontaneous rates and thresholds at CF in one acoustically traumatized animal. Threshold at CF was determined by the automated tuning-curve algorithm at a criterion of 1. This animal was exposed to narrow-band noise centered at 3 kHz (bandwidth of 50 Hz) for two hours at a sound pressure of 108 dB SPL (rms).

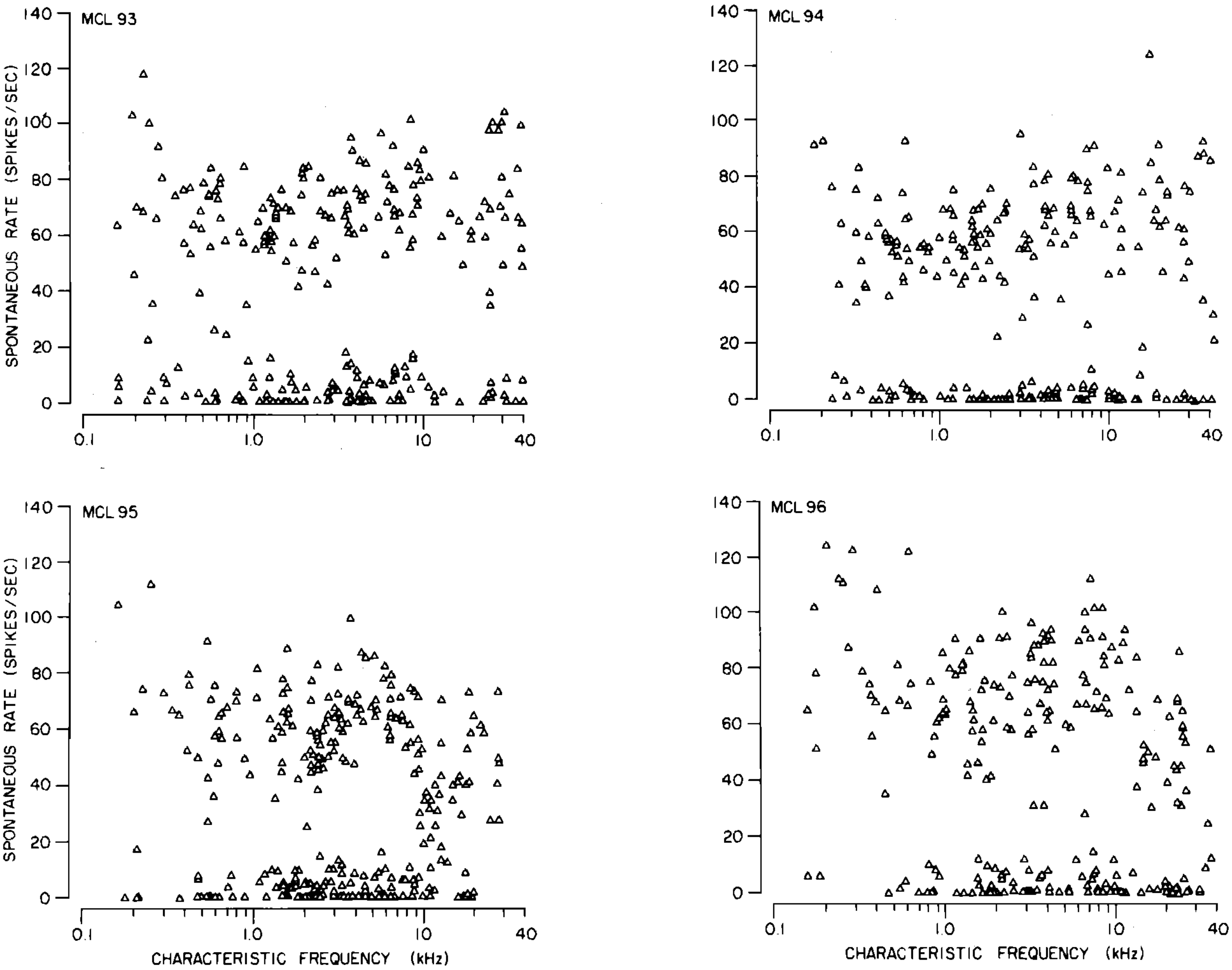

FIG. 6. Distribution of spontaneous rates as a function of CF as seen in each of the four chamber-raised cats. Each panel contains the data from all the units in that particular animal for which electrode contact was maintained long enough to procure both a tuning curve and a 30-s sample of spontaneous activity.

exposure. This was one of the reasons we set out to study animals born and raised in strictly noise-controlled surroundings.

The distribution of spont seen in each of the four "chamber-raised" animals is shown in Fig. 6. In three of the cases the distribution of spont is strikingly bimodal, and the bimodal nature of the distribution is well maintained across the entire CF range. The contrast between the distribution of spont seen in these three animals and that seen in our sample of routine animals is illustrated in Fig. 7.

In the data from one of the chamber-raised animals, there was a clear compression of the spont distribution for CF greater than 9 kHz (Fig. 6, lower left). The high-CF units in this particular animal were also significantly less sensitive (at the CF) than the high-CF units in the other three chamber-raised animals (Fig. 8). Considering only the three most sensitive chamber-raised animals, the histogram of the rates of spont (Fig. 9) is somewhat different from that previously published (Kiang *et al.*, 1965) in that (1) there is a much lower percentage of units with rates between 15 and 40 spikes/s (4% vs 26%); and (2) there is a higher percentage of units with rates below 1 spike/s (20% vs less than 7%).

### C. Relationship between rate of spont and threshold at CF

In routine animals, there can be a spread in threshold of up to 60 or 70 dB among the units in the same animal at the same CF region. It has been known for many years that at least some of this threshold spread could be correlated with rates of spont (Kiang *et al.*, 1965; Kiang, Moxon, and Levine, 1970). More recently, it has been reported that the units with very high relative thresholds were, without exception, units with virtually no spontaneous activity (Kiang, Liberman, and Levine, 1976).

One possible interpretation of these data was that the high-threshold, low-spont units were the result of chronic pathological changes in the cochlea. This represented yet another reason for examining the single-unit data in chamber-raised animals.

The relationship between threshold and spont is especially striking in the data from the chamber-raised animals. To illustrate this relationship for units over a wide range of CF (Fig. 10), it is necessary to normalize the threshold of a unit with respect to the minimum threshold seen in that particular animal at that particu-

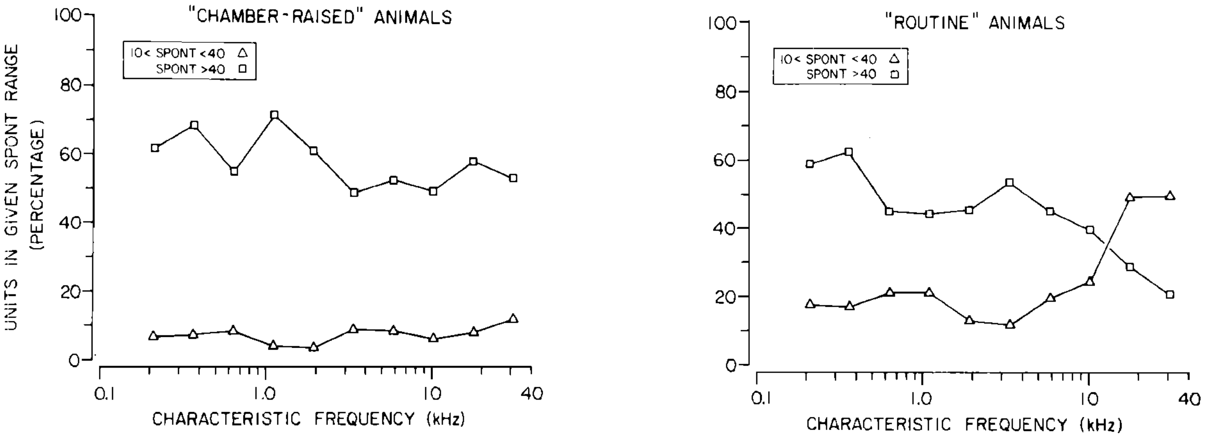

FIG. 7. Compression of the spont rate distribution at high CF in routine animals. The data in the left panel are from three chamber-raised cats (MCL93, MCL94, and MCL96). The data on the right are from 14 animals among those routinely available from local suppliers (MCL14, 47, 49, 75, 79–86, 89, and 90). To make each curve, the units in the sample were divided according to CF into ten logarithmically spaced frequency bins. Each box represents the percentage of units in that CF bin which had spont greater than 40 spikes/s; each triangle represents the percentage of units with spont between 10 and 40 spikes/s. Each symbol is placed in the center of the appropriate CF bin.

lar CF region. Since the lowest thresholds are typically seen in the units with the highest spont, we have found it convenient to use as a normalization function the curve representing, as a function of CF, the average threshold for all the units in the high-rate peak of the spont distribution (rate greater than 18 spikes/s). When threshold is expressed relative to this normalization curve, the relation between threshold and spont is as shown in Fig. 10. The units with spont greater than 18 spikes/s (henceforth called the "high-spont" units) appear to comprise a distinct and homogeneous group with respect to threshold. They appear homogeneous to the extent that (1) a unit with spont of 100 spikes/s is, on the average, no more or less sensitive than a unit of similar CF with spont of 20 spikes/s, and (2) no high-spont unit has a threshold more than 5 dB from the average high-spont threshold in the same CF region. They appear distinct in that (1) the great majority of units with spont less than 18 spikes/s are relatively less sensitive, and (2) there is a complete lack of units with spont near 18 spikes/s.

The units with spont less than 18 spikes/s do not, on the other hand, seem to represent a homogeneous group with respect to threshold. As is particularly well seen in the right panel of Fig. 10, the relative threshold increases dramatically as spont falls below 0.5 spikes/s. This suggests that the units with spont below 18 spikes/s fall into two distinct threshold groups, the "low-" and "medium-spont" units (with a dividing line set at 0.5 spikes/s). In all the data from the four chamber-raised

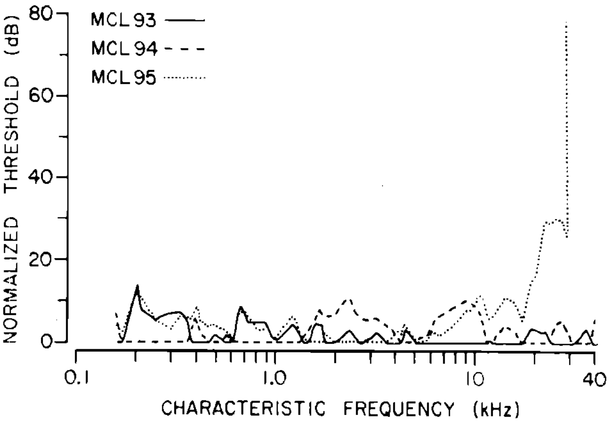

FIG. 8. Comparison of minimum-threshold envelopes for the unit samples in each of three chamber-raised cats. To make these comparisons the curve representing, as a function of CF, the minimum threshold at CF was drawn for each of the three chamber-raised cats for which the automated tuning curves were run at criterion 0. Since the unit sample in each of these animals included better than 250 units, and since these samples were well distributed across CF, there was little ambiguity as to how such minimum-threshold curves should be drawn. The curve for each animal, as it appears in the figure, has been normalized with respect to the minimum-threshold envelope for the entire sample from these three experiments.

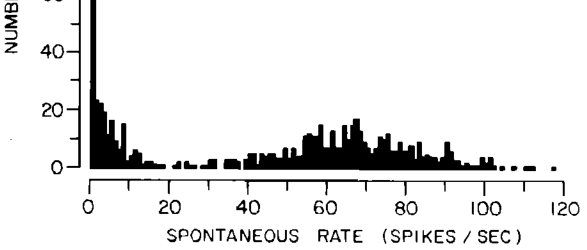

FIG. 9. Histogram of spontaneous rates sampled from the three most sensitive chamber-raised cats (MCL93, 94, 96). The bin width for the histogram is 1 spike/s. The "N" refers to the number of units in the sample.

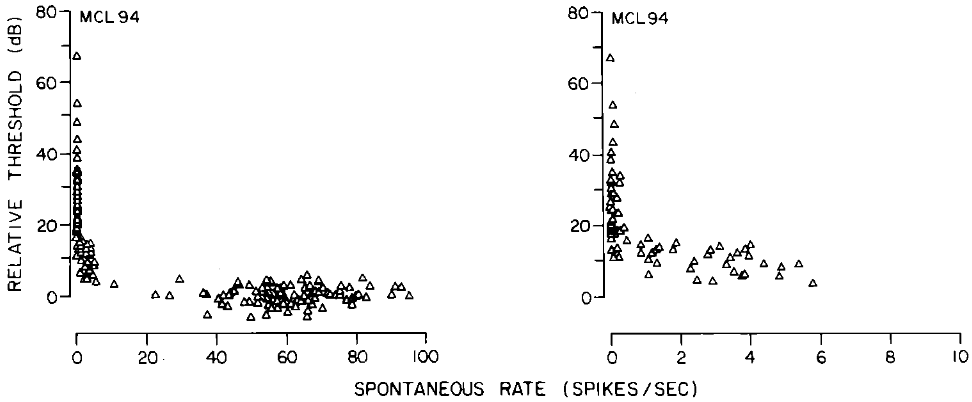

FIG. 10. Relation between spont and relative threshold in one of the chamber-raised animals. In the right panel the data from the low-rate units are displayed on an expanded horizontal scale. The relative threshold of each unit is the difference between its threshold at CF and the average threshold at CF of all the units from the same ear with similar CF and with rates of spontaneous discharge greater than 18 spikes/s. The normalization curve describing the average threshold as a function of CF was derived by dividing the CF continuum into 40 logarithmically spaced frequency bins, averaging the thresholds at CF for all the "high-spont" units within each CF bin and interpolating between the 40 mean-threshold values thus derived. Excluded from these scatter plots are those units with CF below 0.4 or above 15 kHz. Absolute threshold measurements were made with the automated tuning-curve program at criterion 0.

animals, the high-, medium-, and low-spont units comprised 61%, 23%, and 16%, respectively, of the units sampled.

As with the high-spont units, all the medium-spont units appear to have relative thresholds within 10–15 dB of one another. The low-spont units, however, are significantly more inhomogeneous with respect to relative threshold, spanning a range of more than 50 dB. This threshold spread for units with low spont cannot be clearly correlated with the spont rate, at least the rate measured over a 30-s sample. However, as shown in Fig. 11, the spread in relative threshold among the low-spont units does appear to be correlated with CF. Although the low-spont units are relatively insensitive at all CF regions, their relative (as well as absolute) threshold is especially high for units with CF near 3 kHz. Thus, the threshold spread between high- and low-spont units appears to be greatest in the 3-kHz CF region. Note that the medium-spont units (left panel, Fig. 11) maintain approximately the same average relative threshold throughout the entire CF range.

The relationship between threshold and spont in the data from routine animals (Kiang, Liberman, and Levine, 1976) is fundamentally similar to that just described, but the grouping of units has never been so clear as in the data from the chamber-raised animals. In general, as the appearance of the spont distribution becomes less strikingly bimodal, the relationship between spont and relative threshold becomes less strict. As the proportion of units with spont between 10 and 40 spikes/s increases, one sees more medium-spont units which are as sensitive as the most sensitive high-spont units and others with threshold comparable to low-spont units (Fig. 12). The result is that the three spont groups in routine animals appear less distinct and less homogeneous with respect to threshold.

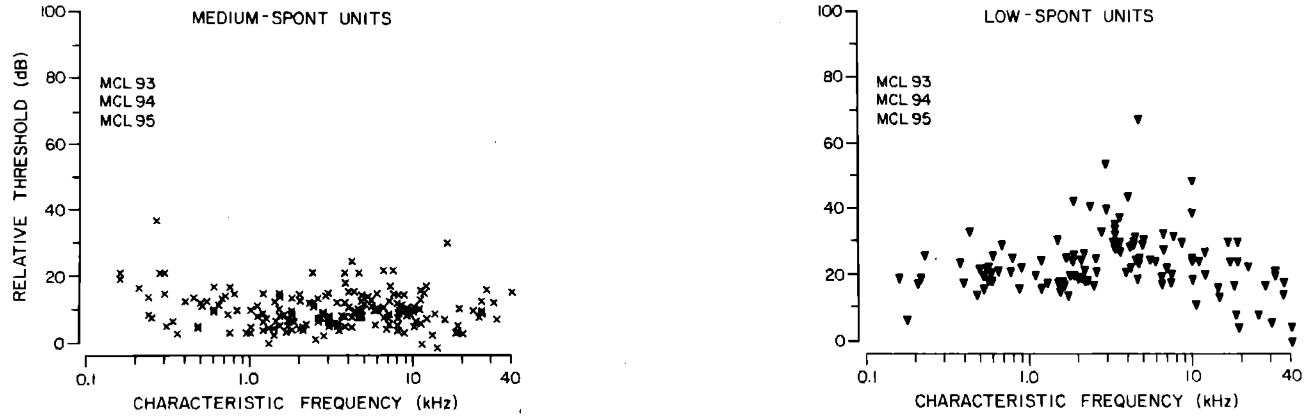

FIG. 11. Relation between relative threshold and CF. As in Fig. 5, relative threshold is defined with respect to the average threshold of the high-spont units. Thus, only plots for medium- and low-spont units are shown. Data are pooled from the three chamber-raised animals for which tuning curves were obtained at criterion 0.

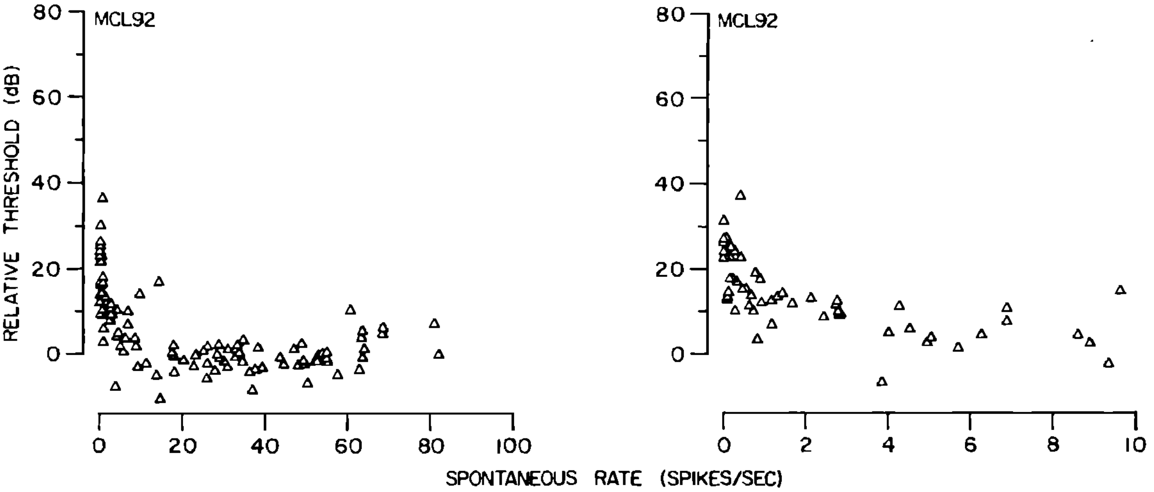

FIG. 12. Relation between spont and relative threshold in one of the routine-normal animals. All methods of data gathering and display are as described in the caption for Fig. 10.

## D. Tuning-curve shape and its relation to spont rate

The classification of units into high-, medium-, and low-spont groups was based on the relation between spont rate and threshold at CF. There is a similar relation between spont rate and thresholds off the CF. Tuning curves from two CF regions are shown in Fig. 13 (data from chamber-raised animals). When units are segregated according to spont group, the tuning curves of all the units in each group are quite similar. In data from routine animals there is not always such homogeneity among the units in each spont group. In the right-hand panel of each row the tuning curves of each spont group have been averaged, and the average curves for each of the three groups have been superimposed. In both CF regions, the average curve for the medium-spont units has been made virtually indistinguishable from the high-spont curve by subtracting a constant threshold value at all frequencies (approximately a 7-dB shift in the top row and an 8-dB shift for the data in the bottom row). Thus, the medium- and high-spont units differ, on the average, by the same number of decibels near the CF as they do below the CF, on the tuning-curve "tails."

The tails of the low-spont units could not be investigated

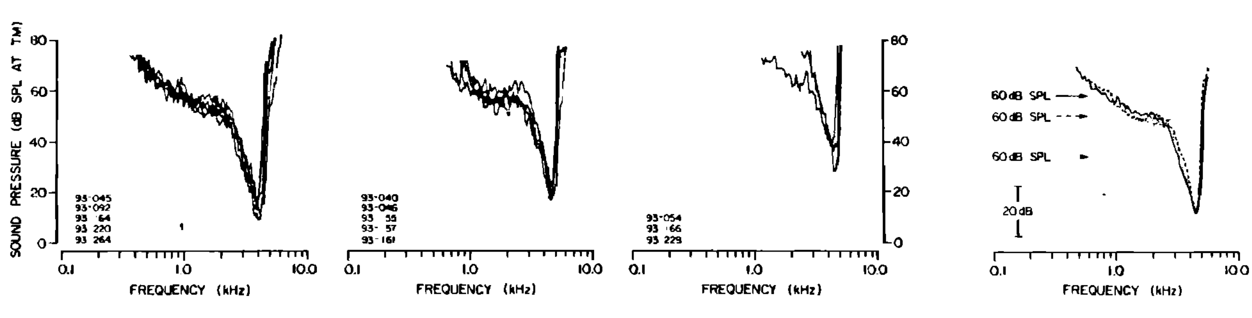

FIG. 13. Comparison of tuning-curve shapes in the three spont groups at two different CF regions. The data in the top and bottom rows are from two different chamber-raised animals. The top row contains all the tuning curves obtained in MCL95 with CF between 1.9 and 2.2 kHz. The bottom row contains all the tuning curves obtained in MCL93 with CF between 4.4 and 5.0 kHz. The curves in each row have been segregated into three groups according to the spont rate with which they were associated: high-spont units at the left, medium-spont units in the middle, low-spont units to the right. In the panel set apart at the far right of each row, the average tuning curves for each of the three spont groups have been superimposed, shifting the curves for the medium-(dashed) and low-spont (dotted) units in the threshold dimension so the tips of the tuning curves coincide. The amount of the threshold shift can be ascertained by comparing the solid, dashed, and dotted arrows to the left of the curves.

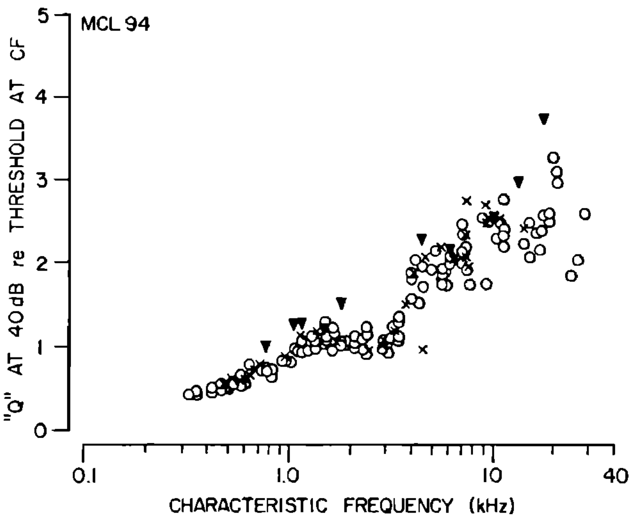

FIG. 14. Tuning curve "Q" as a function of CF with coding for spont rate. "Q" is measured at 40 dB *re* threshold at CF and is defined as the ratio of the characteristic frequency to the bandwidth of the tuning curve. Solid triangles represent low-spont units, crosses represent medium-spont units, and open circles represent high-spont units. The data are taken from one of the chamber-raised animals.

since the low-spont units have such high thresholds and since we avoid high-level stimulation for fear of acute acoustic trauma. We have noted, however, a slight tendency for the tips of some low-spont units to be exceptionally narrow, especially at high intensities. This tendency is not clear in the averaged tuning curves of Fig. 13, but can be seen in Fig. 14 in which a measure of the bandwidth of the individual tuning curves at 40 dB *re* threshold at CF is plotted (as a function of CF). The solid triangles represent low-spont units; the data have been plotted so that none of the points from the low-spont units is obscured. The low-spont units clearly tend to show narrower tuning curves than do the medium- and high-spont units. This phenomenon was also observed in the data from routine-normal animals (Kiang, Liberman, and Levine, 1976).

There is another issue concerning the threshold on the tuning-curve tail for which the data from the chamber-raised ears are especially relevant. In routine-normal animals the thresholds on the tails of the tuning curves for units with CF near 3 kHz tend to be lower than those seen for units in neighboring CF regions (Fig. 15, middle panel). This "dip" in the distribution of tail thresholds is correlated with the "notch" in the distribution of "tip-thresholds" (thresholds at CF) described above. These observations were suggestive of the phenomenon of "tail hypersensitivity" seen in single units from acoustically traumatized ears (Kiang, Liberman, and Levine, 1976). In traumatized ears, for which the thresholds at CF are significantly *elevated*, the thresholds on the tuning-curve tail can be significantly *reduced* (Fig. 15, bottom panel). The tail thresholds in the chamber-raised ears were of interest since the tip thresholds near 3 kHz were the lowest ever seen. As can be seen in the top panel of the figure, the tail thresholds for the mid-CF region were higher than those seen in the routine animals. These observations suggest that there is some cochlear pathology underlying the behavior of the 3-kHz units in routine-normal animals. The observations are

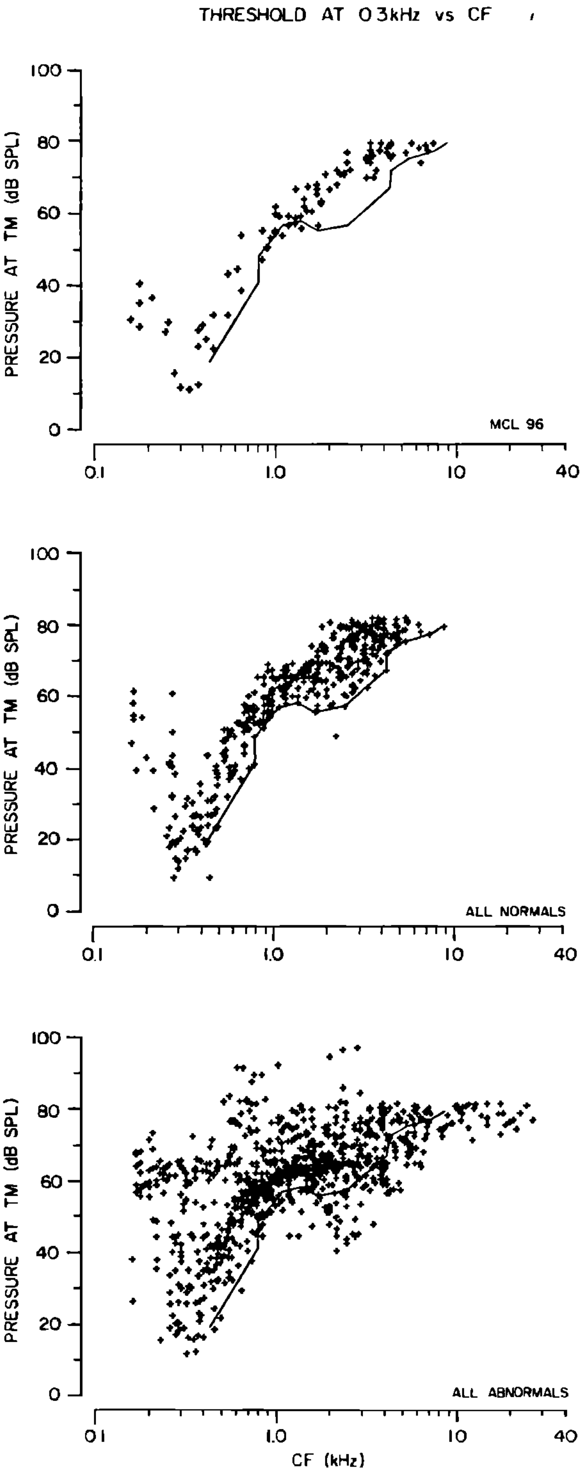

FIG. 15. Thresholds to 300 Hz as a function of CF for three different samples of units. The top graph includes all the high-spont units from a chamber-raised animal (MCL96). The middle row contains threshold data from all the high-spont units from a sample of routine-normal animals; the bottom graph contains threshold data from all the high-spont units from a group of acoustically traumatized animals (exposed to narrow-band noise centered either at 1.5, 3.0, 6.0, or 12 kHz). Each panel also contains a solid curve which is drawn so that almost all the normal thresholds to 300 Hz lie above it.

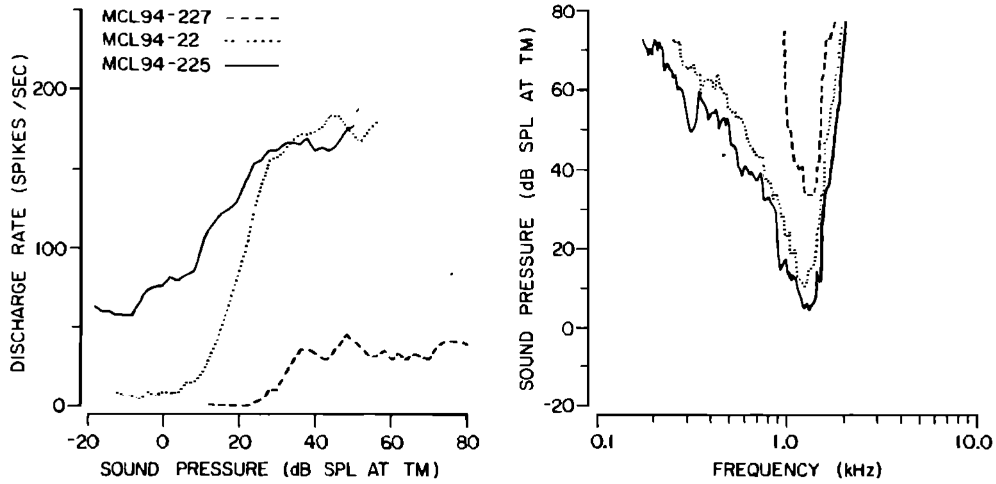

FIG. 16. Typical rate-level functions at the CF for units from the three spont classes in one of the chamber-raised animals. The tuning curves for the three units (criterion 0) are shown in the right-hand panel. The rate-level functions (left) have undergone three-point smoothing. The spont rate for units 227, 22, and 225 were 0.03, 3.83, and 56.3 spikes/s, respectively.

consistent with the notion that this pathology is noise induced.

### E. Relation between spont rate and driven rate to tones at CF

In data from routine-normal animals, it had been noted that when stimulating a unit at its CF, the maximum discharge rate attainable by certain low-spont units was significantly lower than the maximum rates for medium- or high-spont units of similar CF (Liberman, unpublished data). Again, it seemed possible that such a phenomenon was indicative of chronic pathological change, and it was of interest whether the same behavior could be seen in the units from chamber-raised cats.

In two of the chamber-raised cats, we investigated the relation between spontaneous rate and the rate-level function at the characteristic frequency. Sample rate-level functions for a high-, medium-, and low-spont unit of similar CF are shown in Fig. 16. The intensity was taken as high as 54 dB above threshold at CF, which was typically high enough to allow determination of the rate of discharge at saturation. Note that even in the chamber-raised animal the low-spont unit can saturate at a very low discharge rate.

To systematically investigate the relation between saturation rate and spontaneous rate, data must be pooled across CF. However, there is also a difference in saturation rate as a function of CF (Fig. 17). The mean saturation rate appears to climb with increasing CF, especially for CF greater than 4 kHz. Thus, pooling data across CF appears to be justifiable only for CF less than 4 kHz.

The relation between saturation rate and spont rate (for units with CF less than 4 kHz) appears in Fig. 18. Among the high-spont units there appears to be no relation between spont and saturation rate at CF. As a group, they show discharge rates ranging from 160 to 240 spikes/s with a mean near 200 spikes/s. The medium-spont units show saturation rates between 145 and 250 spikes, and the mean is again near 200 spikes/s. (This means, of course, that the percentage increase in discharge rate achievable by stimulation at the CF can be 100 times greater in a unit with spont near 1 spike/s than in a unit with spont near 100 spikes/s.) The low-spont units show markedly different saturation rates from those seen in the medium- and high-spont units. One sees rates as low as 40 spikes/s, and the highest saturation rate for a low-spont unit was only 190 spikes/s. A similar relation between spont rate and saturation rate is seen in data from routine animals.

The low-spont units showed a larger *range* of saturation rates than either the medium- or the high-spont units (Fig. 18). As was shown in Fig. 10, the low-spont units also showed a large range of relative threshold. There was a correlation between these two characteristics. Among the low-spont units, those with the highest thresholds tended to show the lowest discharge rates at saturation (and vice versa).

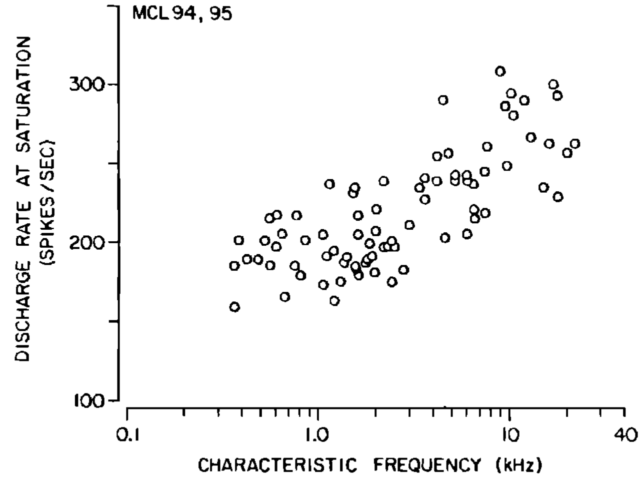

FIG. 17. Discharge rate at saturation as a function of CF. Included in the figure are all the data from the high-spont units in the two chamber-raised animals for which level sweeps were run. The saturation rate is the maximum discharge rate to which each unit was driven by the stimulation at the CF at levels up to and including 54 dB above threshold. Although it is possible that some of the units could have been driven to higher rates had intensity been raised further, virtually all the rate-level functions appeared to have saturated.

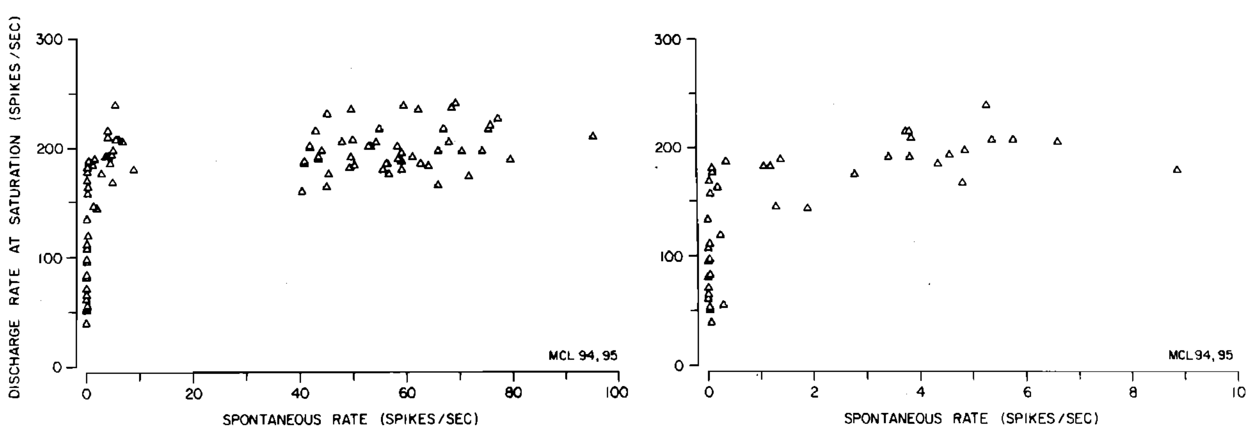

FIG. 18. Discharge rate at saturation as a function of spont rate. Included in this figure are all the data from units with CF less than 4 kHz in the two chamber-raised animals for which rate-level data were obtained. In all cases, level sweeps were run at the CF. Saturation rate is determined as described in the caption for Fig. 17.

## III. DISCUSSION

### A. The issue of pathology in "normal" animals

In any study of normal physiology, one has to deal with the problem of weeding out those data which reflect pathological change. To devise effective screening procedures requires large amounts of data, and, even with such data, any criterion for dividing normal from abnormal will necessarily be arbitrary. One arbitrary screening procedure which is simple to implement is based on the visual detection level (VDL) for the gross neural response (at the round window) to click stimuli. Any animal with a VDL above a certain value can be considered unfit for normal studies.

All of the animals described in the present report, including the one exposed to high-level noise, had VDL's in the range which has been considered acceptable, i.e., "normal." However, there were significant differences in the single-unit data from these animals. One could not consider all these individuals to be "normal," no matter what the definition of the word. If one defines "normal" as that which is most commonly seen, then the compression of the spont distribution is normal for the fiber population in the cat's auditory nerve. However, the data from the chamber-raised animals (specifically the observation that in those ears where the minimum thresholds were exceptionally low at all CF regions the spont distribution was uniform across CF) suggest that the distribution is inherently bimodal at all CF regions and that the single-unit population in routine animals is reflecting a "normal pathology."

If we accept the view that the data from the three most sensitive chamber-raised animals most clearly reflect the inherent characteristics of the peripheral auditory system, then an inherent characteristic of the system is a very strict relationship between the rate of spont and relative threshold. At the high-CF region in routine animals, where the distribution of spont is severely compressed, this relationship can break down almost completely. This phenomenon could be the reason that Manley and Robertson (1976) failed to find any relation between spont and relative threshold in high-CF units from the guinea pig.

Data which we now consider to reflect normal pathology have appeared in previous publications from this laboratory. For example, a distribution of spont from four "untreated" animals (Kiang, Moxon, and Levine, 1970) shows a very large percentage of units with rates between 10 and 40 spikes/s. The threshold data for these same four ears have also been published [Kiang (1968), Fig. 5]. Two of the ears (K448 and K480) showed exceptionally low minimum thresholds at all CF regions and showed a spont distribution which was uniform across CF. The other two ears showed compression of the spont distribution in the high-CF region and thresholds deviating significantly from the BTC.

These observations suggest that a more sophisticated screening procedure is necessary if one wishes to study in detail the inherent relationships between physiological variables in the peripheral auditory system. One reasonable approach would be to compare the minimum thresholds in each animal to the BTC for the appropriate species. In the three most sensitive chamber-raised animals, all the high-spont units were within 20 dB of the BTC at all CF regions. If, in routine animals, one considers only those CF regions where the high-spont units were within 20 dB of the BTC, the distribution of spont is similar to that seen in the most sensitive chamber-raised cats.

With a strict 20-dB-from-the-BTC criterion, the yield of usable data from the routine animals is diminished significantly, especially for CF above 10 kHz. Thus, it would be of considerable practical use, as well as theoretical interest, to know the causes of this "normal pathology." As mentioned earlier, the observation that compression of the spont distribution was sometimes associated with elevated thresholds after experimental acoustic traumatization suggested that noise exposure could be the principal cause of this pathology in routine animals. However, the data from the chamber-raised animals were not entirely in concordance with such a view. Since all four animals must have had very similar noise exposures, the compression of spont rates seen in one of them suggests that the phenomenon is not solely noise induced. A second possibility is that the phenomenon is age related, with a variable time of onset. Since most of the routine animals in our sample were probably more than six months old (the age of the chamber-raised animals), there should be a significantly higher proportion of any pathology related to aging in the former sample of animals.

A second feature of the single-unit response in routine animals which we had suspected was due to previous noise exposure was the notch near 3 kHz in the distribution of thresholds at CF (Kiang, Liberman, and Levine, 1976). One of the major reasons for suspecting an etiology of noise exposure was by analogy to the "4-kHz notch" in the audiograms of humans exposed to environmental noise (Taylor *et al.*, 1965; Paparella and Melnick, 1967; Passchier–Vermeer, 1974). A second reason is that these single units with CF near 3 kHz show a hint of the increase in sensitivity on the tuning-curve tail seen very clearly in animals experimentally exposed to high-intensity noise (Fig. 15). Two additional observations argue against a purely conductive origin for the 3-kHz notch: (1) There is no notch in the low-frequency tails of tuning curves from units with CF higher than 3 kHz, and (2) there was often an increase in the spread of CF thresholds among units with CF near 3 kHz (Fig. 11).

The data from the chamber-raised animals were not entirely consistent with the view that the singularity in the 3-kHz region was solely noise induced. There were small (less than 10 dB) notches in the unit-threshold plots of some of the chamber-raised animals and a noticeable increase in the threshold spread. However, since these effects were among the smallest we have seen, and since these animals were not completely sound deprived, the data are inconclusive in this regard. One possibility that cannot yet be ruled out is that the anomalous behavior in the 3-kHz region is, at least in part, due to temporary threshold shift induced by some part of the surgical procedure prior to the single-unit experiment. This threshold shift could be due, for example, to acoustic trauma from the removal of skull to expose the posterior fossa. Alternatively, it could arise from systemic changes in the animal, correlated, for example, with the reaction to anesthesia levels. Although it is not yet clear whether the 3-kHz anomalies are temporary, permanent, or some combination of the two, it does seem clear that they are cochlear in origin. For some reason, this region of the cochlea behaves somewhat differently from the adjoining regions in virtually every animal.

### B. Significance of physiological unit types

The idea that the rate of spont might be a useful dimension along which to classify unit types in the auditory nerve is not a new one (Kiang *et al.*, 1965). The original observation that the distribution of rates was fundamentally bimodal suggested a possible division into two classes, with spont above and below roughly 18 spikes/s. Now that data can be gathered from hundreds of units in the same animal, it can be demonstrated more convincingly that the units with spont greater than 18 spikes/s comprise a distinct and homogeneous group with respect to threshold (Fig. 10). The suggestion that the units with rates below 18 spikes/s fall into two threshold classes rather than one is most convincing when the overall sensitivity of the experimental animals is exceptionally good.

In data from both chamber-raised and routine animals, we have observed threshold differences of up to 70 dB between the low- and high-spont units of similar CF in the same animal. This is a significantly larger spread than has been reported in recent studies and, as such, deserves further comment. The earliest studies of auditory-nerve activity reported very large threshold spread. Katsuki, Suga, and Kanno (1962) reported that there could be threshold differences of more than 100 dB for units with CF near 3 kHz, and Kiang *et al.* (1965) showed a threshold spread of 60–70 dB in data pooled across many animals. Somewhat later, Kiang (1968) reported that when data are not pooled across animals and when "various experimental controls are tightened," the spread in threshold narrows significantly. His unit-threshold plots show a scatter of less than 20–30 dB at any one CF region. He further suggested that Katsuki's 100-dB threshold spread arose by confusing the "tails" of high-frequency units for insensitive low-frequency units. Evans (1972) reported that in "optimal" preparations the threshold spread was less than 20 dB and that the high-threshold, broadly tuned units which he saw in certain animals were explicable, for the most part, in terms of acute pathological change.

There are several reasons to believe that our high-threshold, low-spont units are neither the result of acute pathological changes nor the tails of higher-frequency units. That they are not the tails of high-CF units is quite clear from the sharpness of their tuning curves and the fact that they can be found at all CF regions (Fig. 11). Their sharp tuning also tends to argue that they are not the result of acute pathological change in the cochlea, as does the observation that high-threshold, low-spont units can be found throughout the course of the experiment, intermixed with sensitive, high-spont units of similar CF. (Compare unit numbers for the curves in the three panels of the bottom row of Fig. 13.) Lastly, the possibility must be considered that the low-spont units are the result of *chronic* pathological change. The only argument which can be advanced against this suggestion is that we see these units in all CF regions in the young animals which were raised from birth in the sound proofed room (as well as in every routine animal we have investigated).

It is likely that these high-threshold, low-spont units were selected against in the sample of units obtained by previous experimenters. Only by using electric stimulation were we able to detect such units, since they had very high acoustic thresholds and virtually no spontaneous discharges. Many such units were encountered which would not respond at all to the acoustic clicks routinely used as search stimuli in this laboratory. That we do, in fact, encounter a higher percentage of low-spont units than when the search stimuli are acoustic, can be easily seen by comparing our spont distribution with that published by Kiang *et al.* (1965).

Also relevant to the question of the degree of threshold spread at one CF region is the method used to determine threshold. The "thresholds" yielded by the automated tuning-curve paradigm (when run at criterion 0) constitute, regardless of spont, those frequency-level points which produce an absolute rate increase of roughly 10 spikes/s over spontaneous rate (Fig. 1). One may argue as to whether a threshold criterion of a *percentage* increase in firing rate is not more appropriate in terms of signal detection by higher auditory centers. Had we used a threshold criterion of percentage increase in firing rate, our threshold spread would be somewhat less. The question of threshold definition is key if one wants to use auditory-nerve data such as these to draw inferences about the mechanisms underlying perceptual phenomena such as the growth of loudness. However, questions concerning the appropriateness of various threshold criteria have no direct bearing on the classification of unit types suggested by the data in Fig. 10. This figure shows the relationship between the spontaneous rate of auditory-nerve units and the way they behave when presented with the particular stimulus paradigm we use to estimate threshold tuning characteristics. The important point remains that this behavior does not appear to vary smoothly as a function of spont; rather, the function appears to consist of three discrete segments, suggesting the existence of three types of auditory-nerve units.

There may be some other property of the auditory-nerve response which suggests a further subdivision of one or more of the unit types, especially the heterogeneous, low-spont units. Thus, the relationship between spont rate and other aspects of auditory-nerve response, such as phase or latency, should be examined systematically. The data accumulated to date leave the overall impression that the low-spont units are in some sense different from both the medium- and high-spont units: (1) The threshold of the low-spont units is often very high relative to both high- and medium-spont units (Fig. 10); (2) the threshold of low-spont units relative to both high- and medium-spont units changes as a function of CF (Fig. 11); (3) the low-spont tuning curves are often significantly narrower at high intensity than those from medium- or high-spont units of similar CF (Fig. 14); and (4) the maximum discharge rate in response to tones at the CF shows a great deal of spread among the low-spont units and is often much lower than that seen in high- or medium-spont units of similar CF (Figs. 16 and 18).

The observations that the low-spont units comprise a small subpopulation in the auditory nerve which (1) is evenly distributed throughout the CF dimensions, (2) can be seen in all normal cats, and (3) have response properties markedly different from the remainder of the single-unit sample have suggested that this group of units is a possible neurophysiological correlate of the longitudinal fiber type. The problem with such an interpretation is that the percentage of units with spont rate less than 0.5 spikes/s is typically 10%–15% of the unit sample while the longitudinal fibers are said to comprise roughly 5% of the fibers in the nerve (Spoendlin, 1969, 1971). Secondly, although at least three unit types have been tentatively identified, only two fiber types have thus far been described. These data suggest the need for more morphological studies as well as further physiological work. One area which should be reexamined is the effect of efferent stimulation on the activity in single auditory-nerve fibers (Wiederhold and Kiang, 1970). Any differences in the effectiveness of stimulation of the crossed olivocochlear bundle in raising the threshold of low-, medium-, and high-spont units would be interesting in light of the report that this bundle terminates exclusively on the outer hair cells (Iurato, 1964).

It should be noted, in passing, that one recent study of auditory-nerve response in cat reported the discovery of a small subpopulation of auditory-nerve units with a distinctive pattern of response to clicks (Pfeiffer and Kim, 1972). The authors suggested that this group might correspond to the longitudinal fibers. They point out that this subgroup, isolated on the basis of click response, ranged in spont from less than 1 to greater than 80 spikes/s. Preliminary observations in this laboratory (Kiang, personal communication) confirm the suggestion that Pfeiffer and Kim's "Population II" units are not the same as the low-spont units. It should also be noted that Pfeiffer and Kim have not demonstrated that Population II units can be found at all CF regions, and that they have demonstrated significant differences in the proportion of Population II units seen in different animals.

Regardless of the morphological significance of the division of auditory-nerve units into low-, medium-, and high-spont classes, this classification has relevance for other studies of auditory-nerve response. It would be useful to reexamine many aspects of these responses, paying more attention to differences as a function of spont and, especially, to the behavior of the low-spont units.

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