Some Effects of Stimulus Intensity on Response of Auditory Nerve Fibers in the Squirrel Monkey

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WE SHALL DESCRIBE in this paper some effects which change in sound pressure level of a tonal stimulus may have on the response of an auditory nerve fiber in the squirrel monkey. We shall focus our attention primarily on those observations which imply the existence of orderly relationships between the mechanical events produced on the cochlear partition and the time structure of the neural response.

METHODS AND MATERIALS

Experimental data were obtained from 48 squirrel monkeys. The surgical procedures to expose the cochlear nerve and the techniques for stimulus delivery and recording were reported previously (1, 14) and will only be summarized briefly here. The frequency and sound pressure level (SPL) of tonal stimuli were set by a LINC computer under program control. For each animal the SPL at the tip of the probe of a calibrated Kellogg condenser microphone was determined for frequencies between 20 and 25,600 Hz when the tip was located at the central end of an earpiece in close proximity to the eardrum. SPL values were determined every 20 Hz up to 5,100 Hz and every 100 Hz at higher frequencies. SPL calibration data were stored in the LINC memory and were used in setting a computer-controlled attenuator in order to present specified SPLs during the experiment. In each experimental run the frequency-SPL domain was explored in an orderly manner. The sequence was from low to high, both for the consecutive SPLs at each frequency and for the successive frequencies. The duration of the stimuli, the interval between stimuli of the same frequency and the interval between stimuli at different frequencies could be set independently. In order to obtain representative samples of spontaneous activity, the computer scheduled spontaneous (no stimulus) sequences at the beginning and end of each run as well as after every eight consecutive stimulus presentations.

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RESULTS

Relation between shape of response area and best frequency of fiber

Figures 1 and 2 illustrate, for eight fibers, response areas graphed in the form of isointensity contours. The samples are arranged in ascending order of best frequencies. The fiber in Fig. 1*A* (best frequency about 200 Hz) responds vigorously to a tone that is 1.5 octaves higher than the best frequency. Moreover, phase-locking is still in evidence at frequencies that are about 2.5 octaves higher. On a linear scale, the response area is highly asymmetrical and is skewed toward higher frequencies. As one examines data for fibers with successively higher best frequencies (Figs. 1*B*–2*C*) the shape of the response area changes systematically, becoming more or less symmetrical for best frequencies of about 800–1,000 Hz. Above 2,000 Hz the response areas assume the well-known shape, that is, they are asymmetrical about the best frequency, spread toward lower frequencies with increasing sound pressure level, and show a sharp cutoff for higher frequencies (see Kiang et al. (10) for references). In Fig. 2*D* the spread toward lower frequencies is not yet apparent since the highest sound pressure level in this case was less than 30 dB above threshold.

The plots suggest that there may be a relation between best frequency and the shape of the response area. We can examine this problem in more detail if we assume that two tonal stimuli which produce the same discharge rate (below the saturation level) do so because the mechanical disturbance on the segment of the cochlear par-

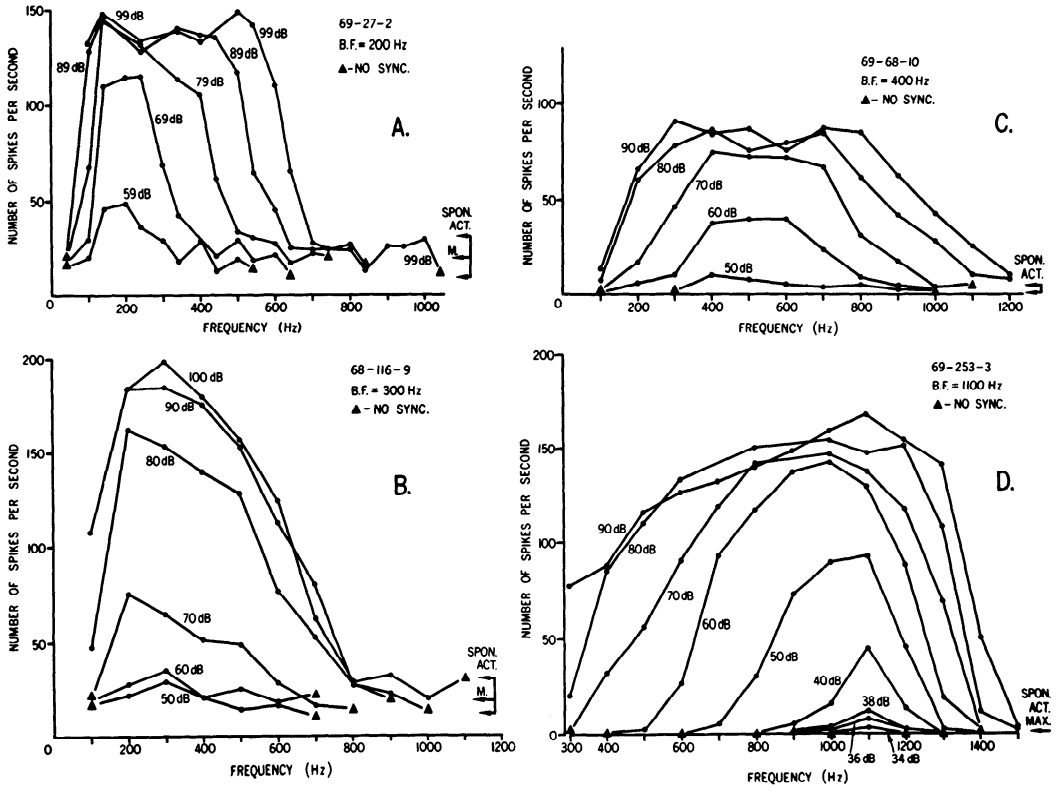

FIG. 1. Isointensity contours for four auditory nerve fibers with best frequencies (BF) below 1,200 Hz. Dots: evident synchronization of discharges with stimulus cycle; triangles: no significant synchronization. Arrows to the right of each figure indicate range, mean (M), or maximal rate of spontaneous discharges. In all figures sound pressure level (SPL) is given in decibels (dB) re 0.0002 dyne/cm^2.

tition supplied by the fiber is of the same amplitude in both cases. While such an assumption is probably not strictly correct it seems reasonable to make it for sound pressure levels near threshold.

It is a simple matter to determine graphically from isointensity contours the frequencies which can be expected to produce the same spike counts at different sound pressure levels. In practice, we have generally drawn a line parallel to the abscissa through the maximum of the isointensity curve for an SPL level near threshold and determined for each response area the frequencies below and above the best frequency which, for a given intensity differential, would be expected to cause the same spike count. Figure 3 plots on a double logarithmic scale two series of such measurements for all fibers for which we have adequate data. In Fig. 3*A* the best frequency determined at a level near threshold is plotted on the abscissa while the ordinate indicates the corresponding frequency below the best frequency which, at a 20 dB greater sound pressure level, was estimated to cause the same number of spikes as the best frequency and thus presumably produce—in the same region of the cochlear partition—a mechanical disturbance of the same amplitude as did the best frequency near threshold. Figure 3*B* is a similar plot for frequencies higher than the best frequency.

A systematic relation is apparent. Data points cluster closely along a straight line for all best frequencies above 2,000 Hz; they depart from this relation for lower best frequencies. Figure 3*B* demonstrates that the large spread toward higher frequencies illustrated in Fig. 1*A, B,* and *C* is a systematic observation for all fibers whose best frequencies are low.

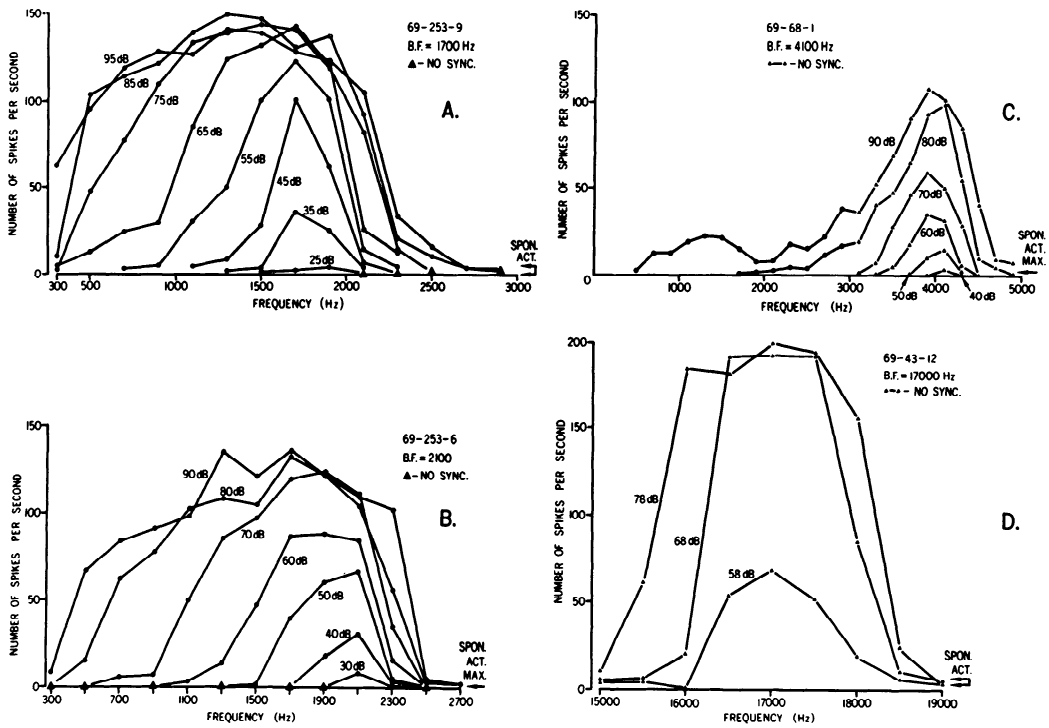

FIG. 2. Isointensity contours for another four fibers. Best frequencies higher than 1,500 Hz.

Figure 3 suggests several significant inferences concerning the shape of the traveling wave envelope, i.e., the spatial distribution of vibration amplitudes along the cochlear partition (2). The straight-line relation for the data above 2,000 Hz is consistent with the generally accepted view that points of maximal amplitude for the higher octaves are, in fact, nearly equidistant along the cochlear partition. Moreover, the excursion caused by a best frequency near threshold is approximately of the same magnitude as the excursion produced—at a 20 dB greater sound pressure level—by a tone which differs from best frequency by a constant ratio regardless of the actual value of best frequency. This in turn implies that the traveling wave envelope has a similar shape and spatial distribution irrespective of the point—between the oval window and the 2,000 Hz region—at which maximal amplitude occurs.

Departure of the data points from a straight-line relation can be interpreted in two ways that are not necessarily mutually exclusive. One could assume that the departure occurs because the shape of the traveling wave envelope changes substantially at some distance from the helicotrema. The other interpretation is that the shape of the traveling wave envelope is similar all along the cochlear partition and that the departure of the data points from the regression line results mainly because the logarithmic scale does not constitute an adequate approximation of the actual spacings between the points of maximal amplitude for the lowest octaves on the cochlear partition. In fact, an assumption that maximal amplitude points below 1,000 Hz are spaced approximately on a linear scale tends to shift the deviant points in Fig. 3*A* and *B* toward the regression line. We favor the second interpretation, mainly because a compression to various degrees of the representations of the lowest octaves has been deduced to exist in cat, guinea pig, man, and other mammals from a variety of experimental approaches (2, 4, 16, 19). We shall consider further implications of these findings in the discussion.

Possible physiological significance of spontaneous discharge rate

It is known that individual auditory nerve fibers differ greatly in spontaneous

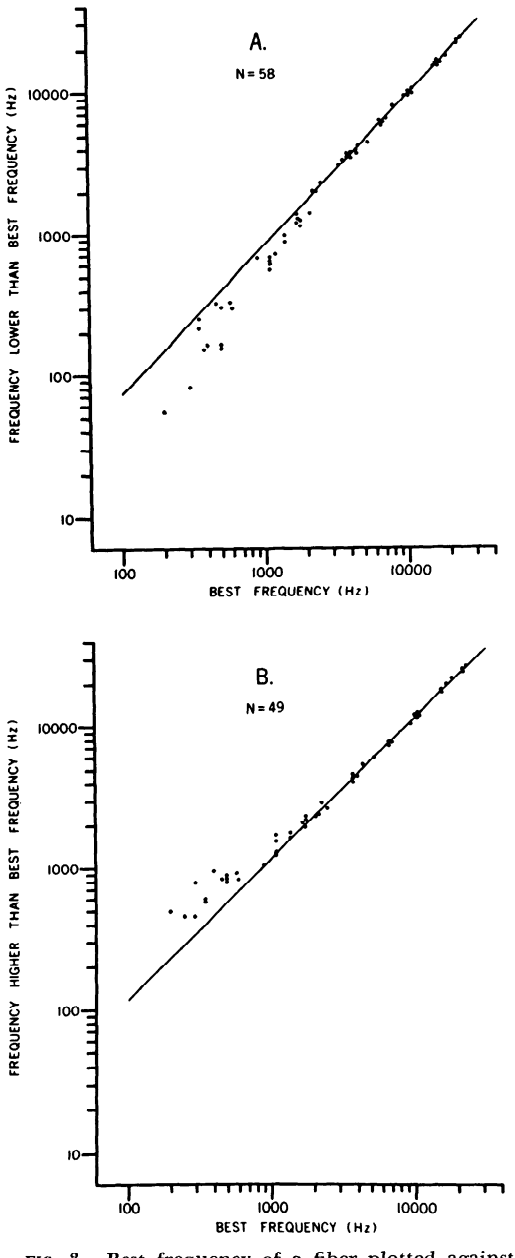

FIG. 3. Best frequency of a fiber plotted against that frequency which would be expected to produce at a 20 dB greater sound pressure level the same discharge rate as did the best frequency near threshold. Ordinate in *A* plots frequencies lower than best frequency; ordinate in *B*, frequencies which were higher. Regression lines were calculated for only those fibers whose best frequencies were equal to or higher than 2,000 Hz. Value of the slope is 1.0469 in *A* and 0.9858 in *B*. A few overlapping points in the graphs were spread apart slightly to indicate the presence of a measurement.

activity (8, 10, 14). In a sample of 124 fibers in which this question was examined in detail, about 23% discharged spontaneously at a mean rate not exceeding 10 spikes/sec and a substantial number of fibers in this subpopulation discharged less than once per second. For about 37% the mean rate was between 11 and 50 spikes/sec, while for about 40% this rate was between 51 and 110 spikes/sec.

No relation was detected between the level of spontaneous activity and the best frequency of the fiber. There was also no obvious dependence of background activity on the maximal discharge rate produced by an adequate stimulus, and some fibers whose maximal driven rate was well over 200 spikes/sec discharged spontaneously at very low rates. However, we had no fiber in our sample for which the maximal driven rate was equal to or lower than the spontaneous activity level but, with the technique employed, we might have overlooked such fibers if they exist.

As a rule, the mean rate of spontaneous activity is a fairly stable value throughout the period of study of the fiber. The absolute variability around the mean tends to be larger when the mean is larger.

Whether the various levels of spontaneous rates reflect a physiological phenomenon or whether injury to the fiber plays a significant role in determining this rate is a difficult question to answer. On the one hand, we often had an impression that in deteriorated preparations the spontaneous rate tends to be high; on the other hand, fibers with high or low rates occur in a single penetration in any animal. Moreover, if timing of the discharges is important for transfer of auditory information then at least some fibers with high spontaneous rates can be shown to transfer such information at markedly lower sound pressure levels than fibers with low spontaneous rates.

It is a routine observation for low frequencies (14) that the first sign of stimulus effectiveness, as sound pressure level is increased from below threshold, is locking of the discharges to the stimulus cycle. Phase-locking occurs, as a rule, before there is an increase in the discharge rate above the spontaneous level. In fact, when locking

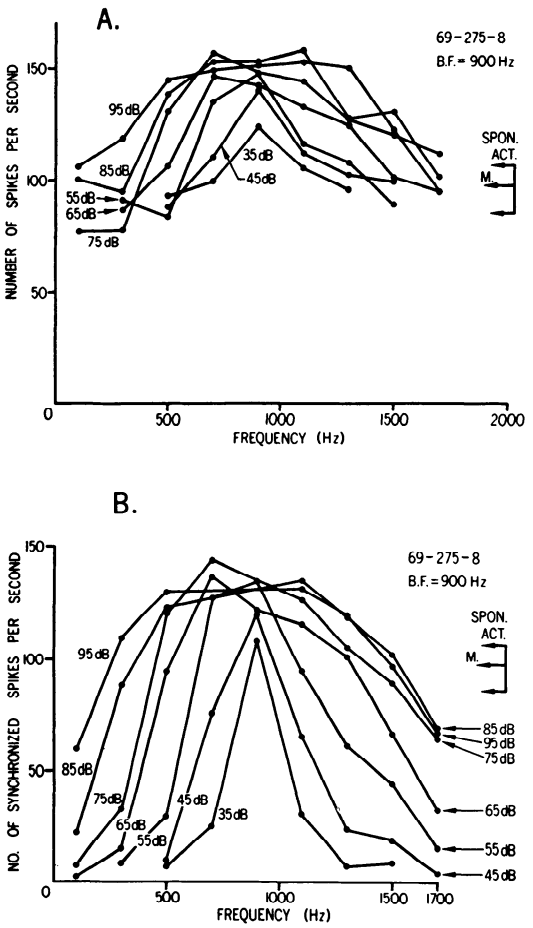

FIG. 4. Isointensity contours for a fiber having a high rate of spontaneous activity. *A:* total discharge rate. *B:* discharge rate of spikes synchronized with stimulus cycle. Further explanations in text.

starts to occur there is rather often a slight drop in rate below the average level of spontaneous activity and, occasionally, such a drop can be profound.

Figure 4*A* shows the response area of a fiber whose spontaneous activity fluctuated between 85 and 106 spikes/sec with a mean of 97 spikes/sec. The response area was relatively flat since the maximal driven discharge rate was less than 160 spikes/sec. For the contour at 35 dB SPL only the best frequency produced a rate clearly above the level of spontaneous activity and even this rate (124 spikes/sec) was but 18 spikes higher than the maximal spontaneous rate.

From consideration of the discharge rate alone it is not easy to see what purpose could be served by a high level of spontaneous discharge. If, however, timing of the discharges conveys information it seems useful to plot on the ordinate not the total discharge rate but the rate of spikes synchronized with the stimulus cycle. One measure of the number of synchronized spikes can be obtained from period histogram values by subtracting the number of spikes occurring in the less effective half of the cycle from that in the more effective one. Clearly, if the stimulus is without effect this difference is near zero. Figure 4*B* replots in this way the data shown in Fig. 4*A*. The result is striking. The isointensity contours become sharp; many stimuli which appear marginally effective or not effective at all in Fig. 4*A* seem, in fact, powerful. Thus, for example, a tone of 900 Hz at 35 dB SPL is not just slightly above threshold; instead, it causes transmittal of synchronized information at a rate of 109 spikes/sec. A tone of 700 Hz at 45 dB SPL —to give still another example—is not doubtfully effective; it produces synchronized information at the impressive rate of 75 spikes/sec.

Findings of this type suggest that moderate or high rates of spontaneous activity may possibly play a role in detecting weak signals, at least for low frequencies. If this be true, one would expect that fibers which are highly active spontaneously should usually have lower thresholds than fibers with low spontaneous rates.

Since individual animals may differ greatly in hearing acuity a desirable way to test this proposition is to compare fibers which stem from the same animal, have the same best frequency, and produce similar maximal discharge rates but which differ in rate of spontaneous activity. We have only a few such samples, but those we have are of interest.

Figure 5 shows the response area for fiber *69-253-7* plotted in terms of synchronized spikes. The range of spontaneous activity is between 39 and 69 spikes/sec with a mean of 50 spikes/sec. The best frequency stimulus at 20 dB produces 48 synchronized spikes/sec. Let us compare this response area with the one shown in Fig. 1*D* which stems from the same animal; here the spon-

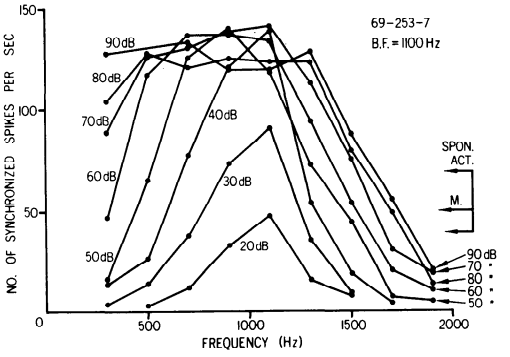

FIG. 5. Isointensity contours in terms of synchronized discharge rates for a fiber whose spontaneous rate was fairly high. Compare with response area shown in Fig. 1*D*.

taneous activity ranges between 0 and 0.8 spike/sec with a mean of 0.1 spike/sec. For the best frequency the threshold can be said to be about 34 dB since this stimulus produces a rate of 3 spikes/sec. However, even at 40 dB the stimulus produces only 40 spikes/sec, of which 38 occur in the most effective half of the stimulus cycle. The fiber in Fig. 5 was thus producing about 26% more synchronized discharges at 20 dB lower sound pressure level than was the fiber in Fig. 1*D* and the obvious major difference between these two fibers is the level of spontaneous activity. One may observe also that the more sensitive fiber is responsive over a substantially larger range of frequencies. Attention may be called to Fig. 2*A* and *B* which shows two other response areas for animal *69-253*. Spontaneous activity levels are low for both these fibers and neither is as sensitive as is the fiber in Fig. 5. However, best frequencies of these fibers are also different.

Figures 6 and 1*C* show three response areas for animal *69-68*. Best frequency is about 400–500 Hz for all three and the maximal discharge rates are also similar. At 50 dB, the best frequency stimulus produces a synchronized discharge rate of 10 spikes/sec for the fiber shown in Fig. 1*C* while this rate is 36 and 65 spikes/sec, respectively, for fibers in Fig. 6*A* and *B*. The mean rates of spontaneous activity are 3, 34, and 46 spikes/sec. It may be noted again that the more sensitive the fiber the wider is the responsive frequency range.

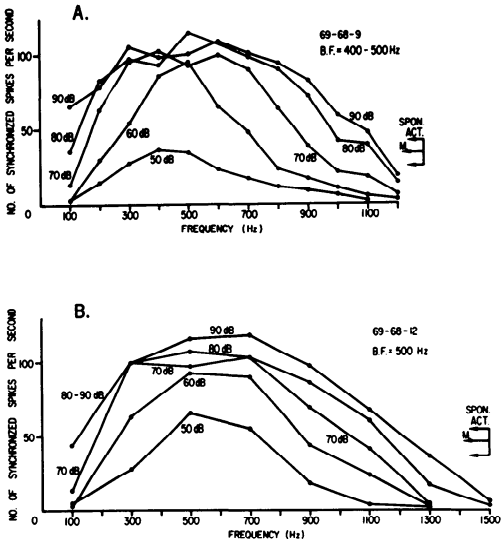

FIG. 6. Response areas for two spontaneously active fibers. Note the different discharge rates elicited by the best frequency stimuli at 50 dB SPL in *A* and *B* and in Fig. 1*C*.

Concept of an acoustic unit

It is a striking experimental observation that the saturation discharge rates caused by the most effective stimuli may be different by an order of magnitude for different fibers even though this rate varies only within narrow limits for an individual fiber. Figures 1 and 2 illustrate the most common saturation rates. The histogram in Fig. 7 indicates the distribution of maximal discharge rates (the upper limit of the saturation rate) for a representative sample of fibers. The modal value is 150 spikes/sec; the distribution is essentially normal about the mean. Note that the highest maximal rate is nearly 10 times the lowest. Figure 8 illustrates that the shape of the response

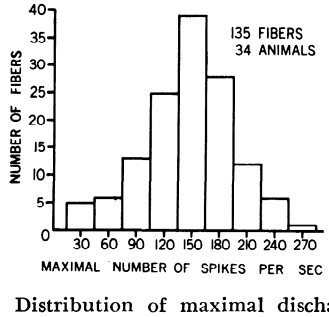

FIG. 7. Distribution of maximal discharge rates for a sample of 135 fibers. Class interval = 30 spikes.

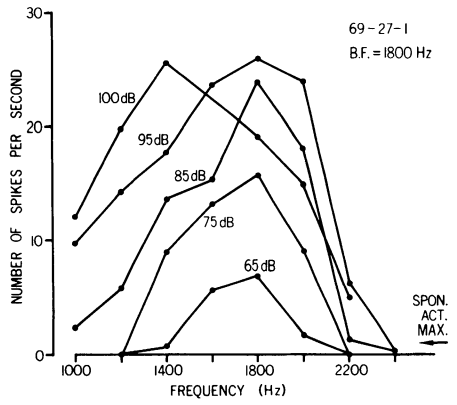

FIG. 8. Isointensity contours for a fiber whose maximal discharge rate was at the lower end of the distribution shown in Fig. 7. Contours for 65–95 dB SPL based on 3-sec tones, that for 100 dB on 10-sec tones.

area need not be affected in any obvious way merely because the discharge rates are low. On the other hand, the curves relating spike count to sound pressure level are likely to have different shapes for fibers with different saturation rates (Fig. 9).

The discharge rates reported here were usually based on stimuli which lasted 3 or 5 sec. Since stimuli were delivered in rather rapid succession throughout the experiment we assume that most of the fibers studied were already adapted by the time they were encountered. Hence it is probable that the observed maximal discharge rates are generally lower than rates for fully rested fibers.

The great differences between maximal discharge rates suggest that individual fibers may differ in the number of hair cells they innervate and thus constitute with their complements of receptors what may be defined as acoustic units of different sizes. We shall consider this question in some detail in the discussion.

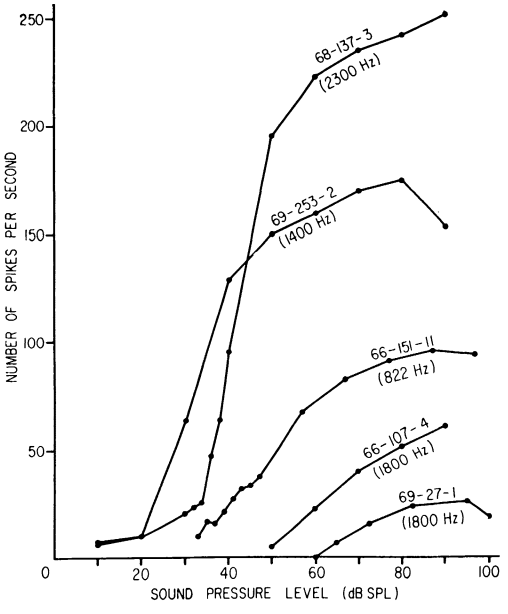

FIG. 9. Spike count vs. SPL functions elicited by best frequency stimuli for five fibers with different saturation rates.

Influence of sound pressure level on time structure of response

A basic and as yet poorly understood aspect of auditory physiology is the ability of the cochlea to function effectively throughout the enormous range of stimulus intensity which the ear is known to discriminate. Some of our results on the responses to low-frequency tones are relevant to this question.

Figure 10 shows a set of period histograms for a fiber responding at its best frequency to various sound pressure levels. The responses are phase-locked to the stimulus cycle and each histogram is fitted with a synthesized stimulus waveform. Figure 1*D* (the response area of the fiber) indicates that 60 dB stimulus causes a rate close to saturation and that the rates for 70, 80, and 90 dB stimuli are all within the saturation range. The pertinent observation here is that the histograms at saturation level can be fitted by a sine wave with about the same accuracy as the histogram near threshold insofar as it is possible to judge by inspection.

The result is representative and holds for all our single-tone data. The statement does not imply that the time structure of the period histogram, which we believe reflects the effective stimulating waveform, on the cochlear partition, never differs from the waveform of the presented sound. In fact, we shall show below that it may, and we have previously reported some preliminary observations to this effect (3). However, regardless of any distortion which may occur, the fiber clearly retains, at least up to 100 dB, its sensitivity to the funda-

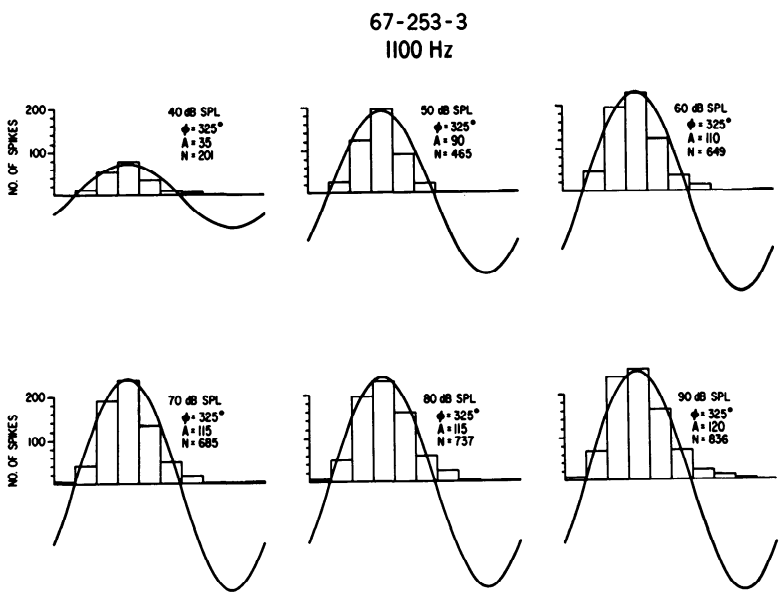

FIG. 10. Period histograms for a fiber responding to best frequency stimuli at different sound pressure levels. Each histogram is fitted by a sinusoid whose phase angle (in respect to the origin of the histogram) and amplitude are stated for each graph. Period of the stimulus: 912 μsec. Each bin = 92 μsec. N = number of spikes in the sample. Duration of the stimulus: 5 sec. In this and other similar figures the frequency of the stimulus is stated in round numbers. The period of the stimulus defines more precisely the actual frequencies used. A small division on the ordinate corresponds always to 10 arbitrary units of amplitude for the fitted waveform.

mental component of the stimulus waveform. In Fig. 10, for example, the nearly supramaximal stimulus at 60 dB and the one at 40 dB cause spike distributions similar to that for the tone at 90 dB although, of course, the amplitude of the latter is greater by factors of approximately 32 and 320 times, respectively. In the same fashion the shape of the period histograms for the data in Fig. 5 remains very similar when the amplitude of the sound pressure is raised roughly 3,200 times above the threshold value and at least 320 times above the amplitude of a supramaximal stimulus. Since such relations occur routinely in our data they raise the possibility that some kind of sensitivity control mechanism exists in the cochlea. If this mechanism were mechanical in nature the receptors would not necessarily be subjected to an unchecked linear increase in the amplitude of vibration as the stimulus intensity increases, and it would be reasonable to expect that the fiber might remain highly sensitive to the waveform of the stimulus, whatever its intensity.

Irrespective of whether or not such a mechanism exists we can use complex stimuli to examine, in a way more sensitive than possible with a single pure tone, to what extent the waveform of the stimulus is reflected in the time structure of the period histogram when the sound pressure level is varied. These experiments involved presentation of two low-frequency tones, the frequencies being locked precisely in the ratio of small integers and the sound pressure level chosen in such a way that the tones interacted to produce complex period histograms. If we now systematically raise the sound pressure levels of two primary tones but maintain the ratio of their amplitudes at a fixed value, all histograms in the series—if they follow the stimulus waveform precisely—should have exactly the same shape and, if the problem of phase shifts is neglected, they should be matchable by a waveform in which the amplitude ratio of the primaries is always the same.

Figure 11 illustrates a typical result. The first three histograms in the series indeed have a similar shape and can be matched by a waveform constructed from primaries

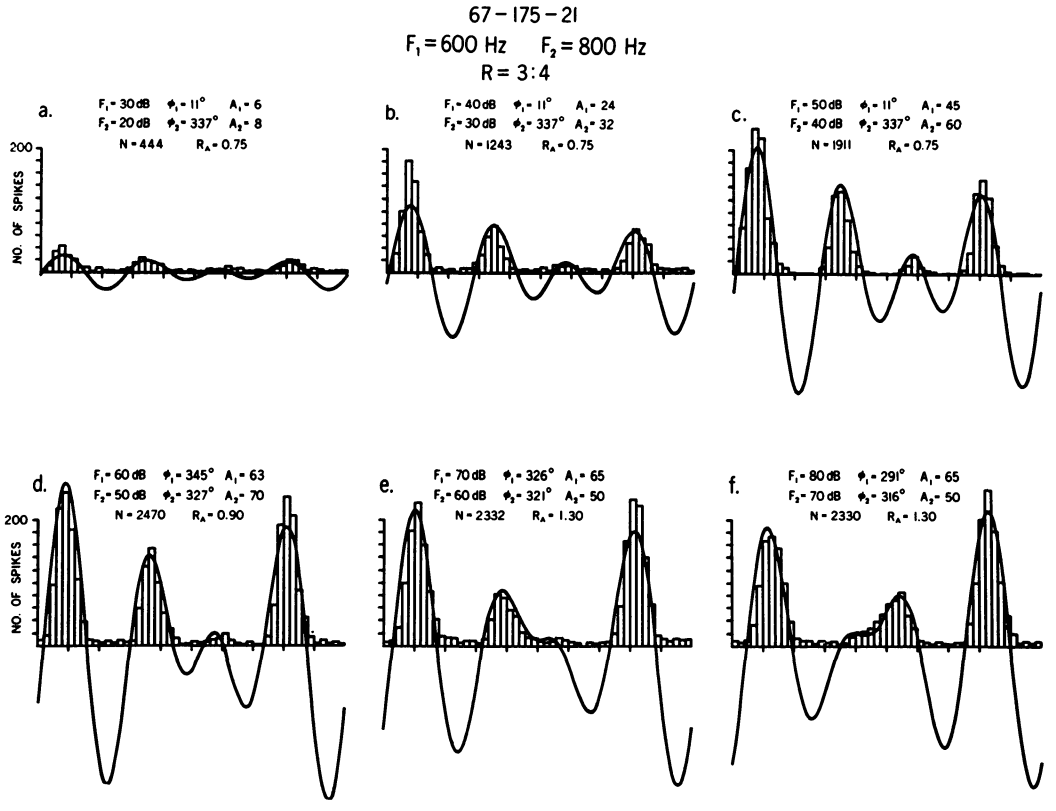

FIG. 11. Period histograms for a fiber responding to a complex periodic sound when the sound pressure level of both primaries is successively raised in 10-dB steps. Tones are locked in a ratio of 3:4. Period of complex sound = 4,998 μsec. Each bin = 100 μsec. Phase angle and amplitude of each primary used in construction of the fitted waveform are specified for each graph. R_a = amplitude ratio. Each histogram based on two stimulus presentations. Stimulus duration: 10 sec.

whose amplitude ratio is 0.75. The histogram in Fig. 11*D* could also be matched using this ratio, but a ratio of 0.90 gives a better result. The last two histograms cannot be matched, even approximately, with a ratio of 0.75 regardless of the phase angles chosen. However, satisfactory fits are obtained with a ratio of 1.3 which is quite unacceptable for reconstructing a waveform to match the first three histograms.

It will be noticed in Fig. 11 that the phase angles of the primaries in the matching waveforms are not the same for all histograms. We have reported elsewhere on the shifts in phase angle observed in the period histogram when single pure tones of increasing sound pressure level are presented (1). The general finding is that there is no shift in phase angle with increasing sound pressure level for best frequency tones; there is a phase lag for frequencies lower than the best frequency and there is a phase lead for frequencies higher than the best frequency. Usually, therefore, there is no expectation that the phase angle should remain constant when the sound pressure level changes.

The data in Fig. 11 are representative of our experiments of this type and the results can be summarized as follows. When a complex sound increases in sound pressure level over a range of about 50–70 dB but the intensity differential between primaries remains constant, the period histograms suggest that the stimulating waveform undergoes changes, both in the phase angles of the primaries and in their amplitude ratios. In our experiments it was always true that the less effective primary (the one which had less influence on the period histogram at low intensity levels) became more dominant as the absolute levels of both

were increased. The time structure of the response, therefore, reveals a marked nonlinearity of the system. The magnitude of the amplitude nonlinearity can be estimated by noting that the amplitude ratio for Fig. 11*F* is approximately 1.73 times that for Fig. 11*A*, a factor equivalent to 4.8 dB. This implies that F_2 in Fig. 11*F* is about 5 dB less effective than would be expected on the basis of its sound pressure level. Other data yield figures of similar magnitude (5–12 dB).

If this estimate is correct, it follows that for a smaller intensity range, say 20 dB, the nonlinearity is correspondingly smaller and therefore the period histograms should reflect rather closely, but (and we stress) not precisely, the amplitude ratios of the delivered sounds. We can examine this inference in a locked-tone situation maintaining one primary at a constant level while varying the other. Figures 12 and 13 illustrate 4 of about 50 similar experiments. In each series the first histogram is matched

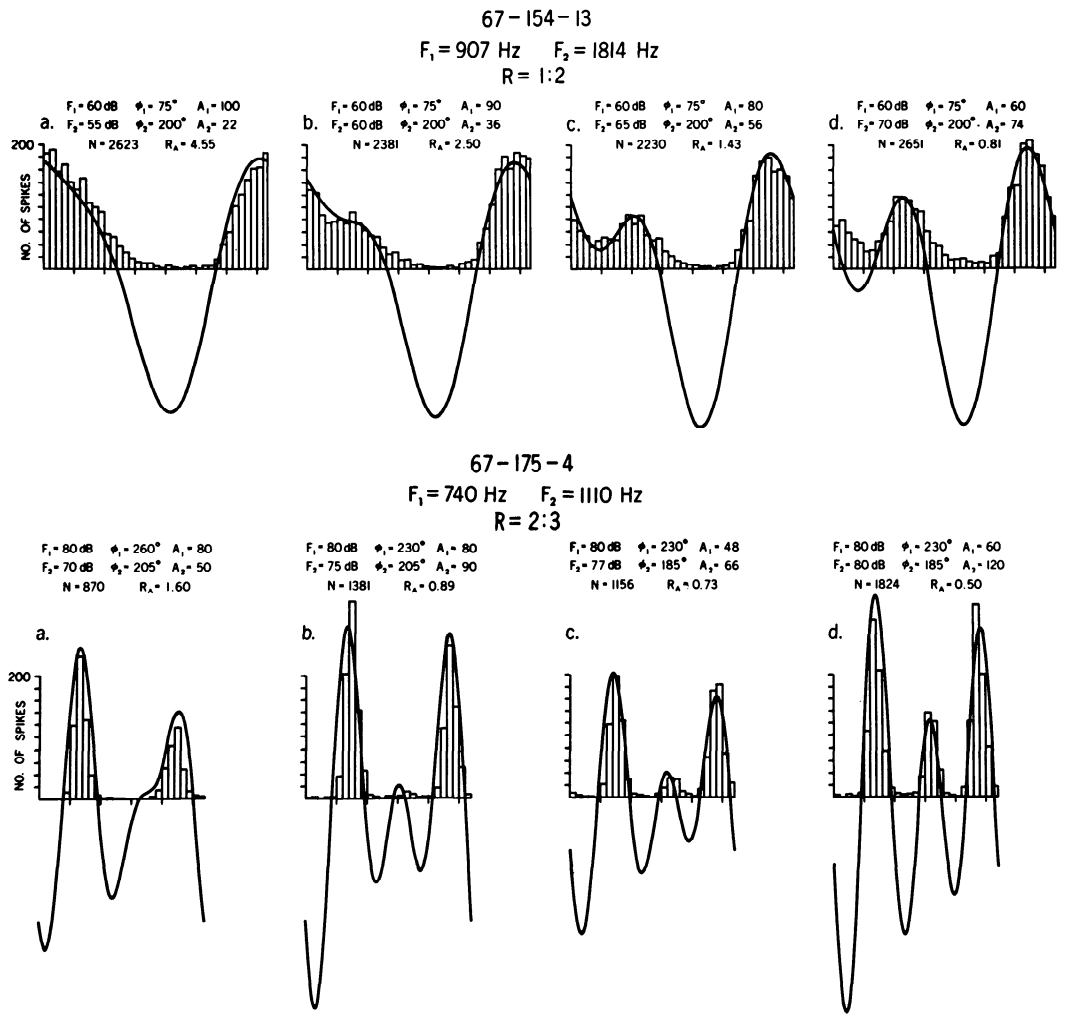

FIG. 12. Period histograms for two fibers responding to complex periodic sound when the sound pressure level of one primary remains constant and that of the other is successively increased in small steps. Parameters for the matching waveform were chosen arbitrarily for the leftmost histogram in each row. Note that the amplitude ratios for the other waveforms in each row were changed in proportion to the amplitude ratios of the acoustic stimuli. Period of the complex sound: 1,102 and 2,700 μsec, respectively. Bin = 100 μsec. Histograms in the upper row based on two, those in the lower row on four presentations of the stimulus. Duration of stimuli: 10 sec.

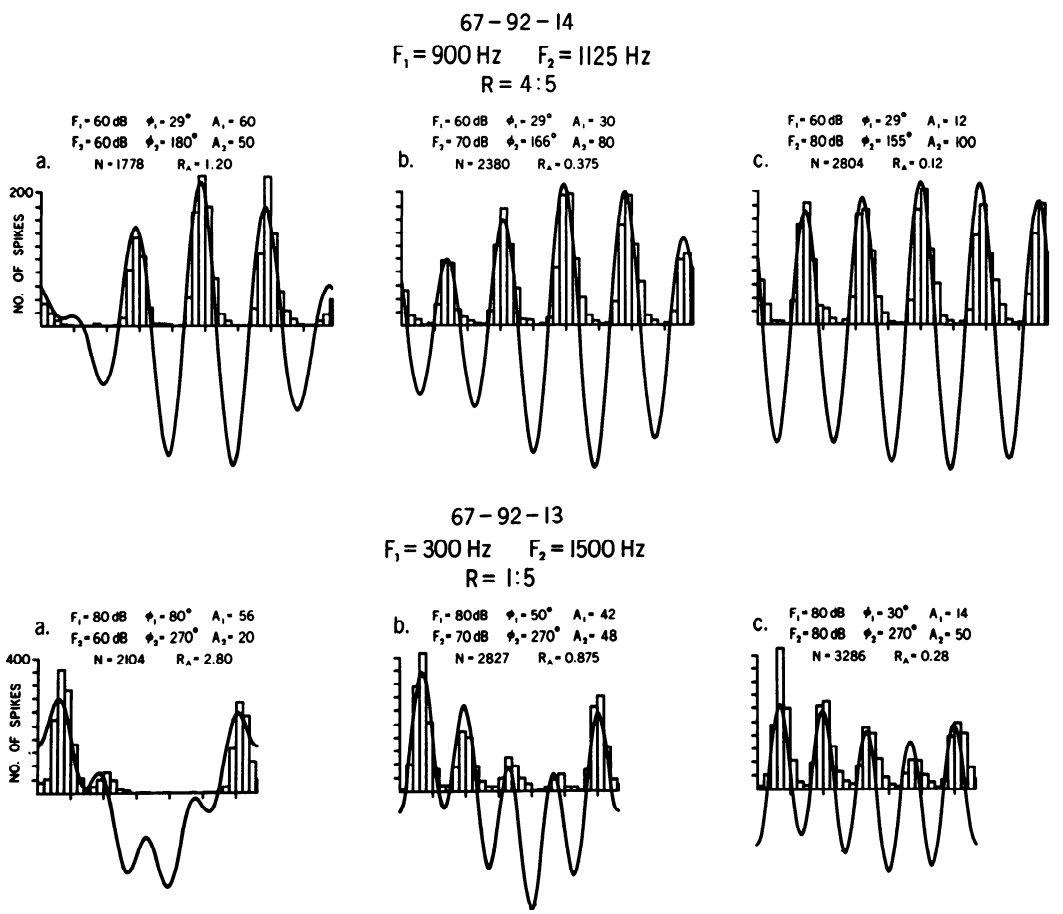

FIG. 13. Two experiments similar to those shown in Fig. 12. However, tones are locked in different ratios and the sound pressure levels of the higher primaries are varied over a larger range. Period of the complex sound is 4,444 and 3,322 μsec, respectively. Bin = 100 μsec. Each histogram based on two presentations of the stimulus. Stimulus duration: 10 sec.

by a waveform whose amplitude ratio is arbitrarily chosen to fit the data. In all other histograms in each series the amplitude ratio corresponds to the ratio in the actual stimulus. The fits, as expected, appear rather satisfactory. Thus, if two tones interact, the stimulating waveforms can be reconstructed to a first approximation over virtually the entire interaction range by a linear addition of the primaries whose amplitudes are in the ratio of the tones actually delivered. We have observed previously (3) that the range of waveform interaction for two tones is usually of the order of 20 dB. The reason for this is clear since a nearly 10-fold increase in amplitude of one of the primaries is likely to make it dominant in the resulting waveform on the cochlear partition.

DISCUSSION

Our findings on the shape of response areas and the spread of responsiveness lead us to infer that: *1*) the traveling wave envelope probably has a similar shape all along the cochlear partition, regardless of where the point of maximum amplitude occurs; *2*) the representation of octaves along the partition is not uniform. Our data suggest that the loci of maximal amplitude for octaves higher than about 1,000 Hz occur at approximately equidistant points, while those for octaves below 1,000 Hz are crowded over a distance which, to a first approximation, may be about equal to that occupied by a representation of a higher octave. Since the length of the cochlear partition is about 20 mm (9) and the audible upper-frequency limit in the squir-

rel monkey is higher than 32 kHz (5) it would follow that the lowest 1,000 Hz and each higher octave are represented over a distance of about 3.0 mm. The anatomical resolution therefore would be, on the average, approximately 3 μ/Hz up to 2,000 Hz and this resolution would diminish by a factor of two with each higher octave. It has often been suggested that the capacity to discriminate frequency is related to frequency representation on the cochlear partition. If this is true, one could infer that the absolute differential frequency limen for the squirrel monkey should be constant up to about 2,000 Hz and rise steeply for higher frequencies. Psychoacoustic observations lend credence to such a supposition since the absolute frequency limen in man (11, 17) is a fairly constant value of 2–3 Hz from about 60–1,000 Hz and rises by approximately a factor of two with each higher octave, which is, of course, another way of stating the classical finding that the relative frequency limen becomes approximately constant for higher frequencies.

Responses to low-frequency stimuli indicate that thresholds of fibers with high spontaneous activity cannot be assessed on the basis of discharge rate alone since locking to the stimulus cycle occurs routinely at intensities lower than those necessary to augment the rate above spontaneous level and locking is obviously an indication that the stimulus was effective.

There are several ways to estimate the degree of synchrony of the discharges with the stimulus cycle. In this report, we have expressed the rate of transmission of synchronized discharges by subtracting the rate in the less effective half of the stimulus cycle from the rate in the more effective half on the assumption that this difference reflects the depth of modulation of the rate due to the stimulus. However, depending on the nature of the neural mechanisms which receive and operate on the information carried by auditory nerve fibers, the total discharge rate in the more effective half-cycle may be a more meaningful measure than the difference. If this were so, the numerical advantage in transmission enjoyed by fibers with high spontaneous levels would be even greater than illustrated in our figures. In any case, our data clearly demonstrate that a fiber with a high rate of spontaneous activity can produce, at a sound pressure level that is lower by at least 20 dB, the same amount of synchronized information as a fiber which is nearly silent in the absence of stimulation. There is, therefore, some reason to believe that spontaneous activity could be utilized to lower the detection threshold for weak, low-frequency signals. However, no correlation was found either by Kiang et al. (10) or by us between best frequency and spontaneous activity level and the great range of these levels is puzzling. On the one hand, a fiber may be almost silent in the absence of a stimulus while, on the other hand, spontaneous activity may be as high as 100 spikes/sec, which is a rate equal to or higher than the maximal driven rate in response to a most efficient stimulus for a substantial population of fibers. An important question, still unresolved, is whether an injury to the fiber by the electrode or conceivably some other unphysiological events contribute significantly to the wide range of spontaneous activity. If moderate and high levels of spontaneous activity are, in fact, physiological phenomena and if it is assumed that the background activity increases with a number of hair cells a given fiber innervates, then one would be inclined to suppose on classical anatomical grounds that a majority of fibers in our sample (see p. 687, last paragraph; 688, first paragraph) was composed of external spiral fibers which innervate outer hair cells. However, Spoendlin (18) has recently suggested that about 90% of all fibers in the cochlear nerve in the cat are activated by the inner hair cells.

Great differences in saturation rate among auditory nerve fibers suggest that individual fibers may differ significantly in the number of hair cells they innervate and thus form acoustic units of different sizes. The classical anatomical knowledge seems in harmony with this view. The question of how many hair cells are innervated by a single afferent attracted much attention in the past since the answer had a bearing on the then current theories of hearing. While the findings were by no means unanimous it soon became clear that a near one-to-one relation, as expected by some

workers, was not likely to be true. Held (7), one of the greatest authorities on the innervation of the organ of Corti, was of the opinion that the principle of multiple innervation prevails. He felt that the innervation of the inner hair cells is too complex to be resolved by silver methods but he provided evidence that an external spiral fiber usually innervates a number of outer hair cells and that this number varies with individual fibers. The observations of Lorente de Nó (12) were rather similar. He concluded that several neighboring inner hair cells are usually supplied by a single radial fiber and thought that an external spiral fiber supplies numerous outer hair cells which may be scattered over a considerable distance along the cochlear partition.

Apart from differences in saturation rate there are two other observations which imply that auditory nerve fibers usually innervate a number of hair cells. First, scrutiny of response areas (Figs. 1 and 2) reveals that saturation rates for the marginal frequencies are fairly often substantially lower than those for the most efficient stimuli. Such an observation would be expected if the receptor surface is composed of a number of elements arranged over a length which cannot be neglected from a functional point of view. The other observation pertains to phase shifts in the period histogram when a tone of increasing sound pressure level is presented. We have shown that for frequencies lower than best frequency a lag in the average phase angle results (1). It is, we believe, difficult to explain such a systematic relation by a simple mechanism unless the assumption is made that the receptor surface of a fiber has an appreciable functional length.

Assuming that acoustic units differ in size, what can be said about the number of receptors an average fiber supplies? Since the modal saturation rate is about 5 times larger than the lowest observed, Fig. 7 suggests a minimum of 4–6 cells for such an average although, of course, this number could be larger by any multiple. While this estimate is in no apparent conflict with anatomical facts it is based on an assumption of unknown validity, namely, that all hair cells cause similar discharge rates. Whether acoustic units of different sizes necessarily have the same functional implications is, at present, a matter for conjecture. The unimodal distribution of the histogram values does not suggest that the sampled fibers might have been members of different populations.

It may be mentioned that Kiang et al. (10) have also observed large differences in saturation rate for auditory nerve fibers in the cat. However, the highest rates observed by them are lower than our figures by about 100 spikes/sec. The reason for this substantial difference is obscure.

We have suggested previously (3) that a single auditory nerve fiber is excited only by unidirectional elevations of the cochlear partition. We have also shown that if a complex periodic sound is presented and the phase angle of one primary is shifted, the time structure of the resulting period histogram faithfully reflects such a shift. Moreover, since any period histogram can be matched, to a first approximation, by a waveform obtained by a linear addition of the component sinusoids, we concluded that the time structure of the period histogram reflects the effective stimulating waveform produced by the sound on the relevant sector of the cochlear partition (3, 15). A later study showed an increase in sound pressure level may cause a shift in the average phase of the period histogram, the occurrence and direction of the shift being dependent on the position of the tonal stimulus within the response area of the fiber (1). Present work discloses a relation between the amplitude ratios of the primaries in the effective stimulating waveform and those in the delivered sound. There is, we believe, no doubt that if the sound pressure level of both primaries is raised over a range of 50–70 dB, but their amplitude ratio remains constant, the amplitude ratio in the stimulating waveform changes. The fibers respond, therefore, in a nonlinear fashion, both in regard to phase and amplitude, when the sound pressure level of the stimulus is increased. It is noteworthy that Goldstein and Kiang (6), who studied the difference tone, interpreted their results as indicating that a nonlinear mechanism must exist in the cochlea of the cat.

The magnitude of the amplitude non-

linearity over the explored intensity range (70 dB) is of the order of only 5–12 dB. Hence, over a range (usually not larger than 20 dB) in which the shape of the period histogram is the resultant of both tones, the amplitude ratio of the effective stimulating waveform changes very nearly as the ratio in the delivered sound.

The capacity of a fiber to reflect the waveform of the stimulus when the latter greatly exceeds that sound pressure level which elicits a saturation discharge rate suggests the existence of a cochlear sensitivity control mechanism which may, but perhaps need not be, mechanical in nature. Such a mechanism could be a major source of the demonstrable nonlinearity of the system and be the result of asymmetry in the vibration of the cochlear partition. While our material is too restricted to permit satisfactory evaluation of this possibility, we have occasionally found it useful to introduce a d-c component in synthesizing the effective stimulating waveform. Asymmetrical vibration of the cochlear partition has been observed in cochlear models by Tonndorf (20) and its importance in cochlear mechanics has been strongly argued by Whitfield (21). As the latter points out, acceptance of nonlinearity drastically revises the classical, but nonetheless quite incredible, conclusion that at threshold the receptors are sensitive to displacements as small as a tiny fraction of the diameter of a hydrogen atom. It is also tempting to think that the receptors are not exposed to enormous variations in the amplitude of vibration as is postulated by the orthodox view. In fact, there is recent direct evidence (13) that the motion of the cochlear partition, in the region of maximal amplitude, is markedly nonlinear and therefore a very substantial error may be introduced in calculating the amplitude of the displacement at threshold by linear extrapolation of values observed at very high sound pressure levels.

SUMMARY

1. The response areas of single auditory nerve fibers imply that the traveling wave envelope has a similar shape all along the cochlear partition but that spatial representation of octaves varies with frequency. Points of maxima for octaves higher than 1,000 Hz are equidistant; those for octaves below 1,000 Hz are crowded into a space approximately equivalent to that occupied by each higher octave.

2. The results suggest that auditory nerve fibers with high spontaneous activity could be of use in lowering the detection threshold for weak, low-frequency signals.

3. It is suggested that individual nerve fibers differ in the number of hair cells they innervate and thus form acoustic units of different sizes.

4. A sensitivity control mechanism may exist in the cochlea since a fiber remains sensitive to the waveform of the stimulus when the latter greatly exceeds the sound pressure level which elicits saturation discharge rate.

5. The time structure of the response implies that the amplitude of the effective stimulating waveform on the cochlear partition behaves in a nonlinear fashion when sound pressure level increases over a range of 50–70 dB. However, over the range where the waveforms of two tones interact, which is about 20 dB, the amplitude ratio in the stimulating waveform changes very nearly as the ratio in the acoustic stimulus.

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