SPIKE DISCHARGE PATTERNS OF SPONTANEOUS AND CONTINUOUSLY STIMULATED ACTIVITY IN THE COCHLEAR NUCLEUS OF ANESTHETIZED CATS

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ABSTRACT   Interspike interval histograms of spontaneous and stimulated activity were computed from spike discharges of single units in the cochlear nucleus. These histograms indicate that a number of different types of spontaneous discharge patterns exist in the nucleus. The type of spontaneous activity of a given unit is related to its activity in response to continuous tones. Correlations were found between the discharge patterns of units and their anatomical locations within the nucleus.

INTRODUCTION

The cochlear nucleus is a complex structure that can be divided into a number of subdivisions based on the nature of cell structure and connections. (Ramón y Cajal, 1952; Lorente de Nó, 1933; Rasmussen, 1960). These distinctive anatomical characteristics provide opportunities to relate the electrical activity of single units with the morphological structures found within the nucleus. In any systematic attempt to study the electrical activity of single units, one important step lies in the description of spontaneous activity, *i.e.,* activity in the absence of controlled stimuli. The possible functional significance of spontaneous activity has been discussed already in several previous studies. (Lowenstein and Sand, 1940; Pumphrey, 1950; Bremer, 1953; Buller, Nicholls, and Strom, 1953; Granit, 1955; Roeder, 1955; Kuffler, FitzHugh, and Barlow, 1957; Bullock, 1958; Burns, 1958; Schlag, 1958, 1959; Grossman and Viernstein, 1961; Werner and Mountcastle, 1963). Although many aspects of spontaneous activity of single units may be studied, this report concerns only the temporal patterns of spike discharge.

METHODS

All experiments were conducted in an electrically shielded, soundproofed, and vibration-isolated chamber. Acoustic stimuli were delivered by a 1-inch Brüel and Kjaer capacitor

microphone (Brüel and Kjaer Instruments, Inc., Naerum, Denmark) used as an earphone. A closed acoustic system was obtained by sealing the earphone coupler into the external ear canal.

Experiments were performed on 49 adult cats. Surgical procedures were carried out after cats were anesthetized with intraperitoneal injections of Dial (75 mg/kg). A gross electrode placed near the round window enabled monitoring of the microphonic and neural potentials from the cochlea. The cochlear nucleus was exposed after the cerebullum was either partially aspirated or displaced medially. Indium-filled, platinum-tipped microelectrodes (Gesteland, Howland, Lettvin, and Pitts, 1959) were placed on the surface of the cochlear nucleus under visual observation. Fine movements of the electrode along a single track within the nucleus were controlled remotely by a hydraulic micromanipulator.

Spike discharges, which were negative in polarity with respect to the headholder, of single units could be recorded for many hours. These electric responses from the animal were amplified and recorded on an FM magnetic tape recorder. The entire recording system had a passband of 35 to 5,000 CPS. Interspike interval histograms were obtained by processing the recorded spike trains on the TX-O digital computer (Gerstein and Kiang, 1960; Rodieck, Kiang, and Gerstein, 1962).

Information concerning anatomical locations of single units was obtained by two different methods. The first method was based on data described by Rose, Galambos, and Hughes (1959). These workers correlated sudden shifts in the orderly tonotopic arrangement of units in the cochlear nucleus with the boundaries of three gross subdivisions of the nucleus. These divisions may be labeled the dorsal cochlear nucleus (DCN), the posterior ventral cochlear nucleus (PVCN), and the anterior ventral cochlear nucleus (AVCN). In the present study the characteristic frequency (frequency of tone burst to which a unit is most sensitive) of each unit as well as its position along an electrode track was noted. Characteristic frequencies (CF) and unit thresholds were determined by finding the frequency and lowest signal level of tone burst (25-millisecond duration, 10 per second repetition rate, 2.5-millisecond rise-fall times) for which spike discharges synchronized with the tone burst stimuli could be observed on an oscilloscope. Electrophysiological data sufficient to localize units are available for 170 units.

The second method of locating units was based on histological determinations of electrode tracks. Animals were perfused either with 10 per cent formalin or with the alcohol-formalin—acetic acid mixture of Bodian (1937). The excised cochlear nuclei were imbedded in paraffin and sections cut at 20-micron thickness. Serial sections were mounted and stained by the protargol method of Bodian (1936). The electrode tracks were reconstructed taking into consideration shrinkage and distortions of the tissue as a result of histological manipulations. The locations of units relative to the beginning and end of each electrode track were superimposed on the reconstructed tracks. In certain cases the position of a particular unit was determined more accurately by producing a small radio-frequency lesion at the tip of the recording electrode after recording from the unit. The histological data necessary for reconstructing electrode tracks are available for 45 units. Altogether a reasonable estimate of location is available for 190 units, both methods of localizing units being available for 25 units.

RESULTS

In a total sample of 269 units, the rates of spontaneous discharge for most units ranged from 0 to 150 spikes/second. Approximately 20 per cent of the units

showed no spontaneous activity during 1 minute of recording. Another 15 per cent had rates of spontaneous activity lower than 5/second. Almost 95 per cent of the total number of units in this study had rates of spontaneous activity less than 100 spikes/second. Two exceptional units had rates of 183 and 289 spikes/second, respectively.

The interspike interval histograms of the spontaneous activity recorded from these units have a variety of shapes as illustrated in Fig. 1. With the exception of four units with histograms similar to that of unit P28-5, all histograms of spontaneous activity were unimodal. Bimodal histograms were thus too rare for systematic study and will not be treated further in this report. The "blank" histogram (unit P20-3) is an explicit reminder that many units do not exhibit spontaneous activity.

If the spontaneous activity of a particular unit is sampled over many hours, the shape of the histogram can be quite stable (Rodieck, Kiang, and Gerstein, 1962). There is no obvious correlation between the CF of the units included in this study and the shapes of their interval histograms. Furthermore, given the rates of spontaneous activity (Fig. 2), the shapes of the interval histograms cannot be predicted.

As a unit is stimulated by a continuous tone at its CF, its rate of discharge increases and the interspike interval histograms of its response activity become narrower than the histogram of its spontaneous activity, (Fig. 3, left column). However, when the time scales of histograms for responses to low and moderate levels of stimulation (within 25 db of the unit's threshold) are expanded by a factor equal to the ratio of the average rates of response and spontaneous activity, the shapes of the histograms for both spontaneous and stimulated conditions are very similar, (Fig. 3, right column). For some units, higher levels of stimulation result in a relative decrease of the number of long interspike intervals. The similarity in the shape of interspike interval histograms for spontaneous and stimulated activity holds for any particular shape (Fig. 4).[1] The shapes of histograms remain similar even in cases for which the rates of response activity are tenfold greater than the rates of spontaneous activity. In addition, the joint interspike interval histograms (Rodieck, Kiang, and Gerstein, 1962) for spontaneous activity are found to resemble closely the corresponding histograms for stimulated activity, provided the time scales are appropriately changed.

Fifteen units with zero spontaneous activity did not respond to continuous tones at their CF, although they did respond to the onsets of tones. Nineteen units with zero spontaneous activity responded to continuous tones with sustained discharges.

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[1] The leading edges of histograms of spontaneous activity with short modal values often differ from the corresponding portion of histograms of response activity (e.g., unit P33-5, Fig. 4). In these cases, increases in stimulus level can not decrease the modal value proportional to the expansion of the time scale of the histograms. Thus, a shift in the relative position of the mode of the histogram leads to a difference in the shape of the leading edges.

SPONTANEOUS

UNIT P32-5

UNIT P33-14

UNIT P87-2

P54-2

P32-11

P64-4

O   MSEC.   125   O   MSEC.   125   O   MSEC.   125

UNIT P28-5

UNIT P20-3

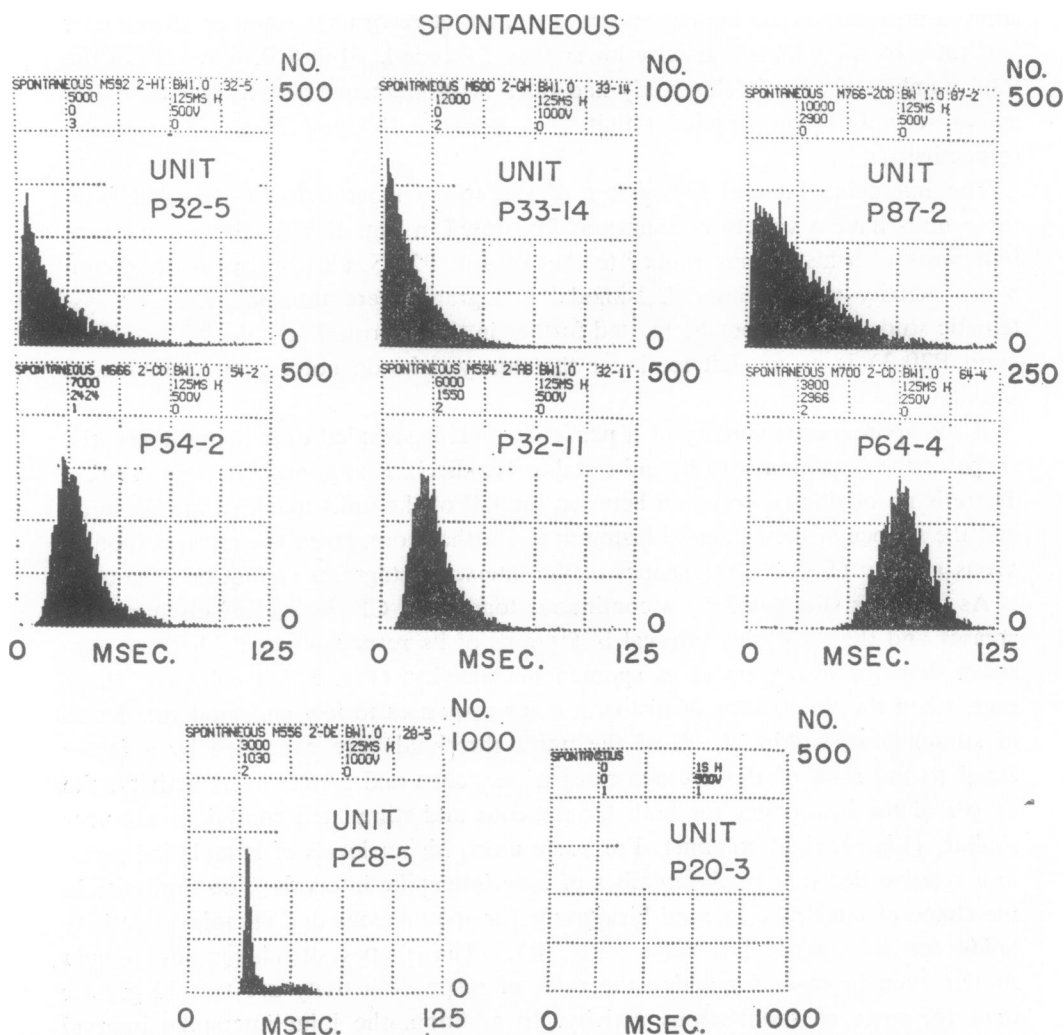O   MSEC.   125   O   MSEC.   1000

FIGURE 1   Sample interspike interval histograms of spontaneous activity for eight units in the cochlear nucleus. These histograms represent a survey of the various shapes of histograms encountered in this study. The height of each bar in the histogram represents the number of intervals with the time duration indicated by the abscissa. The CF and spontaneous rate are:

Unit	CF kc	Spontaneous rate spike/sec
P32–5	11.4	43.1
P33–14	10.3	60.0
P87–2	2.0	33.2
P54–2	2.0	25.8
P32–11	33.7	36.8
P64–4	1.4	12.8
P28–5	Unobtained	29.0
P20–3	1.6	0
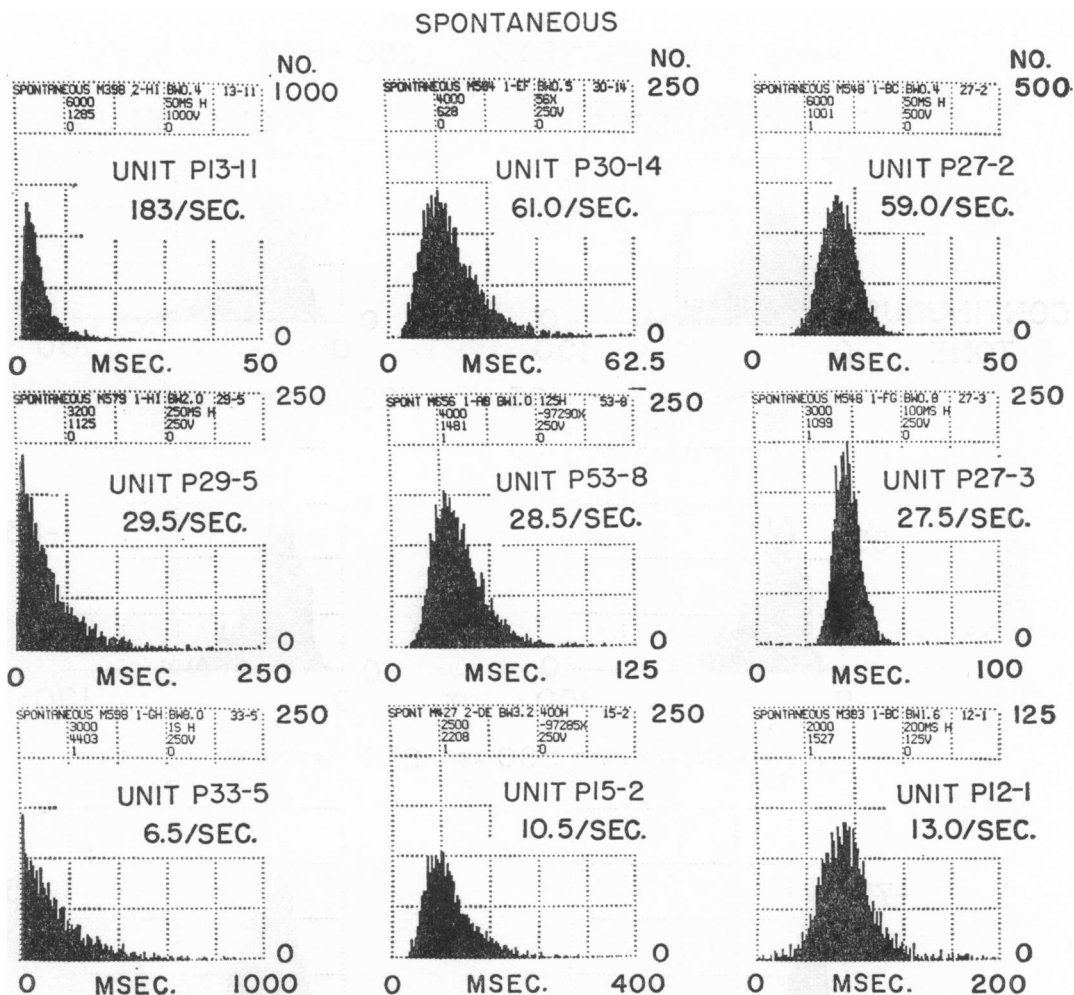
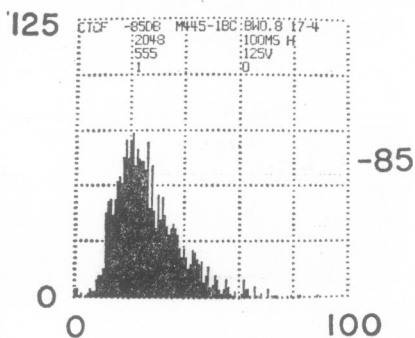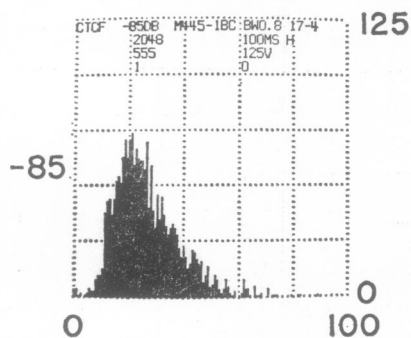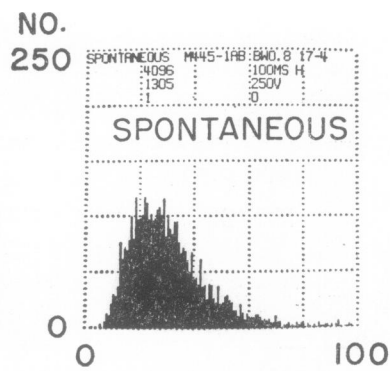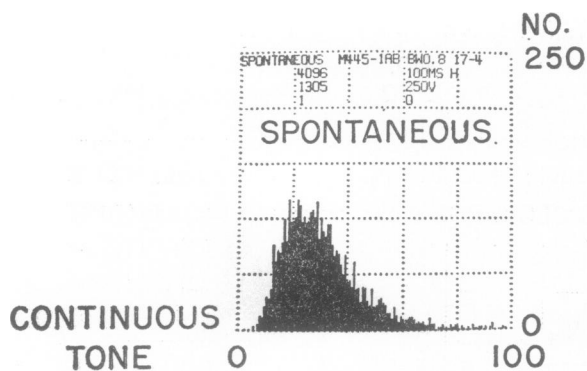FIGURE 2 Interval histograms for units with widely different rates of spontaneous activity. The histograms in each column have been selected for their general similarity of shape. The top row contains histograms for units with high rates of spontaneous activity, the middle row contains histograms for units with intermediate rates of spontaneous activity, the bottom row contains histograms for units with low rates of spontaneous activity. The rates in spikes/second are given under the unit numbers. The CF of the units are:

Unit	CF
	kc
P13–11	15.5
P29–5	16.9
P33–5	38.8
P30–14	16.6
P53–8	25.6
P15–2	14.2
P27–2	12.0
P27–3	11.5
P12–1	Unobtained

SPONTANEOUS MH45-1AB BW0.8 17-4
:4096   :100MS H
:1305   :250V
:1   :0

SPONTANEOUS.

SPONTANEOUS MH45-1AB BW0.8 17-4
:4096   :100MS H
:1305   :250V
:1   :0

SPONTANEOUS

CONTINUOUS
TONE   0   100

0

0   100

125

125

CTQF -85DB MH45-1BC BW0.8 17-4
:2048   :100MS H
:555   :125V
:1   :0

CTQF -85DB MH45-1BC BW0.8 17-4
:2048   :100MS H
:555   :125V
:1   :0

-85

-85

0

0

0   100

0   100

500

250

CTQF -75DB MH45-1CD BW0.8 17-4
:4096   :100MS H
:597   :500V
:3   :0

CTQF -75DB MH45-1CD BW0.4 17-4
:4096   :50MS H
:597   :250V
:3   :0

-75

-75

0

0

0   100

0   50

500

250

CTQF -65DB MH45-1DE BW0.8 17-4
:4096   :100MS H
:352   :500V
:4   :0

CTQF -65DB MH45-1DE BW0.2 17-4
:4096   :25MS H
:352   :250V
:4   :0

-65

-65

0

0

0   MSEC.   100

0   MSEC.   25

These nineteen units constitute exceptions to the observation that the shapes of histograms are similar for spontaneous and stimulated activity.[2]

From the histograms in Fig. 1, the modal value, the degree of symmetry about the mode, and the rise and decay characteristics can be determined. As described previously (Rodieck, Kiang, and Gerstein, 1962) the decay may be compared to an exponential decay by replotting the histograms on semilogarithmic coordinates (Fig. 5). Since this replotting affects neither the mode nor the symmetry, these characteristic features can still be read from Fig. 5. The histogram for unit P64-4, appears to be more symmetrical about its model value (75 msec) than the other histograms. The decay characteristics in the histograms for units P33-14, and P32-11, are relatively well represented by straight lines (exponential); for units P87-2 and P64-4 they are faster than exponential, and for unit P32-5 the decay is slower than exponential. The decay for P54-2 is either faster or slower than exponential, depending on the particular portion of the decay being examined.

The selection of three features of the interspike interval histograms—mode, symmetry, and decay—for detailed examination would seem arbitrary were it not for the fact that these features seem to correlate with the location of units in the cochlear nucleus.

Fig. 6 shows that the histograms whose modes are less than 12 milliseconds are found almost exclusively for units in the VCN (AVCN and PVCN combined). Histograms whose modes exceed 12 milliseconds have never been found for units in the AVCN but have been obtained for units in the PVCN and DCN.
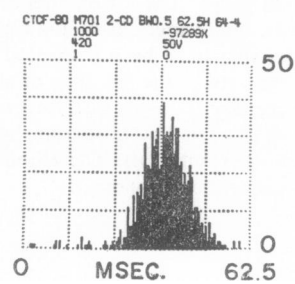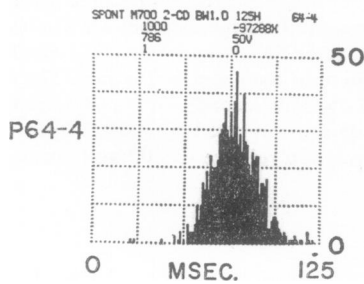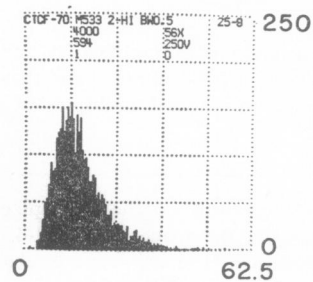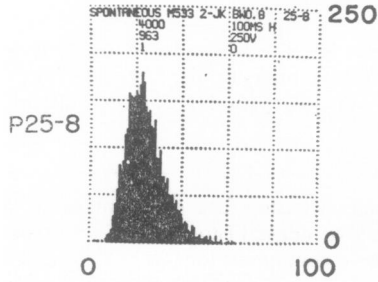
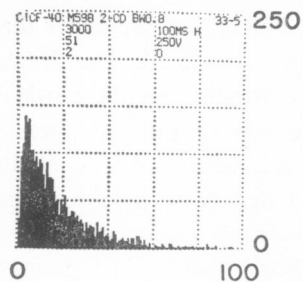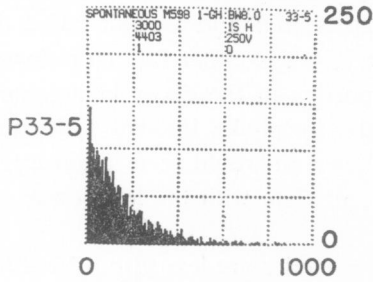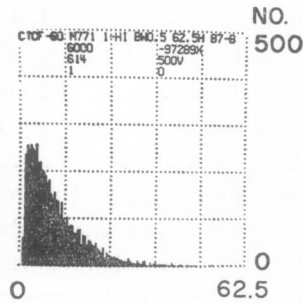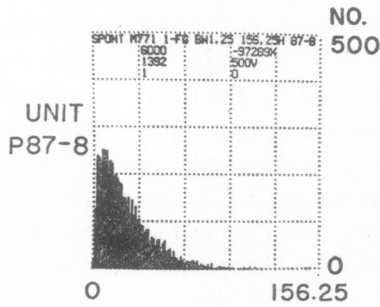The degree of symmetry about the histogram mode may be measured in a number of ways. For present purposes it is sufficient to use the symmetry measure, S, defined in Fig. 7. Fig. 7 also shows that units in the VCN have histograms with low values of S. Histograms that are more nearly symmetrical, i.e., that have values of S closer to 1.0, are found only for units in the DCN. Moreover the histograms

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[2] Another exception is exemplified by units with low CF whose responses to tones are locked to a specific phase of the stimulus and therefore have peaks on the interspike-interval histogram that correspond to integral multiples of the stimulus period (Kiang, Goldstein, and Peake, 1962).

FIGURE 3 Comparison of the interspike interval histograms of spontaneous and stimulated activity from one unit, P17-4. The two upper histograms of spontaneous activity are identical. The unit was stimulated by a continuous tone at its CF (15.3 kc) at three different levels. The histograms on the left are displayed with a time scale of 100 milliseconds; the histograms on the right represent the same data but are displayed with time scales that have been decreased by a factor that is approximately equal to the ratio of spike rate in the presence of stimulation to the spontaneous rate. The discharge rates were: spontaneous, 31.3/second; -85 db, 36.9/second; -75 db, 68.5/second; and -65 db, 116/second. The histograms at -85 db are computed from 2048 intervals, all others from 4096 intervals. The stimulus levels are relative to 200 volts peak-to-peak into the condenser earphone.

SPONTANEOUS   CONTINUOUS TONE AT C.F.

Histograms arranged in a grid. Left column labeled SPONTANEOUS, right column labeled CONTINUOUS TONE AT C.F. Rows labeled UNIT P87-8, P33-5, P29-1, P25-8, P64-4.

Row P87-8: left axis NO. 500 to 0, x-axis 0 to 156.25; right axis NO. 500 to 0, x-axis 0 to 62.5.

Row P33-5: left axis NO. 250 to 0, x-axis 0 to 1000; right axis NO. 250 to 0, x-axis 0 to 100.

Row P29-1: left axis NO. 125 to 0, x-axis 0 to 800; right axis NO. 125 to 0, x-axis 0 to 400.

Row P25-8: left axis NO. 250 to 0, x-axis 0 to 100; right axis NO. 250 to 0, x-axis 0 to 62.5.

Row P64-4: left axis NO. 50 to 0, x-axis 0 to 125 MSEC.; right axis NO. 50 to 0, x-axis 0 to 62.5 MSEC.

having the highest *S*-values are obtained from units in a particular part of the DCN that lies near the border of the PVCN (Fig. 8). Electrolytic lesions placed at the site of three such units have been found to be in the deep portion of the DCN.

The decay characteristics of certain interspike interval histograms also correlate with anatomical location. The 15 histograms that have short modes and decays faster than exponential, were all obtained from units in the AVCN. All 21 histograms with short modes and exponential decays were obtained from units in the PVCN except for a few units for which the possibility of the units being located in the AVCN could not be excluded. Histograms with short modes and slower than exponential decays were obtained from units found in both PVCN and DCN, although the distinction between an exponential decay and a decay slower than exponential is not sharp. The decay characteristics of histograms whose mode exceeds 12 msec are not easily correlated with location within PVCN and DCN. The various correlations that exist between certain histogram characteristics and anatomical location are summarized in Fig. 9.

DISCUSSION

In an earlier paper (Rodieck, Kiang, and Gerstein, 1962) a tentative classification of spontaneous activity in the cochlear nucleus was suggested. Interspike interval histograms were described as:

(*a*) unimodal, asymmetric with exponential decay

(*b*) unimodal, symmetric, with non-exponential decay

(*c*) bimodal, and

(*d*) unimodal, asymmetric, with non-exponential decay.

Some of the histograms in the last category were relatively invariant with respect to a mathematical scaling procedure. (This invariance is not related to the invariance of histogram shape for different time scales for stimulated and non-stimu-

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FIGURE 4 Comparison of interspike interval histograms of spontaneous and stimulated activity for five different units. The units were selected to show a wide variety of histogram shapes. The time scales of the histograms of stimulated activity (right-hand column) have been adjusted as described for Fig. 3. The stimulus variables, the unit threshold, and rate of spontaneous activity for each example are as follows:

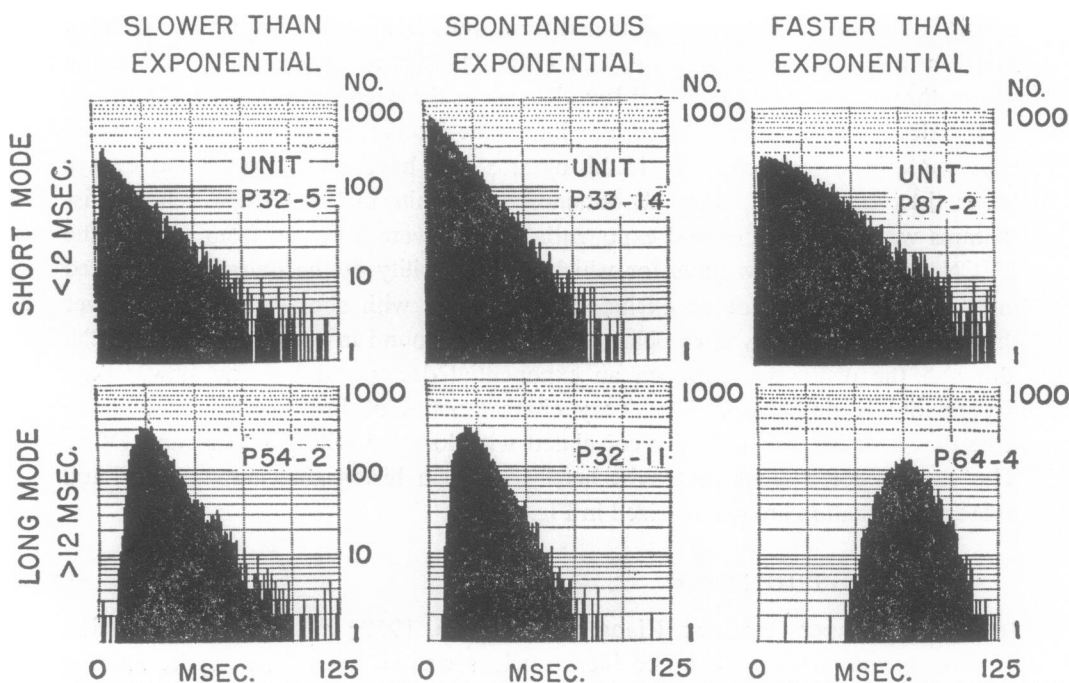| Unit	CF *kc*	Stimulus level Re 200 volts peak-to-peak into the condenser earphone *db*	Unit threshold *db*	Spontaneous rate *spike/sec*	No. of events in histogram
P87–8	1.9	−60	−85	40.5	3000
P33–5	38.8	−40	−48	6.5	6000
P29–1	6.9	−80	−103	6.0	4000
P25–8	13.0	−70	−98	29.5	1200
P64–4	1.4	−80	−100	12.8	1000

FIGURE 5 Semilogarithmic plots of interval histograms for six different units. (Compare with Fig. 1.) The upper row contains histograms whose modal values are less than 12 milliseconds, while in the lower row this value exceeds 12 millseconds. Exponential changes plot as straight lines on these graphs.

lated conditions.) Although the mathematical scaling properties have been useful in stimulating the generation of mathematical models (Gerstein and Mandelbrot, 1964), they have not been helpful in correlating spontaneous activity with anatomical location. One constant difficulty in this respect has been the difficulty in making sharp, explicit criteria for whether a histogram scales in the mathematical sense. The problem of defining quantitative criteria exists also for mode, symmetry, and decay and has been attempted only in crude form in the present study. It is the correlation with anatomical location which seems to justify the separation of histograms into different classes.

Several recent studies have emphasized the relation between spontaneous and stimulated activity. Werner and Mountcastle (1963) have described one type of interspike interval histogram for spontaneous activity of some ventrobasal thalamic neurons. Their data suggest that the spontaneous activity of these neurons differs from the driven (stimulated) activity. Measures of the variability of the intervals of time between successive nerve impulses in the two states—spontaneous and driven—appear to be quite different. They found that the average coefficient of variation, (CV = standard deviation/mean × 100 in per cent) of the time in-
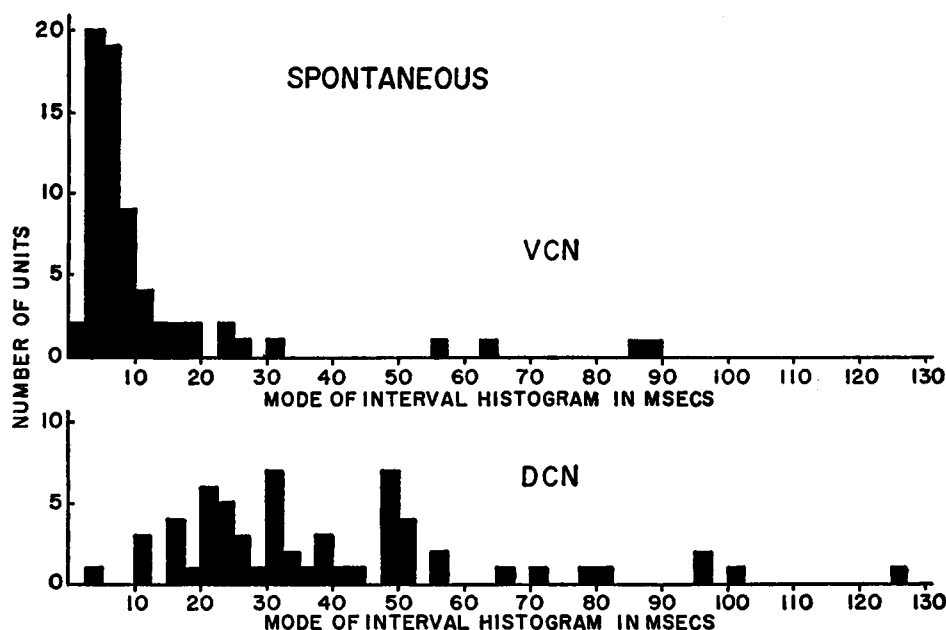
FIGURE 6 Histograms of modal values of the interspike interval histograms for spontaneous activity. The upper graph is for 70 units located in either the AVCN or PVCN, the lower graph is for 61 units located in the DCN.

tervals for 29 periods of spontaneous activity from 27 neurons was 93 ± 2.9 per cent, and for 82 periods of driven activity from 28 neurons was 52 ± 1.7 per cent. Thus individual units in the ventrobasal thalamic region seem to exhibit a marked difference in CV for the two states. However, this marked difference has not been found in units in the cochlear nucleus. For example, the CV of periods of activity, similar in length to those averaged by Werner and Mountcastle, from the spike trains used to obtain some of the histograms for Fig. 4 were: unit P33-5, spontaneous CV = 94 per cent, response CV = 96 per cent; unit 25-8, spontaneous 35 per cent, response 37 per cent; and unit 64-4, spontaneous 19 per cent, response 30 per cent. This result could have been anticipated because of the similarity in the shapes of the histograms of spontaneous and stimulated activity for these units. If the shapes of the interspike-interval histograms for spontaneous and stimulated activity were identical after appropriate time scaling, the corresponding CV would also be identical.

Goldberg, Adrian, and Smith, (1964) describe both spontaneous and stimulated activity for neurons in the superior olivary complex of the cat. It appears, from their data, that interspike interval histograms for spontaneous and stimulated activity of the superior olivary neurons would have similar shapes after appropriate time scaling. These workers propose a model that generates histograms that resemble
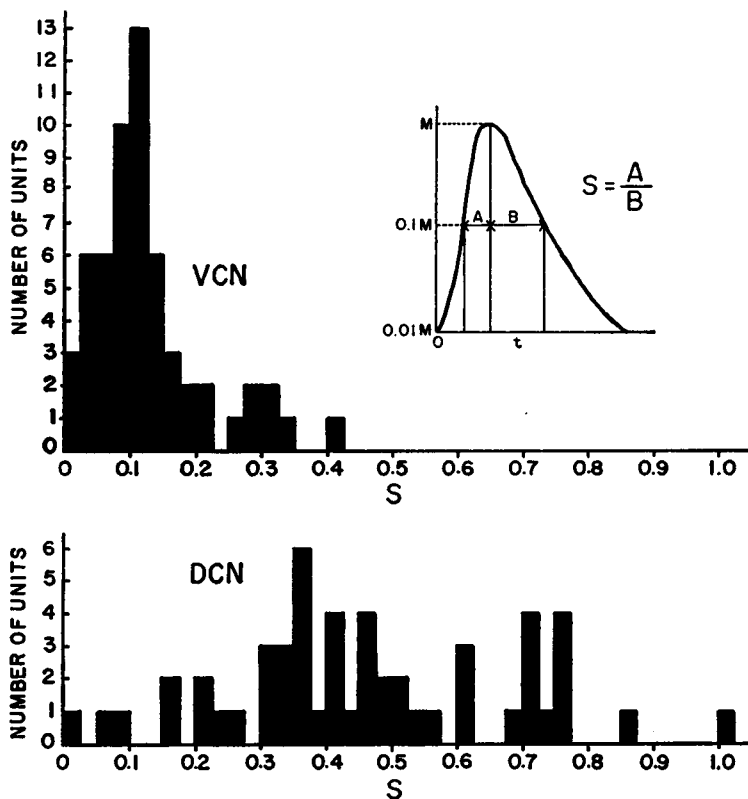
FIGURE 7   Histogram for the different symmetry values (S) of the interspike interval histogram for spontaneous activity. The upper graph is for 58 units located in either the AVCN or the PVCN, the lower graph is for 52 units located in the DCN. The inset shows how S is measured from a sample curve on a semilogarithmic plot. M is the modal value; A and B are measured at the value of the ordinate that is equal to M/10.

those obtained from their experimental data. Histograms corresponding to different groups of units were generated by changing the value of a single parameter. It is not clear whether their model would be applicable to all the units of the cochlear nucleus.

A number of factors may restrict the interpretations of the present experimental results. One such factor is that the present studies are on anesthetized cats. It is entirely possible that the time patterns of spontaneous activity are different in unanesthetized animals (Amassian and Waller, 1958). Moushegian, Rupert, and Galambos (1962) report that comparison of results obtained from the cochlear nucleus of unanesthetized and anesthetized preparations revealed no obvious differences, but it is not clear what measures of the activity were being compared.

27₁ UNIT | C.F. IN KC
30₂ UNIT | C.F. IN KC
31₁ UNIT | C.F. IN KC
33₂ UNIT | C.F. IN KC
52₁ UNIT | C.F. IN KC
64₁ UNIT | C.F. IN KC
77₅ UNIT | C.F. IN KC

0.5 mm

27₁
- 19.7
- P27-14: 17.5, 16.4
- P27-1: 17.1
- 15.7
- 14.1
- 13.7
- P27-13: 12.0
- P27-2: 14.4
- P27-3: 11.5, 17.6
- P27-4: 17.2
- 29.8

30₂
- P30-23: 34.0, 32.0
- 27.0, 28.1
- P30-13: 25.1
- 22.5
- 21.5
- P30-22: 17.5
- P30-14: 17.5, 16.6
- P30-24: 15.3, 13.6
- P30-15: 13.5, 10.3
- 10.0
- 8.0
- P30-16: 5.1
- P30-21: 3.2
- P30-17: 3.0
- approx. 25

31₁
- 32.9
- 23.7
- 26.0
- P31-1: 25.8, 25.0
- P31-2: 24.9, 24.8
- 24.1
- 21.7
- P31-3: 22.3
- 20.3
- P31-4: 20.4, 22.2
- P31-5: 9.5
- 9.1
- P31-6: 7.0, 39.0

33₂
- 32.7, 34.6
- 32.2
- 27.2, 24.4
- 22.2
- 20.8
- 18.5
- P33-2: 19.0, 19.4
- 26.6
- 27.1

52₁
- 26.8
- P52-1: 23.0
- 21.6
- 19.5
- P52-2: 15.7
- P52-3: 14.2
- P52-4: 11.0
- P52-5: 15.3
- 36.4, 36.0

64₁
- 18.9
- 16.6
- 15.5
- 13.6
- P64-1: 11.0
- P64-2: 9.8
- P64-3: 8.3, 8.1
- 5.3
- 5.2
- 3.3
- 3.2
- P64-4: 1.4
- P64-5: 20.7

77₅
- 11.0
- 9.2
- 8.0
- 6.4
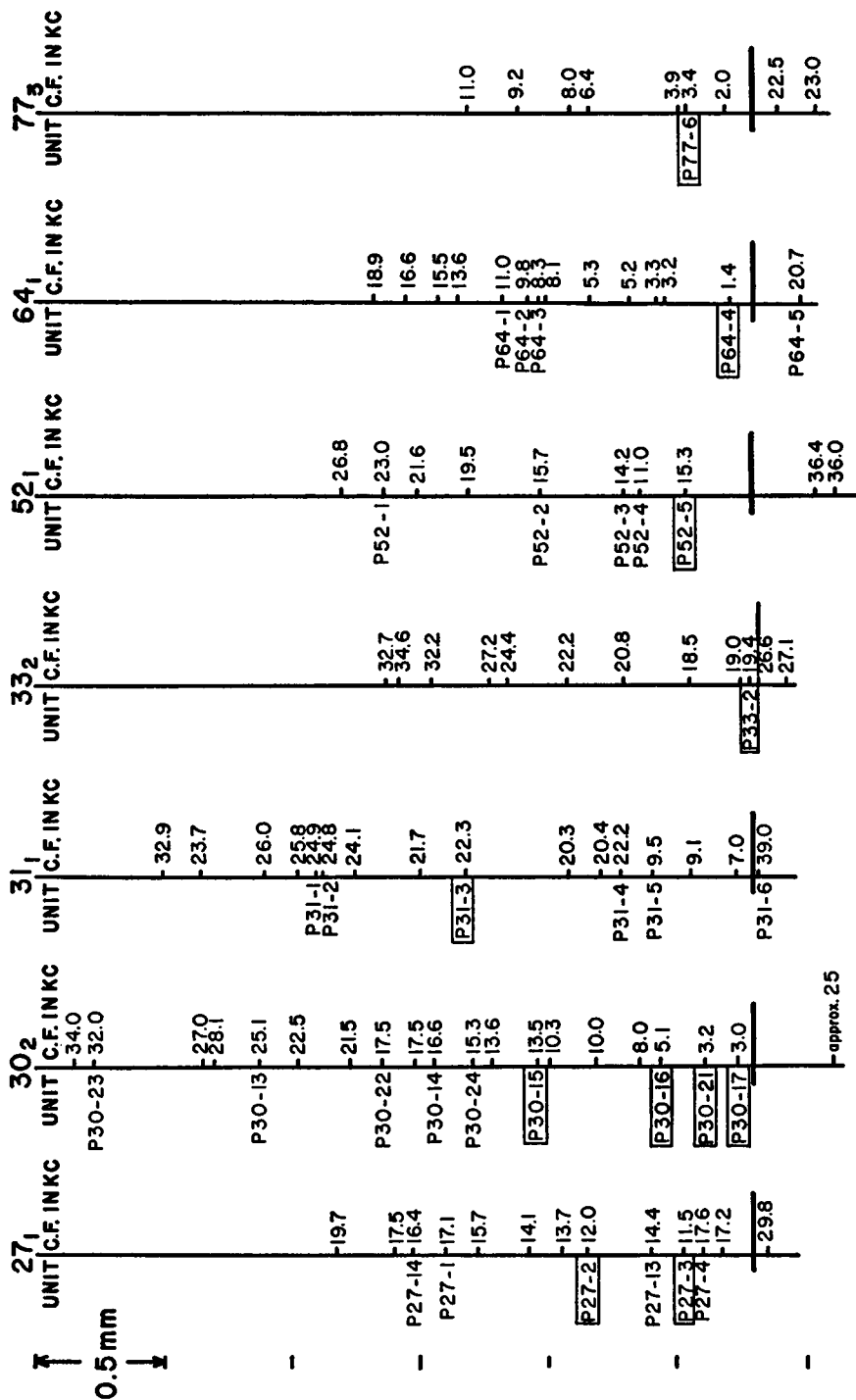- P77-6: 3.9, 3.4
- 2.0
- 22.5
- 23.0

FIGURE 8 Schematic representation of the initial portions of electrode tracks from seven different cats. The numbers above each track designate the cat (large number) and the electrode track number (subscript) for that cat. The numbers to the right of each column show the characteristic frequency for each unit; the numbers to the left of each column are for units from which histograms of spontaneous activity are available. The heavy horizontal bar near the bottom of each track marks the position of the discontinuity in tonotopic organization which presumably corresponds to the boundary between the DCN and the PVCN. The unit numbers that are enclosed in boxes represent those units that have interval histogram S-values greater than 0.7. (See Fig. 7)
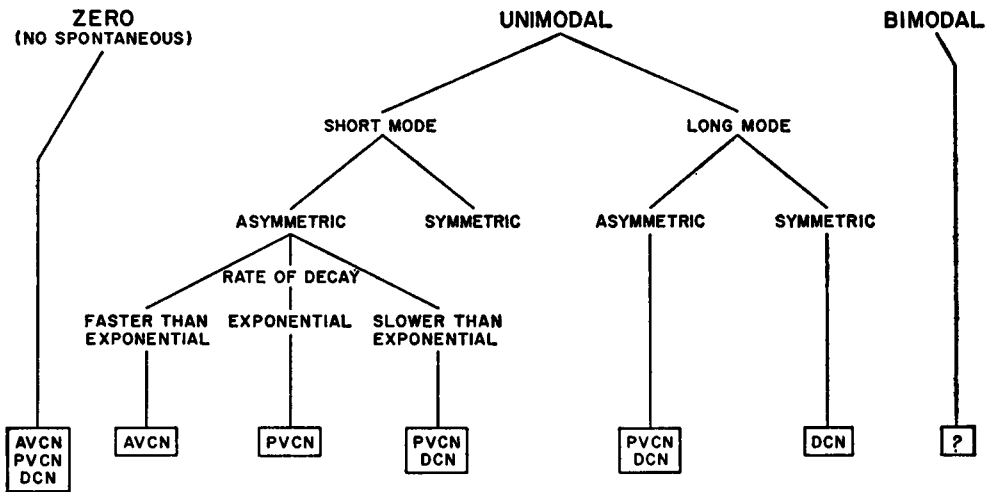
FIGURE 9   Correlation of interspike-interval histograms of spontaneous activity with anatomical location of units. The particular properties of the histograms that are emphasized are the mode, symmetry, and decay characteristics.

Other factors are possible biases in the recording of units introduced by the use of particular electrodes or response criteria.

The fact that for some units histograms do change shape as the stimulus level is raised approximately 25 db above threshold suggests that changes in other stimulus parameters need to be investigated. Perhaps the invariance in histogram shape holds only for a narrow range of stimulus conditions.

The functional significance of spontaneous activity is still largely a matter of conjecture. Whether the detailed time patterns are significant in the functional roles played by these units or are merely indications of "noise" in the system cannot be evaluated at the present time. It would be interesting to examine other regions in the nervous system with cells anatomically similar to those in the cochlear nucleus to see if the "type" of spontaneous activity is correlated with the morphological characteristic of cells.

The various types of spontaneous activity may also be related to their connectivity with other units. If the spontaneous activity is correlated with patterns of responses to other stimulus conditions, it may prove to be a significant indicator of the functional roles of various types of single units (Kuffler, FitzHugh, and Barlow, 1957). An important step in this direction would be the determination of inputs to a particular cell in the cochlear nucleus not only from the auditory nerve fibers but also from efferent fibers (Rasmussen, 1960) (Pfalz, 1962). Studies of potentials obtained from intracellular probes might provide some useful clues

(Nelson and Erulkar, 1963). It may be premature to discuss the functional significance of spontaneous activity in the cochlear nucleus before the activity in the input stages is fully assessed.

BIBLIOGRAPHY

1. AMASSIAN, V. E., and WALLER, H. J., Spatiotemporal patterns of activity in individual reticular neurons, *in* Reticular Formation of the Brain, (H. H. Jasper, L. D. Proctor, R. S. Knighton, W. C. Noshay, R. T. Costello, editors), Boston, Little, Brown and Company, 1958, 69.
2. BODIAN, D., A new method for staining nerve fibers and nerve endings in mounted paraffin sections, *Anat. Rec.,* 1936, **65**, 89.
3. BODIAN, D., The staining of paraffin sections of nervous tissue with activated protargol. The role of fixatives, *Anat. Rec.,* 1937, **69**, 153.
4. BREMER, F., Some Problems in Neurophysiology, London, The Athlone Press, 1953.
5. BULLER, A. J., NICHOLLS, J. G., and STROM, G., Spontaneous fluctuations of excitability in the muscle spindles of the frog, *J. Physiol.,* 1953, **122**, 409.
6. BULLOCK, T. H., Parameters of integrative action of the nervous system at the neuronal level, *Exp. Cell Research,* 1958, suppl. **5**, 323.
7. BURNS, B. D., The Mammalian Cerebral Cortex, London, Edward Arnold Publishers Ltd., 1958.
8. GERSTEIN, G. L., and KIANG, N. Y-s., An approach to the quantitative analysis of electrophysiological data from single neurons, *Biophysic. J.,* 1960, **1**, 15.
9. GERSTEIN, G. L., and MANDELBROT, B., Random walk models for the spike activity of a single neuron, *Biophysic. J.,* 1964, **4**, 41.
10. GESTELAND, R. C., HOWLAND, B., LETTVIN, J. Y., and PITTS, W. H., Comments on microelectrodes, *Proc. IRE (Inst. Radio Engrs.),* 1959, **47**, 1856.
11. GOLDBERG, J. M., ADRIAN, H. O., and SMITH, F. D., Response of neurons of the superior olivary complex of the cat to acoustic stimuli of long duration, *J. Neurophysiol.,* 1964, **27**, 706.
12. GRANIT, R., Receptors and Sensory Perception, New Haven, Yale University Press, 1955.
13. GROSSMAN, R. G., and VIERNSTEIN, L. J., Discharge patterns of neurons in cochlear nucleus, *Science,* 1961, **134**, 99.
14. KIANG, N. Y.-s., GOLDSTEIN, M. H., and PEAKE, W. T., Temporal coding of neural responses to acoustic stimuli, *IRE Trans. Inform. Theory,* 1962, IT-8, 2, 113.
15. KUFFLER, S. W., FITZHUGH, R., and BARLOW, H. B., Maintained activity in the cat's retina in light and darkness, *J. Gen. Physiol.,* 1957, **40**, 683.

16. LORENTE DE NÓ, R., Anatomy of the eighth nerve. III. General plan of structure of the primary cochlear nuclei, *Laryngoscope,* 1933, **43,** 327.
17. LOWENSTEIN, O., and SAND, A., The individual and integrated activity of the semicircular canals of the elasmobranch labyrinth, *J. Physiol.,* 1940, **99,** 89.
18. MOUSHEGIAN, G., RUPERT, A., and GALAMBOS, R., Microelectrode study of ventral cochlear nucleus of the cat, *J. Neurophysiol.,* 1962, **25,** 515.
19. NELSON, P. G., ERULKAR, S. D., Synaptic mechanisms of excitation and inhibition in the central auditory pathway, *J. Neurophysiol.,* 1963, **26,** 908.
20. PFALZ, R. K. J., Centrifugal inhibition of afferent secondary neurons in the cochlear nucleus by sound, *J. Acoust. Soc. Am.,* 1962, **34,** 1472.
21. PUMPHREY, R. J., Hearing, *in* Physiological Mechanisms in Animal Behavior, *Symp. Soc. Exp. Biol.,* 1950, **4,** 1.
22. RAMÓN Y CAJAL, S., Histologie du système nerveux de l'homme et des vértébres. I. Madrid, Instituto Ramón y Cajal, French edition, 1952.
23. RASMUSSEN, G. L., Efferent fibers of the cochlear nerve and cochlear nucleus, *in* Neural Mechanisms of the Auditory and Vestibular Systems, (G. L. Rasmussen, and W. F. Windle, editors), Springfield, Illinois, Charles C. Thomas, Publisher, 1960.
24. RODIECK, R. W., KIANG, N. Y-s., and GERSTEIN, G. L., Some quantitative methods for the study of spontaneous activity of single neurons, *Biophysic. J.,* 1962, **2,** 351.
25. ROEDER, K. D., Spontaneous activity and behavior, *Sc. Monthly,* 1955, **80,** 362.
26. ROSE, J. E., GALAMBOS, R., and HUGHES, J. R., Microelectrode studies of the cochlear nuclei of the cat, *Bull. Johns Hopkins Hosp.* 1959, **104,** 211.
27. SCHLAG, J., A differentiation of spontaneous unit firing in subcortical structures of the cat's brain, *Science,* 1958, **127,** 1184.
28. SCHLAG, J., L'activité Spontanée des Cellules du Système Nerveux Central, Bruxelles, Editions Arscia S.A., 1959.
29. WERNER, G., and MOUNTCASTLE, V. B., The variability of central neural activity in a sensory system, and its implications for the central reflection of sensory events, *J. Neurophysiol.,* 1963, **26,** 958.