AN APPROACH TO THE QUANTITATIVE ANALYSIS OF ELECTROPHYSIOLOGICAL DATA FROM SINGLE NEURONS

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ABSTRACT   The application of a digital computer to the processing of data from single neurons is described. Examples from experimental data are presented to demonstrate the usefulness of certain types of computations. These methods are placed in a descriptive mathematical framework. Other easily attainable computations are suggested.

INTRODUCTION

Since the days of Ramon y Cajal (1), the neuron has been generally accepted as the basic building block of the nervous system. This view has been important in the interpretation of electrical phenomena recorded in nervous tissue by macroelectrodes. Even the most careful of these recordings poses problems of measurement for which we lack satisfactory theoretical formulations. In the (more or less) intact animal, a macroelectrode records electrical activity from a volume that is large compared to that of a single neuron; the recorded activity is not of necessity functionally homogeneous. Thus there arises the problem of meaningfully relating the electrical activity seen by a macroelectrode to the underlying single neuron activity and, more generally, to a valid indicant of the behavior of the nervous system as a whole.

The introduction of microelectrodes has made it possible to obtain greater spatial resolution in recordings. It has become possible to record electrical events from a single nerve cell or even from certain regions of a given neuron. The temporal characteristics of these events cover the range of "fast" action spikes to DC and "slow"

potential changes. Although any and all of these potentials may have functional significance (2-5), the action potentials or spikes have loomed largest, historically, in the analysis of single unit activity. Spatiotemporal patterns of spike activity have frequently been used as indices of nervous system function.[1] Such patterns have conveniently been studied in sensory systems because these systems are particularly accessible to manipulation.

In stimulus response studies, changes in spike activity must be assessed against a background of "spontaneous activity." Stimulation can lead to subtle changes of the temporal distribution of spikes. When these pattern changes occur with long latency and much variability, it hardly seems wise to define the "response" of a neuron as the casually detectable change in background activity that immediately follows stimulation. As closer and more formal examination of single-unit firing patterns becomes possible, the number of units that fall into the "no response" cate-
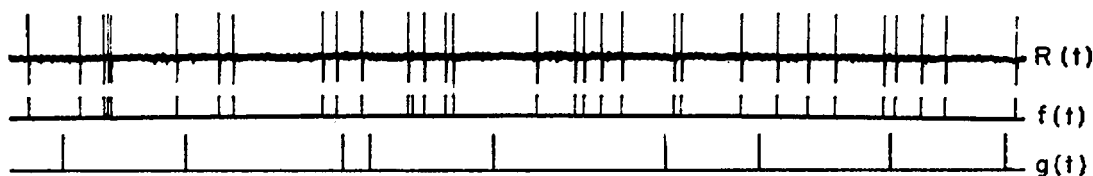

FIGURE 1   Spike and pulse trains discussed in the text. $R(t)$, single-unit activity (spikes) recorded by microelectrodes in cochlear nucleus; $f(t)$, idealization by pulse generator; $g(t)$, externally determined time marker.

gory diminishes strikingly. Potentially more useful categories can be obtained by more exact description of response pattern changes. For this purpose it appears necessary to utilize probabilistic approaches to the quantification of unitary spike activity.

It is the purpose of this paper (a) to illustrate, from our experimental work, the use of several methods of data processing which make possible the quantitative description of single neuron firing patterns and (b) to place these methods in a mathematical framework that makes explicit the interpretations that can be drawn from such analyses. We wish particularly to set forth both the power and the limitations of this approach to the description of firing patterns.

ANALYSIS OF SINGLE-UNIT DATA

If the time pattern of action spikes is selected as the subject of interest, other aspects of the electrical activity (such as details in the spike waveform, slow potentials) can be neglected. This selection is illustrated in Fig. 1 where $R(t)$ is a train

[1] Today it seems much less certain that the analysis of discrete events alone will lead to a complete understanding of the behavior of the nervous system. It is likely that an adequate description of nervous system activity can be obtained only through the analysis of *both* the graded electrical activity and the discrete spikes.

of spikes recorded by a microelectrode, and $f(t)$ is the idealization of $R(t)$ produced by letting the spikes trigger an electronic pulse generator. In such a train of identical pulses of unit amplitude all "information" is carried by the times at which individual pulses occur. In this article we shall consider the spike train $R(t)$ as being equivalent to the corresponding pulse train $f(t)$. In order to analyze the time structure of the train it is necessary to choose an origin (or a series of origins) for time measurements. There are two possibilities for this choice: (*a*) events in the spike train itself, or (*b*) externally determined instants (for example, $g(t)$ in Fig. 1).

The simplest application of the first choice leads to a class of analyses that we shall call "interval histograms;" the second choice leads to a class that we shall call "time histograms."

Within the past few years it has become possible to perform such computations on large masses of data with high resolution, accuracy, and speed. In order to obtain maximum flexibility in choosing the particular type of analysis to be used, it is convenient to work with a general-purpose digital computer. A data-processing system of this type which is in use at this laboratory has already been described (6). With this system, computations of the simplest cases of interval and time histograms have yielded useful analyses of single-unit firing patterns in several neurophysiological studies. In particular, we are using:

(a) an interval histogram—a histogram of the intervals between *successive* spikes.

(b) a poststimulus time (PST) histogram—the distribution of spikes in time relative to the instant of the *most previous* presentation of the stimulus, summed over many repeated stimulus presentations. A peak on an interval histogram shows a preferred interval between firings; a peak on a PST histogram shows a preferred time of firing relative to the stimulus.

(These analyses are, respectively, the second term of equation (3) and the first term of equation (7) below.)

It is not our intention to present the results of completed studies here; rather we wish to indicate certain advantages and disadvantages in the use of these and other methods for the analysis of single-unit data. All of our examples are drawn from work on the auditory system.

In order to formalize most simply the types of computation that we have used, let us assume that the basic spike train results from a process that is statistically stationary in the large. This means, if we are considering an experiment which involves the repeated presentation of the same stimulus, that we assume the statistical properties of all responses to be the same. In other words, we are examining a steady-state process and are not concerned with adaptation effects and other "dynamic" properties that could alter the response to successive identical stimuli. Within the time between presentations of the stimulus, the statistical properties of the process may of course vary. This assumption will avoid difficulties in choosing the segments of data over which calculations are made.

In this framework, interval histograms are selected portions of an estimate of the autocorrelation function for a train of suitably defined spikes. Let the spike train we are investigating be

$$f(t) = \sum_{k=1}^{N} \delta(t - t_k) \tag{1}$$

where $\delta(t)$ is a Dirac δ function (or, alternatively, a unit impulse), and where N is a large number. (For mathematical convenience we are representing the original train of *unit amplitude* spikes by a train of δ functions of unit area, each located at the time of an original spike. To interpret any results we must now consider *areas*.)

An estimate of the autocorrelation of (1) is

$$\varphi_{ff}(\tau) \equiv \int f(t)f(t - \tau)\, dt = \int \sum_{k=1}^{N} \delta(t - t_k) \sum_{l=1}^{N} \delta(t - t_l - \tau)\, dt$$

$$= \sum_{k=1}^{N} \sum_{l=1}^{N} \delta(t_k - t_l - \tau) \tag{2}$$

For convenience, the double sum can be broken up in the following way:

$$\varphi_{ff}(\tau) = N\, \delta(\tau) + \sum_{k=2}^{N} \delta(t_k - t_{k-1} - \tau) + \sum_{k=3}^{N} \delta(t_k - t_{k-2} - \tau) + \cdots . \tag{3}$$

These terms correspond respectively to letting $l=k$, $l=k-1$, $l=k-2$, ... Since the autocorrelation function is symmetric in τ, we have not written the $-\tau$ terms explicitly.

Thus the estimate of the autocorrelation function of (1) is itself expressed as an array of δ functions. The numerical values of the estimated autocorrelation function would be obtained from the envelope of the δ function *areas*.[2]

For convenience we may measure the continuous values of τ as discrete time values τ_j, $j = 1, 2, 3, \ldots$, in such a manner that all τ that satisfy $\tau_j < \tau < \tau_{j+1}$ are measured as τ_j. Thus $\tau_{j+1} - \tau_j \equiv \Delta\tau$ defines a time bin that determines the resolution of the analysis. The choice of bin width is governed by the time scale of the particular phenomena that are being studied. In this case of discrete time values, the *areas* of all δ functions of φ_{ff} which fall between τ_j and τ_{j+1} are added together to give the height of the τ_j—th bar in a histogram.

The first term of equation (3) is a constant contribution to the estimated autocorrelation function at $\tau=0$; its numerical value (area) is N, the total number of spikes in the train. If the time duration of the spike train is known, this term of equation (3) yields the average firing rate in the spike train. The second term is an interval histogram; *i.e.*, a histogram of the intervals between *successive* (k and $k-1$) spikes of the train. The

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[2] This usage is common in text-books. See chapter 2, reference 7. The reader who finds our notation obnoxious can perform a similar development in terms of summations only, without using δ functions, integrals, or integral properties, by starting with a spike train

$$f(t_i) = \sum_{k=1}^{N} \Delta(t_i - t_k) \quad \text{where} \quad \Delta(t_i - t_k) = \begin{matrix} 1, & t_i = t_k \\ 0, & t_i \neq t_k \end{matrix} \text{. For discrete time shifts}$$

τ_m, equation (2) would be $\quad \varphi_{ff}(\tau_m) = \sum_{k=1}^{N} \sum_{l=1}^{N} \Delta(t_k - t_l - \tau_m)$. Interpretation

of results in terms of areas is then unnecessary. Still other forms of notation are possible. However, the particular resolution of components expressed in (3) and (7) remains valid.

third term is an interval histogram of the intervals between every second (k and $k-2$) spike. All subsequent terms are interval histograms for higher order intervals in the spike train.

A peak on an interval histogram shows a preferred periodicity in the train; *i.e.*, a preferred interval between spikes or groups of spikes. The value of this preferred interval is indicated by the position of the peak on the abscissa. The ordinate measures the number of spike intervals falling into each discrete τ_j time bin.

In a similar manner, the time histograms are selected portions of an estimated cross-correlation function between the spike train under study and an external pulse train that can be determined arbitrarily by the experimenter. Again, let the spike train that we are investigating be

$$f(t) = \sum_{k=1}^{N} \delta(t - t_k) \tag{4}$$

and let the externally determined (not necessarily periodic) pulse train be

$$g(t) = \sum_{l=1}^{N} \delta(t - t_l) \tag{5}$$

Generally, very few, if any, t_k and t_l will have the same values. An estimate of the cross-correlation function of functions (4) and (5) is

$$\varphi_{fg}(\tau) \equiv \int f(t)g(t - \tau)\, dt = \int \sum_{k=1}^{N} \delta(t - t_k) \sum_{l=1}^{N} \delta(t - t_l - \tau)\, dt$$
$$= \sum_{k=1}^{N} \sum_{l=1}^{N} \delta(t_k - t_l - \tau) \tag{6}$$

Although (6) looks formally like (2), the t_k and t_l are *not* the same series in this case, and the double sum cannot be broken down as in (3). Instead we write

$$\varphi_{fg}(\tau) = \sum_{l=1}^{N} \left[\sum_{k} \delta(t_k - t_l - \tau) + \sum_{k} \delta(t_k - t_l - \tau) \right] \tag{7}$$

$$t_l < t_k < t_{l+1} \qquad t_k > t_{l+1}$$
$$t_k < t_l$$

Thus the estimate of the cross-correlation function is also expressed as an array of δ functions. Just as for equation (3), the numerical values are obtained from the envelope of δ function *areas*.

As in the discussion of equation (3), the continuous τ can be measured as discrete τ_j, $j = 1, 2, \ldots$

The two right hand terms of equation (7) are time histograms; *i.e.*, histograms of the average times of occurrence of the $f(t)$ spikes relative to origins determined by the external $g(t)$ pulses. The first term describes the average times of occurrence of the $f(t)$ spikes relative *only* to the last previous (lth) $g(t)$ pulse as origin. The second term lumps together the average times of occurrence of the $f(t)$ spikes relative to the $l-1$, $l-2$, $\ldots$, $g(t)$ pulses. In other words, a peak on a time histogram shows, on the average, a preferred time of occurrence of the $f(t)$ spikes relative to the $g(t)$ pulses. The value of this preferred time is indicated by the position of the peak on the abscissa. The ordinate measures the number of spikes that fall into each discrete time bin.

This computation serves to sort the spike train under study in a way that detects pat-

terns that are time-locked to the arbitrary external pulse train. Suppose, for example, that the arbitrary external pulse train marks the delivery of stimuli. Then the first term of equation (7) would detect average evoked response patterns that occur during the time *before* the delivery of the next stimulus. Let us call this particular computation a post-stimulus time (PST) histogram. If the perturbations caused by the first stimulus have not died away by the time the next stimulus is delivered, a part of the pattern that is time-locked to the stimulus would be found in the second term of equation (7). (The physical meaning of the two terms of (7) is most easily visualized in the case in which the stimuli are delivered aperiodically but at a mean interval that is shorter than the duration of the time-locked evoked response pattern.)

We cannot overemphasize that both types of histogram that have been discussed involve averaging the data. This means that in performing these computations, to bring out certain aspects of the spike pattern, we have lost other information. For example, we lose the time sequence of the events contributing to a particular histogram. This could be remedied, in principle, by computing separate time and interval histograms for the first, second, ... , spike, or spike pair after the stimulus. Unfortunately, there are so few data in most experiments that such fractional analyses are statistically impractical.

A far more crucial loss of information is hidden in the assumptions involved in averaging: a meaningful average can be obtained only if the events in the pattern that enter into the average have statistical properties which are similar. If the statistical properties of the events vary during the period of the average, then an "average" of the events can still be computed, but there will be a loss of all information about the changes of the statistical properties. In any real neurophysiological experiment such changes of the statistical properties are associated with inevitable physiological variability. Thus a more complete description of the properties of neural firing patterns must eventually necessitate the use of higher order statistical measures.

There is an interesting difference in the interpretation of the two general types of histogram. In the time histogram, we seek significant variations of the distribution as a function of poststimulus time—a distribution that is flat within statistics, *i.e.*, a DC contribution conveys little of interest. Such a flat distribution represents the events in the spike pattern which are not time-locked to the external pulse train, and which are therefore randomly distributed in time relative to the external train. For the interval histogram, however, all parts of the distribution are pertinent because no criteria external to the spike train are used in the computation.

EXPERIMENTAL METHODS

All experiments were performed on cats anesthetized with either dial or nembutal, given either intraperitoneally or intravenously. Recordings were made from one of two places: (*a*) the cochlear nucleus, or (*b*) the auditory cortex. The cochlear nucleus was approached through the intracranial route with removal of cerebellum. Cortical recordings were made with a closed chamber technique similar to that described by Davies (8). Electrodes were either the indium-platinum type described by Dowben and Rose (9) or the tungsten type described by Hubel (10). In all cases the experiments were conducted in sound-proof chambers, with hydraulic remote control of the microelectrode. Clicks were delivered by a PDR-10 earphone connected to the external auditory meatus through a plastic tube. The intensity of the clicks is stated relative to the VDL (visual detection level), of the appropriate evoked response as recorded by a macroelectrode.

Responses were recorded with an FM tape system. For the cortex both a high-pass (200 to 10 kc) and an "unfiltered" (8 to 10 kc) channel were recorded. This allowed investigation of both unit spike potentials and slow potentials.

The processing of single-unit data by the TX-O general-purpose digital computer has already been described. (6) Output from the computer was obtained as a display of a bar graph and titles, and was photographed with a Polaroid camera.

RESULTS AND DISCUSSION

The fundamental objective of our experimental work is the detection of changes that take place in single neuron activity patterns as a result of changes in stimulus conditions. Neurophysiological spike trains can be considered in two categories: *(a)* spontaneous activity, and *(b)* responses to stimuli. Any stimulus condition results in a spike pattern that is a mixture or interaction of both types of activity. The effect of a discrete stimulus on the over-all spike pattern decreases with time after stimulation; the pattern gradually returns to the spontaneous condition. If the stimuli are spaced far apart in time, the over-all contribution of the stimulus-dependent activity (responses) is low relative to the spontaneous activity. If stimuli are delivered at sufficiently high rates, the contribution of spontaneous activity can become relatively small.

The interval histogram emphasizes *internal* timing relations in the spike train, whether the individual spike be spontaneous or in response to a stimulus. The PST histogram emphasizes the time relations of the spikes in the train to the stimulus time marker.

In general, the spike trains with which we deal represent some interaction of spontaneous and responsive activity, so that both the interval and time histograms are useful in describing the patterns of activity.

In practice, for particular samples of data, we have found that one or the other display is more striking in showing differences in activity patterns. This contrast in effectiveness between the two displays can be attributed to the relative contribution of spontaneous and responsive activities.

Figs. 2 and 3 show applications of interval histogram computations. Fig. 2*a* shows single-unit activity recorded from the cochlear nucleus during various rates of click presentation. Note that the unit exhibits spontaneous activity that appears to be suppressed when clicks are delivered at rates around 10 or 20/sec. At 10/sec. the unit appears to fire once and only once to each click. At 20/sec. there appear to be some clicks to which the unit does not respond, although whenever a spike occurs it seems time-locked to the stimulus. Over considerable stretches of time the unit appears to fire to every other click.

At higher rates, from these pictures, it becomes more difficult to describe the pattern of activity with respect to the stimulus. On a faster time base, there appears to be some following with irregular skipping.
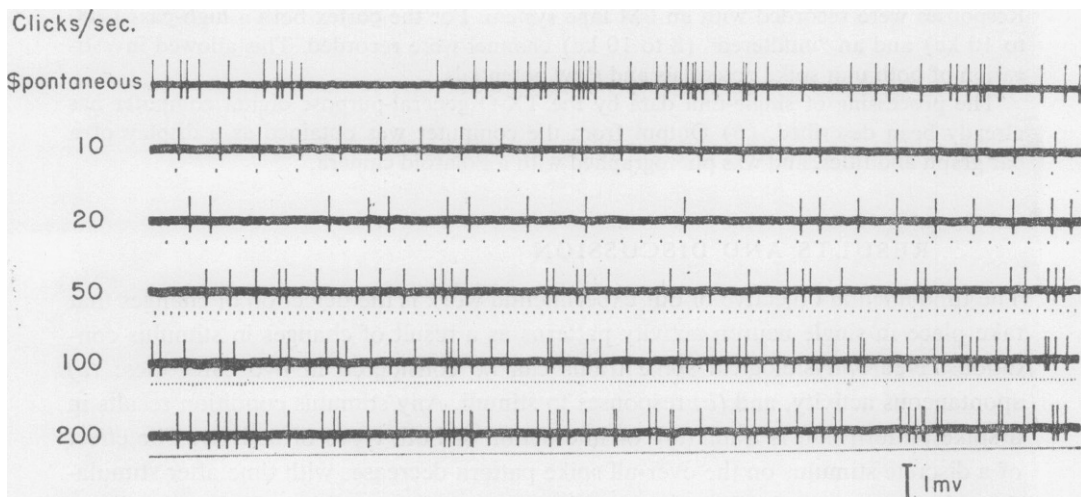
FIGURE 2a Activity of a single unit in cochlear nucleus (unit 165-1) during presentation of clicks at various rates. Click intensity 25 db re VDL.
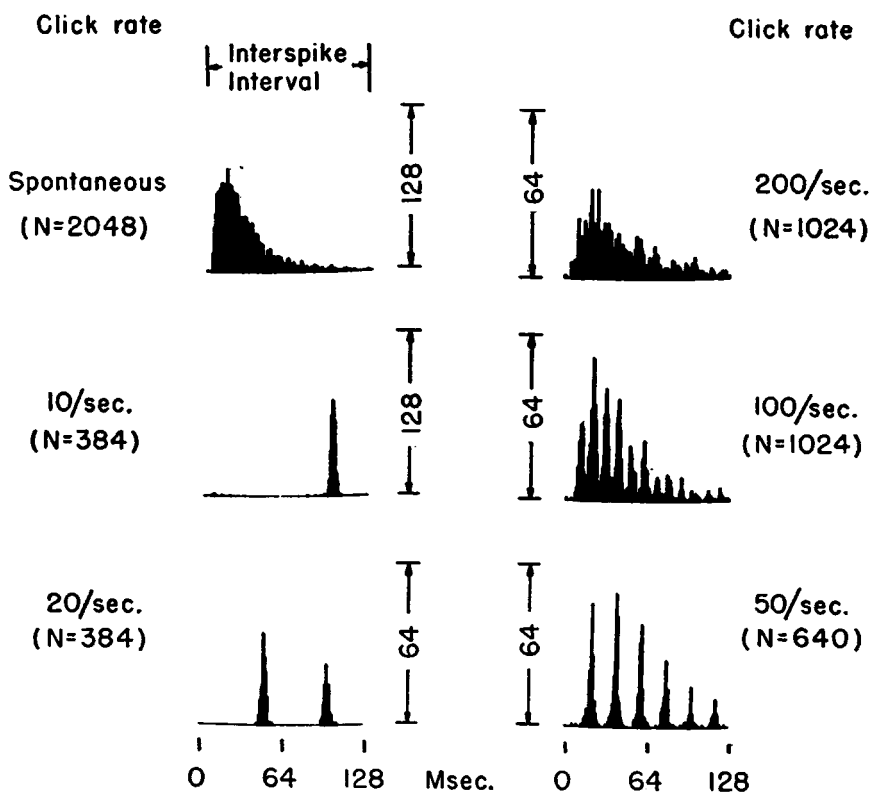
FIGURE 2b Interval histograms of the same data from which Fig. 2a was obtained. The ordinate on all displays is the number of spikes per unit time interval. N is the total number of spikes represented in each histogram.

Fig. 2*b* shows the interval histograms for the same samples of data from which Fig. 2*a* was taken.

The interval histograms show very clearly the marked effect of 10/sec. clicks on the pattern of spontaneous activity. The single sharp distribution at 100 msec. (*i.e.,* time interval between clicks) reflects the one-to-one following seen in Fig. 2*a*. For 20/sec., there is one large peak at 50 msec. (*i.e.,* time interval between clicks) and an additional smaller peak at 100 msec. which corresponds to those intervals when the response skips one stimulus. The relative areas of the two peaks expresses the relative number of times that the unit responds in a one-for-one manner as compared with the number of times that the unit skips one stimulus. Note especially that there is negligible activity with intervals other than at the periods of the stimulus or its subharmonics. At 50/sec. the fundamental period of the stimulus is 20 msec. The first peak in the interval histogram corresponds to this period (*i.e.,* one-for-one responses). Now however, the second peak, representing intervals of 40 msec., is larger than the first peak. This signifies that the unit now fires more often to every other click than to every click. The areas of the peaks at higher interval values indicate the relative occurrence of activity which skips two, three, etc., clicks. At 100/sec., similar observations can be made. At 200/sec., while the individual peaks are no longer clearly separable, the envelope of the interval distribution approaches that of spontaneous activity. It is evident that the interval histogram emphasizes certain "interesting" features of the pattern not easily studied in the original records.

Fig. 3 shows interval histograms for a unit in the auditory cortex (A1). The
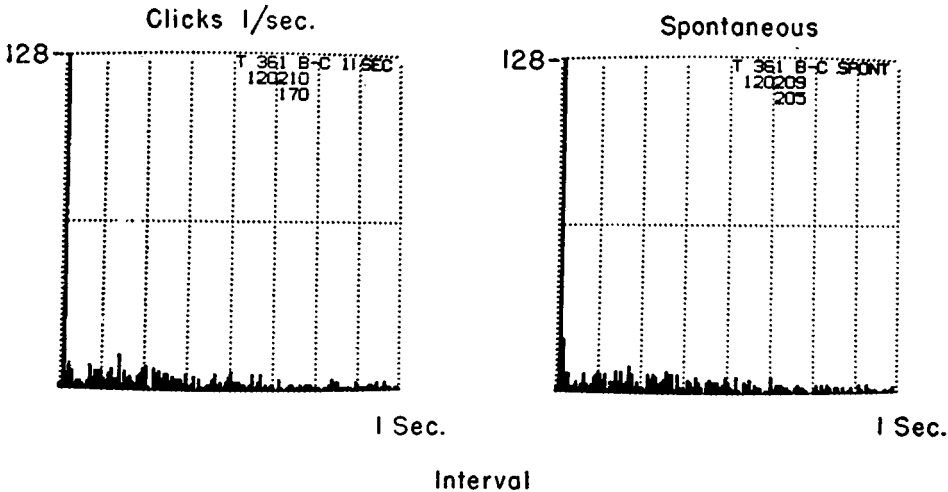
FIGURE 3   Interval histograms for a unit (120-2) in auditory cortex. Left, activity during click presentations. Right, activity during the interleaved spontaneous conditions. Click intensity 20 db re VDL. $N = 576$.

large peak at small interval corresponds to the rapid bursts of 2 or 3 action potentials which were characteristic for this unit. These displays do not show any gross differences between the stimulated and unstimulated conditions. However, observation of the unit's activity during the experiment seemed to indicate that the stimulus had some effect, although there was much spontaneous activity. The similarity of the interval histograms for 1/sec. clicks and the spontaneous condition is probably a reflection of the relatively large "spontaneous" contribution to the over-all activity even during stimulation. This picture is true for most cortical units that we have observed even at higher click presentation rates. The interval histogram does not clearly reflect changes in the pattern of most of our cortical unit responses. Comparison of Figs. 2 and 3 shows that, determined by the particuliar behavior of a unit, the interval histogram may or may not be trivial.
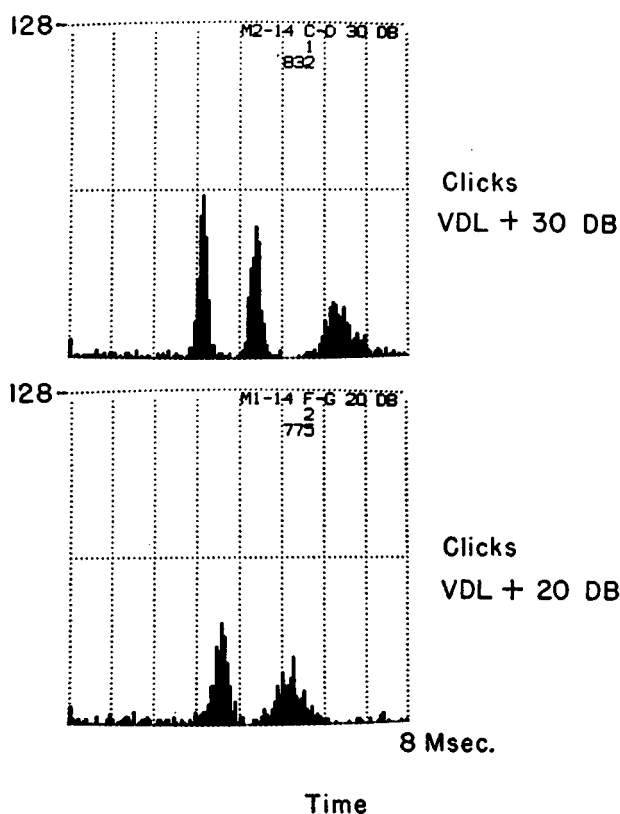

Time

FIGURE 4   PST histograms for a unit in cochlear nucleus (unit K — 173 — 3). Top, activity during presentation of clicks at 30 db re VDL. Bottom, activity during presentation of clicks at 20 db re VDL. $S = 256$, the number of stimulus intervals processed.

Various applications of the time histogram display are shown in Figs. 4 to 6. In each case the time of stimulus presentation or dummy time marker is at the extreme left of the histogram.

Fig. 4 shows the time histogram for a cochlear nucleus unit when two intensities of clicks are used. Under these conditions photographs of the responses show that
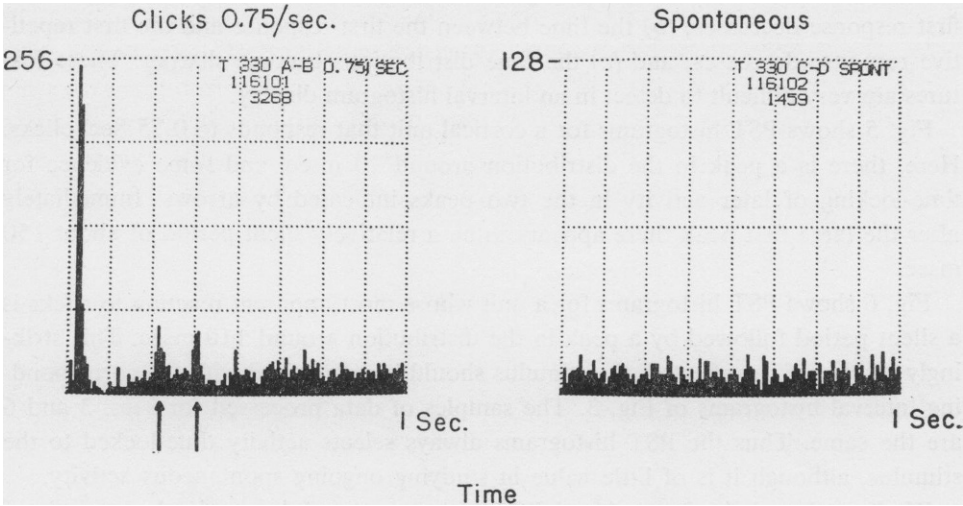
FIGURE 5   PST histograms for a unit in auditory cortex (unit 116-1). Left, activity during clicks presented at 0.75/sec. Right, spontaneous activity. Click intensity 20 db re VDL. $S = 512$.
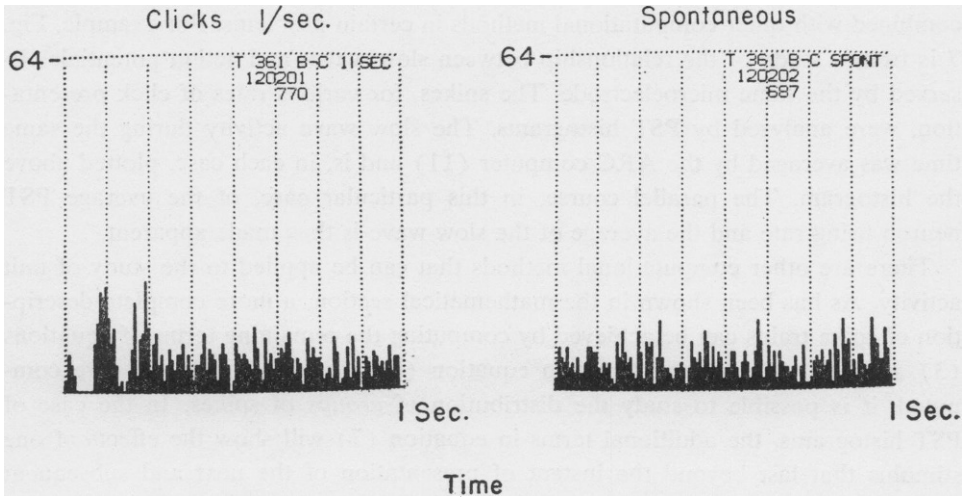
FIGURE 6   PST histograms for the same data as Fig. 3 (unit 120-2 in auditory cortex). Left, activity during clicks presented at 1/sec. Right, interleaved spontaneous activity. $S = 256$.

the unit fires repetitively to each click. The number of repetitives may not be constant. The area under a particular peak in the PST histogram relates to the number of responses that may be identified as that particular repetitive. The increasing width of successive peaks indicates the increasing time jitter of successive repetitives. Not only does the PST histogram show an increase in the number of repetitives with increased stimulus intensity but it also shows that (a) the latency of the first response decreases; (b) the time between the first response and the first repetitive response decreases; and (c) the time distributions become sharper. These features are very difficult to detect in an interval histogram display.

Fig. 5 shows PST histograms for a cortical unit that responds to 0.75/sec. clicks. Here, there is a peak in the distribution around 20 msec. and some evidence for time-locking of later activity in the two peaks indicated by arrows. Immediately after the large first peak there appears to be a relatively silent period of about 150 msec.

Fig. 6 shows PST histograms for a unit whose most apparent reaction to clicks is a silent period followed by a peak in the distribution around 110 msec. This strikingly display of the effect of the stimulus should be contrasted with the corresponding interval histograms of Fig. 3. The samples of data processed for Figs. 3 and 6 are the same. Thus the PST histograms always selects activity time-locked to the stimulus, although it is of little value in studying ongoing spontaneous activity.

We have found the interval and PST histograms useful even in the analysis of response patterns from unanesthetized animals, in which the spontaneous activity is extremely labile.

The type of single-unit data processing that we have used can be advantageously combined with other computational methods in certain problems. For example, Fig. 7 is from a study of the relationship between slow waves and action potentials observed by the same microelectrode. The spikes, for various rates of click presentation, were analyzed by PST histograms. The slow wave activity during the same time was averaged by the ARC computer (11) and is, in each case, plotted above the histogram. The parallel course, in this particular case, of the average PST neuron firing rate and the average of the slow wave is thus made apparent.

There are other computational methods that can be applied to the study of unit activity. As has been shown in the mathematical section, a more complete description of spike trains can be achieved by computing the remaining terms of equations (3) and (7). When these terms in equation (3) (interval histogram) are computed, it is possible to study the distribution of *groups* of spikes. In the case of PST histograms, the additional terms in equation (7) will show the effects of one stimulus that last beyond the instant of presentation of the next and subsequent stimuli. This makes possible the study of responses to patterns of stimuli.

Another extension of our analytical tools is to set more complex criteria for the time markers in the averaging procedures for computing time histograms. This will

FIGURE 7 PST histograms for a unit in auditory cortex (unit 120-1). Left, activity during presentations of 1, 5, 10 clicks/sec., top to bottom. Right, interleaved spontaneous activity. The curves are the average of the slow activity measured by the same microelectrode during the same time. Click intensity 20 db re VDL. $S = 512$; 1536; 2560 respectively, top to bottom.

enable study of response probabilities which are conditional on certain aspects of the response. In Fig. 4 for instance, one could study the dependence of the latency of the first response on the occurrence of repetitives to the preceding stimulus.

As experimental methods begin to permit the simultaneous recording of many functionally connected neurons, it will become necessary to investigate various conditional statistics between the several activity patterns.

These particular extensions over our present work are relatively easy to achieve with the general-purpose computers that we are using. Complete descriptions of the time properties of a spike train involve variances and other higher order statistics that cannot be discussed here. But the various computation techniques we have outlined begin to permit quantitative tests of specific mathematical models of the properties and interactions of single neurons.

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