CONDITIONAL PROBABILITY ANALYSES OF THE SPIKE ACTIVITY OF SINGLE NEURONS

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ABSTRACT With the objective of separating stimulus-related effects from refractory effects in neuronal spike data, various conditional probability analyses have been developed. These analyses are introduced and illustrated with examples based on electrophysiological data from auditory nerve fibers. The conditional probability analyses considered here involve the estimation of the conditional probability of a firing in a specified time interval (defined relative to the time of the stimulus presentation), given that the last firing occurred during an earlier specified time interval. This calculation enables study of the stimulus-related effects in the spike data with the time-since-the-last-firing as a controlled variable. These calculations indicate that auditory nerve fibers "recover" from the refractory effects that follow a firing in the following sense: after a "recovery time" of approximately 20 msec, the firing probabilities no longer depend on the time-since-the-last-firing. Probabilities conditional on this minimum time since the last firing are called "recovered probabilities." The recovered probabilities presented in this paper are contrasted with the corresponding poststimulus time histograms, and the differences are related to the refractory properties of the nerve fibers.

INTRODUCTION

Statistical analyses of the time patterns of action potentials in single neurons have been increasingly employed in recent years. These analyses have been appropriate in many neuronal systems, because of the apparently "random" nature of the firing patterns; i.e., repetition of the same stimulus conditions does not necessarily result in the same pattern of spikes, but certain averages of the firing patterns, taken over several stimulus presentations, do converge. One view of the various data-processing schemes is that they are directed toward a random-process description of the firing patterns. With this view, most data-processing methods may be considered as providing a partial characterization of the spike-train process. It is only rarely that a complete characterization of the process is easily achieved; therefore, it is usually necessary to decide which partial characterizations are most useful. This decision, of course, depends on the objectives of the particular study.

Neuronal spike data have been processed with a variety of objectives, some of which are: (*a*) to draw inferences about the mechanisms of spike generation; (*b*) to develop or employ a sensitive measure of the presence, or character, of a stimulus; (*c*) to describe the firing patterns in terms of characteristics that may be important for processing by "higher centers." A recent review by Moore et al. (Moore, Perkel, and Segundo, 1966) summarizes the kinds of data-processing methods that have been used by various investigators and the conclusions that have been drawn from these calculations.

In studies of the spike activity of auditory nerve fibers poststimulus time (PST) histograms and interspike interval histograms have been useful in providing information about the relations between the firing patterns and the stimulus dependent mechanical motion of cochlear structures (Kiang, 1965). In fact, the relative simplicity of these relations has encouraged efforts to develop a random-process model to describe the spike activity of these fibers (Weiss, 1964; Siebert and Gray, 1963; Gray 1966). Such models usually include two kinds of contributions to the spike patterns. The first is the excitation of the fiber, which is thought to be closely related to the mechanical motion of cochlear structures and the resulting action of the hair cells. The second is that of the refractory properties of the nerve fiber. In most models, these two factors originate in separate components. For purposes of testing and refining such models, it would be useful to separate these two factors in the spike data, but the PST histogram is determined by a rather complicated interaction of both effects; the same is true of the interval histogram except in cases where there is no stimulus-related time structure in the spike data.

The conditional probability analyses introduced in this paper were developed with the objective of removing, or at least controlling, the effects of refractoriness in the spike data. All of the calculations considered here involve estimates of the conditional probability of a firing in a specified time interval (relative to the stimulus), given that the last firing occurred during an earlier specified time interval. This calculation allows the study of the stimulus-related effects with the time-since-the-last-firing as a controlled variable, and thus it facilitates a more direct comparison of some components of the model with the data. For this reason, these calculations have proved quite valuable in analyzing auditory nerve data. It seems likely that they will also be of value with other data, but this of course would depend on the specific characteristics of such other data. The characteristics of the auditory nerve fiber data that led to these conditional probability analyses will be reviewed as the analyses are discussed.

In the application of all of these data-processing methods, there is an implicit assumption that the data are statistically regular in a sense that justifies treating all stimulus presentations identically. If, for example, on 600 repetitions of a stimulus, the calculations performed on data from the first 100 yielded significantly different results from those based on the last 100, it would not seem appropriate to treat all 600 presentations in the same way. This assumption does not preclude nonstationarities that are locked to the stimulus, but it does exclude—or at least assumes to be negligible—nonstationarities that are not related to individual presentations of the stimulus. Fortunately, this assumption can be tested, and with the auditory nerve fibers, at least, adaptation and other effects are small enough that the assumption seems justified (Gray, 1966).

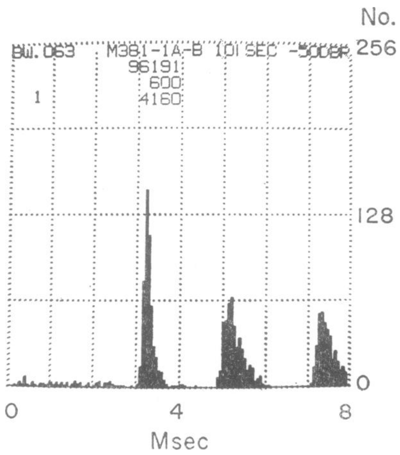
In the discussion that follows, there is a potential confusion between "true" probabilities and the estimates of them, which are based on calculations. Where it seems necessary, the distinction between probabilities and estimates of probabilities is made explicitly. As a matter of convenience, however, much of the discussion depends on context to indicate whether probabilities or their estimates are intended.

All of the calculations presented are based on microelectrode recordings from auditory nerve fibers in cat. Descriptions of the experimental methods (and equipment) may be found in Kiang (1965).

Before discussing the various conditional probability analyses, the PST and interval histogram calculations will be briefly reviewed, in a manner somewhat different from that of Gerstein and Kiang (1960), who discussed these calculations in terms of correlation functions. Following this review, three kinds of conditional probability analyses will be introduced. (As will be elaborated below, the last two are special cases of the first.) This paper has the limited objective of introducing these analyses and demonstrating their value. Results obtained by applying these analyses to auditory nerve data have been discussed elsewhere (Gray, 1966).

POSTSTIMULUS TIME HISTOGRAMS

With acoustic clicks presented 10 times per sec, certain regularities in the firing patterns of auditory nerve fibers may be observed. Fig. 1 shows several samples of the microelectrode recording, each beginning at the time of a click presentation. Note that the patterns of spike activity are not identical for different click presentations, but there are certain preferred times of firing. These preferred times of firing show up more clearly in the poststimulus time (PST) histogram, which also appears in Fig. 1. In the PST histogram, z_k, the height of the kth bar is equal to the total number of spikes which occurred between $k\Delta$ and $(k + 1)\Delta$ time units after a stimulus presentation. (Δ is called the "bin width" of the calculation.) The calculation of the PST histogram can be described in the following way. At each stimulus presentation a clock is set to zero; the clock advances by one unit every Δ time units; at each spike the bar corresponding to the current clock reading is increased in height by one. Often it is convenient to normalize the PST histograms by dividing all of the bar heights by the number of stimulus presentations; these histograms are referred to as "normalized PST histograms."



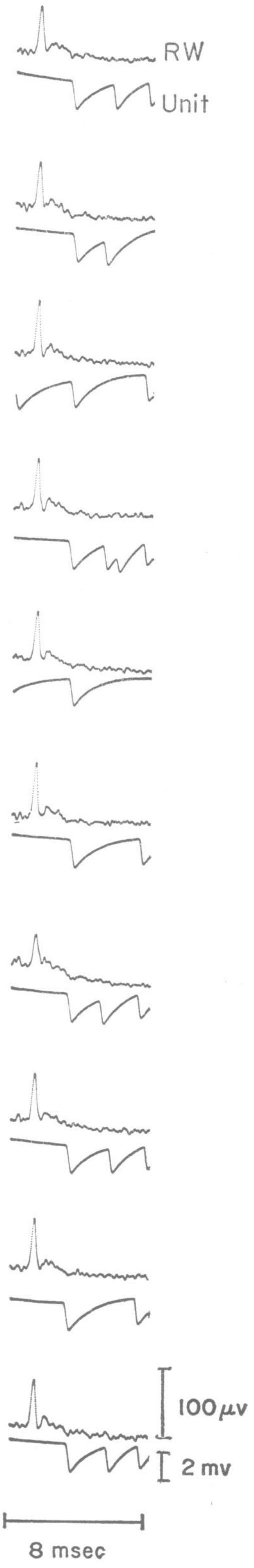


Figure 1 PST histogram and recordings from both round-window electrode and microelectrode at auditory nerve fiber for unit 296-19. Stimulus: 10/sec, −05 *dB* rarefaction clicks. The histogram has a bin width of 0.0625 msec, displays 128 bars, and is based on 1 min of data. The ten pairs of electrode recordings each begin at the time of a click presentation. (The action potentials shown are somewhat distorted by the limited frequency response of the amplifier.) [Fig. 4.1, page 21, in Kiang, 1965 (reproduced by permission of The M.I.T. Press, Cambridge, Mass.).]

The PST histogram can be useful in studying spike patterns that have a time structure related to the stimulus presentation, but there are some important aspects of the data that must be discarded in the calculation of the PST histogram. For example, it cannot be determined whether or not most of the spikes occurring in the interval corresponding to the second peak of the histogram were preceded by a spike in the interval corresponding to the first peak.

INTERVAL HISTOGRAMS AND HAZARD FUNCTIONS

The interval histogram is simply a plot of the first-order distribution of the time intervals between spikes; that is, the height of each bar represents the number of intervals of that length. More precisely, let Δ be the "bin width" of the calculation and y_k, $k = 0, 1, 2, \cdots$, the height of the kth bar, then y_k is the number of intervals of length greater than $k\Delta$ and less than or equal to $(k + 1)\Delta$. (It is convenient, though not strictly correct, to speak of intervals being "of length $k\Delta$" rather than detailing the condition "between $k\Delta$ and $(k + 1)\Delta$.")

It should be emphasized that the interval histogram involves only first-order statistics of the data. Any tendency for long intervals to follow short intervals, or for short intervals to come in bursts, is not directly reflected in this calculation. To explore such a sequential dependence between intervals it would be necessary to perform higher order calculations. One could, for example, count the number of intervals of length $k\Delta$ that are followed immediately by an interval of length $n\Delta$. If carried out for all n and k, this calculation would provide an estimate of the second-order density function for interspike times. This particular calculation has been performed on data from auditory nerve fibers and preliminary results suggest that the times between spontaneous firings may be regarded as independent random variables (Kiang, 1965).

A process that is characterized by independent identically distributed interevent times is called a "renewal process." In a renewal process, the interval histogram takes on special significance, for if a process is known to be a renewal process, the only information needed to completely characterize it is the interval distribution (or some equivalent function). Of course, the interval histogram may be an interesting statistic of other processes, but it is only in the case of a renewal process that it is a complete description of the data.

The number of intervals of length k has been defined as y_k. The (estimate of the) probability that a given interval is of length k is

$$p(k) = \frac{y_k}{\sum_{n=0}^{\infty} y_n} \tag{1}$$

In publications on renewal processes (see, for example, Cox, 1962, or Parzen, 1962) a function that is related to $p(k)$ is often discussed. In current notation this function is defined by

$$\Phi(k) = \frac{p(k)}{\sum_{n=k}^{\infty} p(n)} \tag{2}$$

Equations 1 and 2 are easily combined to give

$$\Phi(k) = \frac{y_k}{\sum_{n=k}^{\infty} y_n} \tag{3}$$

Equation 2 may be interpreted as follows: $p(k)$ is the probability of an interval being of length $k\Delta$; $\sum_{n=k}^{\infty} p(n)$ is the probability of an interval being at least of length $k\Delta$; and $\Phi(k)$ is the conditional probability that an interval is of length $k\Delta$, given that it is at least of length $k\Delta$. Stated another way, if it has been $k\Delta$ time units since the last firing, the conditional probability of a firing during the next Δ is $\Phi(k)$. Similarly, in equation 3, $\sum_{k=n}^{\infty} y_n$ is the number of intervals that are at least $k\Delta$ in length, and $\Phi(k)$ is the fraction of these intervals which are exactly $k\Delta$ in length.

$\Phi(k)$ is an estimate of the conditional probability of a firing during the next Δ, given that it has been $k\Delta$ time units since the last firing. In renewal process discussions, $\Phi(k)$ has been referred to as the hazard function, as the age specific failure rate, or as any of several other names. In a neurophysiological context, Goldberg, Adrian, and Smith (1964) calculated $\Phi(k)$ and referred to this calculation as a conditional probability analysis. In the present paper, however, the calculation of $\Phi(k)$ represents only one of several conditional probability analyses. The term "hazard function" is selected for this discussion, since it is the shortest, commonly used term that is not ambiguous.

In Fig. 2 the interval histogram calculated from a long recording of the spontaneous activity of an auditory nerve fiber is presented along with the corresponding hazard function (also in the form of a histogram). Several features of these two histograms deserve comment. The interval histogram starts near zero, rises to a mode at ~5 msec, and then decays in an exponential manner toward zero. The hazard function starts near zero, implying that the probability of a firing in the next Δ is small if it has only been a millisecond or two since the last firing. With increasing values of time, the hazard function increases toward an asymptotic value of approximately 0.02. It appears that this asymptote is reached somewhere between 20–25 msec. This histogram implies that the probability of a firing in the next Δ is the same for any time-since-the-last-firing greater than 20–25 msec.

It is easy to show that an exponential decay of the interval histogram implies a constant value of the hazard function, for all times after the exponential decay begins. Kiang has reported that the interval histograms obtained from spontaneous activity of auditory nerve fibers seem to be characterized by a mode at less than 10 msec, followed by a decay that is roughly exponential (Kiang, 1965). This suggests that the hazard function of Fig. 2 is typical of auditory nerve fibers, in that it levels off at a constant value, and does so in 20–25 msec. The value of this constant is, of course, related to the rate of spontaneous firing of the fiber.

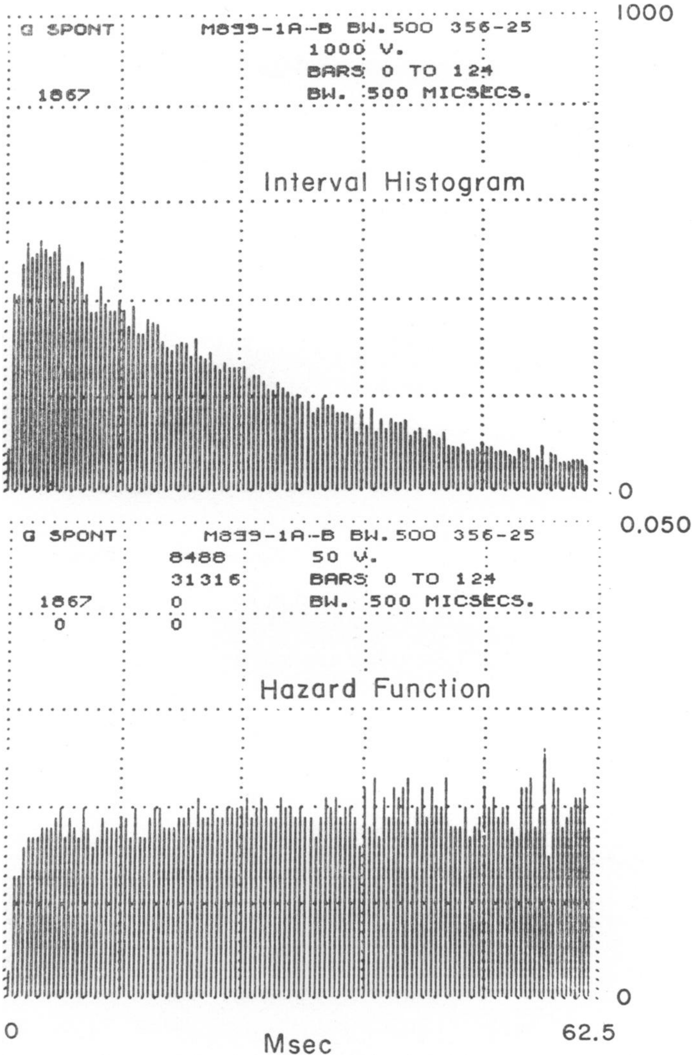


FIGURE 2 Interval histogram and hazard-function histogram (bin width 0.5 msec, 124 bars) calculated from a long (approx. 14 min) recording of the spontaneous activity of unit 356-25.

The hazard function of Fig. 2 is reproduced in Fig. 3, together with the hazard functions calculated from the spontaneous activity of four other units. For purposes of comparison, all of the histograms in Fig. 3 have the same vertical and horizontal scales. For the units with the higher spontaneous rates, relatively few long intervals

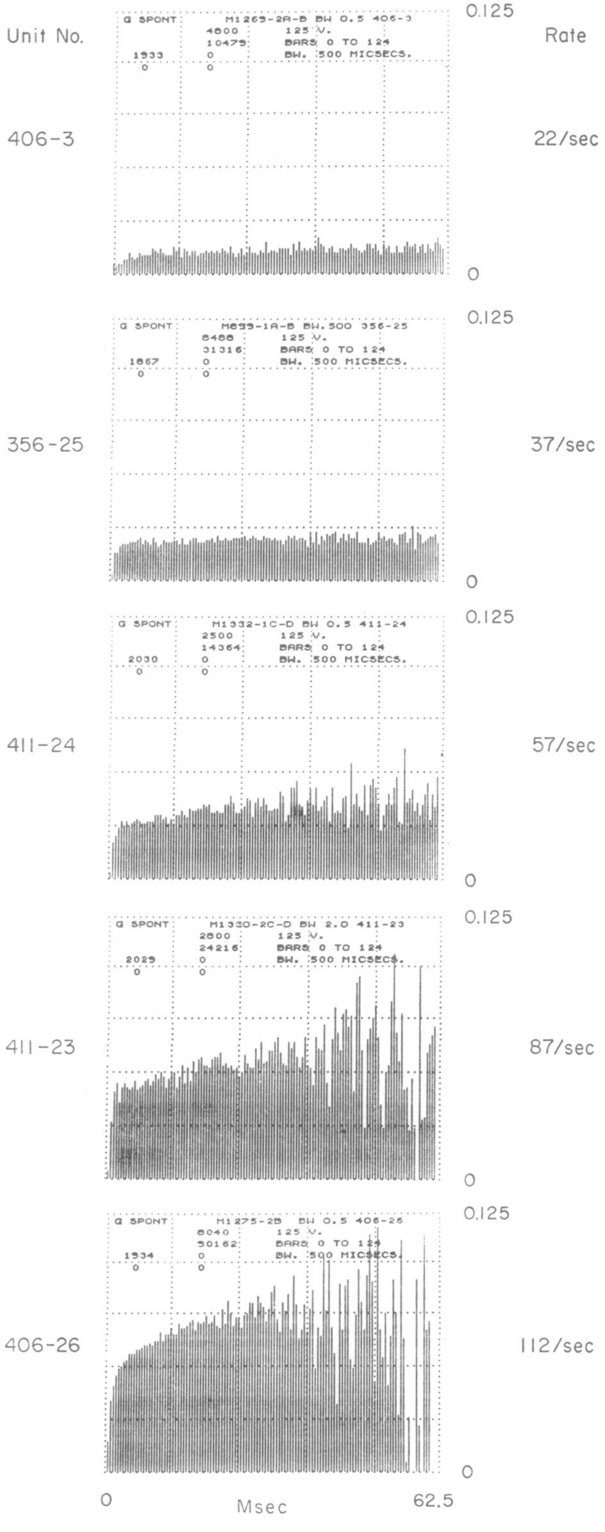


FIGURE 3 Hazard-function histograms (bin width 0.5 msec, 124 bars) calculated from long runs of spontaneous activity with several units.

are available for estimating the hazard functions at the corresponding times. Hence the hazard functions are somewhat "noisy" in the right halves of these histograms.

These histograms appear to be consistent with the suggestion above that the hazard functions calculated from the spontaneous activity of auditory nerve fibers level off at a constant value within 20–25 msec. With these data, however, this cannot be a very precise statement, and whether the hazard functions actually level off or just grow at a much slower rate after 20–25 msec has not been established.

If the hazard function does, in fact, assume a constant value within a certain time after firing, then the following is implied: provided it has been long enough since the last firing, the probability of a firing in the next Δ does not change with time, until, of course, another firing occurs. This suggests that the unit "recovers" from a previous firing in a period of roughly 20 msec. The words "recovery" and "refractory effects" are used in this discussion to refer in a general way to the processes taking place soon after a firing. It should be emphasized, however, that the definitions of these terms are strictly operational and do not necessarily coincide with any underlying physiological phenomena. The neural unit is considered "recovered," that is, the "refractory effects" are considered to be no longer present, when the probability of firing is no longer a function of the time-since-the-last-firing. Conceivably, the neuron could still be undergoing major changes in state and still appear "recovered" by this definition. It has already been suggested that auditory nerve fibers "recover" from spontaneous firing; that they also "recover" in the presence of certain stimuli can be demonstrated by appropriate calculations, and these will be discussed below.

CONDITIONAL PROBABILITY MATRICES

In a stimulus situation such as the click example in the PST histogram discussion, where there is a preferred time structure in the spike pattern, there are several conditional probabilities that might be of interest. For example, what is the conditional probability of a firing in the interval corresponding to the second peak of the PST histogram, given that the last firing occurred during the interval corresponding to the first? How does this probability compare with the conditional probability of a firing, given that it has been a long time since the last firing? The calculations described below have been used to estimate conditional probabilities such as these.

Several time intervals are defined relative to the onset of the stimulus presentation. For each pair of these intervals the conditional probability of a firing in the later one, given that the last firing was in the earlier one, is estimated. This is done on a simple relative frequency basis. To illustrate, suppose that in n of the stimulus presentations there was a firing in interval 5, but no firing in interval 6 or 7. In other words, there were n trials in which the last firing before interval 8 occurred in interval 5. Furthermore, suppose that, considering only these n trials, on m of these there was also a firing during interval 8. Then the estimate of the conditional probability of a firing in interval 8, given that the last firing was in interval 5, is m/n. A con-

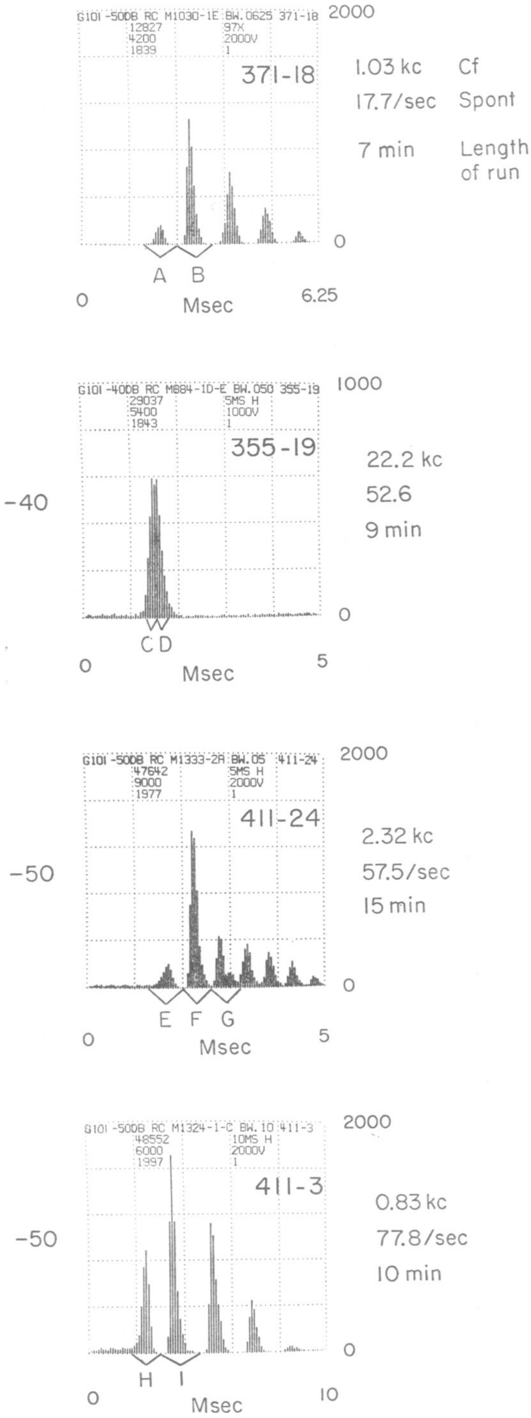


FIGURE 4 PST histograms and interval definitions for Fig. 5, (all histograms display 100 bars, bin widths are 0.0625, 0.05, 0.05, and 0.10 msec for units 371-18, 355-19, 411-24, and 411-3, respectively). Stimuli: 10/sec rarefaction clicks at levels (in *dB* re 100 v into condenser earphone) indicated at left of each histogram. The *CF*, spontaneous rate, and length of data runs used for the calculations are indicated at the right of each histogram.

venient way to present the results of these calculations is in matrix form with, for example, the entry in the 8th column of the 5th row being the conditional probabilty of a firing in interval 8, given that the last firing was in interval 5. Because of this natural scheme of presentation, this calculation is referred to as the "conditional probability matrix" calculation, or simply the "matrix calculation."

By using the matrix calculation, the probability of a firing in a specific interval of time relative to the click may be studied with the time-since-the-last-firing as a controlled variable. Some examples of this application of the matrix calculation are given in Figs. 4 and 5. Conventional PST histograms calculated from long click runs on each of four units are presented in Fig. 4. Two or three intervals are defined on each histogram, and, for each interval, conditional probabilities of firing have been estimated. These estimates are conditional on the last firing being in a specified "conditioning interval." In Fig. 5, these conditional probabilities are plotted as functions of the location of the "conditioning interval." For conditioning intervals preceding the click, each point is plotted at the horizontal coordinate representing the conditioning interval's boundary that is closest (in time) to the click. Time is measured relative to the click, with times before the click being negative. The conditioning intervals following the click are labeled in terms of the peaks of the appropriate histogram. Different intervals were used for different units, so some care is necessary in interpreting this figure. To illustrate the meaning of this

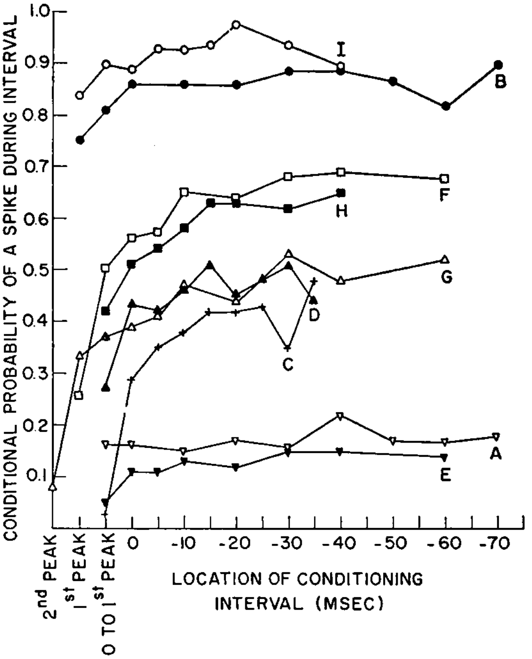


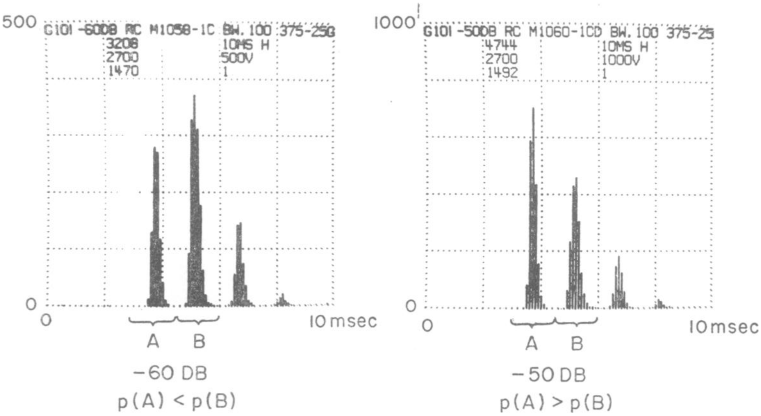
Figure 5 Conditional firing probabilities as functions of the location of the conditioning intervals. The curve labels (*A*-*I*) correspond to the interval definitions of Fig. 4, where stimulus conditions are also given. For conditioning intervals preceding the click, each point is plotted at the horizontal coordinate representing the conditioning interval's boundary that is closest (in time) to the click. The conditioning intervals following the click are labeled in terms of the peaks of the appropriate histogram.

figure, the curve labeled E represents the probability of a firing in interval E, (unit 411-24), conditional on the last firing before E falling in the various conditioning intervals. For the point above -30 msec, the conditioning interval is -30 to -40 msec; above -40 it is -40 to -60 msec; and above -60 it is "before -60 msec" (that is, -60 msec to $-\infty$).

Despite the fact that these calculations are based on a large number of stimulus presentations (4200, 5400, 9000, and 6000), statistical fluctuations in these curves are appreciable, and these make precise inferences inappropriate. It does appear, however, that these curves level off somewhere between 15 and 30 msec. In other words, the probability of firing in the designated interval does not depend on the time since the last firing, provided the last firing preceded the click by at least 20 msec (30 msec would be a more conservative estimate). This result is consistent with (though not implied by) the observation that these units recover from spontaneous firings in roughly 20 msec. The term "recovered probabilities" will be applied to conditional probabilities that are based on a sufficiently long time since the previous firing that there is no longer any dependence on this time. As was noted in the discussion of hazard functions, this is a strictly operational definition of "recovery"; it may not coincide with the actual physiological recovery processes. It is a

(Recovered probabilities)

	p(A)	p(B/A')	p(B/A)	p(B)
-60 DB	0.32	0.61	0.32	0.52
-50 DB	0.76	0.87	0.56	0.64



-60 DB
$p(A) < p(B)$

-50 DB
$p(A) > p(B)$

FIGURE 6 PST histograms (bin width 0.1 msec, 100 bars) and various conditional probabilities for unit 375-25. Stimuli 10/sec, -50 *dB*, and -60 *dB* rarefaction clicks. All probabilities are conditional on no spike for 30 msec before interval A. A [B] is the event: a spike during interval A [B]. $p(B)$ is calculated from $p(B) = p(A)p(B/A) + [1 - p(A)]p(B/A')$. The calculations are based on 4.5 min of data.

most useful concept because in this operational sense, at least, refractory effects are removed from the spike data by the calculation of recovered probabilities.

Further examples of the results of the matrix calculation are presented in Fig. 6, together with the corresponding PST histograms, which were computed from the same data. In this figure, all probabilities are conditional on no firing for 30 msec before interval A. Thus $p(A)$ is the conditional probability of a firing during interval A, given that the last firing was at least 30 msec earlier. Similarly, $p(B/A')$ is the conditional probability of a firing in B, given that the last firing was at least 30 msec before interval A (so, in particular, there was no firing during A). $p(B/A)$ is the conditional probability of a firing in B, given that there was a firing in A (and no firing for 30 msec before A).[1] The conditional probability of a firing in B, given only that no firing occurred in the 30 msec immediately before interval A, is $p(B)$, and this is calculated from the following equation:

$$p(B) = p(B/A)p(A) + p(B/A')[1 - p(A)]$$

With these definitions, $p(A)$ and $p(B/A')$ are recovered probabilities, and $p(B)$ and $p(B/A)$ are not. In examining Fig. 6, it should be noted that the recovered probability for B is larger than that for A at both intensities, that the probability of a firing in B is smaller if the unit has fired in A than if it has not, and that all of the probabilities are higher at the higher click level.

In addition to presenting some typical results of the matrix calculation, Fig. 6 illustrates the usefulness of these calculations in interpreting the conventional PST histogram. The fact that peak A is larger than peak B in the -50 *dB* run could be misleading if the PST histogram were interpreted as a direct measure of the strength of an "effective stimulus." (As an "effective stimulus" for the auditory nerve fiber one might consider some aspect of the mechanical motion of the cochlea or perhaps some electrical or chemical action of the hair cell.) In terms of recovered probabilties, peak B is larger than A, but if there has been a firing during A, the unit is "refractory" during interval B and a smaller probability $[p(B/A)]$ applies. Since, at the -50 *dB* click level, the unit is likely to fire during interval A and hence be "refractory" during interval B, the size of peak B in the histogram is smaller than would be expected from the recovered probability alone. As the recovered probabilities are presumably free of any refractory effects, it seems reasonable to regard them as a measure of an effective stimulus. In these terms, the PST histogram reflects a somewhat complicated combination of both the characteristics of the effective stimulus and the refractory characteristics of the neural unit.

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[1] In fact, this number cannot be determined with the "matrix calculation," and the number given is really the conditional probability of a firing in B, given that a firing occurred in A, without any condition on what happened in the 30 msec before A; this number is probably very close to the desired number, but even if it were not, the qualitative conclusions intended from this example would presumably still apply.

RECOVERED PROBABILITY HISTOGRAMS

The calculation described here, in principle, is a specialization of the conditional probability matrix calculation, but for practical reasons it is employed separately, and it seems appropriate to discuss it separately. The concept of a recovered probability has already been introduced. The conditional probability of a firing in an interval of time defined relative to the stimulus, considered as a function of time since the last firing, appears to reach an asymptote in approximately 20 msec. This asymptotic value is defined as the recovered probability. By definition, the height of each bar in the recovered probability histogram represents the recovered probability of a firing at that time. More precisely, if the "recovered condition" is -20 msec, let m_k be the number of stimulus presentations on which there was no firing during the interval from -20 msec to $+k\Delta$. (-20 msec refers to the time 20 msec before the stimulus presentation.) Considering only these m_k trials, let n_k be the number on which there was a firing between $k\Delta$ and $(k + 1)\Delta$ (so $m_{k+1} = m_k - n_k$). Then n_k/m_k is an estimate of the recovered probability of firing in the interval $k\Delta$ to $(k + 1)\Delta$, and x_k, the height of the kth bar in the recovered probability histogram, is equal to n_k/m_k.

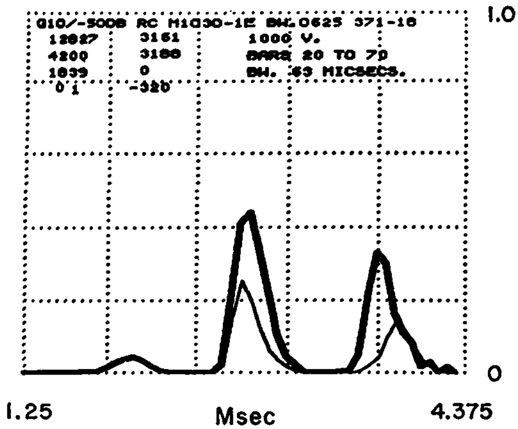


FIGURE 7 Straight-line interpolations between tops of bars 20–69 in recovered probability histograms (heavy line) and normalized PST histograms (light line) (bin width 0.0625 msec, recovered condition: -20 msec). Stimulus: 10/sec, -50 *dB* rarefaction clicks. Calculations are based on 7 min of data.

It is interesting to compare the recovered probability histogram with the conventional PST histogram for the same data; this is done in Fig. 7. To facilitate comparing the two histograms, rather than displaying the customary bar graph, a smooth curve representing the straight-line interpolation between the tops of the bars is given for each histogram. The heavy line represents the recovered probability histograms, hence the height of the curve at a particular time represents the recovered probability of a firing within a bin width of that time. The lighter curve is a conventional PST histogram that has been normalized by dividing by the number of stimuli. Its height, therefore, represents the fraction of stimulus presentations on which there was a firing during the indicated bin width. In comparing these two curves, observe that they are much the same for the small first peak and for the first half of the larger second peak, but that the PST histogram returns toward zero sooner than the recovered probability histogram. Furthermore, the recovered probability histogram rises for the second peak before the conventional PST histogram does. The apparent discrepancy between these two curves can be understood qualitatively in terms of the refractory characteristics of the neural unit. The probability of a firing during the first half of the second peak is sufficiently large that on most stimulus presentations the unit fires somewhere during the early part of the peak and is "refractory"—and hence less likely to fire—for a period of time afterwards. The portion of the PST histogram corresponding to the time when the unit is usually refractory is diminished by this refractory effect. The recovered probability histogram is not affected by the refractoriness, since in estimating the recovered probability of an event at some time in the second half of the first peak, none of the stimulus presentations that involved an event during the first half are used.

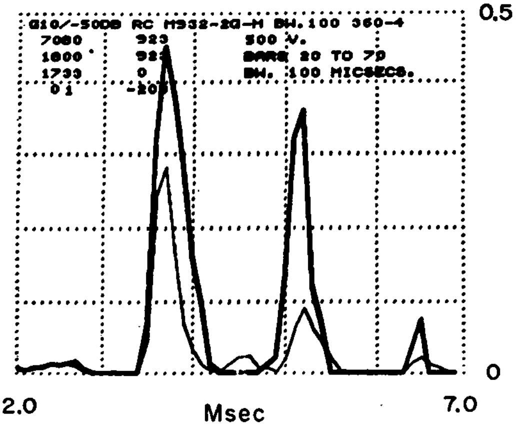


FIGURE 8 Straight-line interpolations between tops of bars 20–69 in recovered probability histogram (heavy line) and normalized PST histogram (light line) (bin width 0.10 msec, recovered condition: −20 msec). Stimulus: 10/sec, −50 *dB* rarefaction clicks. Calculations are based on 3 min of data.

Another kind of difference between the recovered probability histogram and the conventional PST histogram is illustrated in Fig. 8. In this figure there is a small peak in the PST histogram that does not appear in the recovered probability histogram. Considering that the recovered probability is essentially zero in this region, it is curious that the conventional PST histogram indicates so many firings. For this to happen it is necessary that some "unrecovered" probability be larger than the negligible value of the recovered probability. This rather unexpected situation can be studied by using the calculations described below.

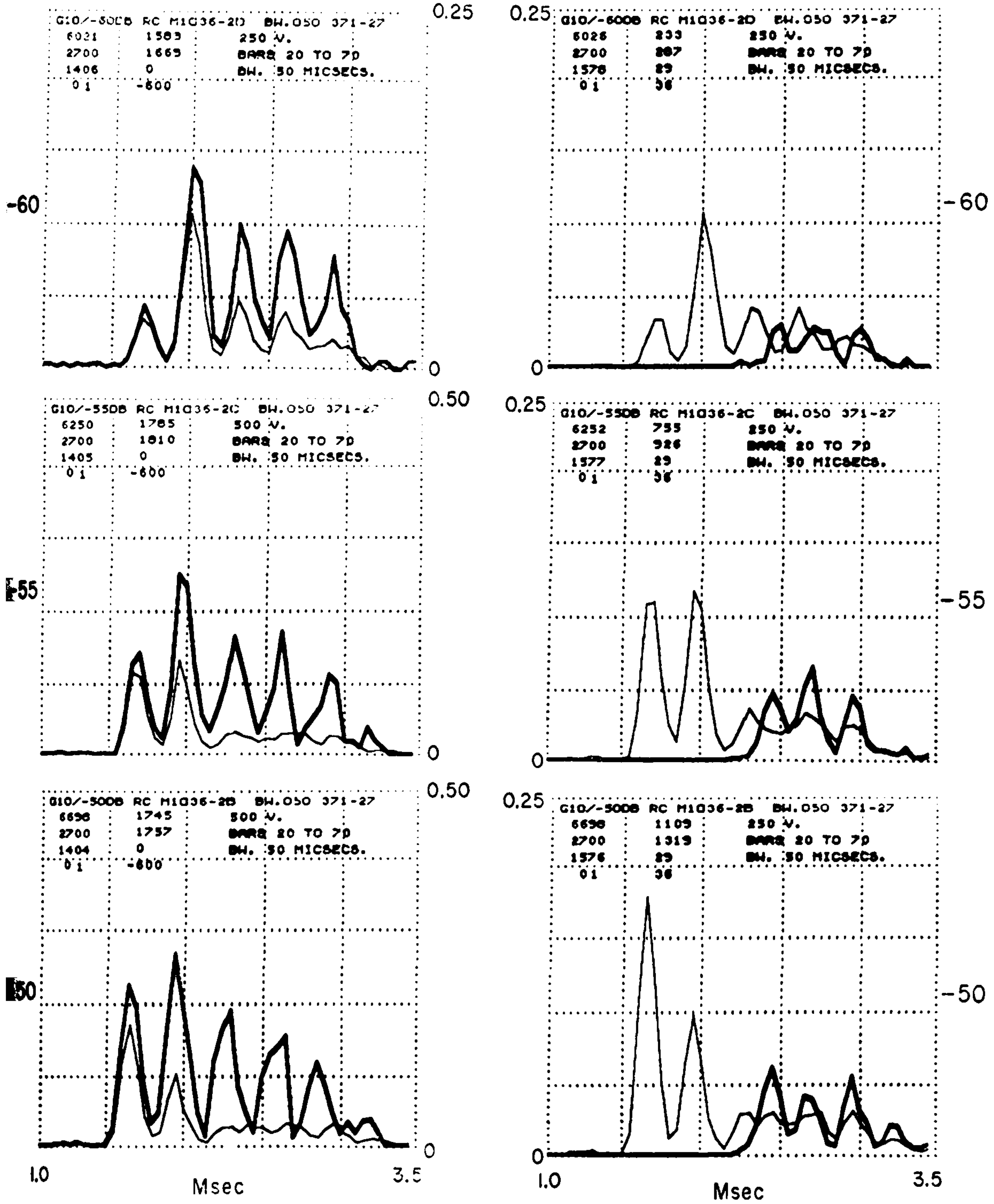
CONDITIONAL PROBABILITY HISTOGRAMS

The height of each bar of the conditional probability histogram represents the conditional probability of a firing at the corresponding time, given that the last firing occurred in the specified "conditioning interval." The recovered probability histogram is a special case of the conditional probability histogram where, for example, the conditioning interval might include all times at least 20 msec before the stimulus. In calculating the conditional probability histogram, the only stimulus presentations that are used are those on which there was a firing during the conditioning interval. If m_k is the number of these trials that involved no firing between the conditioning interval and $+k\Delta$, and n_k the number of these that involved a firing before $(k + 1)\Delta$, $(m_{k+1} = m_k - n_k)$, then x_k, the height of the kth bar, is n_k/m_k. Slightly restated, m_k is the number of stimulus presentations on which there was a firing during the conditioning interval, but no firing between the conditioning interval and $+k\Delta$. Considering only these m_k stimulus presentations, x_k is the fraction of these that involved a firing between $k\Delta$ and $(k + 1)\Delta$. Hence x_k is an estimate of the conditional probability of a firing at $k\Delta$, given that the last firing occurred during the conditioning interval.

In Fig. 9 the normalized PST histogram, the recovered probability histogram, and a conditional probability histogram for three levels of click runs on the same unit are presented. The conditioning interval is defined to correspond to the first peak. Several conclusions can be drawn from this figure. In the left column, the recovered probability histogram appears as the heavy line, and the normalized conventional PST histogram as the light line. Both curves show several peaks spaced at a period of the 3.27–kc characteristic frequency of this unit, but the separate peaks are much clearer in the recovered probability curve than in the PST curve. The reason for this is that the unit often fires a second time during the displayed interval of time and the second firings do not have the same preferred-time structure that applied to the first. This phenomenon can be studied by means of the conditional probability histograms shown in the right column.

At each time indicated on the horizontal axis, the height of the conditional probability curve presents the probability of a firing within the next bin width, conditional on the last firing being during the first peak. The first peak of the conditional probability curve occurs approximately ¾ msec after the first peak of the PST histogram. Examination of the pictures in the left column indicates that this time corresponds to the region between the third and fourth peaks of the recovered probability histogram. Because the time structure of the recovered probabilities does not in this case hold for second firings, the separate peaks are much harder to distinguish in the PST histogram than in the recovered probability histogram.

Incidentally, the tendency to fire a second time, after $\sim$¾ msec, also accounts for the extra peak in Fig. 8. In fact, these calculations applied to several units have indicated that this phenomenon occurs with many auditory-nerve fibers; its effect on the PST histogram depends on the relation between the ¾ msec interval and the spacing of peaks in the histograms.



[illegible]URE 9 Straight-line interpolations between tops of bars 20–69 in recovered probability histograms (heavy [illegible]s in left column), conditional probability histograms (heavy lines in right column), and normalized PST histo[illegible]ms (light lines in both columns) (bin width 0.05 msec; recovered condition: −30 msec; conditioning interval: [illegible]-1.8 msec). Stimuli: 10/sec, −60, −55, and −50 *dB* rarefaction clicks. Calculations are based on 4.5 min [illegible]data.

CONCLUSIONS

Within the general framework of conditional probability calculations, three specific calculations have been discussed: the conditional probability matrix, the recovered probability histogram, and the conditional probability histogram. It has already been pointed out that the recovered probability histogram is a special case of the conditional probability histogram, and that it, in turn, is a special case of the matrix calculation. Practical constraints imposed by limited computer memory and speed preclude computing several conditional probability histograms simultaneously or having more than 10 or 20 intervals for the matrix calculation. The computer program now in use performs three calculations simultaneously: a conventional PST histogram (with 125 bars), a conditional probability histogram (with 125 bars), a conditional probability matrix (with 15 intervals).

A major consideration in employing these calculations, and in gathering the data on which they are based, is the statistical problem of estimating probabilities from a limited number of trials. For example, in calculating a recovered probability histogram, all stimulus presentations that are preceded too closely by a firing are discarded, and in calculating the height of the kth bar, all trials on which a firing occurred during any of the first $(k - 1)$ bin widths are discarded. For this reason, at moderate click levels, it is often difficult to calculate recovered probabilities for any time after the first peak. In general, it is necessary to obtain longer data runs to get reliable probability estimates than are necessary for reliable PST histograms.

The concept of a recovered probability was suggested by the exponential "tails" of the spontaneous interval histograms, and has been verified on data obtained with click stimuli. The calculation of recovered probabilities is particularly useful because in a sense it removes the refractory complications from the data. From the standpoint of developing a model for auditory nerve activity this can be very helpful. Since most attempts at modeling these data treat the refractory properties of the neuron as a somewhat separable part of the model, the comparison of model and data in terms of recovered probabilities is more direct than, for example, comparing the PST histograms predicted by the model with those obtained from the data. Of course, a complete model would have to include refractory effects, but it may be strategically wise in the construction of a model to begin by excluding the refractory complications.

In addition to providing a more direct measure of the nonrefractory aspects of the data, the recovered probability histograms have been useful for pointing out specific phenomena that occur soon after firings. Some of the apparent discrepancies between recovered probability histograms and conventional PST histograms are reasonable in terms of the usual notion of a diminished probability of firing following a firing. Other discrepancies can be explained only in terms of a temporary increase in the probability of firing. These phenomena are suggested by the comparison of the recovered probability and PST histograms, but are best studied in detail by using the more general conditional probability calculations.

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