

A STATISTICAL ANALYZER FOR OPTIC NERVE MESSAGES

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ABSTRACT

A statistical mathematical model of the discharge in a single optic nerve fiber is proposed, based on a discharge with intervals between impulses distributed independently according to a gamma distribution ("gamma discharge"). A light stimulus distorts the time axis of this discharge according to a "frequency function" which is characteristic of the stimulus.

A linear filter is described which calculates the likelihood of a certain stimulus when the nerve fiber message is fed into it. This filter forms the basis of theoretical nerve message analyzers for three visual experiments: (a) The detection of the occurrence of a flash of light of known intensity and time of occurrence, (b) the detection of the time of occurrence of a flash of known intensity, and (c) The estimation of the intensity of a flash occurring at a known time.

Possible neural mechanisms in the brain for analyzing optic nerve messages, based on the above mathematical models, are suggested. Changes of excitability or discharge frequency correspond to the output of the likelihood filter. Any such mechanism must be sufficiently plastic to have a response matched to each expected stimulus for most efficient vision near threshold.

I

INTRODUCTION

The mammalian optic nerve can be thought of as a noisy communication channel. Each of its sensory fibers carries visual information to the brain coded in the form of a sequence of nearly identical nerve impulses. Such messages, when recorded electrically from ganglion cells in the retina of a cat, either in total darkness or under a steady illumination, are found to have an average frequency of between 3 and 80 impulses per second. This discharge is not regular, but random; the durations of the intervals between successive impulses are distributed statistically over a wide range (Granit, 1947, 1955; Kuffler, Barlow, and FitzHugh, 1957). This variation in the duration of the intervals constitutes "noise" which tends to distort the visual message and set a limit to visual sensitivity.

The statistical properties of the maintained discharge were described by

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Kuffler, Barlow, and FitzHugh (1957), and those of the response to a flash near threshold by FitzHugh (1957). In the latter paper a rather simple method of analyzing the messages was used, namely, counting the number of impulses which occurred during a certain critical period following the flash and studying the statistical distribution of this number, with flash intensity as a parameter. With this method of analysis some of the useful information in the message was undoubtedly lost, but an approximate agreement was found between the number of identical flashes required to attain near certainty in measuring the threshold experimentally, and the corresponding number predicted from the statistical analysis. This work suggested two theoretical questions: (1) how, in principle, to extract useful information most efficiently from an optic nerve fiber message, and (2) how to design an analyzing device to perform this task with reasonable accuracy.

The problem of detecting a small signal in the presence of noise has been studied in considerable detail by communication engineers. Much of their theoretical work is based, however, on the assumption of a linear system, in which the magnitude of the total message at any instant is equal to the algebraic sum of the signal and noise. The mammalian optic nerve message does not have this property, however, since it consists of a sequence of identical impulses which cannot be separated into two subsequences, one constituting the signal and the other noise. The effect of the stimulus is to modify the interval durations or "frequency" of the maintained discharge of impulses, rather than to add (or subtract) individual impulses. It is necessary, therefore, to set up a non-linear stochastic model of the nerve discharge and apply to it those more general parts of communication theory which deal with the process of statistical inference, based on the calculation of likelihoods. The solution of this problem presented in this paper is, briefly, to feed the nerve message into an ideal electrical filter which has as its output a weighted sum of the impulses during the recent past. Impulses that arrive at a time when an increase of frequency is expected, following a flash, tend to favor the hypothesis that the flash did actually occur, and are therefore given positive weights, while those arriving during an expected decrease of frequency tend to oppose the hypothesis and are given negative weights. If a flash did occur, then more of the positively weighted impulses are likely to occur, and fewer negatively weighted ones, so that the resultant weighted sum is larger than would occur after no flash. Therefore, the larger the weighted sum, the more likely it is that a flash did occur. The effect of the filter is to transform a nerve message, in which information is distributed over a time interval of the order of 100 msec., into a signal at a single instant of time which contains all the useful information of the nerve message. This new variable can then, according to its magnitude, give rise to a motor report of what was seen. The design of this filter is based on experimentally analyzed statistical properties of single optic nerve fiber discharges in

the cat. It will be shown that this filter can be used to analyze efficiently the stimulus information in a single nerve fiber message in three cases of visual detection: presence or absence of flash, time of occurrence of flash, and intensity of flash.

List of Principal Symbols

$f(t)$ or $f(t; w)$	frequency function
$g(t)h(w)$	$\ln f(t; w)$ for case of intensity detection
G_1	$\int_0^{t_N} g(t) dt$
G_2	$\int_0^{t_N} [g(t)]^2 dt$
I	flash intensity
$L(w)$ or $L(t_s)$	likelihood of w or t_s , respectively
N	number of impulses in message
$P(s)$	distribution of s
$P(t_n; t_{n-1}, w)$	conditional probability distribution of t_n , given t_{n-1} and w
R	likelihood ratio
s	impulse interval duration
t	time
t_n	time of n th impulse
t_s	variable time of stimulus
T	duration of response
T'	duration of period within which flash is presented
$u(t)$	integral of frequency function
w	stimulus intensity
a, k, k', K	constants

II

A STATISTICAL MODEL OF THE DISCHARGE

Before any detailed treatment of the problem can be made, a mathematical model of the ganglion cell discharge is required. The model must have statistical properties like those of the discharge, but it must also be simple enough to manipulate mathematically. A model which is believed to be a satisfactory compromise between these two requirements has been found.

The time of occurrence of each impulse in a ganglion cell depends statistically on the times of occurrence of the preceding impulses and on the previous stimuli. The latter effect can be eliminated, for the moment, by assuming a zero or constant background illumination, and the resulting discharge will be called the *maintained discharge*. The mathematical model designed on this basis will later be modified to include the effect of an added flash of light. The following properties of the maintained discharge were found experimentally (Kuffler, Barlow, and FitzHugh, 1957). (1) The average frequency

is approximately constant over periods of the order of several minutes. (2) The probability distribution of impulse interval duration (s) can be fitted satisfactorily by the gamma distribution (Pearson's type III; Kendall, 1945):

$$p(s) ds = \frac{k^a s^{a-1} e^{-ks}}{\Gamma(a)} ds \quad (1)$$

$$k > 0, \quad a \geq 1, \quad 0 \leq s < \infty$$

For four out of five samples of discharge analyzed, a was in the range from

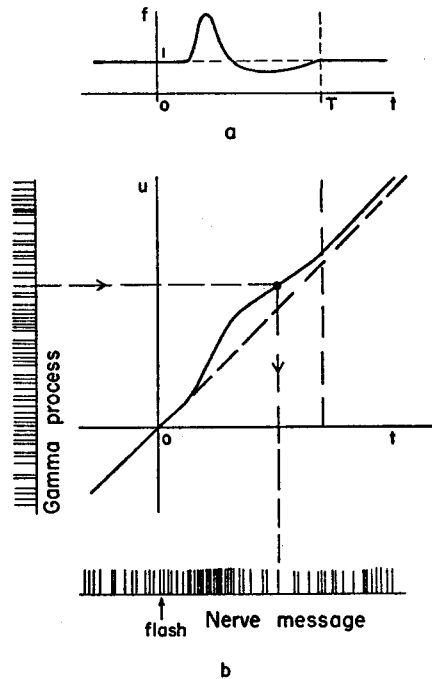


FIG. 1. Diagram of a statistical model of the optic nerve fiber discharge in response to a flash of light on the retina. *a*, a typical frequency function $f(t)$ following stimulus at $t = 0$. *b*, graph showing $u(t)$, the integral of $f(t)$. The impulses in a random gamma process (left) erected along the u -axis, are projected horizontally to the right to meet the $u(t)$ curve, and then vertically down to form the nerve discharge (bottom).

1.8 to 4.1 and k in the range from 0.07 to 0.16 msec.⁻¹ (3) The first serial correlation coefficient between the values of successive intervals was between -0.1 and -0.2; the second and higher order serial correlation coefficients approached zero. Since these correlation coefficients are fairly small, they will be neglected.

The model to be adopted for the maintained discharge consists of a sequence of identical impulses, with the intervals between impulses distributed according to equation (1), and successive intervals statistically independent. Such a model of the maintained discharge will be called a *gamma process*. If $a = 1$, the gamma process becomes a Poisson process (Feller, 1950), which, however, does not represent the data considered here very well. A stimulus flash causes momentary changes in average impulse frequency. In Fig. 1 *a*, t is time and $f(t)$ will be called the *frequency function* of the stimulus. $f(t)$ may be thought of as the ratio of the impulse frequency at any time to the maintained frequency, but the idea of an instantaneous "frequency" must be made more definite. Think of $f(t)$ for the moment as being simply a basic property of the system; its effect on the discharge will be shown as follows. $f(t)$ is a positive, continuous function, differing from unity only for the duration T of the response following the flash. The exact shape of $f(t)$ is not important here, but that shown in Fig. 1 is of a common type, consisting of an increase of frequency or "burst," followed by a decrease, or "pause." Let $u(t)$ be the integral of $f(t)$:

$$u(t) = \int_0^t f(x) dx, \quad u'(t) = f(t). \quad (2)$$

In Fig. 1 *b*, u is plotted against t . Now construct an imaginary gamma process having u as time variable, *i.e.* u_n is the time of occurrence of the n th impulse, and $u_{n+1} - u_n$ is distributed according to (1). Such a typical gamma process is sketched along the left border of Fig. 1 *b*. Each impulse of this gamma process is projected horizontally to the curve of $u(t)$, and then vertically downwards to locate the corresponding impulse in the nerve message erected along the t -axis. Since the nerve message as constructed in this way is formed by a distortion of the time axis of a gamma process, it will be called a *distorted gamma process*. The momentary frequency, or rate at which the process unfolds in real time t , is proportional to $u'(t) = f(t)$. If the stimulus were repeated a large number of times, $f(t) dt = du$ would be proportional to the average number of impulses of the nerve message occurring in the time interval dt . From this point of view, the average number of impulses in an interval du of the gamma process would be $(k/a) du = (ku'/a) dt = (kf/a) dt$, since k/a is the average frequency of the gamma process (1). This, however, is the same as the average number of impulses in the nerve message during the corresponding interval dt , and $kf(t)/a$ is therefore the frequency of the distorted gamma process at time t , when averaged over many repetitions of the same stimulus. Such average frequencies were calculated approximately from experimental data (FitzHugh, 1957), as the number of impulses in successive 10 msec. periods, averaged over the responses to 10 stimuli. The resulting curves of "average frequency," if made with smaller time periods and

with more repetitions of the stimulus, would approach the average maintained discharge frequency times $f(t)$. Therefore $f(t)$ is an experimentally measurable property of the nerve fiber and the stimulus used. $f(t)$ depends also on stimulus intensity, and it was found that the effect of an increase of intensity was to increase the amplitude of $[f(t) - 1]$ without otherwise changing its general shape very much.

The detailed physiological mechanisms in the retina responsible for the statistical properties of the discharge, as just described, are unknown. It still remains as a problem in sensory physiology to explain, in terms of the electrical properties and interactions of retinal neurons, how discharges with these statistical properties are generated. However, this paper is concerned with a different problem, namely what kind of a central neural receiver would theoretically be required to extract the maximum amount of information from such a discharge.

III

THE ANALYSIS OF MESSAGES

A. A Likelihood Filter

The mathematical model just proposed provides a starting point for designing a device to analyze most effectively the messages in an axon. In any communication problem involving loss of information due to noise, there are various possible messages which can be sent through the communication system. Any of these will be distorted in a statistically unpredictable manner, so that in general, it is not possible to reconstruct the message originally sent with certainty from the message actually received. The probability that the received message would occur as a result of a given message sent is known as the likelihood of the message sent. Several methods of analysis of a received signal have been proposed, all of which are based on a comparison of the likelihoods of the various possible messages sent. The first stage in an ideal analyzing device for nerve messages is, therefore, a receiver which computes these likelihoods from the received message. The second step, that of analyzing the likelihood values in an attempt to reconstruct the original stimulus signal, depends on the particular (arbitrary) method of inference chosen, for example, the well known maximum likelihood method of R. A. Fisher, the likelihood ratio criterion of Neyman and Pearson (Cramér, 1951), the construction of the posterior distribution (Woodward, 1953), the maximum expected value criterion and other tests (Peterson, Birdsall, and Fox, 1954). The choice of a method of analysis of the likelihoods depends on how the information is to be used rather than on the properties of the messages themselves, and will not be considered in detail here. This paper will deal principally with the first step of the analysis, the computation of likelihoods,

which is common to all the above methods, but the maximum likelihood solution will also be given in each case considered.

Let t_n be the time of occurrence of the n th impulse in an axon message, w the stimulus intensity, and $P(t_n; t_{n-1}, w)$ the conditional probability distribution of t_n , given t_{n-1} and w . Then the likelihood function $L(w)$ is defined as follows (Cramér, 1951):—

$$L(w) = \prod_{n=1}^N P(t_n; t_{n-1}, w)$$

in which the product is taken over all impulses in the message.

From the assumptions of the previous section,

$$\begin{aligned} P(t_n; t_{n-1}, w) dt_n &= p(u_n - u_{n-1}) du_n \\ &= p(u_n - u_{n-1}) u'(t_n) dt_n \\ P(t_n; t_{n-1}, w) &= \frac{k^a (u_n - u_{n-1})^{a-1} e^{-k(u_n - u_{n-1})}}{\Gamma(a)} f(t_n; w) \end{aligned}$$

$$\begin{aligned} \ln L(w) &= \sum_{n=1}^N \ln P(t_n; t_{n-1}, w) \\ &= N[a \ln k - \ln \Gamma(a)] \\ &\quad + \sum_{n=1}^N [(a-1) \ln (u_n - u_{n-1}) - k(u_n - u_{n-1}) + \ln f(t_n; w)] \end{aligned} \quad (3)$$

(\ln denotes the natural logarithm. $f(t; w)$ is the same as $f(t)$ introduced earlier, except that its dependence on w as a parameter is made explicit.) By the theorem of the mean,

$$u_n - u_{n-1} = (t_n - t_{n-1}) u'(t_n^*) = (t_n - t_{n-1}) f(t_n^*; w)$$

in which

$$t_{n-1} \leq t_n^* \leq t_n$$

Equation (3) becomes:

$$\ln L(w) = NK + \sum_{n=1}^N [(a-1) \ln (t_n - t_{n-1}) + (a-1) \ln f(t_n^*; w) + \ln f(t_n; w)] - k(u_N - u_0) \quad (4)$$

in which K is a constant.

To simplify (4), make the approximation

$$f(t_n^*; w) \doteq f(t_n; w)$$

Then

$$\ln L(w) \doteq NK + \sum_{n=1}^N [(a-1) \ln (t_n - t_{n-1}) + a \ln f(t_n; w)] - k(u_N - u_0) \quad (5)$$

The error in this approximation (5) is e' (using the symbol $f(t)$ again for simplicity):

$$e' = (a - 1) \sum_{n=1}^N [\ln f(t_n^*) - \ln f(t_n)]$$

Let

$$\begin{aligned} e'' &= (a - 1) \sum_{n=1}^N [\ln f(t_n^*) - \ln f(t_{n-1})] \\ e' - e'' &= (a - 1) \sum_{n=1}^N [\ln f(t_{n-1}) - \ln f(t_n)] \\ &= (a - 1) [\ln f(t_0) - \ln f(t_N)] \end{aligned}$$

If N is taken to be large enough, then t_n will be almost always greater than T , and since $f(t_0) = f(t_N) = 1$, $e' = e''$, and

$$e' = \frac{e' + e''}{2} = (a - 1) \sum_{n=1}^N \left\{ \ln f(t_n^*) - \frac{1}{2} [\ln f(t_{n-1}) + \ln f(t_n)] \right\}$$

For a sufficiently smooth $f(t)$, the second term inside the braces may be considered as an interpolated approximation to the first term; if the difference between the first and second term is always less in absolute value than ϵ , then

$$|e'| < (a - 1)N_1\epsilon,$$

in which N_1 is the number of impulses lying in the interval between $t = 0$ and T , during which $f(t) \neq 1$. Usually $|e'|$ will be less than this; since some of the terms of the summation will be positive and some negative, they will tend to cancel each other. In any specific case the error of the approximation could be estimated from a few random samples.

In order to reconstruct the stimulus by any of the methods mentioned above, it is necessary to compute $L(w)$ from the nerve message, and to compare $L(w)$ for all possible values of w . Three cases of stimulation will be considered.

B. Detection of the Presence of a Known Flash

This is the case of the "yes-no choice" experiment used by Blackwell (1953) and by Tanner and Swets (1954) for measuring visual thresholds in man. In this experiment, the subject must report whether or not a flash of light occurred at a certain instant (signalled audibly) and in a specified position in the visual field. He knows that the relative probabilities of a flash and a blank are equal, and that the flashes will all be of a fixed intensity (I). The stimulus intensity w equals zero for a blank and I for a flash. For $w = 0$, $f(t) \equiv 1$, $u(t) \equiv t$. From (4) and (5),

$$\ln L(0) = NK + \sum_{n=1}^N (a-1) \ln (t_n - t_{n-1}) - k(t_N - t_0)$$

$$\ln L(I) = NK + \sum_{n=1}^N (a-1) \ln (t_n - t_{n-1}) + a \sum_{n=1}^N \ln f(t_n; I) - k(u_N - u_0)$$

Since w has only two possible values, 0 and I , all that is needed for the purpose of analysis is the value of the likelihood ratio $R = L(I)/L(0)$:

$$\begin{aligned} \ln R &= \ln L(I) - \ln L(0) \\ &= a \sum_{n=1}^N \ln f(t_n; I) - k[(u_N - t_N) - (u_0 - t_0)] \end{aligned}$$

Choose the zero impulse to be the last one before the stimulus at $t = 0$, and let N be indefinitely large, so that $t_N > T$ nearly always. Then it appears from Fig. 1 that $u_0 = t_0$; and $k(u_N - t_N)$ is almost always equal to

$$k[u(T) - T] = k',$$

so that

$$\ln R = a \sum_{n=1}^N \ln f(t_n; I) - k' \quad (6)$$

Because $\ln f(t; I)$ is different from zero only for $0 < t < T$, only the impulses occurring in that period will contribute to $\ln R$, no matter how large N is. Of the two terms on the right hand side of (6), only the first varies statistically, k' being constant for a fixed value of I .

Expression (6) could be used to design a linear electrical filter which will automatically compute $\log R$ if the nerve message is fed into it. Assume that the output at time t of the filter to a single input impulse at $t = 0$ is

$$[a \ln f(T - t; I)].$$

Fig. 2 shows how the shape of this function is related to the frequency function. From the form of the filter output following an impulse at zero time, it can be seen that the output following an impulse occurring at the time of the expected peak of frequency will be displaced to the right so as to have its maximum at time T . Thus a large filter output at T is evidence that many impulses have occurred during the expected burst and will support the hypothesis that a stimulus did occur at time zero. More precisely, for an input impulse at time v , the output is $[a \ln f(T - t + v; I)]$ and if the input is a sequence of impulses at times t_1, \dots, t_N , the output is

$$a \sum_{n=1}^N \ln f(T - t + t_n; I) \quad (7)$$

The output at $t = T$ will then be

$$a \sum_{n=1}^N \ln f(t_n; I) \quad (8)$$

from which the likelihood ratio can be found by (6). The design of the filter requires a knowledge of $f(t; I)$ and of k' , and is therefore "matched" to a particular sensory fiber and to a particular stimulus. For the yes-no choice experiment, all that is necessary is to choose some criterion value R' of R (according to the method of analysis used) and to report a flash seen when-

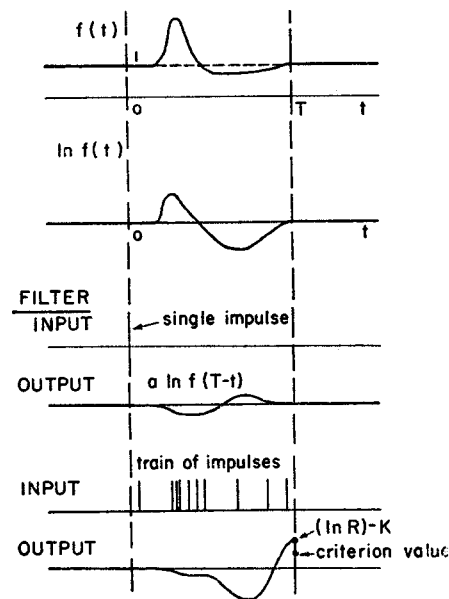


FIG. 2. Diagram of the properties of a likelihood filter designed to analyze the nerve discharge. The output of the filter to a single nerve impulse at $t = 0$ is $a \ln f(T-t)$; this curve is obtained by reversing the time axis of $\ln f(t)$ in the interval $t = 0$ to T . The output at time T of the filter to a train of impulses is $(\ln R) - K$, in which R is the likelihood ratio and K a constant. If this quantity exceeds the criterion value, a flash is reported seen.

ever $R > R'$ (or $\ln R > \ln R'$). For the maximum likelihood method, $R' = 1$, $\ln R' = 0$.

C. Detection of the Time of a Known Flash

The same filter can be used in a more complicated situation, in which a stimulus of fixed intensity is presented at an unspecified time to the subject, who must decide *when* it occurred.

Let t_s be the time of the stimulus, which is specified to occur in the interval $0 < t_s < T'$, in which $T' \gg T$. The frequency function corresponding to this stimulus is $f(t - t_s)$. The likelihood $L(t_s)$ of the flash as a function of its time of occurrence is given by an expression similar to (5):

$$\ln L(t_s) \doteq NK + \sum_{n=1}^N [(a-1) \ln (t_n - t_{n-1}) + a \ln f(t_n - t_s)] - k(u_N - u_0) \quad (9)$$

N is taken large enough so that $t_N > T' + T$ nearly always. The first term in the square brackets is independent of t_s ; so are u_N and u_0 , since

$$\begin{aligned} u_0 &= t_0 & 0 < t_s < T' \\ f(t) &= 1 \begin{cases} t < 0 \\ t > T \end{cases} & t_N - t_s > t_N - T' > T \\ u_N &= \int_0^{t_N} f(t - t_s) dt = \int_{-t_s}^{t_N - t_s} f(t) dt = \int_0^T f(t) dt + t_N - T \end{aligned}$$

Therefore,

$$\ln L(t_s) \doteq a \sum_{n=1}^N \ln f(t_n - t_s) + K' \quad (10)$$

in which K' depends on the t_n 's but not on t_s .

From (7), the output of the filter at time $t_s + T$ is equal to the first term of (10) and the second term of (10) is constant for a given nerve message. Except for an added constant, therefore, the filter gives a continuous record of likelihood with a constant lag T , and from this record the time of occurrence of the flash can be estimated. If the *a priori* probability of the flash is constant through the interval from $t = 0$ to T' , the maximum likelihood method is applicable and the best estimate of t_s is simply the time of the maximum output minus T .

D. Detection of the Intensity of a Flash

In this case the flash is presented at a specified time, but its intensity w can have values over a continuous range; a more complex analyzer will be required than for the previous cases. The nerve message could be analyzed by passing it through a large number of likelihood filters, each one matched to a particular value of w . These values of w would be spaced as closely as necessary to give the desired degree of resolution in estimating w . Then, for the maximum likelihood method of analysis, that value of w corresponding to the filter with the largest output at time T after the stimulus, would be chosen. However, a single likelihood filter will serve near threshold if certain assumptions are satisfied. Let

$$\ln f(t; w) = g(t)h(w) \quad (11)$$

in which $h(w)$ is an increasing differentiable function, $h(0) = 0$, and $g(t)$ is continuous and different from zero only when $0 < t < T$; $g(t)$ is positive during a burst and negative during a pause. This assumption agrees reasonably well with experimental frequency functions (FitzHugh, 1957). Then from (2) and (5):

$$\begin{aligned}\ln L(w) &\doteq a \sum_{n=1}^N g(t_n) h(w) - k \int_0^{t_N} \exp [g(t) h(w)] dt + K'' \\ \frac{d}{dw} \ln L(w) &\doteq h'(w) \left\{ a \sum_{n=1}^N g(t_n) - k \int_0^{t_N} g(t) \exp [g(t) h(w)] dt \right\}\end{aligned}\quad (12)$$

K'' depends on the t_n 's but not on w . If we further assume that $g(t) \cdot h(w)$ is always small compared to one (this limits the range of w), then

$$\begin{aligned}\int_0^{t_N} g(t) \exp [g(t) h(w)] dt & \\ \doteq \int_0^{t_N} g(t) [1 + g(t) h(w)] dt & \\ = \int_0^{t_N} g(t) dt + h(w) \int_0^{t_N} [g(t)]^2 dt & \\ = G_1 + G_2 h(w) &\end{aligned}\quad (13)$$

in which G_1 and G_2 are the integrals of g and g^2 from 0 to t_N .

The expression in braces in (12) is a decreasing function of w and can be zero at only one value of w . Since $h'(w)$ is positive, $d/dw \ln L(w)$ can be zero at only that same single value of w , and $\ln L(w)$ has a maximum there. The maximum likelihood value of w is defined by setting the derivative of $\ln L(w)$ equal to zero. From (12) and (13):

$$\begin{aligned}a \sum_{n=1}^N g(t_n) &\doteq k[G_1 + G_2 h(w)] \\ h(w) &\doteq \frac{1}{G_2} \left[\frac{a}{k} \sum_{n=1}^N g(t_n) - G_1 \right]\end{aligned}\quad (14)$$

But the expression on the right differs only by an added constant and a scale factor from the output of a likelihood filter (8), as can be seen by choosing a reference intensity w_0 . From (11) and (14):

$$\begin{aligned}g(t) &= \frac{\ln f(t; w_0)}{h(w_0)} \\ h(w) &\doteq \frac{1}{G_2} \left[\frac{a}{k h(w_0)} \sum_{n=1}^N \ln f(t_n; w_0) - G_1 \right]\end{aligned}\quad (15)$$

The maximum likelihood value of w is that value of w for which equation (15) is satisfied. $h(w)$ could be found from the output of the likelihood filter by subtraction and multiplication, and then w obtained by passing the resulting signal through a non-linear filter giving as output the inverse function of $h(w)$. Since $h(w)$ is an increasing function, this inverse operation is single valued; therefore a device could in principle be built to estimate from a nerve fiber message the maximum likelihood intensity of a near threshold stimulus, if the assumptions mentioned hold.

IV

DISCUSSION

The use of a frequency function to represent the distortion of the time scale of the maintained discharge was found to be the simplest way to introduce the effect of a stimulus, but this "time-distortion process" contains some inherent assumptions which may not correspond to physiological reality. Since the frequency function $f(t)$ is determined by the stimulus and in turn determines the statistical properties of the discharge, it forms an intermediate step in the model, separating a causally determined process from a statistical one. In the first process the message is coded without loss of information into a form suitable for neural transmission, namely $f(t)$, the running average frequency of impulses, while the second introduces, in the impulse intervals, the statistical variations which destroy information. However, it is not claimed that these two stages correspond to separate physical processes in the retina; they have been separated only to simplify the theoretical analysis. It would, of course, be desirable to test in detail the statistical properties of the distorted gamma process against those of the actual fiber discharge following a flash. Unfortunately this would be much more difficult than for the plain gamma process representing the maintained discharge, since to sample adequately the properties of a brief, time variable response to a stimulus occurring once a second would require the analysis of a long record of the discharge, lasting for many minutes. But slow changes of threshold or average frequency over this time would probably make the results useless. Finally, the complex processes in the retina may not be subject simply to a uniform speeding up or slowing down, following a stimulus, as is implied by the use of a single frequency function.

The principal result of this analysis is the idea of a flexible neural analyzer which is matched to any stimulus expected by the subject, instead of one fixed all purpose device. Such an adaptable analyzer is moreover suggested by the effect of experience and motivation on visual thresholds in human subjects (Hecht, Shlaer, and Pirenne, 1942; Blackwell, 1953).

The theoretical analyzer described here is the most efficient one for extracting information from the nerve message, but the actual central neural analyzer may

not work on the same principle. However, the high efficiency of visual detection near threshold suggests that it may be worth while to look for a mechanism of this sort in the brain. If noise in the optic nerve messages is an unavoidable result of increasing the sensitivity and amplification of the retina, genetic changes tending to increase the efficiency of statistical analysis of these noisy messages would have survival value.

The analyzing process does not necessarily take place all at one site in the brain. The results of experiments on the excitability cycle of ganglion cells in the lateral geniculate suggest the possibility that they function as likelihood filters, each of which has postganglionic impulse frequency as its output variable. It has been pointed out above that impulse frequency is not a continuous function of time, except when averaged over many discharges, but it may be transformed, approximately, into such a function by a suitable mathematical or physical filtering process which counts or averages impulses over a short interval of time past. Such a smoothing filter would differ from the likelihood filter by having a much briefer and less complicated response to a single impulse as input. With this reservation, impulse frequency will be considered below as a possible output variable of a likelihood filter.

Marshall and Talbot (1941) and Marshall (1949), recording from the lateral geniculate of the cat, found that a single volley in the optic nerve of the anesthetized cat was followed by a period of supernormal excitability, as evidenced by summation or recruitment, lasting about 30 msec., followed by a subnormal phase lasting for seconds, with a peak at 50 to 70 msec. Bishop, Jeremy, and McLeod (1953) found that ganglion cells in the dorsal nucleus of the lateral geniculate of lightly anesthetized cats responded repetitively to a single volley of impulses in the optic nerve. They attributed this phenomenon to prolonged internuncial activity and suggested that the nucleus may function as an integrating center rather than simply as a relay station for optic nerve impulses. The repetitive activity disappeared after a previous tetanization of the optic nerve, showing that the excitatory effect of a presynaptic volley is followed by a later inhibition. Thus the excitability changes of the postsynaptic network following a single presynaptic volley are qualitatively similar to the output of one possible type of likelihood filter. It is true that for a presynaptic tetanization of as low a frequency as 2/sec. the inhibitory effect prevailed and eliminated the repetitive response, but the experiments were done under anesthesia, and a deeper anesthesia abolished all repetitive activity. It is therefore possible that with no anesthesia at all, the excitatory component would be relatively stronger, and that the temporal pattern of discharge from the lateral geniculate represents, in the form of a frequency modulated train of impulses, the output of a likelihood filter. This idea might be tested on an unanesthetized preparation as follows. Either allow the maintained discharge from the intact eye to supply optic nerve activity, or tetanize the optic nerve at a frequency of 20 to 80/sec.,

with the eye removed. Record from a single ganglion cell in the lateral geniculate. Add a single impulse volley to the optic nerve activity through stimulating electrodes (or, add a brief, high frequency burst, to increase the effect). The time course of postsynaptic impulse frequency (minus the constant maintained postsynaptic frequency) represents the output of the "filter" to a single added impulse as input. It is necessary to add the single impulse to a maintained discharge, instead of applying it alone, in order to allow for possible large scale non-linearities by working at the physiological "operating point" of the system. Then, by using the formulas developed in this paper (*i.e.*, by taking the inverse logarithm and reversing the direction of time in the output function), one could reconstruct the frequency function to which the postsynaptic cell, acting as a likelihood filter, is matched. It would also be necessary to test whether the filter were locally linear, since the likelihood filter is assumed to be linear. (Compare the behavior of a vacuum tube, which can show a satisfactory local linearity in spite of large scale non-linearities.) For this it would be necessary to add two or more impulses at various times to the maintained discharge, and find out whether the resulting curve of change of frequency *versus* t is the same as that predicted by adding together the separate curves corresponding to each added impulse. Also, if a tetanization is applied artificially to the optic nerve, impulses could be subtracted from the discharge, rather than added to it.

Of course, even if such experiments showed that the ganglion cells in the lateral geniculate had properties like those of a likelihood filter, it would still be necessary to test their behavior following visual stimulation near threshold. Briefly, one would have to find out whether the frequency of such a cell, evaluated at some fixed time following a flash, provided a sensitive "index of response," as discussed in detail by FitzHugh (1957). The nerve discharges could probably best be analyzed with an electronic device for displaying impulse intervals on the screen of a cathode ray oscilloscope, as described by MacNichol and Jacobs (1955). The index of response would be provided by a burst of impulses appearing after a stimulus and having a higher signal-to-noise ratio and a briefer duration than the discharges in the optic nerve fibers. Its function would be to transform by temporal integration (not in the mathematical but in the physiological sense) the variations in frequency spread over many impulses into a more distinct postsynaptic frequency change having a shorter duration and containing only the useful information, in the form of the likelihoods of possible alternative stimuli, of the presynaptic message.

If a likelihood filter could not be found in the geniculate, it is possible that one could be found in the cortex, by experiments similar to those just described.

As shown earlier, the likelihood filter must be matched to the frequency function resulting from a particular stimulus form. Any experimental investigation of such a mechanism must therefore take into account the possible variability of its properties, so as to detect different stimuli, as the result of higher

nervous activities such as motivation and experience. The properties of a likelihood filter in the lateral geniculate, for instance, might depend on the activity of descending fibers from the cortex.

An important restriction of this paper is the consideration of the messages in only a single optic nerve fiber. The process leading to a subjective impression of a stimulus actually involves the simultaneous analysis of many axon messages, in which the contribution of one axon is affected by the messages in the other axons, leading to the perception of spatial patterns as well as of light intensities. Nevertheless the present analysis may be applicable when the stimulus is a large spot and many neighboring retinal ganglion cells are behaving similarly.

The likelihood filter, with its weighting function (response to an impulse) equal to $\ln f(T-t)$, resembles the filter matched to a radar pulse described by Woodward (1953) and others. These radar filters have a weighting function which is proportional to the expected signal itself, rather than the logarithm, but even this difference is mathematically reasonable, since $\ln f(t)$ has the theoretical range $(-\infty \text{ to } \infty)$ while $f(t)$ has the range $(0 \text{ to } \infty)$ as does the radar message.

In an experimental paper (FitzHugh, 1957), the index of response was taken as the number of impulses occurring within a certain critical period following the flash. This rather rough and arbitrary procedure appears more reasonable in the light of the present results. The index used can be considered to be proportional to the output of a hypothetical likelihood filter in which the smooth function $\ln f(t)$ is approximated by a single rectangular pulse and is satisfactory only to the degree of this approximation. A more accurate way to analyze such records is provided by the present paper, namely the calculation of likelihoods from a single nerve fiber message and from the experimental frequency function obtained from an ensemble of such nerve messages. An electric filter might, in fact, be built to analyze messages during an experiment, but would probably not be practical unless a rapid way to measure the frequency function of the unit and to adjust the response of the filter to match it could be found.

The questions of what features of a noisy message in an axon are most important for sensory communication, and how the brain might operate on this message so as to extract the most information from it, have previously been studied for the infrared receptor of the rattlesnake by Bullock (1956). Bullock's suggested mechanism for analyzing nerve fiber messages is concerned principally with correcting for slow drift in the maintained frequency, which in the present paper has been assumed constant. On the other hand he is less specific about the precise time course of the transient frequency change in the response, and simply specifies a mechanism "integrating the frequency over some short time just past." A more complete model could undoubtedly be worked out which would include both aspects of the problem.

The statistical approach used in this paper is applicable only to sensory

systems in which the principal limitation to detection is noise in the form of fluctuations in the time of occurrence of impulses. The maintained discharge from the eye of *Limulus* (Hartline, Wagner, and MacNichol, 1952) and from the stretch receptor of the crayfish (Kuffler, 1954; Eyzaguirre and Kuffler, 1955) under constant stimulation, for instance, are much more regular than in the cat, while statistical studies of responses near absolute threshold in *Limulus* are concerned with the presence or absence of single impulses, in the absence of maintained activity (Hartline and MacDonald, 1947). Different methods of analysis may therefore be more appropriate for other types of sensory messages.

This paper has been written in the belief that the implications of the experimental finding of statistical variations in optic nerve messages should be theoretically explored. It attempts to provide a basis for investigating the efficiency of analysis of nerve messages in the visual system by comparing it with a theoretical analyzing system having the maximum possible efficiency. The specific suggestions regarding possible analyzing mechanisms in the lateral geniculate, in particular, will probably turn out to have been quite naive, but it is hoped that this paper may stimulate productive application of communication theory to the largely unknown processes of detection and integration in the sensory nervous system.

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