

## The Theoretical Channel Capacity of a Single Neuron as Determined by Various Coding Systems\*

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The information channel capacity of a model neuron with a fixed refractory period  $\delta$  has been calculated for optimum continuous time interval coding. Two types of noise perturbations have been considered, a Gaussian probability distribution and a rectangular distribution of the time of occurrence of the response to a stimulus. Laboratory measurements indicate a Gaussian distribution with a standard deviation of latency  $\sigma$ , of about  $5 \mu\text{sec}$  gives the best fit to an actual nerve fiber. This results in a maximum information transmission of slightly over 4000 bits per second. The results are compared with the discrete theory of MacKay and McCulloch.

### LIST OF SYMBOLS

- $\delta$  Dead time of neuron
- $\sigma$  Minimum discriminable time interval
- $a$  Average input rate in pulses per second of a Poisson shower
- $q(\tau)$  Probability frequency distribution of perturbing "noise"
- $\epsilon$  Width of square distribution function
- $H$  Information per signal
- $C$  Channel capacity
- $p(x)$  Probability frequency distribution of input signal
- $p(y)$  Probability frequency distribution of received signal
- $p(x,y)$  Joint probability distribution function

W. S. McCulloch and D. MacKay (1952) have calculated the channel capacity of a "neuronal link" assuming two types of coding, namely, pulse code modulation and pulse interval modulation. In the former type, time is supposedly divided into equal intervals. Each interval contains a signal, which in this case is either the presence or the absence of a

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pulse (the neuron either fires or does not fire). The channel capacity associated with this coding is defined as the maximum rate of information transmission possible under this interpretation of signal. Obviously the greatest average information per signal will be attained when the occurrence or nonoccurrence are equally probable and statistically independent, that is, at the rate of one bit per signal. If this duration is taken as  $\delta$ , the "dead time" of the system, which includes the time of its firing and of the period of absolute refractoriness which follows, then the time rate of information transmission has the maximum value of  $1/\delta$  bits/sec, and this can be taken as the channel capacity associated with pulse code modulation.

In pulse interval modulation, the situation is different. Here the information is supplied not by the answer to the question *whether* the neuron fires in a quantized time interval of fixed length, but to the question *when* it fires on the time axis. If the moment of firing could be ascertained precisely (as a "real number"), the average amount of information per signal would, of course, be infinite, and its calculation would be meaningless. However, there is always some error in determining the exact moment of firing, and this makes the amount of information finite. Now there are two limiting factors to the rate of transmission, namely, the degree of precision in establishing the time of firing and the length of the refractory period.

In pulse interval modulation, McCulloch and MacKay postulate a smallest discriminable time interval. As in pulse code modulation, the time is considered quantized. In the case of our idealized neuron, there must be two of these basic time intervals, namely, the dead time  $\delta$ , which has the same meaning as before, and the minimal discriminable interval  $\sigma$ . Signals can now be interpreted as the numbers of  $\sigma$ 's which elapse between successive firings. In other words, we may still view the system as pulse-code modulated but now the duration of the two signals "Yes" and "No" are not of equal length. The "Yes" signal has duration  $\delta$ , and the "No" signal has duration  $\sigma$ .

If no further restrictions are imposed, the channel capacity of this system can be calculated in a straightforward manner (Shannon, 1949).

Let  $N(t)$  be the number of different messages which can be sent in time  $t$ . Then one must have:

$$N(t) = N(t - \delta) + N(t - \sigma) \quad (1)$$

We can, without loss of generality, let  $\delta = 1$ ,  $\sigma = 1/k$ . For large values

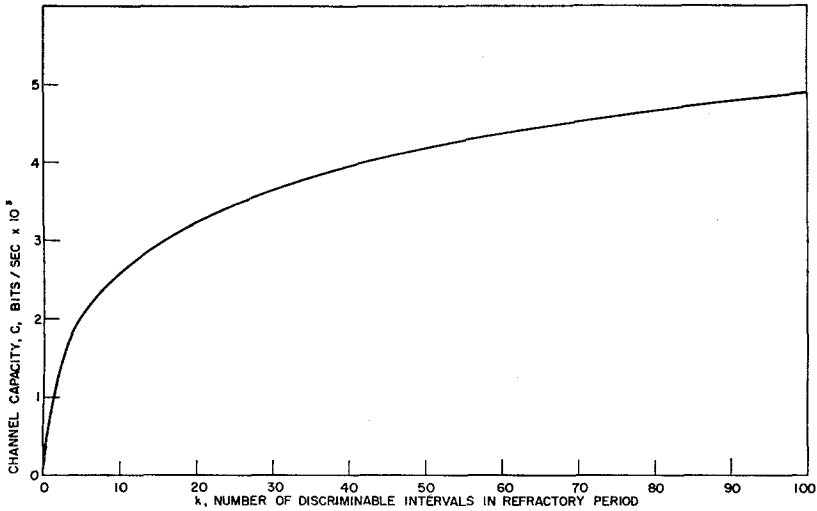


FIG. 1. The calculated channel capacity of a model neuron with a refractory period of 1 msec, using discrete information theory with time quantized into  $1/k$  units of the refractory period.

of  $t$ , the solution of the resulting difference equation is asymptotically equal to  $x^t$ , where  $x$  is the largest real root of the equation:

$$x^{-1} + x^{-1/k} = 1 \quad (2)$$

Thus, the information capacity will be given by  $\log_2 x$  bits per unit time. Therefore, for this system of coding, the information capacity is given by:

$$C = \log_2 x(k) \quad (3)$$

Figure 1 shows the plot of  $C$  as a function of  $k$ , where  $\delta$  has been taken as the unit of time.

In this and in subsequent models, we shall be interested also in the actual rate of information output of the single neuron when a Poisson shower of stimuli impinges upon it. The Poisson shower is characterized by the function  $ae^{-at}$ , which gives the frequency distribution of  $t$ , the time of occurrence of the next stimulus. Moreover, the Poisson shower has the property that the above-mentioned frequency distribution is independent of the choice of the reference moment.

Assume, then, that such a shower impinges on our neuron and take for the origin of the time axis the moment when the refractory period  $\delta$ ,

following a firing, has just elapsed. The time is assumed to be quantized in intervals of length  $\sigma$  and we need to compute the average number of time intervals until the next firing. Since the probability of a "No" response in an interval  $\sigma$  is given by  $e^{-a\sigma}$ , the average number of consecutive "No" responses in an infinite sequence will be given by  $e^{-a\sigma}/(1 - e^{-a\sigma})$ . The average number of signals sent between refractory periods will be this number of "No" signals plus one "Yes" signal, or a total of

$$N = \frac{1}{1 - e^{-a\sigma}}$$

signals in all. Since the nerve will be blocked for a time  $\delta$  and live for a time  $N\sigma$  then a total of

$$\frac{N}{\delta + N\sigma} = \frac{1}{\sigma + \delta(1 - e^{-a\sigma})}$$

signals will be sent per second.

On the other hand, the information per signal can be calculated from the probability of receiving a "No" signal during the time  $\sigma$  following our time origin. Since this is  $e^{-a\sigma}$ , the information per signal can be seen to be:

$$H = a\sigma e^{-a\sigma} - (1 - e^{-a\sigma}) \log_e(1 - e^{-a\sigma}) \quad (4)$$

Combining these results, we have the information in "nits" per second.<sup>1</sup>

$$H^* = \frac{[a\sigma e^{-a\sigma} - (1 - e^{-a\sigma}) \log_e(1 - e^{-a\sigma})]}{\sigma + \delta(1 - e^{-a\sigma})} \quad (5)$$

Figure 2 shows the plot of  $H^*$  as a function of input frequency  $a$  for several values of  $\sigma$  considered as a parameter, where  $\delta$  has been set equal to 0.001 sec.

Note, however, that the capacity (3) is simply inversely proportional to  $\delta$ , but the information output is not. Keeping the value of  $\sigma$  arbitrarily at 0.05 msec,  $H^*$  is shown as a function of  $a$  for different values of  $\delta$  as a parameter in Fig. 3.

#### THE SIGNAL AS A CONTINUOUS VARIABLE

Now instead of viewing the intervals between pulses as an integral number of "smallest distinguishable intervals," consider these intervals

<sup>1</sup> One nit =  $\log_2 e$  bits. This unit and the natural base for logarithms will be used throughout our calculations.

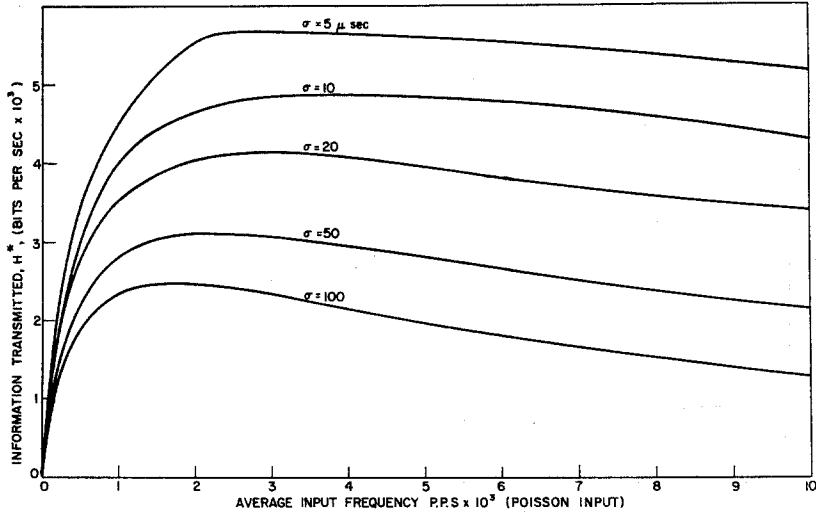


FIG. 2. The information transmitted by a model neuron as a function of average input frequency for a Poisson distribution of stimuli. Calculated by discrete information theory for different values of the least discriminable time interval,  $\sigma$ . The refractory period is fixed at 1.0 msec.

as real numbers. The impossibility of determining these numbers exactly will be represented by a perturbing function  $q(\tau)$ . Thus, if an interval is measured to be of length  $x$ , the probability that its true value departs from  $x$  by  $\tau$  is given by a probability frequency distribution  $q(\tau)$ .

As for the probability frequency distribution of  $x$  we shall take the distribution which maximizes the integral

$$-\int_0^{\infty} p(x) \log p(x) dx$$

under the constraints,

$$\int_0^{\infty} p(x) dx = 1, \quad \int_0^{\infty} xp(x) dx = 1/a \quad (6)$$

and will neglect for the time being the refractory period. That is to say we take the frequency distribution of the signals which maximizes the "relative entropy" for a given fixed average frequency. Later, we shall find the maximizing frequency under the constraint of the refractory period and thus the capacity.

The maximizing probability frequency distribution is known to be

$$p(x) = ae^{-ax} \quad (7)$$

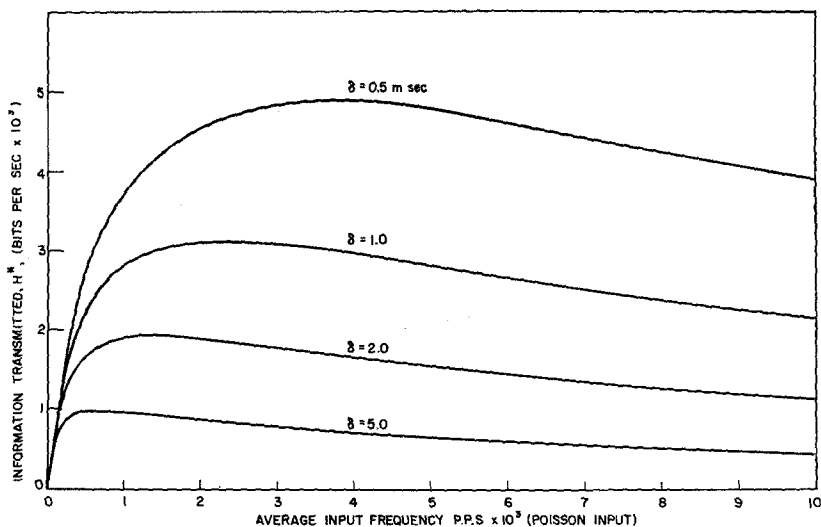


FIG. 3. Information transmitted by a model neuron as a function of average input rate with a Poisson distribution of stimuli. Calculated by discrete information theory with the least discriminable time interval fixed at 0.05 msec and the refractory period,  $\delta$ , varied from 0.5 to 5.0 msec.

that is, the probability frequency distribution of the Poisson shower of impulses.

For our "noise," that is, the perturbing function  $q(\tau)$  we take first the "square" distribution

$$\begin{aligned} q(\tau) &= 1/\epsilon \quad \text{for } |\tau| \leq \epsilon/2 \\ q(\tau) &= 0 \quad \text{for } |\tau| > \epsilon/2 \end{aligned} \quad (8)$$

That is to say, there is an uncertainty interval of length  $\epsilon$  around the apparent time of each firing.

The general formula for the information transmission of a continuous noisy channel is given (Shannon, 1949) by

$$H = \iint p(x,y) \log \frac{p(x,y)}{p(x)p(y)} dx dy \quad (9)$$

Here  $p(x)$  is the probability frequency of  $x$ , the signal sent;  $p(y)$  is the probability frequency of  $y$ , the signal received;  $p(x,y)$  is the joint probability. Obviously if  $x$  and  $y$  are independent,  $p(x,y) = p(x)p(y)$ , the logarithm and therefore the integrand vanishes, and  $H = 0$ .

The distribution  $p(x)$  is given by (7). We will calculate  $p(x,y)$  and

$p(y)$  and thus reduce the problem of calculating  $H$  to a double quadrature.

Using (5) and (6), we note that

$$\begin{aligned} p(x,y) &= \frac{a}{\epsilon} e^{-ax} & \text{if} & \quad |x - y| \leq \frac{\epsilon}{2} \\ p(x,y) &= 0 & \text{if} & \quad |x - y| > \frac{\epsilon}{2} \end{aligned} \quad (10)$$

Using this result and the fact that  $x$  must not be negative, we note that  $p(y)$  consists of three parts:

$$\begin{aligned} p(y) &= \int_0^{y+(\epsilon/2)} \frac{a}{\epsilon} e^{-ax} dx & \text{if} & \quad -\frac{\epsilon}{2} \leq y \leq \frac{\epsilon}{2} \\ p(y) &= \int_{y-(\epsilon/2)}^{y+(\epsilon/2)} \frac{a}{\epsilon} e^{-ax} dx & \text{if} & \quad y > \frac{\epsilon}{2} \\ p(y) &= 0 & \text{if} & \quad y < -\frac{\epsilon}{2} \end{aligned} \quad (11)$$

Although the value of  $x$ , the interval between successive pulses, is by definition nonnegative, the value of  $y$  may be negative as indicated in (11). This is a consequence of our formal model. In practice, of course,  $y$ , the interval measured between two successive pulses, will be nonnegative; but then, if we apply our uncertainty interval  $q(\tau)$  to infer the "true" intervals, some of these may be negative, which is to say the relative positions on the time axis of two pulses may be transposed.

For the purpose of formal calculation, the two interpretations are equivalent, and we have adopted the convention that  $x$  is nonnegative.

Performing the integrations indicated in (11), we get

$$\begin{aligned} p(y) &= \frac{1}{\epsilon} [1 - e^{-ay - a(\epsilon/2)}] & \text{for} & \quad -\frac{\epsilon}{2} \leq y \leq \frac{\epsilon}{2} \\ p(y) &= \frac{e^{-ay}}{\epsilon} [e^{a(\epsilon/2)} - e^{-a(\epsilon/2)}] & \text{for} & \quad y > \frac{\epsilon}{2} \end{aligned} \quad (12)$$

From this, it follows that our integration in (9) must be performed in two regions, defined by the following limits:

$$\begin{aligned} \text{I} \quad & 0 \leq x \leq y + \frac{\epsilon}{2}, & -\frac{\epsilon}{2} \leq y \leq \frac{\epsilon}{2} \\ \text{II} \quad & y - \frac{\epsilon}{2} \leq x \leq y + \frac{\epsilon}{2}, & \frac{\epsilon}{2} \leq y \leq \infty \end{aligned} \quad (13)$$

These are the regions in which none of the factors in the integrand of (9) vanish. Substituting the expressions for  $p(x,y)$  and  $p(y)$  into (9), canceling wherever possible, and taking the limits given in (13) into account, we now obtain:

$$H = - \int_{-(\epsilon/2)}^{\epsilon/2} \int_0^{y+(\epsilon/2)} \frac{a}{\epsilon} e^{-ax} \log[1 - e^{-ay-a(\epsilon/2)}] dx dy \\ - \int_{-(\epsilon/2)}^{\infty} \int_{y-(\epsilon/2)}^{y+(\epsilon/2)} \frac{a}{\epsilon} e^{-ax} \log[e^{-ay}(e^{+a(\epsilon/2)} - e^{-a(\epsilon/2)})] dx dy \quad (14)$$

Integrating with respect to  $x$ , this reduces to:

$$H = - \int_{-(\epsilon/2)}^{\epsilon/2} \frac{1}{\epsilon} (1 - e^{-ay-a(\epsilon/2)}) \log(1 - e^{-ay-a(\epsilon/2)}) dy \\ - \int_{\epsilon/2}^{\infty} \frac{1}{\epsilon} (e^{-ay+a(\epsilon/2)} - e^{-ay-a(\epsilon/2)}) \log(e^{-ay+a(\epsilon/2)} - e^{-ay-a(\epsilon/2)}) dy \quad (15)$$

To simplify the first integral of (15), we introduce the change of variable  $z = 1 - e^{-ay-a(\epsilon/2)}$ , which transforms this integral to

$$- \frac{1}{a\epsilon} \int_0^{1-e^{-a\epsilon}} \frac{z \log z}{1-z} dz \quad (16)$$

In the second integral we let  $z = e^{-ay}(e^{+a(\epsilon/2)} - e^{-a(\epsilon/2)})$ , which transforms that integral into

$$- \frac{1}{a\epsilon} \int_0^{1-e^{-a\epsilon}} \log z dz \quad (17)$$

Noting that the limits of the two integrals are now identical, we combine (16) and (17), obtaining

$$H = - \frac{1}{a\epsilon} \int_0^{1-e^{-a\epsilon}} \frac{\log z}{1-z} dz \quad (18)$$

It is convenient to introduce still another change of variable, namely,  $z = 1 - t$  which yields:

$$H = - \frac{1}{a\epsilon} \int_{e^{-a\epsilon}}^1 \frac{\log(1-t)}{t} dt \quad (19)$$

In spite of the singularity of the integrand at the upper limit, the integral in (19) can be easily shown to be convergent. Expressed as a



series in  $a\epsilon$ , its value is given by:

$$\sum_{j=1}^{\infty} \frac{1}{j^2} - \sum_{j=1}^{\infty} \frac{e^{-a\epsilon j}}{j^2} \quad (20)$$

The sum of the first series is known to be  $\pi^2/6$ . We obtain, therefore, as our final expression for the information transmitted by a neuron, receiving a Poisson shower of impulses of frequency  $a$ , without a refractory period:

$$H = \frac{1}{a\epsilon} \left[ \frac{\pi^2}{6} - \sum_{j=1}^{\infty} \frac{e^{-a\epsilon j}}{j^2} \right] \quad \text{nits/signal} \quad (21)$$

This channel capacity must, of course, be a function of the product  $a\epsilon$  not of each parameter independently, because it must be independent of the unit of time ( $a\epsilon$  is dimensionless).

Consider now  $H$  as a function of its single parameter ( $a\epsilon$ ). Obviously  $H(\infty) = 0$ . At the other extreme  $H(0)$  is indeterminate, since the summation in the bracket approaches  $\pi^2/6$  as  $a\epsilon$  approaches zero. We can, however, calculate  $\lim_{a\epsilon \rightarrow 0} H(a\epsilon)$  by L'Hospital's rule from (19), where both the numerator and the denominator approach zero. Differentiating both with respect to  $a\epsilon$ , we obtain:

$$\lim_{a\epsilon \rightarrow 0} H = -\log(1 - e^{-a\epsilon}) \quad (22)$$

which tends to infinity as  $a\epsilon$  tends to zero. The result is intuitively evident since  $H$  should increase as  $\epsilon$  decreases and also as  $a$  decreases (because the variance of the interval length increases with the average interval length).

Our principal concern is the rate of transmission per unit time under the restraint of a finite refractory period  $\delta$ . To introduce the refractory period, we take for our  $p(x)$  the function:

$$\begin{aligned} p(x) &= 0 & \text{for } x &\leq \delta \\ p(x) &= ae^{-a(x-\delta)} & \text{for } x &> \delta \end{aligned} \quad (23)$$

Calculation analogous to the above leads to exactly the same expression for  $H$ , which is intuitively evident since the variance of the intervals can be taken from the moment the refractory period is over. Time delays make no difference in how much information is transmitted *per signal*, provided that the probability frequency distribution of the next firing is independent of the moment chosen as the origin of time. But it

is so independent in the case of a Poisson shower; hence the result follows. However, the time rate capacity becomes, with the introduction of the refractory period  $\delta$ ,

$$C = \frac{1}{\epsilon(1 + a\delta)} \int_{e^{-a\epsilon}}^1 \frac{\log(1-t)}{t} dt \quad (24)$$

This is because the refractory period "blots out" blocks of signals of duration  $\delta$ . Accordingly the average frequency of impulses put out by the neuron is not  $a$  but  $a(1 + a\delta)^{-1}$ .

Here the parameter  $a$  can be regarded as the frequency of a Poisson shower impinging on our neuron from the outside, to which the neuron responds as a "counter" with dead time  $\delta$ . It is intuitively evident that as  $a$  becomes infinite, the limiting frequency of the response approaches  $1/\delta$  and its variance becomes infinitesimal. Therefore,  $C$  should tend to zero as  $a$  tends to infinity, as the inspection of (24) shows to be the case. On the other hand  $C$  (like  $H$ ) vanishes for  $a = 0$ . Therefore, by the continuity properties of that expression,  $C$  must have a maximum for some value of  $a$ . That is to say, given  $\delta$  and  $\epsilon$ , there is an *optimum* frequency of the impinging Poisson shower which causes the neuron to put out signals at the maximum rate of information per unit time.

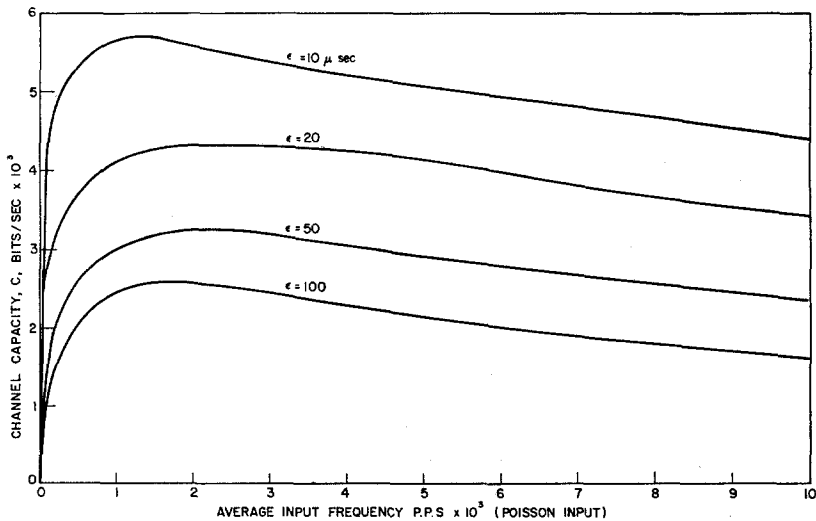


FIG. 4. The channel capacity of a model neuron calculated by continuous information theory for a rectangular noise distribution of total width  $\epsilon$ . Refractory period taken to be 1 msec.

Figure 4 shows the plot of (24) as a function of  $a$  for several values of  $\epsilon$  with  $\delta = 1$  msec.

Let the perturbation function now be Gaussian, namely,

$$q(\tau) = \frac{1}{\sqrt{2\pi}\sigma} e^{-\tau^2/2\sigma^2}$$

Then:

$$\begin{aligned} p(x,y) = p(x)p_x(y) &= \frac{ae^{-ax}}{\sqrt{2\pi}\sigma} \exp\left(-\frac{(x-y)^2}{2\sigma^2}\right) \\ &= \frac{a}{\sqrt{2\pi}\sigma} \exp\left[\frac{-x^2 + 2x(y - a\sigma^2) - y^2}{2\sigma^2}\right] \end{aligned} \quad (25)$$

The last expression can be written also as:

$$\frac{a \exp(-ay + \frac{1}{2}a^2\sigma^2)}{\sqrt{2\pi}\sigma} \exp\left\{-\frac{[x - (y - a\sigma^2)]^2}{2\sigma^2}\right\} \quad (26)$$

Then:

$$\begin{aligned} p(y) &= \int_0^\infty p(x,y) dx \\ &= a \exp\left(-ay + \frac{a^2\sigma^2}{2}\right) \Phi(y - a\sigma^2) \end{aligned} \quad (27)$$

where

$$\Phi(z) = \int_{-\infty}^z q(\tau) d\tau$$

Combining these results, we can write  $H$  as a sum of three integrals:  $H = I_1 + I_2 + I_3$ , where

$$\begin{aligned} I_1 &= \int_{-\infty}^\infty \int_0^\infty \frac{ae^{-ax}}{\sqrt{2\pi}\sigma} \exp\left[\frac{-(x-y)^2}{2\sigma^2}\right] \frac{1}{2\sigma^2} \\ &\quad \cdot (-x^2 + 2xy - y^2 + 2a\sigma^2y - a^2\sigma^4) dx dy \end{aligned} \quad (28)$$

$$I_2 = \int_{-\infty}^\infty \int_0^\infty \frac{ae^{-ax}}{\sqrt{2\pi}\sigma} \exp\left[\frac{-(x-y)^2}{2\sigma^2}\right] \log(\sqrt{2\pi}a\sigma) dx dy \quad (29)$$

$$I_3 = \int_{-\infty}^\infty \int_0^\infty \frac{ae^{-ax}}{\sqrt{2\pi}\sigma} \exp\left[\frac{-(x-y)^2}{2\sigma^2}\right] \log[\Phi(y - a\sigma^2)] dx dy \quad (30)$$

Integrating  $I_1$ , first with respect to  $y$ , we note that the integrand con-

tains the Gaussian frequency function of  $y$  with mean  $x$  and standard deviation  $\sigma$ . Let us transform this into a Gaussian distribution with mean zero and the same standard deviation. Thus, let  $y - x = z$ . Then the polynomial in the bracket reduces to the following polynomial in  $x$  and  $z$ :

$$\frac{1}{2\sigma^2} (-z^2 + 2a\sigma^2 x + 2a\sigma^2 z - a^2\sigma^4) \quad (31)$$

Noting that the first moment of  $z$  vanishes, while the second moment is  $\sigma^2$ , we have, after integrating with respect to  $y$ , the following quadrature:

$$\int_0^\infty a e^{-ax} \left( -\frac{1}{2} + ax - \frac{a^2\sigma^2}{2} \right) dx \quad (32)$$

This, upon integration with respect to  $x$ , gives us the value of:

$$I_1 = \frac{1}{2}(1 - a^2\sigma^2) \quad (33)$$

The integration of  $I_2$  is straightforward and yields immediately:

$$I_2 = -\log(\sqrt{2\pi} a\sigma) \quad (34)$$

To evaluate  $I_3$ , we integrate first with respect to  $x$  and accordingly "complete the square" so as to get a Gaussian distribution in  $x$  whose mean is  $y - a\sigma^2$ , namely:

$$\int_0^\infty \frac{a}{\sqrt{2\pi}\sigma} \exp\left\{ \frac{-[x - (y - a\sigma^2)]^2}{2\sigma^2} \right\} dx \quad (35)$$

This leaves outside the integral sign the expression

$$a \exp\left( -ay + \frac{a^2\sigma^2}{2} \right) \quad (36)$$

The integral (35) is not the complete Gaussian integral, since its lower limit is zero, not  $(-\infty)$ . However, its value is immediately apparent, namely

$$\Phi(y - a\sigma^2) \quad (37)$$

Therefore, the integration with respect to  $y$  to be performed to obtain the value of  $I_3$  is:

$$-\int_{-\infty}^\infty a \exp\left( -ay + \frac{a^2\sigma^2}{2} \right) \Phi(y - a\sigma^2) \log \Phi(y - a\sigma^2) dy \quad (38)$$

Here it is convenient to introduce a change of variable,  $z = y - a\sigma^2$ . The limits and the differential are left unaltered, and (38) becomes:

$$-\int_{-\infty}^{\infty} a \exp\left(-az - \frac{a^2\sigma^2}{2}\right) \Phi(z) \log \Phi(z) dz \quad (39)$$

This integral must be shown to be a function of a  $\sigma$  only, by the same argument that was advanced following Eq. (21). This we will now show. Let  $a\sigma = \omega$ . Then

$$\Phi(z, \sigma) = \int_{-\infty}^{az} \frac{\exp\left(-(\omega^2/2a^2\sigma^2)\right)}{\sqrt{2\pi} a\sigma} d\omega = \Phi(az, a\sigma) \quad (40)$$

Now let  $az = v$ . Then (40) becomes:

$$-e^{-\gamma^2/2} \int_{-\infty}^{\infty} e^{-v} \Phi(v, \gamma) \log \Phi(v, \gamma) dv \quad (41)$$

where  $\gamma = a\sigma$ , i.e., a function of  $a\sigma$  alone. Combining these results, we have:

$$H = \frac{1}{2}(1 - \gamma^2) - \log(\sqrt{2\pi} \sigma) - e^{-\gamma^2/2} \int_{-\infty}^{\infty} e^{-v} \Phi(v, \gamma) \log \Phi(v, \gamma) dv \quad (42)$$

The last term can now be expanded in powers of  $\Phi$  as follows: Using the well-known relation:  $\Phi(-x) = 1 - \Phi(x)$  and introducing  $x = -v$ , we can write the last term as follows:

$$e^{-\gamma^2/2} \int_{-\infty}^{\infty} e^x [1 - \Phi(x)] \log[1 - \Phi(x)] dx \quad (43)$$

Expanding the logarithm in powers of  $\Phi$ , which converges for all values of  $x < \infty$ , and multiplying out, we get:

$$e^{-\gamma^2/2} \int_{-\infty}^{\infty} e^x \left[ -\Phi(x) + \sum_{j=2}^{\infty} \frac{1}{j(j-1)} \Phi^j(x) \right] dx \quad (44)$$

We proceed to integrate by parts, putting  $e^x dx = dv$  and  $u$  equal to the expression in the brackets. The integrated product vanishes at both limits. We have reduced the integral to:

$$-e^{-\gamma^2/2} \int_{-\infty}^{\infty} e^x q(x, \gamma) dx + e^{-\gamma^2/2} \int_0^1 \sum_{j=2}^{\infty} \frac{e^x d\Phi^j}{j(j-1)} \quad (45)$$

where  $q(x, \gamma)$  is the Gaussian distribution with standard deviation  $\gamma$ .

The limits of the second integral are now  $(0,1)$ , because we have changed our variable of integration to  $\Phi^j$ . The first of these integrals has the value  $-1$ . Let us examine the second which has an interesting probabilistic interpretation.

Consider the average value of  $e^x$  with respect to the Gaussian distribution,  $q(x,\gamma)$ . This average value can be obtained as follows: Select from a large Gaussian-distributed population of  $x$ 's a sequence of single representatives, note the value of  $e^x$  each time, and obtain the average of this value. As the number of  $x$ 's in the sequence increases to infinity, the average of  $e^x$  will approach the true average.

Now instead of selecting a single representative  $x$  at a time, select two at a time and note the value of  $e^x$  where  $x$  is the larger of the two  $x$ 's drawn. The average thus obtained can be shown to be

$$\int_0^1 e^x d(\Phi^2) \quad (46)$$

In general, if  $j$   $x$ 's are drawn each time and the value of  $e^x$  for the largest of the  $j$   $x$ 's noted, the average thus obtained will be given by

$$\int_0^1 e^x d(\Phi^j) \quad (47)$$

Call these "jth power" averages  $\rho_j$ . We have, then, the following expression for  $H$ , combining the results so far obtained:

$$H = -\frac{1}{2}[1 + \gamma^2 + \log(2\pi\gamma^2)] + e^{-\gamma^2/2} \sum_{j=2}^{\infty} \frac{\rho_j}{j(j-1)} \quad (48)$$

Another interpretation can be obtained by noting that

$$\begin{aligned} \sum_{j=2}^{\infty} \frac{e^x d(\Phi^j)}{j(j-1)} &= \sum_{j=1}^{\infty} \frac{e^x \Phi^j e^{-(x^2/2\gamma^2)}}{j\sqrt{2\pi}\gamma} dx \\ &= e^{\gamma^2/2} \sum_{j=1}^{\infty} \frac{\Phi^j \exp[-(x-\gamma)^2/2\gamma^2]}{j\sqrt{2\pi}\gamma} dx \end{aligned} \quad (49)$$

The quantity represented by the integral

$$\int_{-\infty}^{\infty} \frac{\Phi^j \exp[-(x-\gamma)^2/2\gamma^2]}{\sqrt{2\pi}\gamma} dx \quad (50)$$

is the  $j$ th moment of the function  $\Phi(x)$  with respect to a Gaussian distribution of  $x$  having the same standard deviation but with its mean at  $\gamma$

instead of at zero. Call this quantity " $\eta_j$ ." We have then as an alternative representation of  $H$ , the expression

$$H = -\frac{1}{2}[1 + \gamma^2 + \log(2\pi\gamma^2)] + \sum_{j=1}^{\infty} \frac{\eta_j}{j} \quad (51)$$

As a check on our calculations, we note that  $H(0) = \infty$ . This is so because the quantity in the brackets increases without bound as  $\gamma$  tends to zero, while the other term always remains positive. Further we must have  $H(\infty) = 0$  and we must have the infinite sums converging for all finite  $\gamma$ . These checks will not be derived here rigorously. Plotted graphs are in conformity with the results.

The channel capacity is given as before:

$$C = \frac{Ha}{a\delta + 1} \quad (52)$$

Figure 5 shows the plot of (52) as a function of  $a$  for several values of  $\sigma$ .

#### ESTIMATES OF $\epsilon$ AND $\sigma$

Actual data on the probability distribution and variance of the response time of a neuron are scarce. McCulloch and MacKay in their calculation assume a  $\sigma$  of 50  $\mu$ sec for a synaptic junction. Some careful

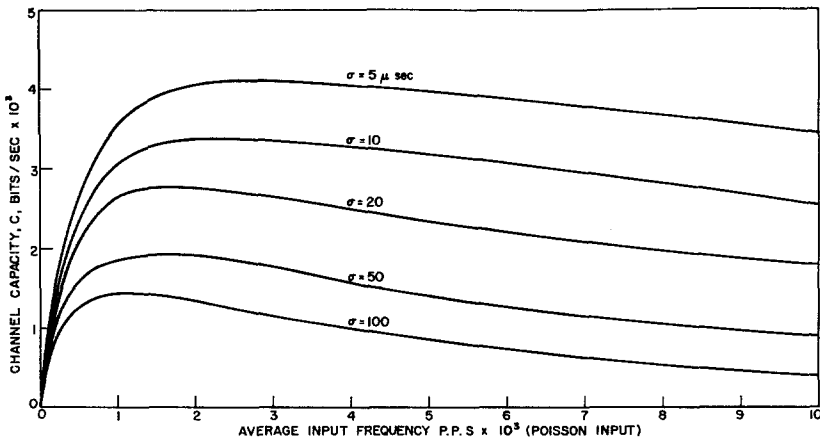


FIG. 5. The channel capacity of a model neuron calculated by continuous information theory for a Gaussian noise distribution with a standard deviation  $\sigma$ . Refractory period taken to be 1 msec.

measurements carried out by Dr. Paul Halick in our laboratory on single fibers from the sciatic tract of a frog showed a Gaussian distribution of latencies with  $\sigma$  varying from 3.6 to 4.6  $\mu\text{sec}$ . It appears, therefore, that the top curve of Fig. 5 is the best representation of the channel capacity of a single fiber employing an optimum pulse interval code.

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