

Firing Rates of Neurons with Random Excitation and Inhibition

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The expectation of the interspike interval for a Stein model neuron receiving Poisson excitation and inhibition is determined by solving a differential-difference equation with both forward and backward differences. The method of solution relies on an asymptotic expansion at large initial hyperpolarizations. The asymptotic solution is continued to near threshold depolarization whereupon the boundary condition is employed along with recursion relations to obtain the complete solution. The dependency of the mean firing rate on excitation at fixed inhibition and on inhibition at fixed excitation is investigated as well as the threshold dependence at fixed input rates. The results are discussed in relation to those for intracellular current injection and synaptic input to real neurons.

1. Introduction

In the construction of models of the activity of populations of neurons, knowledge is needed of the local response in terms of the strengths and natures of the synaptic inputs from spatially distributed sources which may originate extra- or intracortically (Wilson & Cowan, 1972, 1973). A given nerve cell receives excitatory and inhibitory postsynaptic potentials randomly in time so that any model which purports to incorporate the local response should be stochastic rather than deterministic. We will focus on a greatly simplified picture of single neuron activity and determine the average firing pattern for various kinds of input.

It is generally accepted that across the neuronal membrane, in the absence of synaptic inputs, is a resting electric potential which is often about 60 or 70 mV, inside negative. Let $V(t)$ be the depolarization from rest at time t . Excitatory inputs tend to increase $V(t)$ whereas inhibitory inputs tend to drive $V(t)$ in the negative direction. Spike generation is understood for a few types of neurons and we will assume that the cell under consideration is such

that when $V(t)$ reaches a particular value called the threshold (typical values being about 10 or 12 mV (Eccles, 1964; Calvin, 1975)), then a spike occurs. It is implicit in this simplified approach that the threshold at a local patch of the membrane is much lower than that over the rest of the neuronal surface. It is at this patch or trigger zone where the depolarization is in fact $V(t)$. We are aware of the complicated nature of the real problem of random input to a neuron but since this simplified model has proven itself very difficult to obtain answers for, we consider this as a necessary first step in the development of a more elaborate theory.

Stein (1965) introduced a stochastic model for single neuron activity which incorporates some of the physiological features of real neurons. This model can be described by a stochastic differential equation for $V(t)$, a Markov random process. Let $P(f_e; t)$ and $P(f_i; t)$ be independent temporally homogeneous Poisson processes (with rates f_e and f_i) whose values are initially zero. Then $V(t)$ satisfies

$$dV(t) = -sV(t) dt + a_e dP(f_e; t) - a_i dP(f_i; t), \quad V(0) = 0, \quad (1)$$

where a_e and a_i are positive quantities representing the amplitudes of the excitatory and inhibitory postsynaptic potentials and s is the reciprocal of the membrane time constant, τ . The time derivatives of the processes $P(f_e; t)$ and $P(f_i; t)$ are random time sequences of delta functions so that $V(t)$ jumps either up by a_e or down by a_i when events occur in these processes. Let θ be the threshold and let $T(x)$ be the random variable

$$T(x) = \inf \{t | V(t) \geq \theta | V(0) = x \in (-\infty, \theta)\}, \quad (2)$$

which is the time of first escape of the depolarization to suprathreshold values for an initial value of x . It has been shown (Gihman & Skorohod, 1972; Tuckwell, 1976a) that the expected value of $T(x)$, which we denote by $F(x)$, satisfies the differential-difference equation

$$-sxF'(x) + f_e F(x + a_e) + f_i F(x - a_i) - (f_e + f_i)F(x) = -1 \quad (3)$$

where the prime indicates differentiation. The boundary condition is $F(x) = 0$ when $x \geq \theta$. Similar equations can be written down for the higher moments of $T(x)$.

Though there have been extensive studies of the properties of the solutions of many kinds of functional equations (Bellman & Cooke, 1963; Hale, 1974), little progress has been made on equations such as (3) with forward and backward differences. Analytic results have been obtained for small θ and $f_i = 0$ (no inhibition) (Tuckwell, 1976b,c) and numerical results reported for excitation only and ratios of θ/a_e up to 10 (Tuckwell & Richter, 1978). An

analytic approximate solution in the case of weak inhibition was found by putting

$$F(x - a_i) \simeq F(x) - a_i F'(x), \quad (4)$$

thus converting the equation to one with only single differences (Tuckwell, 1975). The only other progress made with Stein's model including inhibition has been through computer simulation (Tuckwell, 1978, 1979).

Inclusion of inhibition makes the solution of (3) difficult for the following reason. When one utilizes the boundary condition for $x \geq \theta$, one obtains on the interval $(\theta - a_e, \theta)$ an equation

$$-sx F'(x) + f_i F(x - a_i) - (f_e + f_i) F(x) = -1, \quad (5)$$

which cannot be integrated without a knowledge of F on the previous interval. It is feasible that numerical solutions could be obtained for (3) by methods used for excitation only (Tuckwell & Richter, 1978), but this would require confining $V(t)$ to a finite interval thereby raising the problem of escapes at both ends, only some of which lead to a spike. We have utilized the asymptotic behavior of solutions of (3) for large negative x to obtain solutions for more positive values of x , and in particular the value of $F(0)$ which is the expected time to a spike when the membrane potential is originally at resting level. It should be pointed out that several other models for random neuronal activity have been proposed (see Holden (1976) for a review and also Yang & Chen (1978) for further references) but we feel that of the simplified models, Stein's is the most appropriate.

Equation (3) is to be solved with the given boundary condition which does not ensure uniqueness. Generally uniqueness follows with the additional constraint that $F(x)$ be continuous on $(-\infty, \theta)$. One exceptional case arises however, when $\theta = a_e$ because a discontinuity necessarily occurs at either $x = 0$ or $x = -a_i$. Generally, in the continuous solution, the discontinuity in $F(x)$ at θ propagates to cause a discontinuity in $F'(x)$ at $\theta - a_e$ etc.

It is natural to try a Laplace transform method of solution of (3). Setting

$$F^*(k) = \int_{-\infty}^{\theta} e^{kx} F(x) dx \quad (6)$$

one finds that $F^*(k)$ satisfies an ordinary differential equation. This equation can be converted to an exceedingly complicated integral equation for $F^*(k)$ whose solution is particularly difficult because there seems to be no way of picking the continuous solution from among generally discontinuous ones.

2. Method of Calculation of the Mean Firing Rate

We shall illustrate our method of finding the mean interspike interval in the case of equal amplitudes for the excitatory and inhibitory postsynaptic potentials. The method is nevertheless not restricted to the case $a_e = a_i$, but this does make for a simplification in the formulas. It is convenient to introduce new variables in order to eliminate some of the parameters. We set

$$y = x/a_e, \quad \hat{\theta} = \theta/a_e, \quad (7a)$$

$$G(y) = f_e F(x), \quad r = s/f_e, \quad R = f_i/f_e, \quad (7b)$$

whereupon equation (3) becomes

$$ryG'(y) - G(y+1) - RG(y-1) + (1+R)G(y) = 1, \quad (8)$$

with boundary condition $G(y) = 0$ for $y \geq \hat{\theta}$ and with the constraint that $G(y)$ be continuous on $(-\infty, \hat{\theta})$.

Our first step is to find an asymptotic form for the solution of this equation for large negative values of y . Recalling that y represents the initial value of the depolarization, it is apparent that when y does become large and negative, the exponential decay towards the resting value ($y = 0$) will dominate the behavior of the random process which satisfies the stochastic equation (1). This implies that $G(y)$ will not vary significantly over small ranges of values of y . That is, we expect that $G(y-1)$ and $G(y+1)$ will have values about the same as $G(y)$. Utilizing this approximation and solving the ordinary differential equation which then comes from (8) we have

$$G(y) \underset{y \rightarrow -\infty}{\sim} r^{-1} \log y + C(\hat{\theta}) \quad (9)$$

where $C(\hat{\theta})$ is a constant to be determined. The approximation (9) suggests that the solution of (8) can be accurately represented for large negative y by an asymptotic expansion of the form

$$G(y) \sim r^{-1} \log |y| + C(\hat{\theta}) + \sum_{n=1}^{\infty} A_n y^{-n}, \quad (10)$$

and substitution into equation (8) enables us to find the coefficients A_n from

$$A_1 = (R-1)/r^2 \quad (11a)$$

and the recursion relations

$$nrA_n + \sum_{m=1}^{n-1} \binom{n-1}{m-1} (R + (-1)^{n-m}) A_m = (R + (-1)^n)/nr, \quad n \geq 2. \quad (11b)$$

This substitution does not, however, determine $C(\hat{\theta})$. Before describing the evaluation of this constant, we consider how the solution can be continued

from large negative y to values of y near $\hat{\theta}$, where its values are needed in order to utilize the boundary condition. Defining $G^*(y) = G(y) - C(\hat{\theta})$, we have the explicit continuation formula

$$G^*(y) = -1 - RG^*(y-2) + r(y-1)G^*(y-1) + (1+R)G^*(y-1). \quad (12)$$

The idea now is to assume that the asymptotic expansion (10) is valid on two consecutive unit intervals $(\hat{\theta} - N - 1, \hat{\theta} - N + 1)$, whereupon equation (12) can be used repetitively to obtain $G^*(y)$ on $(\hat{\theta} - N + 1, \hat{\theta} - N + 2)$ and subsequently up to $(\hat{\theta} - 1, \hat{\theta})$.

In carrying out this procedure it is convenient to number the unit intervals from $(\hat{\theta} - N - 1, \hat{\theta} - N)$ to $(\hat{\theta} - 1, \hat{\theta})$ as intervals $0, 1, \dots, N$, and on interval n to assume the following form for the solution

$$G^*(y) = A_{n0} \log |y - n + 1| + \sum_{m=1}^{\infty} A_{nm} (y - n + 1)^{-m} \\ + B_{n0} \log |y - n| + \sum_{m=1}^{\infty} B_{nm} (y - n)^{-m}, \quad (13)$$

where in practice the sums are finite as only finitely many terms of (10) are used. Substitution in (12) gives the following recursion relations

$$A_{0,m} = 0 \text{ for } m \geq 0, \quad B_{0,0} = 1/r \quad \text{and} \quad B_{0,m} = A_m \text{ for } m \geq 1, \\ A_{1,0} = 1/r \quad \text{and} \quad A_{1,m} = A_m \text{ for } m \geq 1, \quad B_{1,m} = 0 \text{ for } m \geq 0, \quad (14a)$$

$$r(A_{n-1,0} + B_{n-1,0}) - 1 = 0, \quad (14b)$$

$$A_{n,0} = (1+R)A_{n-1,0} - RA_{n-2,0}, \quad B_{n,0} = (1+R)B_{n-1,0} - RB_{n-2,0}, \quad (14c)$$

$$A_{n,1} = r[(n-2)A_{n-1,0} - A_{n-1,1}] + (1+R)A_{n-1,1} - RA_{n-2,1}, \\ B_{n,1} = r[(n-1)B_{n-1,0} - B_{n-1,1}] + (1+R)B_{n-1,1} - RB_{n-2,1}, \quad (14d)$$

and for $m \geq 2$,

$$A_{nm} = -r[mA_{n-1,m} + (m-1)(n-2)A_{n-1,m-1}] + (1+R)A_{n-1,m} - RA_{n-2,m}, \\ B_{nm} = -r[mB_{n-1,m} + (m-1)(n-1)B_{n-1,m-1}] + (1+R)B_{n-1,m} - RB_{n-2,m}, \quad (14e)$$

It should be noted that (14a) and (14b) are consistent.

Determination of $C(\hat{\theta})$

The continuation formula can be used to determine G^* but not G and we

now show how to find $C(\hat{\theta})$. We observe that application of the boundary condition at $y \geq \hat{\theta}$ gives, on $(\hat{\theta} - 1, \hat{\theta})$,

$$ryG^*(y) - RG^*(y-1) + (1+R)G^*(y) + C(\hat{\theta}) - 1 = 0. \quad (15)$$

Multiplying by $(\hat{\theta} - y)^n$, integrating the resulting equation from $\hat{\theta} - 1$ to $\hat{\theta}$, and introducing the notation

$$I_{n,m} = \int_{\hat{\theta}-m-1}^{\hat{\theta}-m} (\hat{\theta} - m - y)^n G^*(y) dy, \quad m, n = 0, 1, 2, \dots, \quad (16)$$

we obtain

$$r[\hat{\theta}G^*(\hat{\theta}) - (\hat{\theta} - 1)G^*(\hat{\theta} - 1)] + C(\hat{\theta}) - 1 + (1+R-r)I_{0,0} - RI_{0,1} = 0 \quad (17a)$$

$$r[-(\hat{\theta} - 1)G^*(\hat{\theta} - 1)] + [C(\hat{\theta}) - 1]/(n+1) + (1+R - (n+1)r)I_{n,0} + nr\hat{\theta}I_{n-1,0} - RI_{n,1} = 0, \quad n > 0. \quad (17b)$$

It would seem that the method outlined so far could lead to the required firing rate. However, when we tried to use equations (17) to find $C(\hat{\theta})$ and hence $G(0)$, we noticed large discrepancies between the resulting mean interspike interval and known results from exact calculations and computer simulations when these were available. The discrepancies apparently arise because values of $G^*(y)$ were used close to $\hat{\theta}$ where after several uses of the continuation formula the solution is least accurate. Thus we had to find $C(\hat{\theta})$ utilizing information concerning $G^*(y)$ for smaller values of y .

This was achieved as follows. The integrals (16) satisfy recursion relations which enable us to express $I_{n,0}$ ($n = 0, 1, 2, \dots$) and $I_{n,1}$ in terms of

$$(\hat{\theta} - 1)G^*(\hat{\theta} - 1), (\hat{\theta} - 2)G^*(\hat{\theta} - 2), \dots,$$

and integrals whose evaluation depends on $G^*(y)$ further away from $\hat{\theta}$.

$$I_{0,m} = -1 + r[(\hat{\theta} - m - 1)G^*(\hat{\theta} - m - 1) - (\hat{\theta} - m - 2)G^*(\hat{\theta} - m - 2)] + [1 + R - r]I_{0,m+1} - RI_{0,m+2}, \quad (18a)$$

$$I_{n,m} = -1/(n+1) - r(\hat{\theta} - m - 2)G^*(\hat{\theta} - m - 2) + [1 + R - (n+1)r]I_{n,m+1} - RI_{n,m+2} + nr(\hat{\theta} - 1 - m)I_{n-1,m+1}, \quad n = 1, 2, \dots \quad (18b)$$

As a result of finding $I_{n,0}, I_{n,1}$ in this fashion, the equations (17) become a system of linear equations for

$$C(\hat{\theta}), \hat{\theta}G^*(\hat{\theta}), (\hat{\theta} - 1)G^*(\hat{\theta} - 1), \dots$$

If we use M of the equations (17), then we regard

$$(\hat{\theta} - 1)G^*(\hat{\theta} - 1), \dots, (\hat{\theta} - M + 2)G^*(\hat{\theta} - M + 2)$$

as unknowns in using the recursion relations (18) and use the continuation formula (12) to evaluate the remaining required values of $G^*(y)$.

In principle, by choosing M sufficiently large, it is possible to avoid the use of the continuation formula (12) altogether, since the only values of $G^*(y)$ needed would be those on an interval of length 2 where the asymptotic expansion (10) is assumed valid. However, in practice this could lead to solving large linear systems of equations whereas the use of the continuation formula allows us to work with relatively small systems. The values for

$$(\hat{\theta}-1)G^*(\hat{\theta}-1), \dots, (\hat{\theta}-M+2)G^*(\hat{\theta}-M+2),$$

calculated by solving the linear system can then be compared with values calculated from the continuation formula (12) as a heuristic check on the accuracy of the asymptotic expansion.

3. Results and Discussion

The above procedure for calculating the expected time between nerve impulses (i.e. the value of $F(0)$) was performed by computer program as follows. First, a certain number (typically through $0(1/y^2)$) of terms of the asymptotic expansion for $G^*(y)$ is employed on two consecutive intervals $(\hat{\theta}-N-1, \hat{\theta}-N+1)$, with N to be determined. For various values of N the continuation formula (12) is used to extend the solution up to $y = \hat{\theta}$. However, since the asymptotic solution is only an approximation, discontinuities appear at $\hat{\theta}-N+2, \dots, \hat{\theta}-1$. The actual solution is continuous, so we seek an N yielding the smallest maximum discontinuity on $(\hat{\theta}-N-1, \hat{\theta})$. Although one might expect larger N to automatically give smoother results, the magnitude of the maximum discontinuity was found to first decrease with increasing N and then to increase. The reason for the increasing size of the discontinuity seems to be the accumulative errors arising from repetitive use of the continuation formula. For example, with $\hat{\theta} = 3, r = R = 1$, the maximum discontinuities in $G^*(y)$ for $N = 6, 11, 16$ are 0.4535, 0.0193 and 18.6875, respectively, and the best value is for $N = 9$ with a maximum discontinuity of 0.0092.

To determine $C(\hat{\theta})$, we use the recursion relations (17) to set up a system of M linear equations involving

$$C(\hat{\theta}), \hat{\theta}G^*(\hat{\theta}), I_{n,0} \text{ and } I_{n,1}.$$

Using equations (19) to replace $I_{n,0}, I_{n,1}$ by quantities involving

$$(\hat{\theta}-1)G^*(\hat{\theta}-1), \dots, (\hat{\theta}-M+2)G^*(\hat{\theta}-M+2)$$

and integrals involving $G^*(y)$ away from $\hat{\theta}$, a system of linear equations for these quantities is obtained. To illustrate, the use of four recursion relations for $\hat{\theta} = 3$, $r = R = 1$, gives the linear system

$$3G^*(3) + (C(\hat{\theta}) - 1)G^*(2) - G^*(1) = -0.3851 \quad (19a)$$

$$0.5(C(\hat{\theta}) - 1) + 2(2G^*(2)) = 3.7471 \quad (19b)$$

$$0.3333(C(\hat{\theta}) - 1) - (2G^*(2)) + 7(G^*(1)) = 19.3018 \quad (19c)$$

$$0.25(C(\hat{\theta}) - 1) - (2G^*(2)) - 7(G^*(1)) = 46.7245 \quad (19d)$$

Solution of this system gives $C(3) = 65.4062$, $G^*(3) = -22.3778$, $G^*(2) = -7.1140$, and $G^*(1) = -2.3421$. As a consistency check we note that the value of $G^*(1^-)$ as given by the continuation formula is -2.4861 , showing good agreement between these two different ways of finding $G^*(1)$ and indicating that $G^*(y)$ is accurate for $y \leq 1$. In some cases it was found that the linear system may become singular (for example, with $\hat{\theta} = 2$, $r = R = 1$ and 5 recursion relations) but this problem only occurred for low values of $\hat{\theta}$. The above-mentioned consistency check was useful because it was found that when it was met, the mean firing interval calculated by the method proposed here and known results either by previous numerical or analytic work (Tuckwell & Richter, 1978) or by computer simulation (Tuckwell, 1979), agreed within a few percent.

To indicate the smoothness of the final solution of equation (8) [and hence of equation (3)], we have shown our computed $G(y) = G^*(y) + C(\hat{\theta})$ for two cases in Fig. 1. The values of the parameters are $\hat{\theta} = 3$, $f_e = s$, $f_i = s$ for the upper curve and $f_i = 0.6s$ for the lower one. Dashed lines in the Figure indicate values of $G(y)$ calculated from the continuation formula [plus the value of $C(\hat{\theta})$] whereas the solid curves are drawn through values calculated by solving the linear system (17). Notice that $G(y)$ calculated from the continuation formula actually has discontinuities at integer values of y but the magnitudes of these discontinuities are so small they are not discernible on the graphs.

We have determined the expected interspike interval for the neural model with depolarization given by the stochastic differential equation (1) for values of $\hat{\theta} = 2, 4, 6, 8$ and 10 and for various values of the frequencies of excitation and inhibition. Generally these input frequencies were chosen to make the expected time between firings between one and a few hundred time constants which seems to cover the physiological range for most central nervous system cells. Though values of $\hat{\theta}$ could be as large as 100 and higher, for some cells postsynaptic potentials can be a large fraction of the threshold

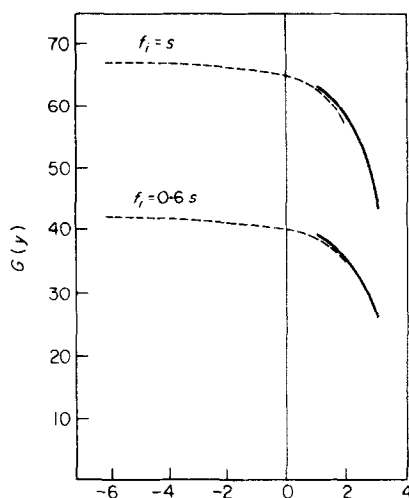


FIG. 1. Numerically computed solutions of equation (8) for $\hat{\theta} = 3$, $f_e = s$, and values of $f_i = s$ (upper curve) and $f_i = 0.6s$. The dashed lines indicate values of $G(y)$ computed from the continuation formula whereas the heavy lines have been drawn through points calculated from the recursion relations.

depolarization (Kuno & Miyahara, 1968; Eide, Fedina, Jansen, Lundberg & Vyklicky, 1969; Calvin, 1972). The method used here can be used for higher $\hat{\theta}$ but would involve considerable amounts of computer time. We will thus focus on general principles and confine our attention to what may be called intermediate values of $\hat{\theta}$.

To illustrate the accuracy of the method it is instructive to compare the results obtained with no inhibition with the values obtained either by exact analytic solution (Tuckwell, 1975; 1976a,b,c; Tuckwell & Richter, 1978) or accurately determined numerical values (Tuckwell & Richter, 1978). For example, values obtained for $F(0)$, in units of the time constant, with $f_e = 2s$, $f_i = 0$ in the present study and corresponding previously known values in parentheses were, for $\hat{\theta} = 2$ and 4, $F(0) = 1.74$ (1.82) and 9.47 (9.48), respectively. The errors here are 4.4% and 0.1%. The magnitude of the error was found to correspond with the ratio of the value of $G(\hat{\theta} - M + 2)$ calculated from the recursion relations to the value calculated from the continuation formula (i.e., the value of $G^*(\hat{\theta} - M + 2) + C(\hat{\theta})$). Here $\hat{\theta} - M + 2$ is the smallest value of y at which $G^*(y)$ is found from the recursion relations. The values of this ratio in the cases just described were 1.0614 and 0.9993. These figures indicate that when no other results are available for a comparison, the accuracy of the value of $F(0)$ obtained by the method

outlined above can be estimated by seeing how close the ratio of the two values of $G(\hat{\theta} - M + 2)$ is to unity. In further support of this, when we used an increasing number of recursion relations for a particular set of values of $\hat{\theta}$, f_e and f_i , the values of $F(0)$ became closer and closer to the known value while the ratio became closer and closer to unity.

We have obtained a large number of numerical results, and some of the calculated values of the mean firing interval, $F(0)$, are collected in the appendix. For ease of inspection we have also plotted in Figures 2 through 4 the frequency of firing, f , given by

$$f = 1/(F(0) + T_R), \quad (20)$$

where T_R is the absolute refractory period, as functions of various parameters. In order to make the frequencies more physiologically meaningful, all these plotted values are based on a time constant $\tau = 12$ msec, which is close to the value (12.3 ms) reported for fast pyramidal tract neurons of *cat* (Calvin & Sybert, 1976). It is not, however, implied that Stein's model provides an accurate description of spike generation in these cells. With this value of τ , we have $s = 83.3 \text{ sec}^{-1}$ and all input frequencies are given in units of s whereas output frequencies are given in sec^{-1} . The value of T_R was set at 1 msec which is approximately the spike duration in fast pyramidal tract neurons.

Figures 2 and 3 show the dependence of f , for $\hat{\theta} = 10$, firstly on frequency of inhibition at fixed frequencies of excitation and secondly on excitation at various fixed levels of inhibition. In Fig. 2, over considerable ranges of f_i , f is

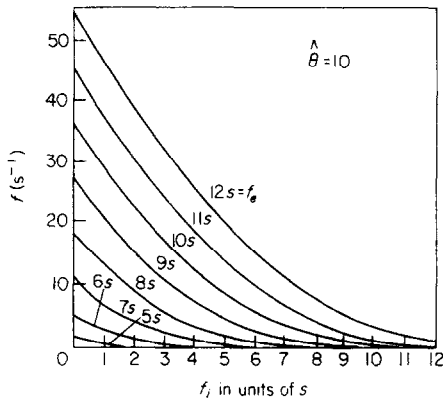


FIG. 2. Output frequency f for Stein's model neuron as a function of the frequency of inhibition f_i for various values of frequency of excitation f_e . The threshold parameter here is $\hat{\theta} = 10$ and the time constant τ has been set at 12 msec. Note that $s = 1/\tau$.

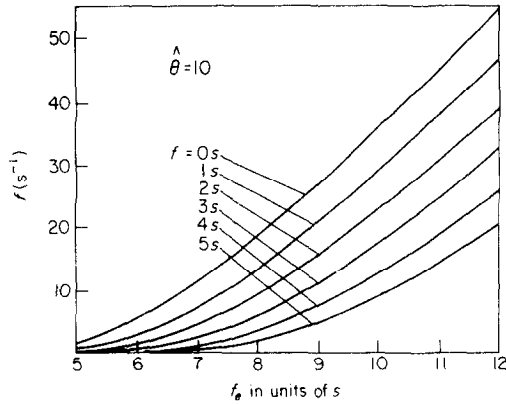


FIG. 3. Frequency of spikes f as a function of f_e at various f_i for $\hat{\theta} = 10$ and $\tau = 12$ msec.

an approximately linearly decreasing function of f_i at a fixed value of f_e . The approximate linearity gives way to an exponential type decline at larger f_i . At a particular $\hat{\theta}$, the family of f vs. f_i curves is approximately parallel over considerable ranges of f_e . When we plotted the results for other values of $\hat{\theta}$, it was noticed that at fixed f_i , the increase in f as f_e increased by s , is much smaller at $\hat{\theta} = 10$ than it is at $\hat{\theta} = 2$, for example.

The results for increasing excitation at fixed inhibition shown in Fig. 3, indicate that the firing rate is approximately a linear function of f_e over fairly wide ranges. For different f_i the curves obtained are almost parallel for large f_e . Thus, though the input currents are arriving randomly according to a Poisson process, there is still an approximate linearity in the f vs. f_e relation, where f is now the mean frequency of spikes. This can be compared with the linearity in the relation between frequency of rhythmic spikes and input current (f/I relation) in real neurons (Granit, Kernell & Lamarre, 1966; Schwindt & Calvin, 1973). The approximate parallel nature of the family of f vs. f_e curves can also be compared with the "algebraic summation" of depolarizing and hyperpolarizing currents, whether these be produced by current injection or by synaptic input. Note that f is actually a sigmoid function of f_e because in the limit as $f_e \rightarrow \infty$, $f \rightarrow 1/T_R$.

The chief differences between the random current case (Stein's model) and the ("more") deterministic cases are: (i) with random input the mean output frequency of spikes is always positive for all positive f_e and any value of f_i , whereas with deterministic current injection there is a threshold input level below which there is no sustained firing; (ii) with intracellular current injection into some cells (e.g., cat spinal motoneurons) one usually sees a fairly abrupt change of slope in the frequency vs. current relation at the

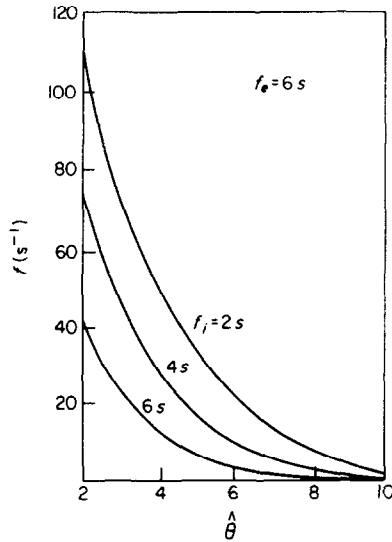


FIG. 4. Frequency f as a function of $\hat{\theta}$ for fixed values of f_e and f_i .

beginning of the secondary and sometimes tertiary ranges, whereas no such phenomena occur in the random input model considered here. The absence of a secondary range for the mean firing rate with randomly arriving postsynaptic potentials is presumably an expression of the deficiencies of Stein's model whereby known electrophysiological complications such as afterhyperpolarization and soma-dendritic invasion by the spikes are ignored. The results should, nevertheless, be useful for moderate firing rates and will certainly be more accurate descriptions of a neuron's response than linear decay models (Gerstein & Mandelbrot, 1964) and diffusion approximations (Ornstein-Uhlenbeck process) to Stein's model (Johannesma, 1968; Roy & Smith, 1969).

We also illustrate the dependence of firing rate on the threshold $\hat{\theta}$ by considering f as a function of $\hat{\theta}$ for fixed f_e and f_i . Figure 4 contains this functional dependence for the cases $f_e = 6s$ and for the three levels of inhibition $f_i = 2s, 4s$ and $6s$. It can be seen that in all these cases f declines approximately exponentially as θ increases. This is similar to the result obtained with excitation only (Tuckwell & Richter, 1978).

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APPENDIX

TABLE 1

Calculated expected interspike intervals in units of the time constant for $\hat{\theta} = 10$ and various values of frequencies of excitation and inhibition. Lack of an entry means an excessively long or excessively short interval. The unit for f_e and f_i is the reciprocal of the membrane time constant.

f_e	f_i							
	0	2	4	6	8	10	12	14
4	356.0	—	—	—	—	—	—	—
5	52.0	303.2	—	—	—	—	—	—
6	15.5	58.3	312.8	—	—	—	—	—
7	7.3	19.1	70.8	354.0	—	—	—	—
8	4.4	9.0	24.3	89.6	415.0	—	—	—
9	3.0	5.4	11.4	31.9	117.1	502.5	—	—
10	2.2	3.6	6.6	14.7	42.5	151.5	583.8	—
11	—	2.7	4.4	8.3	19.4	56.8	194.6	—
12	—	—	3.2	5.4	10.6	25.9	75.5	263.1
13	—	—	—	3.8	6.6	13.8	34.6	100.5