LETTER TO THE EDITOR

Low firing-rates in a compartmental model neuron

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Abstract. A nonlinear relationship is obtained between the membrane potential of a compartmental model neuron as a function of input stimulation. This is used to show how shunting effects can lead to low output firing-rates in associative memory networks.

In a recent paper, Abbott [1] has shown how shunting effects can lead to a nonlinear relationship between the input current to a neuron's soma and the incident rates of excitatory inputs synapsing on the neuron's dendritic tree. Such a nonlinearity produces a low output firing-rate in the presence of high levels of excitation, thus providing a solution to the problem of high firing-rates found in network models based on neurons whose input current varies linearly with synaptic inputs. When these latter networks are in a state of self-sustained firing corresponding, say, to a dynamical fixed point of an attractor network [2], the neurons tend to fire at their maximum rate. Cortical neurons, on the other hand, tend to operate well below their maximum rate. Such a problem has received considerable attention within the context of associative memory networks, where the self-sustained firing patterns are interpreted as memory states [3–5].

The analysis of Abbott [1] is based on Rall's cable theory of current flow in a passive dendritic tree [6]. A complementary approach to representing the electrical properties of a neuron's dendritic tree is to use a compartmental model [7]. In this model, the dendritic system is divided into sufficiently small regions or compartments, such that spatial variations of the electrical properties within a region are negligible. The advantage of the compartmental approach, which is used extensively in computational studies of neuronal systems [8], is that it provides a greater flexibility in modelling neurons and a greater economy of computation.

In this letter, we derive an analogous result to Abbott's [1], *vis-à-vis* the effects of shunting on the firing-rate of a neuron, using recent work on temporal pattern processing in a compartmental model neuron [9]. (In [1], a compartmental model neuron is used in computer simulations rather than as the basis of analytical work.) We assume that the compartmental model neuron consists of a soma connected to a single dendritic tree idealized as a one-dimensional chain of $2M+1$ compartments labelled $\alpha = -M, \ldots, M$. The equivalent circuit of the αth compartment consists of a membrane leakage resistor R_α in parallel with a capacitor C_α, with the ground representing the extracellular medium (assumed to be an isopotential). Each compartment is joined to its immediate neighbours in the chain by the junctional resistors $R_{\alpha\alpha-1}$ and $R_{\alpha\alpha+1}$. Assuming that each compartment α has N synapses labelled (αk), $k = 1, \ldots, N$, then the current at synapse (αk) is governed by a time-varying conductance $\Delta g_{\alpha k}$ *in series*

with a fixed reversal potential $S_{\alpha k}$. It then follows from Kirchhoff's law that the time evolution of the membrane potentials V_α is given by

$$C_\alpha \frac{dV_\alpha}{dt} = -\frac{V_\alpha}{R_\alpha} + \sum_{\langle\beta;\alpha\rangle} \frac{V_\beta - V_\alpha}{R_{\alpha\beta}} + \sum_{k=1}^{N} \Delta g_{\alpha k}[S_{\alpha k} - V_\alpha] \tag{1}$$

where $\langle\beta; \alpha\rangle$ indicates that the summation over β is restricted to immediate neighbours of α. The last term on the right-hand side of equation (1) incorporates shunting effects; the change in a compartment's membrane potential induced by a synaptic input depends on the size of the deviation of the membrane potential from the resting potential. Since each $\Delta g_{\alpha k}$ is positive, the effect of each term $\Delta g_{\alpha k}[S_{\alpha k} - V_\alpha]$ is for V_α to tend towards $S_{\alpha k}$. Hence positive and negative $S_{\alpha k}$ correspond respectively to excitatory and inhibitory synapses.

To obtain a complete picture of the input–output response of a neuron, it is necessary to supplement the leaky-integrator equations (1) with details concerning action potential generation at the axon hillock of the soma [8]. It will be adequate for our purposes simply to view the soma as a point processor that is isopotential with the dendritic compartment nearest to it, taken to be $\alpha = 0$. We shall assume that the neuron fires whenever $V_0(t)$ exceeds a time-dependent threshold h. The time-dependence of h represents the effects of *refractory period*. That is, if Δt denotes the time that has elapsed since the neuron last fired then $h(\Delta t) = \infty$ for $0 < \Delta t \le t_R$ and $h(\Delta t) = h_0 + h_1 \exp(-\Delta t/\tau_a)$ for $\Delta t > t_R$ (until the neuron fires again). Here t_R is the absolute refractory period, whereas τ_a determines the relative refractory period.

Since equation (1) is formally linear in $V = (V_\alpha, \alpha = 0, \pm 1, \ldots, \pm M)$, it may be written as a matrix equation of the form [9, 10]

$$\frac{dV}{dt} = H(t)V(t) + U(t) \tag{2}$$

where $H_{\alpha\beta}(t) = Q_{\alpha\beta} + \bar{Q}_{\alpha\beta}(t)$

$$Q_{\alpha\beta} = -\frac{\delta_{\alpha,\beta}}{\tau_\alpha} + \frac{\delta_{\beta,\alpha+1}}{\tau_{\alpha\alpha+1}}(1 - \delta_{\alpha,M}) + \frac{\delta_{\beta,\alpha-1}}{\tau_{\alpha\alpha-1}}(1 - \delta_{\alpha,-M}) \tag{3a}$$

$$\frac{1}{\tau_\alpha} = \left[\sum_{\langle\beta';\alpha\rangle} \frac{1}{\tau_{\alpha\beta'}} + \frac{1}{C_\alpha R_\alpha}\right] \qquad \frac{1}{\tau_{\alpha\beta}} = \frac{1}{C_\alpha R_{\alpha\beta}} \tag{3b}$$

$$\bar{Q}_{\alpha\beta}(t) = -\frac{\delta_{\alpha\beta}}{C_\alpha}\sum_k \Delta g_{\alpha k}(t) \qquad U_\alpha(t) = \frac{1}{C_\alpha}\sum_k \Delta g_{\alpha k}(t)S_{\alpha k}. \tag{4}$$

Formally, equation (2) may be solved as [9, 11]

$$V(t) = \int_0^t dt' \, T\left[\exp\left(\int_{t'}^t dt'' \, H(t'')\right)\right]U(t') + T\left[\exp\left(\int_0^t dt'' \, H(t'')\right)\right]V(0) \tag{5}$$

where T denotes the time-ordered product, $T[H(t)H(t')] = H(t)H(t')\theta(t - t') + H(t')H(t)\theta(t' - t)$, which is required since H is a time-dependent, non-commuting matrix. The term $T[\exp(\int_{t'}^t dt'' \, H(t''))]_{\alpha\beta}$ is the Green's function or response function $\mathcal{G}(\alpha, t; \beta, t')$ of the system.

In general, equation (5) is difficult to analyse due to the dependence of H on the time-dependent conductances $\Delta g_{\alpha k}$. (Note that this is a direct consequence of the inclusion of shunting effects in equation (1). For if the time-dependent part of H is absent, as occurs when the shunting term $-V_\alpha \sum_k \Delta g_{\alpha k}$ is dropped from equation (1),

then the Green function $\mathscr{G}(\alpha, t; \beta, t')$ reduces to the much simpler form $[e^{(t-t')Q}]_{\alpha\beta}$.) Therefore, we shall make two major simplifying assumptions concerning $\Delta g_{\alpha k}$ to facilitate our analysis [9]: (i) each action potential and post-synaptic potential is idealized as a Dirac delta-function spike, i.e. details of pulse-shape are neglected and (ii) the arrival times of the action potentials are restricted to be integer multiples of a fundamental unit of time t_D. The time varying conductance $\Delta g_{\alpha k}(t)$ induced by an incoming stream of action potentials is then a sequence of conductance spikes of the form

$$\Delta g_{\alpha k}(t) = \varepsilon_{\alpha k} \sum_{m \geqslant 0} \delta(t - mt_D) a_{\alpha k}(m) \tag{6}$$

where $a_{\alpha k}(m) = 1$ if an action potential arrives at the discrete time mt_D and is zero otherwise. The size of each conductance spike, $\varepsilon_{\alpha k}$, is determined by factors such as the amount of neurotransmitter released on arrival of an action potential and the efficiency with which these neurotransmitters bind to receptors [11].

The discrete time condition imposed on the arrival times, assumption (ii), means that the inputs to the neuron are specified completely by the sequence of patterns $A(m) = (a_{\alpha k}(m), \alpha = 0, \pm 1, \ldots, \pm M, k = 1, \ldots, N)$, integer m. Each pattern $A(m)$ is a $(2M + 1) \times N$ matrix. We shall use a more concise representation of an input pattern by assuming that each compartment consists of two groups of identical synapses, one excitatory and the other inhibitory. The input $A(m)$ is then specified by the set $\{N_\alpha^{(e)}(m), N_\alpha^{(i)}(m)\}$ where $N_\alpha^{(e)}(m), N_\alpha^{(i)}(m)$ are the number of excitatory and inhibitory synapses respectively that receive an action potential at time m. Substituting equation (6) into (4) and using this representation of input patterns we obtain

$$\bar{Q}_{\alpha\beta}(t) = \delta_{\alpha\beta} \sum_{m \geqslant 0} \delta(t - mt_D) q_\alpha(m) \qquad U_\alpha(t) = \sum_{m \geqslant 0} \delta(t - mt_D) u_\alpha(m) \tag{7}$$

$$q_\alpha(m) = \varepsilon_\alpha^{(e)} N_\alpha^{(e)}(m) + \varepsilon_\alpha^{(i)} N_\alpha^{(i)}(m)$$
$$u_\alpha(m) = \varepsilon_\alpha^{(e)} S^{(e)} N_\alpha^{(e)}(m) + \varepsilon_\alpha^{(i)} S^{(i)} N_\alpha^{(i)}(m) \tag{8}$$

where for convenience the capacitance C_α has been absorbed into each $\varepsilon_\alpha^{(e,i)}$ so that $\varepsilon_\alpha^{(e,i)}$ is dimensionless. The excitatory and inhibitory reversal potentials $S^{(e,i)}$ are taken to be α-independent. Observe that $S^{(e)}$, $\varepsilon_\alpha^{(e,i)} > 0$ whereas $S^{(i)} \leqslant 0$.

The presence of Dirac delta-functions in equation (7) allows the integrals in (5) to be performed explicitly. In particular, the time-ordered product may be calculated using standard path-integral techniques to give, on setting $t_D = 1$ and $V(0) = 0$ [9]

$$V_\alpha(t) = \sum_\beta [e^{(t-m)Q} e^{-G(m)}]_{\alpha\beta} X_\beta(m) \qquad m < t < m+1 \tag{9}$$

for all positive integers m, where $G_{\alpha\beta}(m) = \delta_{\alpha\beta} q_\alpha(m)$ and $u_\alpha(m), q_\alpha(m)$ satisfy equation (8). Here X_β is a discrete-time variable defined iteratively according to $X_\alpha(0) = u_\alpha(0)$ and, for $m > 0$

$$X_\alpha(m) = \sum [e^Q e^{-G(m-1)}]_{\alpha\beta} X_\beta(m-1) + u_\alpha(m). \tag{10}$$

The main effect of shunting is to alter the local decay-rate of a compartment according to $1/\tau_\alpha \to 1/\tau_\alpha + q_\alpha(m)/(t-m)$ for $m < t \leqslant m+1$. Since each q_α is proportional to the number of concurrent inputs to the αth compartment (equation (8)), this suggests a mechanism whereby shunting can limit the size of response of the neuron. That is, constant high rates of stimulation can lead to fast rates of decay so that the steady-state values of the membrane potentials are lower than those that would occur

in the absence of shunting. To show how this can occur, we shall determine the steady-state values of the variables $X_\alpha(m)$ in the presence of constant synaptic inputs. Suppose that the Lth compartment receives excitatory inputs at a constant rate E whilst every other compartment receives inhibitory inputs at a constant rate F. In other words, $N_\alpha^{(e)}(m) = E\delta_{\alpha L}$, $N_\alpha^{(i)}(m) = F(1 - \delta_{\alpha L})$ for all m. Furthermore we shall take $\varepsilon_\alpha^{(e,i)}$ to be α-independent with $\varepsilon^{(i)}F = \varepsilon^{(e)}E$, and set $S^{(i)} = 0$. (An analogous pattern of stimulation is considered by Abbott [1].) Then using equations (8) and (10) we obtain

$$X_\alpha(m) = \varepsilon^{(e)}S^{(e)}E \sum_{n=0}^{m} [\exp(nQ(E))]_{\alpha L} \tag{11}$$

where $Q(E)_{\alpha\beta} = Q_{\alpha\beta} + \delta_{\alpha\beta}\varepsilon^{(e)}E$.

It remains to determine the matrix $\exp(Q(E))$. As shown in [9], many of the qualitative features of the model can be determined by assuming that all compartments have identical properties and taking the limit $M \to \infty$. (In the case of an infinite dendritic chain, we do not have to worry about edge effects arising from the compartments at $\pm M$.) Setting $R_\alpha = R$, $C_\alpha = C$, $R_{\alpha\alpha+1} = \tilde{R}$ for all α in equation (3) gives $\tau_\alpha = \tau$, $\tau_{\alpha\alpha+1} = \gamma = \tau_{\alpha+1\alpha}$ where $1/\tau = 2/\gamma + 1/\tilde{\tau}$, $\gamma = \tilde{R}C$, $\tilde{\tau} = RC$. Using standard results from the theory of random walks, it follows that for a uniform, infinite dendritic chain [9], $[\exp(nQ(E))]_{\alpha\beta} = \exp(-n/\tau - n\varepsilon^{(e)}E)I_{|\alpha-\beta|}(2n/\gamma)$ where I_n is the modified Bessel function of integer order. The steady-state value of $X_\alpha(m)$ is then given by

$$X_\alpha^\infty = \varepsilon^{(e)}S^{(e)}E \lim_{m\to\infty} \sum_{n=0}^{m} \exp\left(-n\left(\frac{1}{\tau} + \varepsilon^{(e)}E\right)\right)I_{|L-\alpha|}(2n/\gamma). \tag{12}$$

The series on the right-hand side of (12) is convergent so that the steady-state X^∞ is well-defined. Note that X^∞ determines the long-term behaviour of the membrane potentials V according to equation (9); we shall refer to X_α^∞ as the *steady-state membrane potential* of the αth compartment. For small levels of excitation E, X_α^∞ is approximately a linear function of E. However, as E increases, the contribution of shunting inhibition to the effective decay-rate becomes more and more significant so that X_α^∞ eventually begins to decrease. This is illustrated in figure 1, where $X_0^\infty/S^{(e)}$ is plotted as a function of $\varepsilon^{(e)}E$ for $\tilde{\tau} \gg \gamma$, $\gamma = 1$ and $L = 1$ in equation (12) (cf figure 3 of [1]).

Finally, using similar arguments to Abbott [1] it can be shown that the nonlinear relationship between X_α^∞ and E in equation (12) provides a solution to the problem of high firing-rates. First, it is necessary to determine the output firing-rate of the
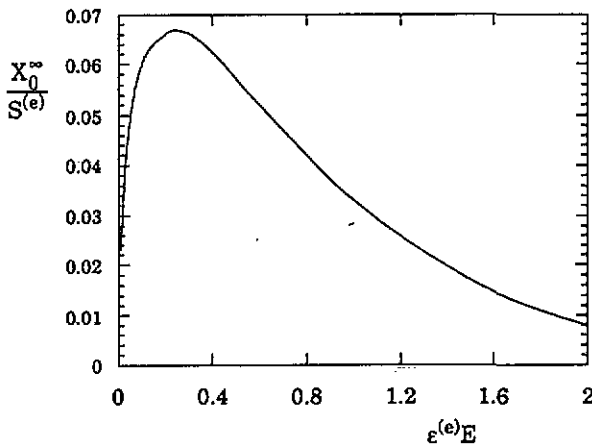

Figure 1. Steady-state value of the membrane potential at the soma as a function of the excitatory rate of inputs to the compartment at $\alpha = 1$.

neuron. In the presence of constant inputs, the membrane potential at the soma will reach some (time-averaged) steady-state $\bar{V}_0$. The larger $\bar{V}_0$, the faster the decreasing threshold $h(\Delta t)$ is crossed from below after firing and thus the greater the firing-rate z of the neuron. As shown by Amari [12], a reasonable approximation for z is a sigmoid function of $\bar{V}_0$. Hence, noting from (9) and (12) that $\bar{V}_0 \propto X_0^\infty$, the average firing-rate of the neuron is $z = f(E) = f_{max}/(1 + \exp[g(\kappa - X_0^\infty(E))])$ for some gain g and threshold κ. Here f_{max} is the maximum firing-rate, which is determined by the absolute refractory period.

Now consider a population of excitatory neurons in which the effective excitatory rate E impinging on a neuron is determined by the average firing-rate $\langle z \rangle$ of the population. Similarly, the inhibitory rate F is determined by the average firing-rate of a population of inhibitory interneurons. For a self-consistent picture, it is necessary to restrict the firing times of the neurons to be integer multiples of t_D. However, since t_D could be made arbitrarily small, this is not a serious restriction. Alternatively, we can simply interpret equation (10) as representing a discrete time, compartmental model neuron with the X_α identified as the state variables of the neuron and, say, f/f_{max} equal to the probability that the neuron fires at each time step. (Such a discrete time model is a natural extension of the standard binary neuron used in artificial neural networks that incorporates spatio-temporal aspects of real neurons.) For a large population of neurons, a reasonable approximation is to take $E = c\langle z \rangle$, for some constant c. Within a mean-field approach, the steady-state behaviour of the population is then determined by the self-consistency condition $E = cf(E)$ [1]. Using graphical methods one finds that there are two stable solutions to this equation, one corresponding to the silent state $E = 0$ and the other to a state in which the firing-rate is considerably below f_{max}. On the other hand, if X_0^∞ were a linear function of E then this latter stable state would have a firing-rate close to f_{max}.

This is illustrated by curve (b) of figure 2 where f/f_{max} is plotted as a function of E with X_0^∞ satisfying (12), $\varepsilon^{(e)} cf_{max} = 1$, and $g^{-1} = 0.03$, $\kappa = 1.0$. On the other hand, if X_0^∞ is a linear function of E, i.e., the contribution of the term $\varepsilon^{(e)}E$ to the exponential in equation (12) is dropped, then this latter stable state has a firing-rate close to f_{max}, see curve (a) of figure 2. (The proof of these results is identical to that of [1].) Note that for certain choices of parameter values there is an additional solution to the self-consistency condition but this is unstable.
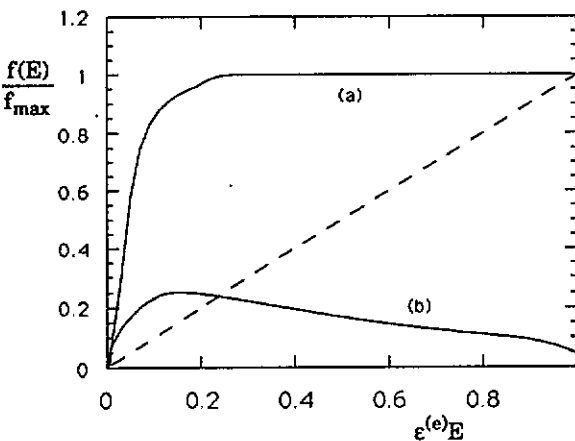

Figure 2. Firing-rate/maximum firing-rate f/f_{max} as a function of input excitation E for (a) linear and (b) nonlinear relationship between steady-state membrane potential X_0^∞ and E. Points of intersection with straight line are states of self-sustained firing.

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