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Diffusion Approximation for a Multi-Input Model Neuron

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Abstract. A generalization of an earlier paper (Capocelli and Ricciardi, 1971), dealing with a diffusion approximation for a neuron subject to one excitatory and one inhibitory Poisson input, is provided by not imposing any restrictions on number and magnitude if synaptic inputs. An equation for the neuron's transition p.d.f. is derived, use of which is made to determine the moments of the membrane potential. It is finally shown that a diffusion approximation is possible and that the resulting diffusion process is characterized by constant infinitesimal variance and linear drift.

1. Introduction

In principle every differential equation derived to provide the description of a physical system should contain a random term to account for the unavoidable perturbations that arise because of the interaction of the system with its environment. However, in physics not always the effect of these perturbations is large enough to make such procedure mandatory. Quite contrary, the reason why stochastic differential equations are being increasingly utilized in biology is mostly due to the impossibility of accounting for the essential interaction of the system under study with its surroundings. It appears then necessary to resort to the "heat bath" assumption, namely to direct attention only to a subsystem and to model the effect of its environment as a "random force" whose stochastic properties are conjectured on the basis of intuition and common sense.

The most illustrious physical example where the above procedure has been successfully employed is the well known study of the motion of a Brownian particle. As for biology, the studies by Reichardt and coworkers [cf., for instance, Poggio and Reichardt (1973), and cited references] of the pattern induced flight orientation of the fly must be recalled.

The stochastic equations approach has also been widely used to arrive at some statistical description of the output of spontaneously active neurons belonging to complex networks and has proven useful to solve the *inverse problem* as well, i.e., the prediction of the neuron's input on the basis of the experimentally determined interspike interval histogram (Ricciardi, 1976, and quoted references). Nevertheless, the procedure that consists of adding a "random force" term to the equation expressing the spontaneous exponential decay of the neuron's membrane potential in the absence of inputs appears to be open to criticism unless it is at least plausible that such force is of the Langevin type. Unfortunately, thus far no systematic method is known for deciding whether any proposed choice is correct. This is the main reason why in an earlier paper (Capocelli and Ricciardi, 1971) a diffusion approximation was derived for a model neuron without resorting to any stochastic equation.

The purpose of this paper is to provide a generalization of the model discussed in Capocelli and Ricciardi (1971) in a way to include an arbitrary number of excitatory and inhibitory inputs. We shall prove that a reasonable diffusion approximation is still possible for the time course of the neuron's membrane potential under suitable assumptions on the neuron's inputs. Such approximation can *a posteriori* be looked at as generated by a stochastic equation of the Langevin type.

Apart from minor obvious changes, the formalism, the motivations and the general background is that of Capocelli and Ricciardi (1971).

2. Formulation of the Model and Moments of the Membrane Potential

Let x denote the variation of the potential difference across the neuron's membrane (*membrane potential*, in the following), so that $x=0$ is the *resting potential*. In the absence of neuronal inputs x exponentially decays toward the resting potential:

$$x(t)=x(t_0)\exp\left(-\frac{t-t_0}{\theta}\right), \tag{2.1}$$

where θ is the time constant of the neuron's membrane, typically of the order of a few milliseconds. Generalizing the situation described in Capocelli and Ricciardi (1971) we assume that the neuron's input consists of $p+q$ sequences of approximately zero-width impulses Poisson distributed in time with rates $\alpha_1, \alpha_2, \ldots, \alpha_p$ and $\beta_1, \beta_2, \ldots, \beta_q$, respectively. The pulses characterized by the rates α_k $(k=1, 2, \ldots, p)$ are excitatory while those arriving at rate β_k $(k=1, 2, \ldots, q)$ are inhibitory. Denoting by $e_k>0$ $(k=1, 2, \ldots, p)$ and by $i_k<0$ $(k=1, 2, \ldots, q)$ the corresponding excitatory and inhibitory post synaptic potentials, the instantaneous transition

$$x \to x+e_k \quad (k=1, 2, \ldots, p) \tag{2.2}$$

depicts the effect of an excitatory input pulse belonging to the sequence characterized by the rate α_k, whereas

$$x \to x+i_k \quad (k=1, 2, \ldots, q) \tag{2.3}$$

is the instantaneous transition occurring when the neuron is hit by a pulse belonging to the sequence that has rate β_k.

It should be noted that these assumptions about the neuron's input appear to be quite reasonable if one thinks of them in the framework of the asymptotic theorems characterizing the superposition of a large number of weakly correlated point processes (Capocelli and Ricciardi, 1973). Furthermore, they imply that $x(t)$ is a homogeneous Markov process so that its transition p.d.f. satisfies the Chapman-Kolmogorov equation:

$$f(x, t+\Delta t|x_0) = \int_{-\infty}^{\infty} dz\, f(x, \Delta t|z) f(z, t|x_0), \tag{2.4}$$

where $x_0=x(0)$ and $t+\Delta t>t>0$ are arbitrary instants. Equation (2.4) can be thrown in to a simpler form by noting that, apart from quantities $o(\Delta t)$, there results:

$$\begin{aligned} f(x, \Delta t|z) = &\left\{1-\Delta t\left[\sum_{k=1}^{p} \alpha_k + \sum_{k=1}^{q} \beta_k\right]\right\} \delta\left[x-\left(z-z\frac{\Delta t}{\theta}\right)\right] \\ &+\Delta t \sum_{k=1}^{p} \alpha_k \delta\left[x-\left(z-z\frac{\Delta t}{\theta}+e_k\right)\right] \\ &+\Delta t \sum_{k=1}^{q} \beta_k \delta\left[x-\left(z-z\frac{\Delta t}{\theta}+i_k\right)\right], \end{aligned} \tag{2.5}$$

where $\delta(\cdot)$ is the Dirac delta function. Substituting (2.5) in (2.4) and making use of the approximation

$$\left(1-\frac{\Delta t}{\theta}\right)^{-1} \approx 1+\frac{\Delta t}{\theta} \tag{2.6}$$

one thus obtains:

$$\begin{aligned} &f(x, t+\Delta t|x_0) \\ &= \left(1+\frac{\Delta t}{\Theta}\right)\left\{1-\Delta t\left[\sum_{k=1}^{p} \alpha_k + \sum_{k=1}^{q} \beta_k\right] f\left(x+x\frac{\Delta t}{\theta}, t|x_0\right)\right. \\ &\quad +\Delta t \sum_{k=1}^{p} \alpha_k f\left[x-e_k+(x-e_k)\frac{\Delta t}{\theta}, t|x_0\right] \\ &\quad \left.+\Delta t \sum_{k=1}^{q} \beta_k f\left[x-i_k+(x-i_k)\frac{\Delta t}{\theta}, t|x_0\right]\right\}. \end{aligned} \tag{2.7}$$

It is finally seen that, in the limit as $\Delta t \to 0$, Equation (2.7) yields:

$$\begin{aligned} \frac{\partial f}{\partial t} = \frac{\partial}{\partial x}\left(\frac{x}{\theta} f\right) &+ \sum_{k=1}^{p} \alpha_k [f(x-e_k, t|x_0) - f(x, t|x_0)] \\ &+ \sum_{k=1}^{q} \beta_k [f(x-i_k, t|x_0) - f(x, t|x_0)]. \end{aligned} \tag{2.8}$$

This is a differential-difference equation for the transition p.d.f. describing the time course of the neuron's membrane potential in the absence of threshold. This equation will be used in Section 3 to construct a diffusion approximation. In the remaining of this Section we shall instead make use of Equation (2.8) to obtain a closed form expression for the moments $M_n(t|x_0)$ of the membrane potential. This task will be achieved without actually solving Equation (2.8) or determining the characteristic function of the process. To this purpose we set:

$$M_n(t|x_0) = \int_{-\infty}^{\infty} dx\, x^n f(x, t|x_0) \quad (n=0, 1, \ldots). \tag{2.9}$$

Clearly there results:

$$\begin{aligned} &M_0 = 1 \\ &M_n(0|x_0) = x_0^n \quad (n=1, 2, \ldots). \end{aligned} \tag{2.10}$$

We now differentiate with respect to t both sizes of Equation (2.9) and make use of Equation (2.8) to express $\partial f/\partial t$. Under the legitimate assumption that $f(x, t|x_0)$ vanishes rapidly enough at infinity, a straightforward calculation yields:

$$\frac{dM_n}{dt} = -\frac{n}{\theta} M_n + \sum_{r=0}^{n-1} \binom{n}{r} \mu_{n-r} M_r \quad (n=1, 2, \ldots), \tag{2.11}$$

where we have set:

$$\mu_j \equiv \sum_{k=1}^{p} \alpha_k e_k^j + \sum_{k=1}^{q} \beta_k i_k^j \quad (j=1, 2, \ldots, n). \tag{2.12}$$

Solving recursively the ordinary differential Equations (2.11) with the initial conditions (2.10) one thus easily obtains the moments of the process describing the time course of the neuron's membrane potential. Setting in (2.11) $n=1$ gives the equation for the mean membrane potential, whose solution is:

$$M_1(t|x_0) = \theta\mu_1 - (\theta\mu_1 - x_0)e^{-t/\theta}, \tag{2.13}$$

where μ_1, the rate of the mean net excitation induced on the neuron, is defined by (2.12). The variance $V(t|x_0)$ of the membrane is also easily determined as solution of the equation

$$\begin{aligned} &\frac{dV}{dt} = -\frac{2}{\theta} V + \mu_2 \\ &V(0|x_0) = 0 \end{aligned} \tag{2.14}$$

obtained by differentiating both sides of the identity

$$V(t|x_0) = M_2(t|x_0) - [M_1(t|x_0)]^2 \tag{2.15}$$

and by using (2.11). The result is:

$$V(t|x_0) = \frac{\theta\mu_2}{2}(1 - e^{-2t/\theta}) \tag{2.16}$$

with μ_2 given by (2.12). It should be noted that in the particular case $p = q = 1$, that is when the neuron's input consists of only one excitatory and one inhibitory pulse train, Equations (2.13) and (2.16) yield a result earlier found by Stein (1965) by a less straightforward procedure.

3. Diffusion Approximation

The outlined procedure allows one to achieve a satisfactory description of the sub-threshold behavior of the neuron's membrane potential. However, because of the discontinuities of the sample paths of the underlying process it is exceedingly hard to get some information on the distribution of the firing times. To make some progress in this direction it is expedient to "smooth down" the sample paths, if at all possible, in a way to change Equation (2.8) into a partial differential equation of the diffusion or Fokker-Planck type. Thus doing one is allowed to use the various techniques available in the literature to estimate the firing distribution as a first passage time distribution through the neuron's threshold value. Here we do not intend to enter details or technicalities as the method has been already outlined in Capocelli and Ricciardi (1971) and it can be used in a straightforward way for the present model. Instead, we wish to point out that a sensible diffusion approximation is possible for the present model neuron and derive the appropriate Fokker-Planck equation.

The starting point is to expand the functions $f(x - e_k, t|x_0)$ and $f(x - i_k, t|x_0)$ on the right hand side of Equation (2.8) as Taylor series about x. Thus doing, Equation (2.8) can be rewritten in the following form:

$$\frac{\partial f}{\partial t} = -\frac{\partial}{\partial x}\left[\left(-\frac{x}{\theta} + \mu_1\right)f\right] + \sum_{j=2}^{\infty} \frac{(-1)^j}{j!}\mu_j \frac{\partial^j f}{\partial x^j} \tag{3.1}$$

where the μ_j's are given by (2.12). Equation (3.1) is the Smolukowski series expension of Equation (2.4) for the transition p.d.f. It simplifies into a diffusion equation of the Fokker-Planck type only if the coefficients $\mu_j\,(j = 3, 4, \ldots)$ vanish. For this to occur, it is necessary to envisage a suitable limit procedure that makes infinitesimal the postsynaptic potentials e_k's and i_k's while simultaneously allowing the input arrival rates α_k's and β_k's to become infinitely large.

In Capocelli and Ricciardi (1971), where only one excitatory and one inhibitory input sequence was considered, an analogous limit has been explicitly carried out. The resulting diffusion equation is identical to the one describing the velocity distribution of a Brownian particle subject to an elastic restoring force. In order to obtain a meaningful limit process suitable conditions on rates and magnitudes of post synaptic potentials had to be imposed, which prevented a constant contribution to appear in the drift term. Consequently, the transition p.d.f. of the membrane potential turned out to have a maximum exponentially drifting toward the resting potential, no matter how large the absolute mean rates of the postsynaptic potentials.

Much more satisfactory is the behavior of the present model. Indeed, as we shall see, it yields a limit diffusion process whose mean drifts toward the neuron's threshold whenever there is a surplus of excitatory input over inhibitory input. To this purpose, and without loss of generality, let us assume that the number of excitatory inputs exceeds the number of inhibitory inputs, i.e., $p > q$. The coefficients μ_j's in Equation (3.1) can then be made all vanishing with the exception of μ_1 and μ_2 if the limit values of rates and magnitudes of the postsynaptic potentials are taken as follows:

$$\left.\begin{aligned}
\alpha_k &= \lim_{y\to 0}\frac{a_k}{y^2}, & a_k &> 0\\
\beta_k &= \lim_{y\to 0}\frac{b_k}{y^2}, & b_k &> 0\\
i_k &= \lim_{y\to 0} d_k y, & d_k &< 0\\
e_k &= \lim_{y\to 0} c_k y, & c_k &= \frac{|d_k| b_k}{a_k}
\end{aligned}\right\}\quad (k = 1, 2, \ldots, q) \tag{3.2}$$

and

$$\left.\begin{aligned}
\alpha_r &= \lim_{y\to 0}\frac{a_r}{y}, & a_r &> 0\\
\beta_r &= \lim_{y\to 0}\frac{b_r}{y}, & b_r &> 0\\
i_r &= \lim_{y\to 0} d_r y, & d_r &< 0\\
e_r &= \lim_{y\to 0} c_r y, & 0 < c_r &\neq \frac{|d_r| b_r}{a_r}
\end{aligned}\right\}\quad (r = q+1, q+2, \ldots, p) \tag{3.3}$$

where e_k's, b_k's, c_k's, and d_k's are otherways arbitrary constants. Indeed, recalling (2.12) and making use of (3.2) and (3.3), in the limit $y \to 0$ one obtains:

$$\begin{aligned}
\mu_1 &\to \lim_{y\to 0}\left[y^{-1}\sum_{k=1}^{q}(a_k c_k - b_k|d_k|)\right] + \sum_{r=q+1}^{p}(a_r c_r - b_r|d_r|) \equiv \delta\\
\mu_2 &\to \sum_{k=1}^{q} b_k d_k^2\left(1 + \frac{b_k}{a_k}\right) + \lim_{y\to 0}\left[y\sum_{r=q+1}^{p}(a_r c_r^2 + b_r d_r^2)\right] \equiv \mu > 0\\
\mu_j &\to \lim_{y\to 0}\left\{y^{n-2}\sum_{k=1}^{q} b_k d_k\left[1 + (-1)^n\left(\frac{b_k}{a_k}\right)^{n-1}\right] + y^{n-1}\sum_{r=q+1}^{p}\left[a_r c_r^n + (-1)^n b_r|d_r|^n\right]\right\} = 0 \quad (j = 3, 4, \ldots).
\end{aligned} \tag{3.4}$$

We have thus proved that Equation (3.1) tends to the Fokker-Planck equation

$$\frac{\partial f}{\partial t} = -\frac{\partial}{\partial x}\left[\left(-\frac{x}{\theta}+\delta\right)f\right]+\frac{\mu}{2}\frac{\partial^2 f}{\partial x^2}, \tag{3.5}$$

where μ denotes the infinitesimal variance. The quantity δ in the drift term is the net rate of excitation impinging on the neuron. Should inhibitions prevail over excitations, the limit equation would still be (3.5), however with $\delta<0$. The case $\delta=0$ corresponds to the situation described in Capocelli and Ricciardi (1971).

Under the diffusion approximation just introduced, a closed form expression for the membrane potential transition p.d.f. is readily available as the process described by Equation (3.5) can be derived from the Wiener process (Ricciardi, 1976). For the sake of brevity we shall not insist on this. Rather, we wish to point out that the method used in Section 2 also yields the moments $m_n(t|x_0)$ and the variance $v(t|x_0)$ of the membrane potential when Equation (3.5) holds. Now the basic equations are:

$$\begin{aligned}\frac{dm_n}{dt} &= -\frac{n}{\theta}m_n+n\delta m_{n-1}\\ &\quad+\frac{1}{2}H(n-1)\,\mu n(n-1)m_{n-2} \qquad (n=1,2,\ldots)\\ m_n(0|x_0) &= x_0^n\,,\end{aligned} \tag{3.6}$$

where $H(z)$ is the Heaviside unit step function. One thus easily finds:

$$\begin{aligned}m_1(t|x_0) &= \delta\theta-(\delta\theta-x_0)e^{-t/\theta}\\ v(t|x_0) &= \frac{\theta\mu}{2}(1-e^{-2t/\theta}),\end{aligned} \tag{3.7}$$

as was to be expected.

Let us now note that if μ is small the sample paths describing the time course of the membrane potential are clustered around $m_1(t|x_0)$ with fluctuations whose amplitude vanishes in the limit $\mu\to 0$. Therefore, if μ is small the mean time T necessary for the membrane potential to attain for the first time the neuron's threshold $S<\delta\theta$ is approximately given by:

$$T\approx\theta\ln\frac{\delta\theta-x_0}{\delta\theta-S}. \tag{3.8}$$

Setting $x_0=0$ in (3.8) we see that for large values of the net excitation rate the mean time necessary for the neuron to fire again after a spike has been elicited (i.e., the mean interspike distance) is approximately given by

$$T\approx\frac{S}{\delta}\left(1-\frac{S}{2\delta\theta}\right) \tag{3.9}$$

thus becoming roughly inversely proportional to the net excitation rate when the excitatory inputs largely override the inhibitory ones. If, however, μ is large the estimates (3.8) and (3.9) are dangerously misleading. In such case the firing time distribution problem has to be tackled with the help of the mathematical machinery outlined in Capocelli and Ricciardi (1971) and in Sugiyama et al. (1970).

In conclusion, it should be pointed out that Equation (3.5) could have been *postulated* by assuming that a "force" of the Langevin type appears in the equation expressing the exponential decay of the membrane potential:

$$\frac{dx}{dt}+\frac{1}{\theta}x=\delta+F(t) \tag{3.10}$$

where $F(t)$ is a stationary delta-correlated normal process with zero mean. However, it is not *a priori* obvious that Equation (3.10) has any neurobiological significance for the reasons outlined in Section 1. The justification for attaching to $F(t)$ the properties characterizing a Langevin force rests exactly, and exclusively, in the diffusion approximation limit carried out above.

References

Capocelli, R. M., Ricciardi, L. M.: Diffusion approximation and first passage time problem for a model neuron. Kybernetik **8**, 214 (1971)

Capocelli, R. M., Ricciardi, L. M.: A continuous Markovian model for neuronal activity. J. theor. Biol. **40**, 369 (1973)

Poggio, T., Reichardt, W.: A theory of the pattern induced flight orientation of the fly *Musca domestica*. Kybernetik **12**, 185 (1973)

Ricciardi, L. M.: Diffusion approximations to neuronal activity and to the time dependent threshold problem. To appear in Proc. 3rd European Cong. Cybern. System Res. (R. Trappl, Ed.)

Ricciardi, L. M.: On the transformation of diffusion processes into the Wiener process. J. Math. Anal. Appl. **54**, 185 (1976)

Stein, R. B.: A theoretical analysis of neuronal variability. Biophys. J. **5**, 173 (1965)

Sugiyama, H., Moore, G. P., Perkel, D. H.: Solution for a stochastic model of neuronal spike production. Math. Biosci. **8**, 323 (1970)

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