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A Dynamical System for the Approximate Moments of Nonlinear Stochastic Models of Spiking Neurons and Networks

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Abstract—We consider multidimensional systems of coupled nonlinear stochastic differential equations suitable for the study of the dynamics of collections of interacting noisy spiking neurons. Assumptions based on the smallness of third and higher central order moments of membrane potentials and recovery variables are used to derive a system of ordinary differential equations for the approximate means, variances, and covariances. We show the usefulness of such a derivation for different cases of model neurons under the action of white noise currents.

Keywords—Neuronal modeling, Stochastic, Spiking neurons.

1. INTRODUCTION

Stochastic models of neural activity are considered here at the single and network level. We are mainly concerned with biological neurons for which state variables are governed by systems of nonlinear stochastic systems of the diffusive type. Examples are those in [1–4], or reduced systems such as those in [5–7] under the action of white noise perturbations.

A general form for such dynamical models of stochastic neuronal networks or single neurons leads to the following system of pN coupled nonlinear stochastic differential equations (N neurons):

$$dX_j = \left[\phi\left(X_j, \underset{\sim}{Y_j}\right) + I_j(t) + \sum_{k=1}^{N} J_{jk}\Theta(X_k)\right] dt + \beta_j\, dW_j, \tag{1}$$

$$d\underset{\sim}{Y_j} = \underset{\sim}{\psi}\left(X_j, \underset{\sim}{Y_j}\right) dt. \tag{2}$$

Here X_j, $\underset{\sim}{Y_j}$, $j = 1, 2, \dots, N$ are, respectively, voltage and $(p-1)$-dimensional subsidiary variables including possible recovery variables, J_{jk} are synaptic weights for the connection from neuron k to

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neuron j, and $\Theta(\,.\,)$ is a threshold function, often taken as sigmoidal in shape. I_j, $j = 1, 2, \ldots, N$ are applied currents for neuron j and $\beta_j(t)$, $j = 1, 2, \ldots, N$ are noise parameters.

The functions $\phi(.,.)$ and $\underset{\sim}{\psi}(.,.)$ may take different forms according to the individual neuronal properties depending on particular nonlinear conductance dynamics and the kinetics of ionic currents.

The transition probability density function could be obtained, at least numerically by solving the Fokker Planck Equation for these diffusion processes. This may present a very large computational task in the case of a great number of connected cells. Other methods for noisy systems in other contexts include Monte Carlo [8] or moment calculations [9]. We present here an approach of this latter type suitable for describing the statistical properties of stochastic processes occurring in neurodynamics. There also have been direct analytical approaches to problems involving networks of integrate and fire [10] and spiking model neurons with synaptic stochastic inputs [11].

2. THE GENERAL CASE AND THE MAIN RESULT

Actually, for our purpose, it is possible to consider a general system of multidimensional diffusion processes. Applications to neural systems will then be developed.

Let $\mathbf{X} = \{\mathbf{X}(t),\ t \geq 0\} = \{(X_1(t), X_2(t), \ldots, X_n(t)),\ t \geq 0\}$, with $n \geq 1$ be an n-dimensional random process with components satisfying the stochastic differential equations

$$dX_j(t) = f_j(\mathbf{X}(t), t)\, dt + \sum_{k=1}^{m} g_{jk}(\mathbf{X}(t), t)\, dW_k(t), \tag{3}$$

where $j = 1, 2, \ldots, n$ and $m \geq 1$. The $W_k = \{W_k(t),\ t \geq 0\}$, $k = 1, 2, \ldots, m$, are standard Wiener processes (that is, each of then has zero mean, initial value is zero with probability one, and variance equal to t at time t) which we assume to be independent. Conditions for existence and uniqueness of solutions are assumed to hold [12].

Define the n means for the various components, $\overline{X}_j(t)$, where $j = 1, \ldots, n$, and the n^2 covariances $C_{ij}(t)$ where $i, j = 1, \ldots, n$.

Let us assume that the distribution function of $\mathbf{X}(\mathbf{t})$ is concentrated near the mean point $\overline{\mathbf{X}}(t) = (\overline{X}_1(t), \overline{X}_2(t), \ldots, \overline{X}_n(t))$ (that is, $\Pr\{|\mathbf{X}(t) - \overline{\mathbf{X}}(t)| < \epsilon\}$, for some (usually small) positive ϵ, is close to 1) and is symmetric around this point. We may find, with the help of numerical integration, some conditions under which these assumptions are valid. Third- and higher-order odd central moments are in this case, close to zero, fourth- and higher-order even moments are small relatively to the second moment.

This enables us to derive the following system of $(1/2)n(n+3)$ nonlinear ordinary differential equations for the approximate means $\mathbf{m}(t) = (m_1(t), m_2(t), \ldots, m_n(t)$ and covariances $C_{ij} = C_{ij}(t)$ where $i, j = 1, \ldots, n$ (see [13])

$$\frac{dm_j}{dt} = f_j(\mathbf{m}, t) + \frac{1}{2} \sum_{l=1}^{n} \sum_{p=1}^{n} \left\{ \frac{\partial^2 f_j}{\partial x_l \partial x_p} \right\}_{(\mathbf{m},t)} C_{lp}, \tag{4}$$

$$\begin{aligned}
\frac{dC_{ij}(t)}{dt} = {} & \sum_{l=1}^{n} \left\{ \frac{\partial f_i}{\partial x_l} \right\}_{(\mathbf{m},t)} C_{lj} + \sum_{l=1}^{n} \left\{ \frac{\partial f_j}{\partial x_l} \right\}_{(\mathbf{m},t)} C_{il} \\
& + \sum_{k=1}^{m} l \left\{ g_{ik} g_{jk} + \frac{1}{2} \sum_{l=1}^{n} \sum_{p=1}^{n} \left[\partial x_p g_{jk} \frac{\partial^2 g_{ik}}{\partial x_l \partial x_p} \right.\right. \\
& \left.\left. + \frac{\partial g_{ik}}{\partial x_l} \frac{\partial g_{jk}}{\partial x_p} + \frac{\partial g_{ik}}{\partial x_p} \frac{\partial g_{jk}}{\partial x_l} + g_{ik} \frac{\partial^2 g_{jk}}{\partial x_l \partial x_p} r \right] r \right\}_{(\mathbf{m},t)} C_{lp}.
\end{aligned} \tag{5}$$

At this stage, we remark that if all n stochastic equations (3) are linear, the above approximation procedure gives known exact results (see [14] for moment equations in this case).

We will now apply the above framework to determine the means and second-order central moments of a four-component neuron model with additive white noise in the first component.

3. STATISTICAL PROPERTIES OF A STOCHASTIC HODGKIN-HUXLEY NEURON MODEL

We consider the Hodgkin-Huxley System which exhibits the known properties of biological neuron including subthreshold responses, solitary waves (action potentials or spikes) in response to suitable stimuli as well as repetitive activity (periodic solutions) in certain ranges of stimuli. In the case of an input current perturbed by noise, the system, as described by equations (1) and (2), is four-dimensional where X is the membrane potential variable and $\underset{\sim}{Y}$ is a three-dimensional vector containing the sodium and potassium conductances. One has, with

$$\underset{\sim}{Y} = (m, h, n),$$
$$\phi(X, \underset{\sim}{Y}) = \frac{1}{C}\left[(v_L - X)g_L + (v_K - X)\overline{g_k}n^4 + (v_{Na} - X)\overline{g_m}m^3h\right], \tag{6}$$

$\underset{\sim}{\psi} = (\psi_1, \psi_2, \psi_3)$ with

$$\psi_i(X, Y_i) = \alpha_i(X)(1 - Y_i) - \beta(X)Y_i, \qquad i = 1, 2, 3. \tag{7}$$

The nonlinear functions $\{\alpha_i(X)\}$ and $\{\beta_i(X)\}$ have the following forms:

$$\alpha_1(X) = \frac{(2.5 - 0.1X)}{e^{2.5-0.1X} - 1}, \qquad \beta_1(X) = 4e^{-X/18}, \qquad \alpha_2 = 0.07e^{-X/20}, \tag{8}$$

$$\beta_2(X) = \left(e^{3-0.1X} + 1\right)^{-1}, \qquad \alpha_3(X) = \frac{0.01(10 - X)}{e^{1-0.1X} - 1}, \qquad \beta_3(X) = 0.125e^{-X/80}, \tag{9}$$

while C, v_L, v_K, v_{Na}, g_L, $\overline{g_K}$, and $\overline{g_m}$ are constants (see [1,6]).

The dynamical system which can be obtained from the general formulation (4),(5) has dimension 14 consisting of four means, $\overline{X}$, $\overline{m}$, $\overline{h}$, $\overline{n}$, four variances, S_X, S_m, S_h, S_n and six covariances, C_{Xm}, C_{Xh}, C_{Xn}, C_{mh}, C_{mn}, C_{hn}.

We have considered input synaptic currents consisting of sequences of pulses which are generated in a random way, with a random amplitude. For any given choice of this sequence, an extra white noise term is applied with amplitude β. The means and variances are obtained by numerical integration of the stochastic system, using a standard Euler method, and a given number of trials (here 200 trials were used, $\beta = 0.1$ and the maximum current is $20nA$). This scheme is called simulation. Then, these values are compared to the solution of the approximate dynamical system. The time step was $\delta t = 0.01$ ms and calculations have been done in double precision.

As we can show in Figure 1, means obtained by simulation and solution of the differential system coincide almost exactly. The agreement is rather good for the variance of the potential. The input current is also shown. In Figure 2, the variance of the potential calculated by the two methods is shown in a region where there is no spike.

When β is increased, there exists an upper value of this parameter above which the moment method yields solution which become unstable. For example, with the same current as above, this upper value is $\beta = 0.3$ and the solution is unstable after around 50 ms. When β is taken between 0.1 and 0.3, it remains a good agreement for the means. However, the variances which are calculated around instants where there is a spike emission are over-estimated by the moment method while they are well estimated when the membrane potential remains under-threshold.

When a sustained mean current of constant amplitude is applied, the agreement between the moment method and simulation is not as good as was the case when the current was a series of pulses. For example, in order to compare with the above results, we have considered the case of a

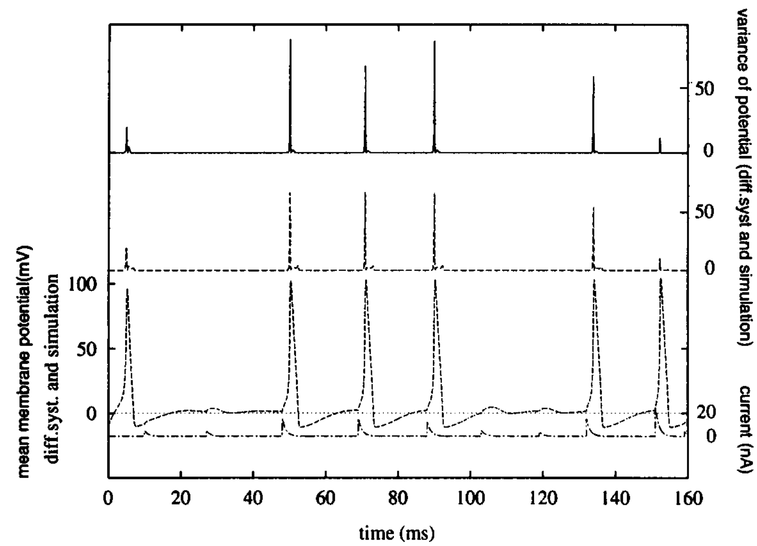

Figure 1. Showing the mean and the variance of the potential for a synaptic current plus noise, $\beta = 0.1$. The mean time course of the current is shown at the bottom of the figure. The means obtained by simulation and by solving the differential system are practically indistinguishable. We also show the variance of the potential calculated by the two methods.

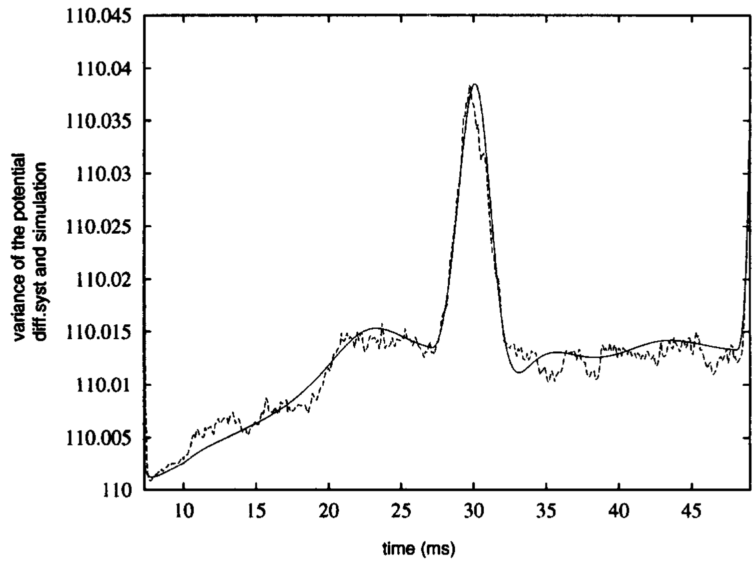

Figure 2. Variance of the potential for the same value of β and the same current as in Figure 1, in a region where the input current does not produce spike emission. Continuous line: variance obtained by solving the differential system. Dashed line: variance determined by simulation.

constant current of $10nA$ which is perturbed by white noise with amplitude $\beta = 0.1$. Repetitive pulse solutions are obtained and, as is shown in Figure 3, the means and variances which are obtained by the two methods exhibit some differences which may be important and which may be lowered if one takes much smaller values of β (of the order of 0.005).

Similar results were obtained for the Fitzhugh-Nagumo System (see [15]).

4. ESTIMATES OF FIRING ACTIVITY IN A NETWORK

When the general system (4),(5) is considered for a network of n cells, it is possible to get estimates on firing probabilities in terms of its solutions. In the case of two-dimensional reduction

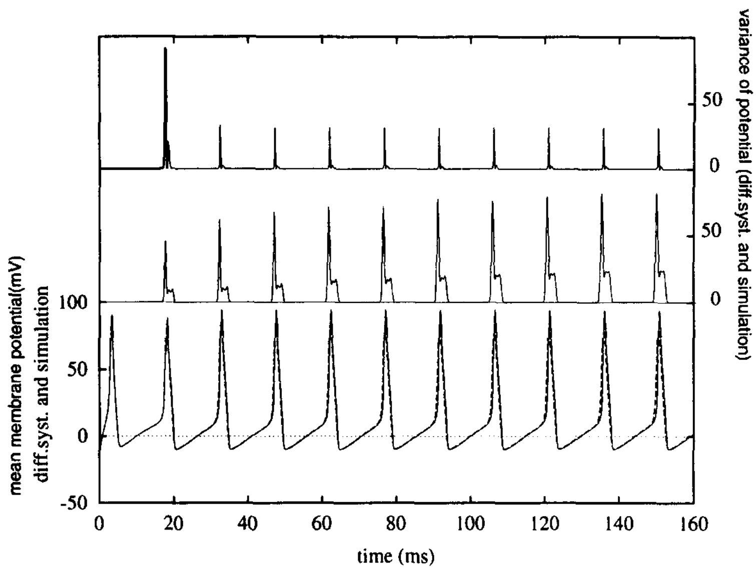

Figure 3. Showing a typical case where the moment method gives different results from those obtained directly from simulation. A constant mean current of $10nA$ is applied to the model neuron and is perturbed by a white noise, $\beta = 0.1$.

as in Fitzhugh-Nagumo case (see also [15]), it is useful to rename the $2n$ dynamical variables as $U_j = X_j$, $U_{j+n} = Y_j$, $j = 1, \dots, n$, so that the system may be written

$$dU_j = \left[\phi(U_j, U_{j+n}) + I_j(t) + \sum_{k=1}^{n} J_{jk}\Theta(U_k)\right] dt + \beta_j\, dW_j, \tag{10}$$

$$dU_{j+n} = h(U_j, U_{j+n})\, dt, \qquad j = 1, 2, \dots, n. \tag{11}$$

Then, it follows from (4),(5) that the following differential equations hold for the approximate means of the voltage and recovery variables of the n neurons:

$$\begin{aligned} \frac{dm_j}{dt} &= \phi(m_j, m_{j+n}) + I_j(t) + \sum_{k=1}^{n} J_{jk}\Theta(m_k) + \frac{1}{2}\Bigg[\phi_{xx}(m_j, m_{j+n})S_j \\ &+2\phi_{xy}(m_j, m_{j+n})C_{j,j+n} + \phi_{yy}(m_j, m_{j+n})S_{j+n} + \sum_{k=1}^{n} J_{jk}\Theta''(m_k)S_k r\Bigg] \end{aligned} \tag{12a}$$

and

$$\begin{aligned} \frac{dm_{j+n}}{dt} &= h(m_j, m_{j+n}) + \frac{1}{2}\; l[h_{xx}(m_j, m_{j+n})S_j \\ &+2h_{xy}(m_j, m_{j+n})C_{j,j+n} + h_{yy}(m_j, m_{j+n})S_{j+n}r], \qquad j = 1, 2, \dots, n. \end{aligned} \tag{12b}$$

We can also find the equations satisfied by the second-order moments for each network neuronal variable. We have, for $1 \le j \le i \le n$,

$$\begin{aligned} &\frac{dC_{ij}}{dt} \left(\phi_x(m_i, m_{i+n}) + \phi_x(m_j, m_{j+n})\right) C_{ij} \\ &+\phi_y(m_i, m_{i+n})C_{i+n,j} + \phi_y(m_j, m_{j+n})C_{i,j+n} + \beta_i^2 + \beta_j^2. \end{aligned} \tag{13a}$$

When $n + 1 \le i \le 2n$, $1 \le j \le n$, we find

$$\begin{aligned} \frac{dC_{n+q,j}}{dt} &= \left[\phi_x(m_j, m_{n+j}) + h_y(m_q, m_{n+q})\right] C_{n+q,j} + \phi_y(m_j, m_{n+j})C_{n+q,n+j} \\ &+h_x(m_q, m_{n+q})C_{qj} + \sum_{k=1}^{n} \Theta'(m_k)J_{kk}C_{n-q,k}, \end{aligned} \tag{13b}$$

whereas when $n \leq j \leq i \leq 2n$, the covariances are

$$\begin{aligned}\frac{dC_{n+q,n+r}}{dt} &= h_x(m_q, m_{n+q})C_{q,n+r} + h_x(m_r, m_{n+r})C_{n+q,r} \\ &+ \left[h_y(m_q, m_{n+q}) + h_y(m_r, m_{n+r})\right] C_{n+q,n+r},\end{aligned} \tag{13c}$$

where q and r range from $1, \dots, n$.

The following differential equations for the variances are obtained:

$$\frac{dS_i}{dt} = 2\left[\phi_x(m_i, m_{i+n})S_i + \phi_y(m_i, m_{i+n})C_{i,i+n} + \beta_i^2\right], \qquad i = 1, \dots, n, \tag{14a}$$

and

$$\frac{dS_{n+q}}{dt} = 2\left[h_x(m_q, m_{n+q})C_{q,n+q} + h_y(m_q, m_{n+q})S_{n+q}\right], \qquad q = 1, \dots, n. \tag{14b}$$

The more important statistical properties of the network may be obtained when the random disturbances are not very large and any deterministic stimuli are fairly small and intermittent. The numerical solution of these equations, even for considerably large n, does not present major problems with modern computers. Now, under the assumption that the $2n$ network dynamical variables are jointly Gaussian distributed, which is expected to be approximately true for small $\{\beta_j\}$, the complete probability distribution of network variables can be obtained in terms of means, variances and covariances obtained as solutions of system (12),(14). Thus, if $P_k(t;\theta_k)$ is the probability that neuron k is firing at time t in the sense that its voltage is above some threshold value θ_k, whatever the values of recovery and potential variables of other cells, we can deduce the estimate $P_k(t;\theta) = 1 - \psi\left((m_k(t) - \theta_k)/\sqrt{S_k(t)}\right)$, where $\psi(\,.\,)$ is the standard normal distribution, $m_k(t)$ and $S_k(t)$ are the mean and variance of voltage variable.

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