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Noisy spiking neurons and networks: useful approximations for firing probabilities and global behavior

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Abstract

Electrophysiological properties of spiking neurons receiving complex stimuli perturbed by noise are investigated. A semi-analytical estimate of firing probabilities and subthreshold behavior of the stochastic system can be made in terms of the solution of a purely deterministic system. The method comes from an approximation for the distribution function and moments of the underlying non linear multidimensional diffusion process. This so called moment method works for general conductance-based systems and an application is presented for the Hodgkin–Huxley neuronal model. Statistical properties obtained from the moment method are compared with direct numerical integration of the stochastic system. The firing probability due to external noise is derived as a closed formula. Results are given for different forms of the deterministic component of the stimulus. A generalization to neural networks of conductance-based systems with internal currents perturbed by noise can be obtained using the same approach. In the case of fully connected networks, a mean field population equation is derived which may be compared to Kuramoto's master equation for weakly coupled neural oscillators. © 1998 Elsevier Science Ireland Ltd. All rights reserved.

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1. Statistical properties of noisy conductance-based models

It is a general rule that spatiotemporal patterns of neural responses are noisy. Thus, one may ask how the coding and decoding of stochastic signals is performed by neurons. This fluctuating aspect of neuronal activity has been analyzed by many authors during the last two decades (Guttman et al., 1974; Bryant and Segundo, 1976; Tuckwell, 1989; Kurrer and Schulten, 1991; Blanchard et al., 1993; Rospars and Lansky, 1993; Softky and Koch, 1993; Mainen and Sejnowski, 1995). For example, it has been shown (Softky and Koch,

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1993) that recordings in some cortical preparations, which exhibit a high degree of variability in the interspike interval, cannot be modeled by integrate and fire models. Moreover, one may consider that the finer details of the firing between spikes in a train can carry information (Barlow, 1963; Abeles and Gerstein, 1988; Hopfield and Hertz, 1995; Lestienne and Tuckwell, 1998). Thus, concerning these coding aspects and the role of noise, biologically plausible models neurons now have to incorporate sufficient physiological detail. Numerical integration of the non linear differential stochastic systems which govern the behavior of such single neurons or networks is often the only helpful tool.

In that way, one can analyze the role of noise in the spike event triggering mechanism. Actually, this task may be a rather tedious one in the case of large networks because of the necessary use of sufficiently many trials. In some cases, however, analytical formulas (Lecar and Nossal, 1971; Horikawa, 1992; Tuckwell, 1992; Rodriguez, 1995) can be obtained for the firing probabilities of nonlinear individual neuronal models under the action of noise. Recently, (Rodriguez and Tuckwell, 1996), we have proposed a semi analytical scheme which may be useful for the case of networks and which can give accurate estimates for the firing probabilities, in a direct manner, namely without sampling. The Fitzhugh–Nagumo single neuron and network models were also considered in relation to random spike trains (Tuckwell and Rodriguez, 1998). The inclusion of more realistic ionic currents is now described. Our derivation is applicable to a large class of space clamped neuronal models for which several ionic currents are necessary in order to reproduce the correct behavior.

A deterministic system may be obtained for the first and second moments of all variables of the system from which one can get the estimates of the probabilities of firing. In order to clarify the presentation, only the single neuron case has been considered here, while the results in (Rodriguez and Tuckwell, 1996) may be used to give results for the network. Finally, an illustration has been given for the original Hodgkin–Huxley model (Hodgkin and Huxley, 1952).

1.1. The stochastic system

In the following, we shall consider space clamped models of individual spiking neurons whose evolution may be described by an equation of the form, in the presence of white noise perturbation:

$$C\frac{\mathrm{d}V}{\mathrm{d}t} = \phi(V,\{U_i\}) + I_{\mathrm{ext}}(t,V) + \eta_t \tag{1.1}$$

where V is the membrane potential and $\{U_i\}_{i=1,2\ldots m}$ is an m-dimensional set of auxiliary variables. $\phi(V, \{U_i\})$ is a function describing the total ionic current I_{ions} across the neuronal membrane with capacitance C, $I_{\mathrm{ext}}\,(t, V)$ is an applied current and η_t is a white noise perturbation such that $<\eta_s\eta_t> = \beta\delta(s-t)$ where δ is the Dirac function. The dynamics of the auxiliary variables takes the form

$$\frac{\mathrm{d}U_i}{\mathrm{d}t} = \psi_i(V,\{U_i\}) \quad i = 1, 2\ldots m \tag{1.2}$$

where $\psi_i(V,\{U_i\}) = A_i^1(V)(1-U_i) - A_i^2(V)U_i$. The factors $(A_i^k(V))_{k=i,2,\, i=1,2\ldots m}$ are non linear functions of the potential V and may take different forms according to the type of cell considered.

1.2. The moment method

Our aim is to derive directly from the stochastic differential Eqs. (1.1) and (1.2), a deterministic dynamical system for the moments. This can be done with the help of the following assumptions which concern the distribution of the solutions. Let us assume that the transition function of the process $Z(t) = (V(t),\{U_i\}(t))$ is concentrated near its mean point and is symmetric about this point. Then third and higher order odd central moments are close to zero, fourth and higher order even moments are small relative to the second moments (see also Jaswinski, 1970).

Thus, it is possible to obtain approximate formulas for means of continuous functionals $G(Z(t),t)$ by retaining up to 2nd order terms in a Taylor expansion of the distribution function about the mean. In the following, we call $(\nu,\{\mu_i\})$ the means of the membrane potential V and the recovery variables $\{U_i\}$. S_V is the variance of V,

C_{VU_k} (resp $C_{U_lU_m}$) is the covariance of V and U_k (resp. U_l and U_m) while $H_\alpha = (\partial H/\partial\alpha)$, $H_{\alpha\beta} = (\partial^2 H/\partial\alpha\partial\beta)$ represent the first and second derivative of $H(v,\{\mu_i\})$ which are evaluated at the mean point. Using Ito calculus, one obtains the differential system:

$$\frac{\mathrm{d}v}{\mathrm{d}t} = \phi(v,\mu_1,\mu_2,\ldots,\mu_m) + I_{\mathrm{ext}}(t,v) + \frac{1}{2}\phi_{vv}S_V + \sum_{k=1}^{M}\phi_{v\mu k}C_{VUk} + \frac{1}{2}\sum_{k,l=1}^{m}\phi_{\mu k\mu l}C_{U_kU_l} \qquad (1.3)$$

Thus, there is a coupling of the mean with the variance S_V and covariances of all other variables. The means of the variables $U_1,U_2,\ldots,U_m$ satisfy a system of the form

$$\frac{\mathrm{d}\mu_i}{\mathrm{d}t} = \psi_i(v,\mu_1,\mu_2,\ldots,\mu_m) + \frac{1}{2}\psi_{i,vv}S_V + \psi_{i,v\mu_i}C_{VU_i} \qquad i = 1,2\ldots m \qquad (1.4)$$

A term like $\psi_{i,v\mu_i}$ represents the second derivative of $\psi_i(V,U_1,U_2,\ldots,U_m)$ with respect to V and U_i evaluated at $(v,\mu_1,\mu_2,\ldots,\mu_m)$.

Now, it can be shown that the variance S_V of the potential obeys the following differential equation

$$\frac{\mathrm{d}S_V}{\mathrm{d}t} = 2(\phi_v + I_{ext,v})S_V + 2\sum_{k=1}^{m}\phi_{\mu_k}C_{VU_k} + \beta^2 \qquad (1.5)$$

Finally, the systems of equations for the covariances C_{VU_i} between the potential and the recovery variables U_i and the covariances $C_{U_iU_j}$ between the recovery variables U_i and U_j are such that

$$\frac{\mathrm{d}C_{VU_i}}{\mathrm{d}t} = \psi_{i,v}S_V + (\phi_v + I_{\mathrm{ext},\,v} + \psi_{i,\mu_i})C_{VU_i} + \sum_{l=1}^{m}\phi_{\mu_l}C_{U_lU_i} \qquad i = 1,2\ldots m \qquad (1.6)$$

$$\frac{\mathrm{d}C_{U_iU_j}}{\mathrm{d}t} = \psi_{i,\,v}C_{VU_j} + \psi_{j,\,v}C_{VU_i} + (\psi_{i,\,\mu_i} + \psi_{j,\,\mu_j})C_{U_iU_j} \qquad i \le j = i, 2\ldots m \qquad (1.7)$$

Thus, we obtain a system $(\boldsymbol{\Gamma})$ of $((m+1)(m+4)/2)$ differential equations for the approximate first and second order moments of the noisy conductance-based neural system. Moreover, it can be shown (Tuckwell and Rodriguez, 1998), that the probability that, at a given time t, the voltage variable $V(t)$ is above some threshold θ, can be approximated by

$$P_\theta(t) = 1 - G\left(\frac{v(t)-\theta}{\sqrt{S_V(t)}}\right)$$

where $G(.)$ is the standard normal distribution, $v(t)$ and $S_V(t)$ being the mean and variance of $V(t)$ which are obtained as solutions of $(\boldsymbol{\Gamma})$.

As a result, the derivation of the solutions of this later system is helpful for the knowledge of the firing probability at any time. Generally, however, analytical solutions of $(\boldsymbol{\Gamma})$ cannot be obtained and the only way to go further rests on numerical integration of this deterministic system. As compared with the integration of the stochastic system (1.1, 1.2) with the use of sufficiently many samples, it can be said that the integration of $(\boldsymbol{\Gamma})$ is quite efficient with respect to computer time. Actually, this task has been done for relatively small noise amplitude in order to justify the hypothesis initially made on the distribution function. However, this amplitude has been chosen sufficiently high to allow the neuron to produce additional spikes.

2. Application to the Hodgkin–Huxley neuronal system

2.1. *The dynamical system of approximate moments*

The stochastic neuronal model of Hodgkin–Huxley is a particular case of the conductance-based system where $m = 3$ and the ionic currents function is given by $\Phi(V, U_1, U_2, \ldots U_m) = (v_{\mathrm{L}} - V)g_{\mathrm{L}} + (v_{\mathrm{K}} - V)g_{\mathrm{K}}n^4 + (v_{\mathrm{Na}} - V)g_{\mathrm{Na}}m^3h$ where $g_{\mathrm{L}}, g_{\mathrm{K}}, g_{\mathrm{Na}}, v_{\mathrm{L}}, v_{\mathrm{K}}, v_{\mathrm{Na}}$ are constants and the recovery variables (U_1, U_2, U_3) are usually denoted (m, h, n) with the meaning of sodium activation and inactivation and potassium activation. Their dynamics is such that $\Psi_i(V, U_1, U_2, \ldots, U_m) = A_i^1(V)(1 - U_i) - A_i^2(V)\,U_i$ where $(A_i^k(V))_{k=1,2.\,i=1,2,3}$ are of the type

$$A_i^k(V) = \frac{f_i^k(V)}{a_i^k e^{g_i^k(V)} + b_i^k}.$$

The functions $(f_i^k(V), g_i^k(V))_{k=1,2.i=1,2,3}$and the constants $(a_i^k, b_i^k)_{k=1,2.i=1,2,3}$ are given by:

$$f_1^1(V) = (2.5 - 0.1V) \quad a_1^1 = 1 \quad f_1^2(V) = 4 \quad a_1^2 = 1$$

$$g_1^1(V) = (2.5 - 0.1V) \quad b_1^1 = 1 \quad g_1^2(V) = 0.055V$$

$$b_1^2 = 0$$

$$f_2^1(V) = 0.07 \quad a_2^1 = 1 \quad f_2^2(V) = 1 \quad a_2^2 = 1$$

$$g_2^1(V) = 0.05V \quad b_2^1 = 0 \quad g_2^2(V) = 3 - 0.1V$$

$$b_2^2 = 1$$

$$f_3^1(V) = (0.1 - 0.01V) \quad a_3^1 = 1 \quad f_3^2(V) = 0.13$$

$$a_3^2 = 1$$

$$g_3^1(V) = 1 - 0.1V \quad b_3^1 = -1 \quad g_3^2(V) = 0.012V$$

$$b_3^2 = 0$$

The various derivatives of $\Phi(V, U_1, U_2, \ldots, U_m)$ which are taken at the mean values $(v, \mu_1, \mu_2, \ldots, \mu_m)$ are:

$$\Phi_v = g_L + \overline{g_k}\mu_3^4 + \overline{g_m}\mu_1^3\mu_2$$

$$\Phi_{v\mu_1} = -3\overline{g_m}\mu_1^2\mu_2, \ \Phi_{v\mu_2} = -\overline{g_m}\mu_1^3, \ \Phi_{v\mu_3} = -4\overline{g_k}\mu_3^3$$

$$\Phi_{\mu_1} = 3(v_{Na} - v)\overline{g_m}\mu_1^2\mu_2, \ \Phi_{\mu_2} = (v_{\mathrm{Na}} - v)\overline{g_m}\mu_1^3, \ \Phi_{\mu_3} = 4(v_{\mathrm{K}} - v)\overline{g_k}\mu_3^3$$

$$\Phi_{\mu_1\mu_1} = 6(v_{\mathrm{Na}} - v)\overline{g_m}\mu_1\mu_2, \ \Phi_{\mu_3\mu_3} = 12(v_{\mathrm{K}} - v)\overline{g_m}\mu_3^2$$

$$\Phi_{\mu_1\mu_2} = 3(v_{\mathrm{Na}} - v)\overline{g_m}\mu_1^2, \ \Phi_{vv} = \Phi_{\mu_2\mu_2} = \Phi_{\mu_1\mu_3} = \Phi_{\mu_1\mu_3} = \Phi_{\mu_2\mu_3} = 0 \tag{2.1}$$

The derivatives of Ψ_i, for each $i = 1, 2, 3$, are

$$\Psi_{i,v} = A_{i,v}^1(v)\,(1 - \mu_i) - A_{i,v}^2(v)\mu_i$$

$$\Psi_{i,vv} = A_{i,vv}^1(v)\,(1 - \mu_i) - A_{i,vv}^2(v)\mu_i$$

$$\Psi_{i,v\mu_j} = -\delta_{ij}(A_{i,v}^1(v) + A_{i,v}^2(v)) \quad j = 1, 2, 3$$

$$\Psi_{i,\mu_j} = -\delta_{ij}(A_{i,v}^1(v) + A_{i,v}^2(v)) \quad j = 1, 2, 3$$

$$\Psi_{i,v_l\mu_m} = 0 \quad \forall l, m = 1, 2, 3 \tag{2.2}$$

Finally, the system (Γ), which is composed here of 14 equations, can be obtained in terms of these formulas. It describes the evolution of the approximate means and variances of all variables and the covariances between potential and auxiliary variables of the Hodgkin–Huxley system.

2.2. The input current I_{ext} (t, V)

We have performed the numerical integration of this system for various input currents $I_{\mathrm{ext}}(t, V)$. They have been taken as the sum of a potential and time dependent current, $I_{\mathrm{syn}}(t, V)$ and an external current $I_0(t)$ which is only time dependent, namely $I_{\mathrm{ext}}(t, V) = I_{\mathrm{syn}}(t, V) + I_0(t)$.

The first part has the meaning of a synaptic current where there appear three groups of variables which are chosen in a random way and then fixed with respect to the white noise perturbation: $I_{\mathrm{syn}}(t, V) = \Sigma_{i=1}^{N} a_i\alpha(t - t_i)(-V + E_i)$. These variables are: $\{a_i\}_{i=1,\ldots,N}$ which are independent and identically uniformly randomly distributed on $\{0, 1\}$. These variables represent amplitudes of synaptic currents occurring at instants t_i which are randomly chosen in such a way that time intervals $t_{i+1} - t_i$ are exponentially distributed with parameter δ. Moreover, for each i, $g_i(t)$ is a synaptic conductance, for a synaptic event occurring at time t_i, which is defined as $g_i(t) = a_i\alpha(t - t_i)$.$\alpha$ is an alpha function of the form $\alpha(t) = \alpha_{\max}(\exp(-t/\tau_1) - \exp(-t/\tau_2))$. Finally, for a given choice of gaussian variables v_i with mean v and standard deviation σ,$E_i =$ $Esyn * v_i \quad i = 1, 2, \ldots, N$ represent synaptic reversal potentials. The second part of the input current $I_0(t)$ is only time dependent. It has been chosen as a step function $I_0(t) = i\mathrm{max}$ for $T_1 <$ $t < T_2$ and $I_0(t) = i\mathrm{min}$ for $0 \leq t \leq T_1$ or $T_2 \leq t \leq$ T_3. By taking various values for the parameter $\alpha_{\max}$ which modulates the amplitude of the synaptic conductances, it has been possible to control the spiking and non spiking activity of the model neuron when the amplitude of noise β is varying. All other parameters have been fixed at the following values: $\tau_1 = 1.0$ ms, $\tau_2 = 0.01$ ms, $\delta = 15$ ms, $E_{\mathrm{syn}} = 70$ mV, $imax = -1.0$ pA, $imin = -2.5$ pA, $T_1 = 35.0$ ms, $T_2 = 95.0$ ms, $T_3 = 100.0$ ms.

2.3. Numerical results

As a first step, the parameter $\alpha_{\max}$ may be chosen such that the behavior is under-threshold

$$A_i^k(V) = \frac{f_i^k(V)}{a_i^k e^{g_i^k(V)} + b_i^k}.$$

The functions $(f_i^k(V), g_i^k(V))_{k=1,2.i=1,2,3}$and the constants $(a_i^k, b_i^k)_{k=1,2.i=1,2,3}$ are given by:

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2.3. Numerical results

As a first step, the parameter $\alpha_{\max}$ may be chosen such that the behavior is under-threshold without noise. When the noise is acting and when $0 < \beta < 1$, one or more spikes may be created. When $\alpha_{\max}$ belongs to an interval $\{\alpha_0, \alpha_1\}$, only one spike is emitted (here $\alpha_0 = 0.1$, $\alpha_1 = 0.14$). In Fig. 1, we show a typical result which is obtained when $\alpha_{\max} = 0.13$ and $\beta = 0.3$. Several sample trajectories are plotted on the top of the figure with the occurrence of a spike which is due to noise. The means of the potential and the sodium inactivation variable are shown as they are obtained from the direct integration of the stochastic system with 1000 trials. It has been plotted on the same figure means as solutions of the system (**Γ**). Actually, the two curves are quite indistinguishable, except around the times of occurrence of spikes. In the same way, a comparison may be made for the potential and sodium inactivation variances (see Fig. 2).

Firing probability estimates can be made for events of the kind considered above (spike emission around $t_0 = 75$ ms, Fig. 1). This has been done when $\alpha_{\max}$ takes different values. In Fig. 3, $Max(P_\theta(t))$, where $P_\theta(t)$ has been defined above, is plotted (dashed lines) for $\alpha_{\max} = 0.12, 0.13, 0.14$ using (**Γ**) (from left to right). On the same figure, with values of $Max(P_\theta(t))$ which are restricted to the indicated range, is shown, using 1200 trials, the fraction of all trials such that $V > \theta$ with an evaluation around the time of spike emission. Along the same lines, we have considered, in a second step, the case where $\alpha_{\max}$ is high enough ($\alpha_{\max} = 3$, for example). There may be spiking without noise, additional spikes may take place due to noise and the results are of the same kind as before.

3. Mean field theory for stochastic conductance-based neural networks

It is possible to extend the results of Section 1 to networks of conductance-based models (see Rodriguez and Tuckwell, 1996). We present here another way which may be useful for the study of the global behavior of these systems. Here also, this problem is generally difficult to solve but there are some situations where approximation methods may give new insights. One such case occurs when neurons are globally coupled in networks. Actually, our aim is to go beyond weak coupling between cells, which may be viewed as oscillators, along a phase reduction procedure (Ermentrout and Kopell, 1990; Kuramoto, 1991; Hansel et al., 1995) and to derive a mean field population equation which may incorporate all the dynamical variables of the cells. Let us recall that such an approach has been done for integrate and fire neurons (Usher et al., 1993). We give here only a sketch of the derivation. The dynamical variables of each neuron are denoted $\tilde{X} = (V, \{U_i\}, s)$ where V is the membrane potential, $\{U_i\}$ are activation-inactivation variables, s is a

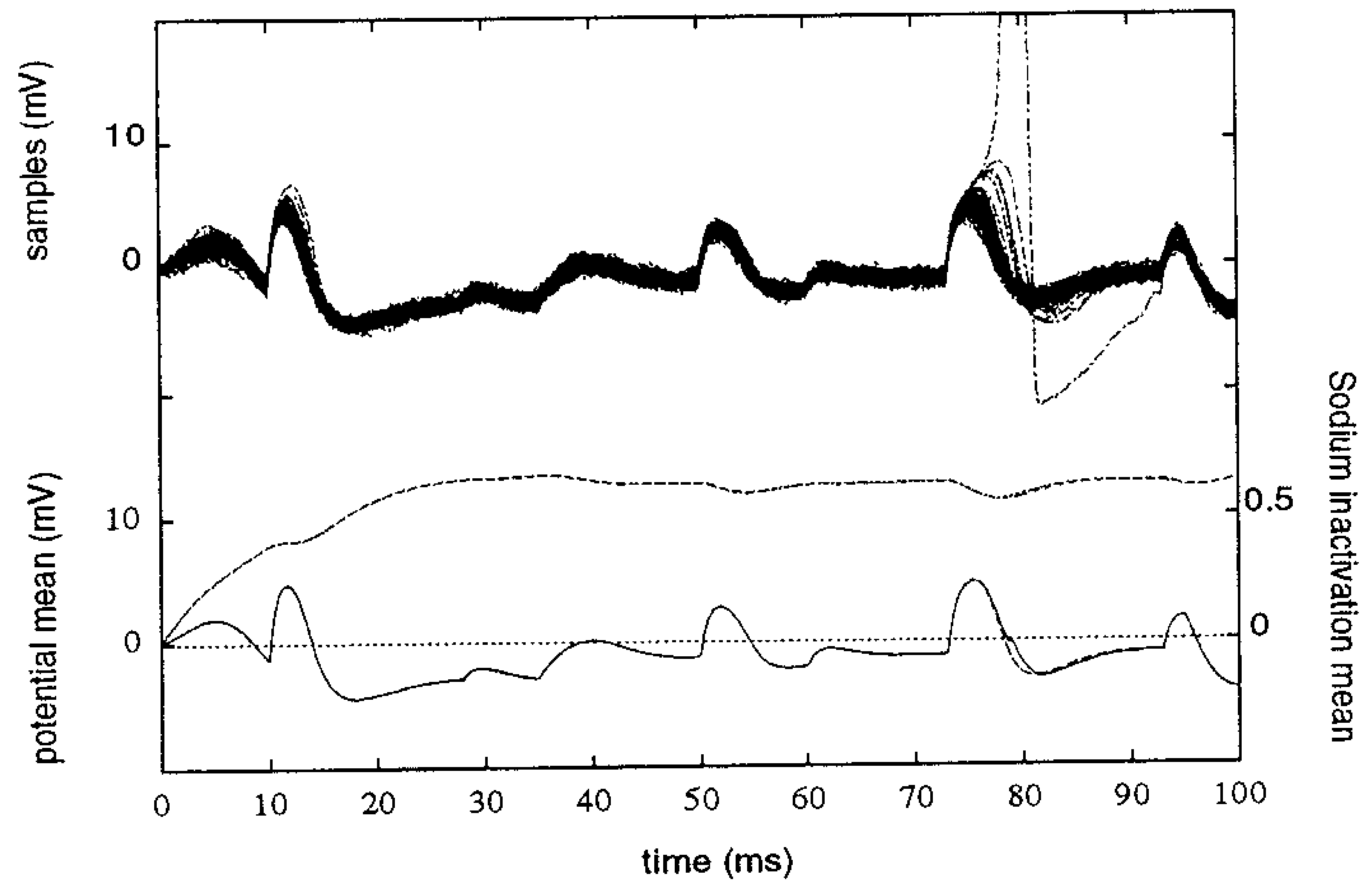

Fig. 1. Potential and Sodium inactivation means.

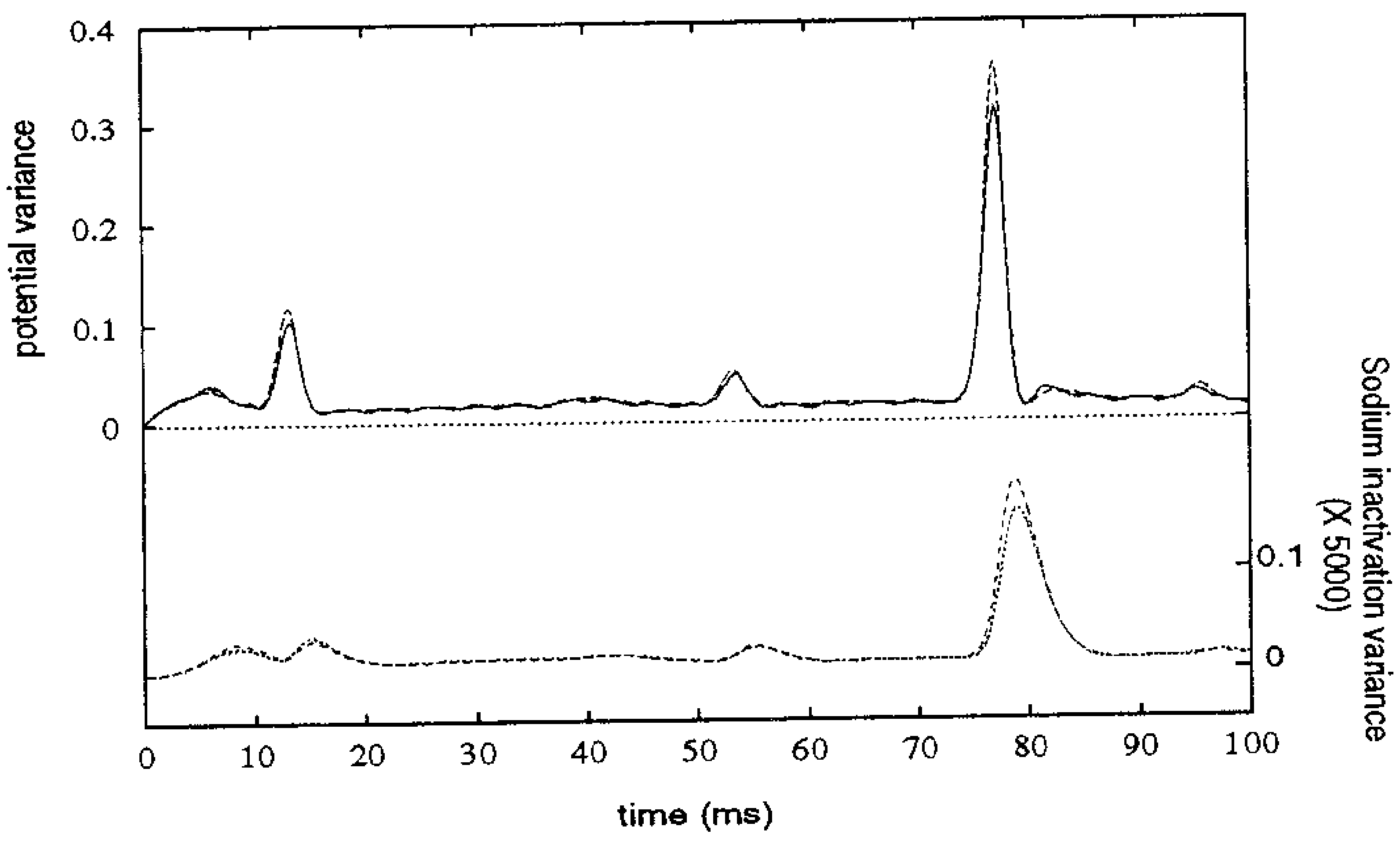

Fig. 2. Potential and Sodium inactivation variances.

synaptic variable. A typical system (Golomb and Rinzel, 1994) for N globally coupled neurons, with $k = 1, 2, \ldots, N$, is given by:

$$C\frac{\mathrm{d}V^k}{\mathrm{d}t} = \phi(V^k, \{U_i^k\}, s^k) + \frac{J_{\mathrm{syn}}}{N}(V^k - V_{\mathrm{syn}}) \sum_{l=1}^{N} s^l(t) + \beta^k \gamma_t^k$$

$$\frac{\mathrm{d}U_i^k}{\mathrm{d}t} = \psi_i^k(V^k, \{U_i^k\}) \quad i = 1, 2 \ldots m$$

$$\frac{\mathrm{d}s^k}{\mathrm{d}t} = M_1(V^k)(1 - s^k) - M_2 s^k \tag{3.1}$$

We have used in (3.1) the same notations as in Section 1. Moreover, γ_t^k are white noises such that $\langle \gamma_s^k \gamma_t^l \rangle = \delta^{kl}\delta(s - t)$ where δ^{kl} is the Kronecker symbol. $M_1(.)$ is a given sigmoidal function of the potential, M_2 is a constant, J_{syn} and V_{syn} are the maximal conductance and reversal potential of the synaptic currents. A general formulation of the dynamical behavior of such interacting neurons is

$$\frac{\mathrm{d}\tilde{X}^k}{\mathrm{d}t} = \tilde{\tilde{F}}(\tilde{X}^k) + \frac{J_{\mathrm{syn}}}{N} \sum_{j \neq k}^{N} \tilde{\tilde{G}}(\tilde{X}^j, \tilde{X}^k) + \tilde{\tilde{\beta}}^k \tilde{\eta}^k(t)$$

$$k = 1, 2, \ldots, N \tag{3.2}$$

where $\tilde{X}^k, \tilde{\eta}^k(t) \in R^n$, $\tilde{\tilde{F}}, \tilde{\tilde{\beta}}^k: R^n \to R^n$, $\tilde{\tilde{G}}: R^n * R^n \to R^n$ and $n = m + 2$.

In what follows, we shall consider noise perturbations as acting only on potential variables and the probability distribution of the stochastic variables $X = \{\tilde{X}^k\}_{k=1 \ldots N}$ will be denoted $p_t(\tilde{X}^1, \tilde{X}^2, \ldots, \tilde{X}^N)$. We define the ensemble variables as given, for each $\tilde{U} \in R^n$, by $n_X^*(\tilde{U}) = \frac{1}{N} \Sigma_{m=1}^{N} \delta(X_1^m - U_1) \ldots \delta(X_n^m - U_n)$ and we take expectations of these variables w.r.t p_t, namely: $n(\tilde{U}, t) = < n_X^*(\tilde{U}) >_{pt}$.

With the help of the Fokker Planck equation, it is possible to evaluate $(\partial n / \partial t)$. One obtains:

$$\frac{\partial n}{\partial t}(\tilde{U}, t) = \frac{\partial}{\partial \tilde{U}}(\tilde{\tilde{F}}(\tilde{U}) n(\tilde{U}, t)) + J_{\mathrm{syn}} \frac{\partial}{\partial \tilde{U}} \int d\tilde{X} \tilde{\tilde{G}}(\tilde{X}, \tilde{U}) \langle n*(\tilde{U}) n*(\tilde{X}) \rangle_{pt} + \frac{\partial}{\partial \tilde{U}} \left(\tilde{\tilde{\beta}} \frac{\partial}{\partial \tilde{U}} n(\tilde{U}, t) \right) \tag{3.3}$$

Here

$$\frac{\partial}{\partial \tilde{U}} \tilde{\tilde{H}}(\tilde{U}) = \sum_{i=1}^{n} \frac{\partial}{\partial U_i} H_i(\tilde{U}).$$

This equation is exact for these globally connected systems. To go further, we remark (as in Kuramoto (1991), for phase systems) that fluctuations of $n*(\tilde{U})$ are small, for N sufficiently high and are of the order $(1/\sqrt{N})$. Thus, one has the following estimate $\langle n*(\tilde{U}) n*(\tilde{X}) \rangle_{pt} \approx n(\tilde{U}, t)) n(\tilde{X}, t))$.

Finally, a mean field non-linear equation may be derived from the above exact equation

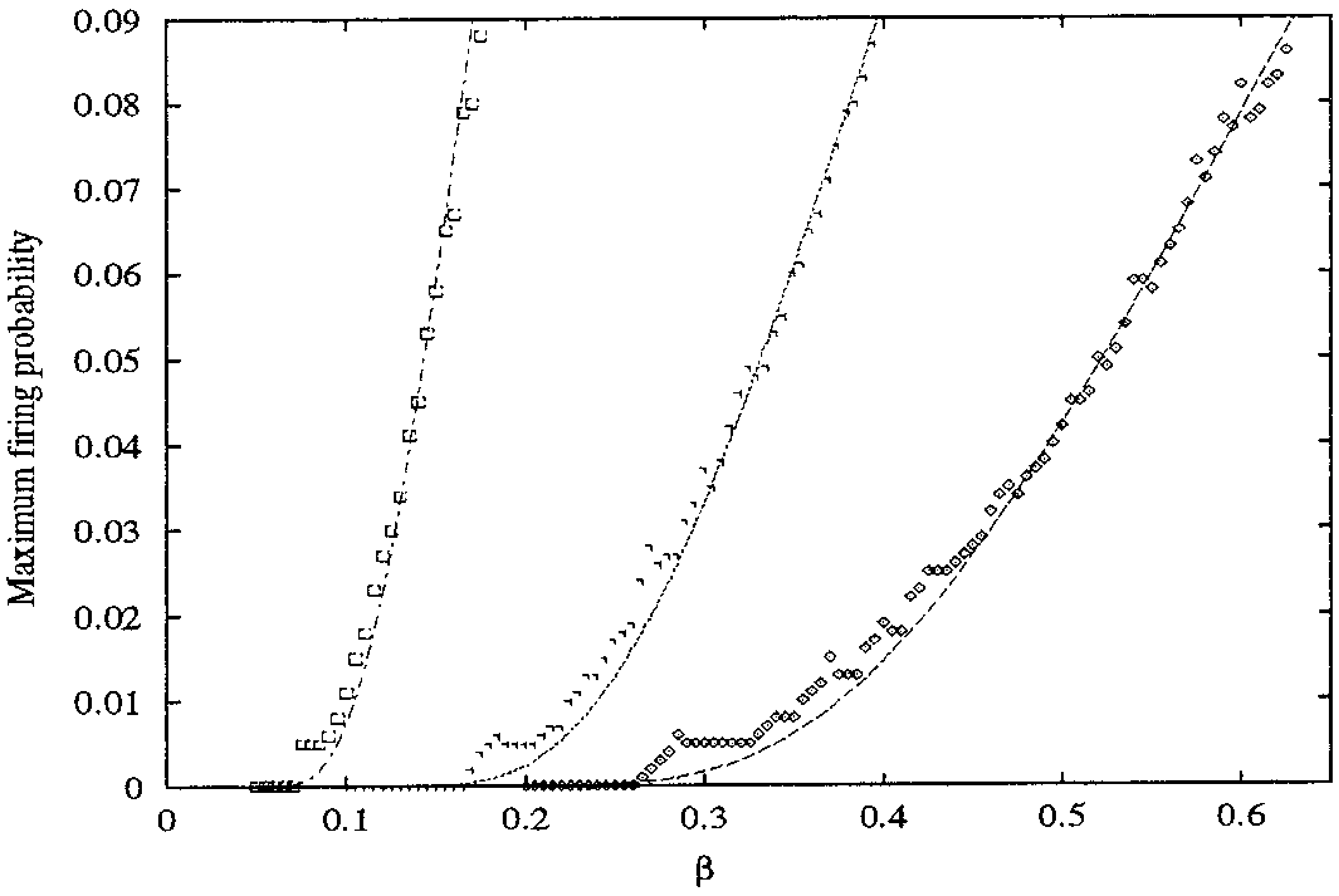

Fig. 3. Firing probabilities.

$$\frac{\partial n}{\partial t}(\tilde{U}, t) = \frac{\partial}{\partial \tilde{U}}\Bigg((\tilde{\tilde{F}}(\tilde{U})n(\tilde{U}, t)) + J_{\text{syn}} \int d\tilde{X}\tilde{\tilde{G}}(\tilde{X}, \tilde{U})n(\tilde{U}, t)n(\tilde{X}, t) + \tilde{\tilde{\beta}} \frac{\partial}{\partial \tilde{U}} n(\tilde{U}, t)\Bigg) \tag{3.4}$$

This non linear partial integro-differential equation may be viewed as a generalization of the population equation of Kuramoto (1991) (this later has been derived for oscillatory neurons under weak coupling). In a work in preparation, (Gandolfo et al., 1998), solutions of this equation are investigated in order to derive informations about synchronization and clustering effects of these globally coupled conductance-based neuronal systems.

4. Conclusion

We have shown that the moments of complex conductance based models of the Hodgkin–Huxley type which are perturbed by noise can be obtained as solutions of purely deterministic systems. Moreover, this moment method has appeared to be rather efficient in the prediction of firing probabilities when the noise is superimposed to rather general external synaptic inputs which are acting on the neuronal model. These statistical quantities may be readily obtained from simulations of the stochastic system. However, as it avoids the necessary use of many trials, the moment method appears to be useful in the case of systems with a great number of recovery variables and when such neuronal models are connected in networks. In that case, for globally coupled neurons, the smallness of fluctuations of the population variables allows the derivation of a mean field equation which may be used for a description of the global dynamics of the network.

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