Statistical properties of stochastic nonlinear dynamical models of single spiking neurons and neural networks

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Dynamical stochastic models of single neurons and neural networks often take the form of a system of $n \geqslant 2$ coupled stochastic differential equations. We consider such systems under the assumption that third and higher order central moments are relatively small. In the general case, a system of $\frac{1}{2}n(n+3)$ (generally) nonlinear coupled ordinary differential equations holds for the approximate means, variances, and covariances. For the general linear system the solutions of these equations give exact results—this is illustrated in a simple case. Generally, the moment equations can be solved numerically. Results are given for a spiking Fitzhugh-Nagumo model neuron driven by a current with additive white noise. Differential equations are obtained for the means, variances, and covariances of the dynamical variables in a network of n connected spiking neurons in the presence of noise. [S1063-651X(96)03511-8]

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I. INTRODUCTION

There has been much recent interest in stochastic models of neural activity either at the single neuron or network level [1–5]. In realistic such models of biological neurons the principal state variables are governed by systems of nonlinear differential equations such as those of Hodgkin and Huxley [6] or reduced systems such as those of Fitzhugh, Nagumo, Arimoto, and Yoshizawa [7,8]. We will refer to the latter systems as Fitzhugh-Nagumo systems.

In this article our main aim is to present and illustrate a method for analyzing the behavior of nonlinear stochastic neural models for both spiking neurons and networks of neurons. The types of model for which the analysis is most suitable are those in which a cell or a network of connected neurons is represented by dynamical equations of the form of a multidimensional system of coupled nonlinear stochastic differential equations. One example of such a model [3] consists of a collection of n noisy Fitzhugh-Nagumo model neurons. A general form for such dynamical models for stochastic neuronal networks or single neurons leads to the following system of $2n$ coupled nonlinear stochastic differential equations:

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

$$dY_j = h(X_j, Y_j) dt. \quad (2)$$

Here the X_j, $j=1,2,\ldots,n$ are voltage variables, the Y_j, $j=1,2,\ldots,n$ are recovery variables, J_{jk} are synaptic weights for the connection from neuron k to neuron j, and $\Theta(\ )$ is a threshold function, often taken as sigmoidal in shape [9], 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. On the other hand, models for the large-scale activity of neural networks may also be governed by coupled nonlinear equations such as those of Wilson and Cowan [10].

In order to study the properties of such multidimensional diffusion processes, one may consider solving the Kolmogorov or Fokker-Planck equation for the transition probability density function. However, it is a partial differential equation with, in the case of an n-component system, $n+1$ independent variables which presents, in the case of large n, a large computational task even on modern large computing systems. It is useful to have analytical or semianalytical techniques to apply to these problems in addition to that of numerically solving the Fokker-Planck equation. In practical computations with multidimensional diffusion processes, the most frequent methods employed are Monte Carlo simulation [11] or moment calculation [12]. In addition, in some cases a stationary probability distribution can be found [13] either analytically or numerically.

Because there are many different forms for the stochastic differential equations which arise in modeling of single neurons and networks of connected neurons, we will obtain, in a general case, differential equations for moments up to those of order 2 (though this can easily be extended) for each component in a multidimensional nonlinear system of diffusion processes. The form of the system studied includes many of the above mentioned neurobiological models, both for single neurons [14] and for networks, including that described by Eq. (1) [1,3,4].

II. GENERAL RESULTS

Although the primary motivation for this article comes from the need for neurodynamical theories, because nonlinear systems of stochastic differential equations have frequently been employed as mathematical models in the physical, chemical, and biological sciences [13,15], we will first consider a general system of coupled diffusion processes.

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We shall then consider, in Sec. III, the specialization of the techniques to a biologically realistic model of a spiking single neuron, with an example of the numerical results obtained, and a general neural network model in Sec. IV.

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

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

where $j=1,2,\ldots,n$ and $m\geqslant 1$. The $W_k=\{W_k(t),t\geqslant 0\}$, $k=1,2,\ldots,m$ are standard Wiener processes (that is, they each have zero mean, initial value zero with probability one, and variance equal to t at time t) which we assume are independent. The latter assumption can be relaxed without difficulty but it usually is taken to hold. It is also assumed that existence and uniqueness conditions [16] for the solution of Eq. (3) are fulfilled.

Define the n means for the various components

$$\overline{X_j}(t)=E[X_j(t)],$$

where $j=1,\ldots,n$, and the n^2 quantities

$$K_{ij}(t)=E[(X_i(t)-\overline{X_i}(t))][(X_j(t)-\overline{X_j}(t))],$$

where $i,j=1,\ldots,n$. Of these n^2 quantities there are n variances,

$$V_j(t)=E[(X_j(t)-\overline{X_j}(t))]^2,$$

where $j=1,\ldots,n$, and $\frac{1}{2}n(n-1)$ distinct covariances, $K_{ij}(t)$ with $i<j$. These $\frac{1}{2}n(n+3)$ first and second order central moments, under certain assumptions about the probability distribution of $\mathbf{X}(t)$, satisfy a system of $\frac{1}{2}n(n+3)$ nonlinear ordinary differential equations. This system of deterministic equations, associated with the stochastic system described by Eq. (3), is found by first finding differential equations for these moments which hold exactly. For the means we have immediately, on using general integration according to the Itô definition [17], the integro-differential equation

$$\frac{d\overline{X_j}(t)}{dt}=E[f_j(\mathbf{X}(t),t)]. \qquad (4)$$

The application of Itô's formula [16] to the quantities $K_{ij}(t)$, including the cases $i=j$, in conjunction with (3) yields the following integro-differential equations for the covariances and variances:

$$\frac{dK_{ij(t)}}{dt}=E\Bigg[(X_i(t)-\overline{X_i}(t))f_j(\mathbf{X}(t),t)+(X_j(t)-\overline{X_j}(t))\times f_i(\mathbf{X}(t),t)+\sum_{k=1}^{m} g_{ik}(\mathbf{X}(t),t)g_{jk}(\mathbf{X}(t),t)\Bigg]. \qquad (5)$$

Note that Eqs. (4) and (5) hold exactly.

From these equations, approximate differential equations can be found for the first and second order moments under the assumption that the distribution function of $\mathbf{X}(\mathbf{t})$ is concentrated near the mean point $\mathbf{X}(t)=(X_1(t),X_2(t),\ldots,X_n(t))$ [that is, $\Pr\{|\mathbf{X}(t)-\mathbf{X}(t)|<\epsilon\}$, for some (usually small) positive ϵ, is close to 1] and is symmetric about this point [18]. It then follows that third and higher order odd central moments are close to zero and that fourth and higher order even moments are small relative to the second moment. Expectations can thus be calculated approximately by retaining up to second order terms in a Taylor expansion of the distribution function about the mean. Thus if $G(x_1,x_2,\ldots,x_n)$ is a real-valued function of n variables, then one has the following approximation formula:

$$E[G(\mathbf{X}(t),t)]\approx G(\mathbf{m},t)+\frac{1}{2}\sum_{l=1}^{n}\sum_{p=1}^{n}\left\{\frac{\partial^2 G}{\partial x_l\partial x_p}\right\}_{(\mathbf{m},t)} C_{lp}, \qquad (6)$$

where $\mathbf{m}=\mathbf{m}(t)$ is the approximation to $\overline{\mathbf{X}}(t)$ and $C_{lp}=C_{lp}(t)$ is the approximation to $K_{lp}(t)$. The notation

$$\left\{\frac{\partial^2 G}{\partial x_l\partial x_p}\right\}_{(\mathbf{m},t)}$$

means evaluation of the (deterministic) indicated derivative of the indicated (real) function $G(x_1,x_2,\ldots,x_n,t)$ at the deterministic point $(m_1(t),m_2(t),\ldots,m_n(t),t)$.

Applying (6) to Eqs. (4) for the means gives immediately the required n differential equations for these quantities:

$$\frac{dm_j}{dt}=f_j(\mathbf{m},t)+\frac{1}{2}\sum_{l=1}^{n}\sum_{p=1}^{n}\left\{\frac{\partial^2 f_j}{\partial x_l\partial x_p}\right\}_{(\mathbf{m},t)} C_{lp}. \qquad (7)$$

To obtain approximate differential equations for the variances and covariances we first consider the first part of (5). On applying (6) we find that this is given by

$$E[(X_i(t)-m_i(t))f_j(\mathbf{X}(t),t)]$$
$$=\frac{1}{2}\sum_{l=1}^{n}\sum_{p=1}^{n}\left\{\frac{\partial^2}{\partial x_l\partial x_p}[(x_i-m_i)f_j]\right\}_{(\mathbf{m},t)} C_{lp}. \qquad (8)$$

Since

$$\left\{\frac{\partial^2}{\partial x_l\partial x_p}[(x_i-m_i)f_j]\right\}_{(\mathbf{m},t)}=\left\{\delta_{il}\frac{\partial f_j}{\partial x_p}+\delta_{ip}\frac{\partial f_j}{\partial x_l}\right\}_{(\mathbf{m},t)}, \qquad (9)$$

where δ_{jk} is Kronecker's delta (equal to 1 for $j=k$ and 0 otherwise), we find after some algebra, and utilizing the fact that the term $E[(\mathrm{X_j(t)-m_j(t)})\mathrm{f_i}(\mathbf{X}(t),t)]$ is just (8) with i and j reversed,

$$\frac{dC_{ij}(t)}{dt}=\sum_{l=1}^{n}\left\{\frac{\partial f_i}{\partial x_l}\right\}_{(\mathbf{m},t)}C_{lj}+\sum_{l=1}^{n}\left\{\frac{\partial f_j}{\partial x_l}\right\}_{(\mathbf{m},t)}C_{il}$$
$$+\sum_{k=1}^{m}\left\{g_{ik}g_{jk}+\frac{1}{2}\sum_{l=1}^{n}\sum_{p=1}^{n}\left[g_{jk}\frac{\partial^2 g_{ik}}{\partial x_l\partial x_p}+\frac{\partial g_{ik}}{\partial x_l}\frac{\partial g_{jk}}{\partial x_p}+\frac{\partial g_{ik}}{\partial x_p}\frac{\partial g_{jk}}{\partial x_l}+g_{ik}\frac{\partial^2 g_{jk}}{\partial x_l\partial x_p}\right]\right\}_{(\mathbf{m},t)}C_{lp}. \tag{10}$$

Thus (10), in general, gives the sought after differential equations for the second order central moments, including the required covariances. In the event that $i=j$ Eq. (10) yields the following differential equation for the variances $S_j(t)\approx V_j(t)$:

$$\frac{dS_j(t)}{dt}=2\left[\left\{\frac{\partial f_j}{\partial x_j}\right\}_{(\mathbf{m},t)}S_j+\sum_{l\neq j}^{n}\left\{\frac{\partial f_j}{\partial x_l}\right\}_{(\mathbf{m},t)}C_{lj}\right]+\sum_{k=1}^{m}\left[g_{jk}^2(\mathbf{m},t)+\sum_{l=1}^{n}\left\{\left(\frac{\partial g_{jk}}{\partial x_l}\right)^2+g_{jk}\frac{\partial^2 g_{jk}}{\partial x_l^2}\right\}_{(\mathbf{m},t)}S_l\right.$$
$$\left.+\sum_{l=1}^{n}\sum_{p=1}^{n}{}'\left\{\frac{\partial g_{jk}}{\partial x_p}\frac{\partial g_{jk}}{\partial x_l}+g_{jk}\frac{\partial^2 g_{jk}}{\partial x_l\partial x_p}\right\}_{(\mathbf{m},t)}C_{lp}\right], \tag{11}$$

where the prime denotes summation with $l\neq p$.

Although in general Eqs. (7) and (10) are quite complicated, simplifications may occur in certain cases; and in others, it is found that these equations actually give exact rather than approximate values for the means, variances, and covariances of the dynamical variables. These special cases are discussed in the Appendix.

III. A NONLINEAR STOCHASTIC SPIKING NEURON MODEL

We will apply the above framework to determine the means and second order central moments of a two-component neuron model with additive white noise in the first component. There are several such systems [19] but we have chosen the Fitzhugh-Nagumo system which has been employed to provide insight into the more complex Hodgkin-Huxley system of four equations. It shares with the latter the properties of 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. Then,

$$dX=[f(X)-Y+I]dt+\beta dW, \tag{12}$$

$$dY=b(X-\gamma Y)dt, \tag{13}$$

where $X=X(t)$ is the ‘‘voltage’’ variable, $Y=Y(t)$ is the recovery variable, $W=\{W(t),t\geqslant 0\}$ is a standard Wiener process, I is a deterministic input current (stimulus) which is taken to be a constant, and b and γ are positive constants. The function f is a cubic,

$$f(x)=kx(x-a)(1-x), \tag{14}$$

where $0<a<1$. Usually one takes $a<\frac{1}{2}$ in order to obtain suitable suprathreshold responses.

Application of the method outlined in the preceding section gives the following five coupled differential equations for the approximate means, variances, and the covariance between the two components:

$$\frac{dm_1}{dt}=f(m_1)-m_2+\frac{1}{2}f''(m_1)S_1+I, \tag{15}$$

$$\frac{dm_2}{dt}=b(m_1-\gamma m_2), \tag{16}$$

$$\frac{dS_1}{dt}=2f'(m_1)S_1-2C_{12}+\beta^2, \tag{17}$$

$$\frac{dS_2}{dt}=2b(C_{12}-S_2), \tag{18}$$

$$\frac{dC_{12}}{dt}=bS_1-S_2+C_{12}[f'(m_1)-\gamma b]. \tag{19}$$

With $f'(m_1)=k[2m_1(1+a)-a-3m_1^2]$ and $f''(m_1)=k[2(1+a)-6m_1]$, Eqs. (15)–(19) may be solved numerically.

We give an illustrative example of the computation of the moments with the following parameter values: $k=0.5$, $a=0.1$, $b=0.015$, γ=0.2, $I=1.5$, β=0.01. We employed a fourth order Runge-Kutta method with a step size of $\Delta t=0.1$ or smaller. Initial conditions were chosen as $m_1(0)=m_2(0)=1$, $S_1(0)=S_2(0)=C_{12}(0)=0$.

Results are shown in Fig. 1 for the means, $m_1(t)$ and $m_2(t)$, in Fig. 2 for the variance of the first or potential variable, $S_1(t)$, and in Fig. 3 for the variance of the recovery variable, $S_2(t)$, and the covariance of the two components. For these quantities, excellent agreement was obtained with the corresponding quantities for Monte Carlo simulations which are not shown here. When the noise parameter β increases sufficiently, the systems (15)–(19) for the moment approximations may eventually become unstable and periodic solutions no longer pertain. We plan to make a more detailed study of simulation studies in the future.

We note that not only can a single space-clamped neuron model be treated with the present method, but also a compartmental model in which the cell is represented by a system of coupled ordinary differential equations, one for each

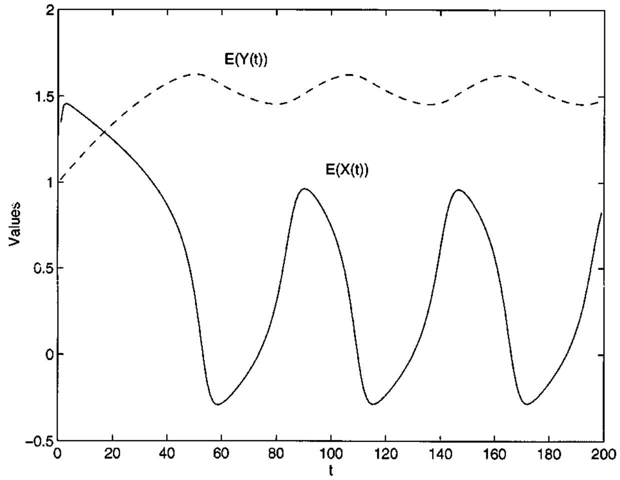

FIG. 1. The means of $X(t)$ and $Y(t)$ in the Fitzhugh-Nagumo model obtained from the system of differential equations (15)–(19). Parameter values here and in the next two figures are given in the text.

dendritic (and possibly axonal) segment and for the soma. We also plan to illustrate this in a future article.

IV. A NETWORK OF SPIKING NEURONS

In this section we will derive dynamical equations for the first and second order moments in a neuronal network governed by the stochastic system (1). Note that even when delays due to transmission of nerve impulses or synaptic delays are included, this form of model can still be appropriate if the delays are not very large.

It is useful to rename the $2n$ dynamical variables as $U_j = X_j$, $U_{j+n} = Y_j$, $j = 1,\ldots,n$, so that the system may be written

$$dU_j = \left[\phi(U_j, U_{j+n}) + I_j(t) + \sum_{k=1}^{n} J_{jk}\Theta(U_k) \right] dt + \beta_j dW_j, \tag{20}$$

$$dU_{j+n} = h(U_j, U_{j+n})dt,$$

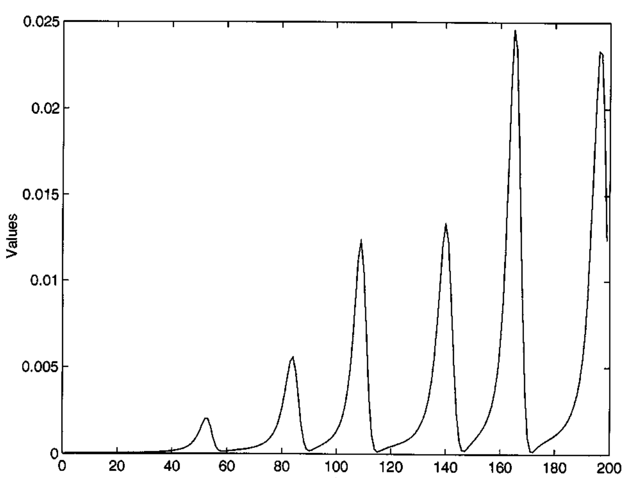

FIG. 2. The variance, $S_1(t)$, of the neuronal potential variable, determined by solving the differential equations.

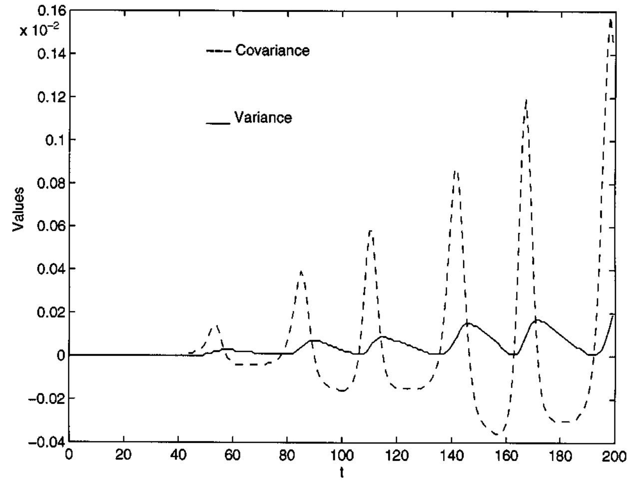

FIG. 3. The variance, $S_2(t)$, of the recovery variable in the model neuron, and the covariance, $C_{12}(t)$, of the voltage and recovery variables calculated from the differential equations (15)–(19).

where again $j = 1,2,\ldots,n$. Then it follows from (7) that the following differential equations hold for the approximate means of the voltage and recovery variables of the n neurons:

$$\frac{dm_j}{dt} = \phi(m_j, m_{j+n}) + I_j(t) + \sum_{k=1}^{n} J_{jk}\Theta(m_k) + \frac{1}{2}\Bigg[\phi_{xx}(m_j, m_{j+n})S_j + 2\phi_{xy}(m_j, m_{j+n})C_{j,j+n} + \phi_{yy}(m_j, m_{j+n})S_{j+n} + \sum_{k=1}^{n} J_{jk}\Theta''(m_k)S_k \Bigg], \tag{21a}$$

and

$$\frac{dm_{j+n}}{dt} = h(m_j, m_{j+n}) + \frac{1}{2}[h_{xx}(m_j, m_{j+n})S_j + 2h_{xy}(m_j, m_{j+n})C_{j,j+n} + h_{yy}(m_j, m_{j+n})S_{j+n}], \tag{21b}$$

where $j = 1,2,\ldots,n$, and subscripts x,y denote derivatives.

We can also find the equations satisfied by the second order moments for each network neuronal variable. Using (10) we have, for $1 \leqslant j \leqslant i \leqslant n$,

$$\frac{dC_{ij}}{dt} = [\phi_x(m_i, m_{i+n}) + \phi_x(m_j, m_{j+n})]C_{ij} + \phi_y(m_i, m_{i+n})C_{i+n,j} + \phi_y(m_j, m_{j+n})C_{i,j+n} + \beta_i^2 + \beta_j^2. \tag{22a}$$

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

$$\frac{dC_{n+q,j}}{dt}=[\phi_x(m_j,m_{n+j})+h_y(m_q,m_{n+q})]C_{n+q,j}+\phi_y(m_j,m_{n+j})C_{n+q,n+j}+h_x(m_q,m_{n+q})C_{qj}+\sum_{k=1}^{n}\Theta'(m_k)J_{kk}C_{n+q,k}, \quad (22b)$$

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

$$\frac{dC_{n+q,n+r}}{dt}=h_x(m_q,m_{n+q})C_{q,n+r}+h_x(m_r,m_{n+r})C_{n+q,r}+[h_y(m_q,m_{n+q})+h_y(m_r,m_{n+r})]C_{n+q,n+r}, \quad (22c)$$

where q and r range from 1 to n.

The following relatively simple differential equations for the variances are obtained:

$$\frac{dS_i}{dt}=2[\phi_x(m_i,m_{i+n})S_i+\phi_y(m_i,m_{i+n})C_{i,i+n}+\beta_i^2], \quad i=1,\ldots,n \quad (23a)$$

and

$$\frac{dS_{n+q}}{dt}=2[h_x(m_q,m_{n+q})C_{q,n+q}+h_y(m_q,m_{n+q})S_{n+q}], \quad q=1,\ldots,n. \quad (23b)$$

Using (21)–(23) 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. For example, in the Fitzhugh-Nagumo case, one takes

$$\phi(x,y)=f(x)-y,$$

where $f(\ )$ is given by (14). The numerical solution of these equations, even for considerably large n, does not present major problems with modern computers. We plan to report solutions and their properties for various network dynamics and architectures elsewhere.

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APPENDIX

In this appendix we consider some simplifications which occur in certain special cases of the system of equations considered in Sec. II.

1. Additive noise terms

If we assume that all coefficients of the dW_k in (3) are functions of time only, $g_{jk}=g_{jk}(t)$, we may set

$$\sum_{k=1}^{m} g_{jk}^2(t)=\beta_j^2(t), \quad (A1)$$

in which case the differential equations for the variances simplify to

$$\frac{dS_j(t)}{dt}=2\left[\left\{\frac{\partial f_j}{\partial x_j}\right\}_{(\mathbf{m},t)}S_j+\sum_{l\neq j}^{n}\left\{\frac{\partial f_j}{\partial x_l}\right\}_{(\mathbf{m},t)}C_{lj}\right]+\beta_j^2(t). \quad (A2)$$

Two components

There are many classical nonlinear models in which there are two components. Examples are the Lotka-Volterra system of predator-prey interactions and many reduced neuronal models, one of which was considered above. We let the governing stochastic differential equations be

$$dX=f(X,Y,t)dt+a_1(t)dW_1+a_2(t)dW_2 \quad (A3)$$

and

$$dY=g(X,Y,t)dt+b_1(t)dW_1+b_2(t)dW_2, \quad (A4)$$

where the coefficients of the noise terms are deterministic functions of time. Then we have the following five coupled, generally nonlinear, equations for the two means, two variances, and the covariance:

$$\frac{dm_1}{dt}=f(\mathbf{m},t)+\frac{1}{2}[f_{xx}(\mathbf{m},t)S_1+f_{yy}(\mathbf{m},t)S_2+f_{xy}(\mathbf{m},t)C_{12}], \quad (A5)$$

$$\frac{dm_2}{dt}=g(\mathbf{m},t)+\frac{1}{2}[g_{xx}(\mathbf{m},t)S_1+g_{yy}(\mathbf{m},t)S_2+g_{xy}(\mathbf{m},t)C_{12}], \quad (A6)$$

$$\frac{dS_1}{dt}=2[f_x(\mathbf{m},t)S_1+f_y(\mathbf{m},t)C_{12}]+\alpha^2(t), \quad (A7)$$

$$\frac{dS_2}{dt}=2[g_y(\mathbf{m},t)S_2+g_x(\mathbf{m},t)C_{12}]+\beta^2(t), \quad (A8)$$

$$\frac{dC_{12}}{dt}=f_y(\mathbf{m},t)S_2+[f_x(\mathbf{m},t)+g_y(\mathbf{m},t)]C_{12}+g_x(\mathbf{m},t)S_1, \quad (A9)$$

where $\alpha^2=a_1^2+a_2^2$ and $\beta^2=b_1^2+b_2^2$ and subscripts denote differentiation with respect to the indicated variables.

2. The general linear stochastic system

If all of n stochastic equations (3) are linear we may write

$$dX_j(t)=\left(\sum_{q=1}^{n} A_{jq}(t)X_q(t)+a_j(t)\right)dt+\sum_{k=1}^{m}\left(\sum_{q=1}^{n} B_{jqk}(t)X_q(t)+b_{jk}(t)\right)dW_k(t). \tag{A10}$$

In this case the differential equations for the means become

$$\frac{dm_j(t)}{dt}=\sum_{q=1}^{n} A_{jq}(t)m_q(t)+a_j(t), \tag{A11}$$

and this system may be solved explicitly by employing its fundamental matrix. The equations for the covariances are

$$\frac{dC_{ij}}{dt}=A_{ji}S_i+A_{ij}S_j+\sum_{l\neq i}^{n} A_{jl}C_{il}+\sum_{l\neq j} A_{il}C_{lj}+\sum_{k=1}^{m}\left[g_{ik}(\mathbf{m},t)g_{jk}(\mathbf{m},t)+\sum_{l=1}^{n} B_{ilk}B_{jlk}S_l+\sum_{l\neq p}^{n} B_{ilk}B_{jpk}C_{lp}\right], \tag{A12}$$

where

$$g_{jk}(\mathbf{x},t)=b_{jk}(t)+\sum_{q=1}^{n} B_{jqk}(t)x_q. \tag{A13}$$

The differential equations for the variances follow from this formula on setting $i=j$. The variances and covariances may thus also be obtained explicitly using the fundamental matrix because the inhomogeneous terms are known. Furthermore, all the differential equations for the means, variances, and covariances so obtained are the same as those satisfied by these quantities exactly [20]. We may conclude, appealing to uniqueness theorems for the solutions of linear systems of differential equations, that the above approximation procedure gives exact results for a general linear stochastic system of the form of (A10). A simple verification of this follows.

An example

We will illustrate in a one-dimensional linear case that the first and second order moments predicted by the approximation procedure coincide exactly with the known values. The following stochastic differential equation has arisen in various applications [21]:

$$dX=\mu X dt+\sigma X dW, \tag{A14}$$

where it is assumed that $X(0)=x_0$ with probability one. The transition probability densities for $X(t)$ and its moments are known exactly, since a monotonic transformation takes X to a Wiener process. Letting the mean and variance of $X(t)$ be $m(t)$ and $S(t)$, respectively, application of the above formulation gives the following differential equations for m and S:

$$\frac{dm}{dt}=\mu m, \tag{A15}$$

$$\frac{dS}{dt}=\sigma^2 m^2+(2\mu+\sigma^2)S. \tag{A16}$$

The solutions of these equations with $m(0)=x_0$ and $S(0)=0$ are

$$m(t)=x_0 e^{\mu t}, \tag{A17}$$

$$S(t)=x_0^2 e^{2\mu t}(e^{\sigma^2 t}-1), \tag{A18}$$

which are exactly the known mean, $\overline{X(t)}$, and variance $V(t)$ for $X(t)$.

[1] D. Golomb, X-J. Wang, and J. Rinzel, J. Neurophysiol. **72**, 1109 (1994).

[2] Y. Horikawa, Biol. Cybern. **67**, 253 (1992).

[3] L. Kruglyak and W. Bialek, Neural. Comp. **5**, 21 (1993).

[4] R. Rodriguez, *Modern Group Theoretical Methods in Physics*, edited by J. Bertrand *et al.* (Kluwer, Amsterdam, 1995), pp. 233–242.

[5] H. C. Tuckwell, Phys. Scr. **46**, 481 (1992).

[6] A. L. Hodgkin and A. F. Huxley, J. Physiol. **117**, 500 (1952).

[7] R. Fitzhugh, Biophys. J. **1**, 445 (1961).

[8] J. S. Nagumo, S. Arimoto, and S. Yoshizawa, Proc. IRE **50**, 2061 (1962).

[9] J. J. Hopfield, Phys. Today **47**, 40 (1994).

[10] E. R. Grannan, D. Kleinfeld, and H. Sompolinsky, Neural. Comp. **5**, 550 (1993); H. R. Wilson and J. D. Cowan, Biophys. J. **12**, 1 (1972).

[11] V. Loreto, G. Paladin, and A. Vulpiani, Phys. Rev. E **53**, 2087 (1996).

[12] H. K. Leung, Phys. Rev. A **30**, 2609 (1984).

[13] C. Van den Broeck, J. M. R. Parrondo, and R. Toral, Phys. Rev. Lett. **73**, 3395 (1994); M. Malek-Mansour and J. Houard, Phys. Lett. A **70**, 366 (1979); R. F. Fox, Phys. Rep. **48**, 179 (1978).

[14] H. C. Tuckwell, *Stochastic Processes in the Neurosciences* (SIAM, Philadelphia, 1989).

[15] M. Roncadelli, Phys. Rev. E **52**, 4661 (1995).

[16] I. I. Gihman and A. V. Skorohod, *Stochastic Differential Equations* (Springer-Verlag, Berlin, 1972).

[17] Note that processes defined by stochastic differential equations such as (1) are specified if a definition of stochastic integral is chosen. Specifying that this is an Itô integral is a matter of convenience as the drift terms can then be read directly from the equations. Any such system can be transformed to that appropriate for Stratonovich integration.

[18] A. H. Jaswinski, *Stochastic Processes and Filtering Theory* (Academic, New York, 1970).

[19] C. Meunier, Biol. Cybern. **67**, 461 (1992).

[20] L. Arnold, *Stochastic Differential Equations: Theory and Applications* (Wiley, New York, 1974).

[21] H. C. Tuckwell, *Elementary Applications of Probability Theory: With an Introduction to Stochastic Differential Equations*, 2nd ed. (Chapman and Hall, London, 1995).