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Single effective neuron

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We consider a network of N symmetrically interconnected neurons. Through the procedure of adiabatic elimination (separation of time scales), the dynamics of a single neuron is obtained, in closed form, from the system of coupled differential equations that describe the N-neuron problem. For the deterministic case, our approach yields an explicit form for the single-neuron "self-coupling" term J_{11}. The case of noisy neurons containing both Langevin and multiplicative noise (in the synaptic connections) is also considered.

I. INTRODUCTION

Since the work of Hopfield,[1,2] considerable interest has been generated in physics and engineering in mathematical neuron network models having the idealized properties of their biological counterparts.[3–6] These information processing networks containing relatively simple constituents have allowed the analysis and also the simulation of thousands of elements. If, furthermore, the synaptic connections are taken to be symmetric, the model is equivalent to a spin-glass system and the ideas of mean-field theory and statistical mechanics may be utilized in the analysis.[3,7–10] It has been recognized that these admittedly gross oversimplifications of the biological arena may indeed represent new insights into the cognitive processes of the brain as well as suggest new nonlinear methods of computing.

In contrast to nonlinear coupled neural networks, there has been a recent upsurge of interest in *single*- (isolated) or few-neuron nonlinear dynamics. In particular, Babcock and Westervelt[11] have examined simple models involving one or two nonlinear threshold switching elements, which they model as coupled Hopfield neurons. By introducing inertial terms in the dynamics they demonstrate complicated bifurcation behavior including chaos. Their model of a single neuron with additive and multiplicative noise terms was considered by Bulsara, Boss, and Jacobs.[12] It was found that multiplicative noise (in the synapic connection) could suppress the bistable character of the deterministic system as well as introduce bistability in the "thermodynamic potential" in parameter regimes where such behavior might not normally be expected. Li and Hopfield[13] have considered the neural processings in the olfactory bulb. They find that the oscillatory activities in the bulb (as observed in electrophysiological experiments) may be modeled by a small group of coupled nonlinear oscillators. There is also a commonly held belief amongst physicists that simple models involving only a few degrees of freedom can frequently describe, quite accurately, the dynamics of very complex systems. An excellent example in which microscopic complexity may be sacrificed in order to obtain the broader, macroscopic dynamics is afforded by the renormalization-group approach to second-order phase transitions; this approach leads to the description of the universal behavior (in terms of critical exponents) in the neighborhood of a second-order phase transition. Even though the Hopfield neuron is an oversimplification of real neuron behavior, it is expected that some collective features (which are relatively insensitive to the dynamics of individual neurons) of real neural networks might be extracted from it. It is precisely the relationship between the many-neuron connected model and a single-effective-neuron nonlinear dynamics that we want to examine here. In this context it is worth pointing out that Skarda and Freeman[14] have evaluated electroencephalograph data from the olfactory bulb. They find that many of their observations may be explained on the basis of simple "connectionist" models such as that of Hopfield.

In this work, we use the technique of "adiabatic elimination" to obtain the dynamics of a single neuron, in closed form, from the dynamics of the network. In this method, a set of fast relaxing variables is identified and the long-time solutions to their dynamics utilized to form one or more slow time-scale single-mode dynamic equations for the relevant (i.e., "slow") variable. We will term this an *effective* neuron in the coupled-neuron system under consideration. The adiabatic method is well known in the statistical mechanics of strongly interacting systems as well as quantum optics, both for deterministic and stochastic dynamics.[15–17] In particular, when one considers generalized Ginzburg-Landau equations for multimode nonequilibrium systems, one may use the technique to eliminate a set of "fast" variables in the vicinity of a nonequilibrium phase transition. We are then left with a set of equations of greatly reduced dimensionality that can be readily treated. An example of the application of this procedure is the single-mode laser in which one begins with a set of coupled equations for the photon field and the atomic populations in the lasing levels of the atoms in the laser cavity. By assuming the atoms to be in or close to their steady states, one derives a closed differential equation for the photon number density. This procedure has been described by Haken.[15]

For simplicity, we will adopt the deterministic Hopfield model[1–3] of the form

$$C_i \frac{dU_i}{dt} = \sum_{j \neq i, ji=1}^{N} J_{ij} \tanh U_j - \frac{U_i}{R_i} . \tag{1}$$

Here U_i is the potential of the i^{th} neuron with input capacitance C_i and a leakage current due to the intermembrane resistance R_i. The simple change of variables $U \to \beta U$, $J_{ij} \to \beta \alpha_j T_{ij}$ transforms Eq. (1) to the basic model of Ref. 2. The interesting first term on the right-hand side of (1) represents the (biological) input to the soma from the other neurons with the characteristic saturation with potential of their firing rates, taken for simplicity to be a hyperbolic tangent function. A nice discussion of this equation is given by Shamma.[4] We will take the neuron connectivity to be symmetric:

$$J_{ij} = J_{ji}, \quad J_{ii} = 0 . \tag{2}$$

It is the latter condition which focuses upon the question as to the meaning of a single-neuron effective equation. Self-excitation is not easily understood, but has been assumed in the literature.[2,11] We wish to understand the relationship between an effective J_{ii} and the J_{ij} $(i \neq j)$ and the other parameters of the network.

In Sec. II we use the adiabatic elimination procedure to obtain the effective-neuron equation. This is compared to the results of Babcock and Westervelt.[11] Approximate solutions are obtained and compared to numerical integration. In Sec. III we turn to the solution with noise, both Langevin and multiplicative.[17,18] We set $J_{ij} = \bar{J}_{ij} + \delta J_{ij}$, where δJ_{ij} is a noise source. In addition, we add to the right-hand side of (1) a random current source $F(t)$. With these additions, Eq. (1) becomes a system of coupled stochastic differential equations. The adiabatic elimination is carried out, in a stochastic context, on the associated Fokker-Planck equation for the case of two coupled neurons. The generalization of these results to larger networks of neurons, however, is complicated by the fact that the Fokker-Planck equation in two or more dimensions cannot be easily solved in the steady state because of detailed balance considerations. We consider the three-neuron case explicitly, and invoke a local Gaussian approximation[19] to obtain the steady-state solution of the Fokker-Planck equation for the fast neurons. The details of the calculation are relegated to the Appendix. Thereafter it becomes a simple matter to write down, formally, the N-neuron result. Specifically, we write down the stochastic differential equation for a single neuron in a "bath" of N-1 fast neurons (these neurons are assumed to have relaxed to their steady states on a much faster time scale than the slow neuron). The equation takes into account the details of the synaptic coupling between all the neurons as well as the additive and multiplicative noise (in the synaptic couplings) in the network. The results obtained are compared to the single-neuron stochastic model generalization[12] of the (deterministic) Babcock-Westervelt model.[11] Finally, some comments are made in Sec. IV.

II. DETERMINISTIC EFFECTIVE NEURON

Let us consider Eq. (1). For simplicity of notation, we will consider a three-neuron network; the results may be readily generalized to N neurons. We focus on the neuron $i=1$ and assume that the other two neurons may relax to a steady state on a much shorter time scale[15] than the $i=1$ neuron. To do this, we assume $R_i \ll R_1$ $(i=2,3)$. Thus we may set

$$C_i \frac{dU_i}{dt} \approx 0, \quad i=2,3$$

and obtain

$$C_1 \dot{U}_1 = -\frac{U_1}{R_1} + J_{12} \tanh U_2 + J_{13} \tanh U_3 , \tag{3a}$$

$$U_2 = R_2 (J_{21} \tanh U_1 + J_{23} \tanh U_3) , \tag{3b}$$

$$U_3 = R_3 (J_{31} \tanh U_1 + J_{32} \tanh U_2) . \tag{3c}$$

Since the R_i $(i=2,3)$ are small by definition, we may take the tanh in the steady solutions, Eqs. (3b) and (3c), and use the approximation

$$\tanh(R_i J_{ij} \tanh U_i + R_i J_{ik} \tanh U_k) \approx R_i J_{ij} \tanh U_j + R_i J_{ik} \tanh U_k . \tag{4}$$

Since Eqs. (3b) and (3c) are linear in $\tanh U_i$ $(i=2,3)$, one may solve for these variables in terms of $\tanh U_1$ and substitute the result into (3a). The result is a closed equation for U_1 in which the variables U_2 and U_3 have been adiabatically eliminated:

$$C_1\dot{U}_1=-\frac{U_1}{R_1}+(J_{12}^2R_2+J_{13}^2R_3+2J_{12}J_{23}J_{31}R_2R_3)D^{-1}\tanh U_1\ , \quad (5)$$

where $D\equiv 1-J_{23}^2R_2R_3$. We may further simplify the above equation by dropping terms of $O(R_2R_3)$. Then we obtain

$$C_1\dot{U}_1=\frac{-U_1}{R_1}+(J_{12}^2R_2+J_{13}^2R_3)\tanh U_1\ , \quad (6)$$

which may be readily generalized to yield

$$C_1\dot{U}_1=-\frac{U_1}{R_1}+\sum_{j=2}^{N}J_{1j}^2R_j\tanh U_1 \equiv -\frac{U_1}{R_1}+J_{11}\tanh U_1\ , \quad (7)$$

where the self-connection is

$$J_{11}=\sum_{j=2}^{N}J_{ij}^2R_j\ . \quad (8)$$

This is the single-neuron equation written by Babcock and Westervelt.[11] The Hebb rule for storing memories[1,3,20] is the initial assignment

$$J_{ij}=N^{-1}\sum_{p=1}^{M}\xi_i^p\xi_j^p\ , \quad (9)$$

and J_{ij} may be positive or negative. From (8) we see that $J_{11}>0$ consistent with the work of Babcock and Westervelt.[11] It should be noticed that the self-term need not be assumed but depends on the assignment of the parameters of connectivity and resistance to the *other* neurons.

The two-neuron problem has been considered by Hopfield[2] and, earlier, by Andronov, Vitt, and Khaikin[21] in connection with the analysis of an electron tube trigger circuit. An analysis of the phase flows indicates that $J_{12}^2R_1R_2=1$ is a bifurcation point. For $J_{12}^2R_1R_2>1$, $U_1=U_2=0$ becomes an unstable fixed point with two stable attracting points away from the origin. It can easily be understood that in this case the single-effective-neuron mode is a motion in the potential valley joining these fixed points seen in Eq. (3); the fast motion is transverse to the valley (see Fig. 1).

Some comments are now made concerning the analytic solution to the effective equation, which is the problem of integrating Eq. (7):

$$\int dU_1\frac{1}{J_{11}R_1\tanh U_1-U_1}=\frac{t}{R_1C_1}\ . \quad (10)$$

The left-hand side is easy to evaluate numerically, but seemingly intractable analytically. One may make the replacement

$$|\tanh x|\approx\frac{cx^2}{1+cx^2}\ , \quad (11)$$

c being an adjustable parameter. The solution (10) may then be written in the form

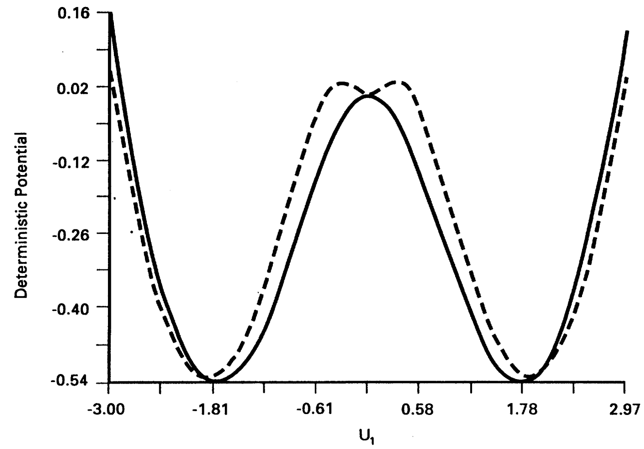

FIG. 1. Effective 1D deterministic potential. Solid curve reprents the numerical integration results; the dashed curve represents the analytic approximation [using Eq. (11)]. $(R_2,R_1C_1,c,J_{11})\equiv(0.125,1,4,2)$.

$$U_1(t)\frac{2cU_1(t)+L_2}{2cU_1(t)+L_3}=U_1(0)\frac{2cU_1(0)+L_2}{2cU_1(0)+L_3}\times\exp\left[-\frac{t}{R_1C_1}\right]\ . \quad (12)$$

This is written for $U_1(t)>0$, the piece for $U_1(t)<0$ being obtained via the replacement $L_{2,3}\rightarrow -L_{2,3}$. Here we have defined

$$L_1\equiv J_{11}c(J_{11}^2c^2-4c)^{-1/2}\ ,$$
$$L_2\equiv -(J_{11}^2c^2-4c)^{1/2}(1+L_1)\ , \quad (13)$$
$$L_3\equiv(J_{11}^2c^2-4c)^{1/2}(1-L_1)\ .$$

This has behavior similar to the original integral in (10) except that the fixed point at the origin remains a stable

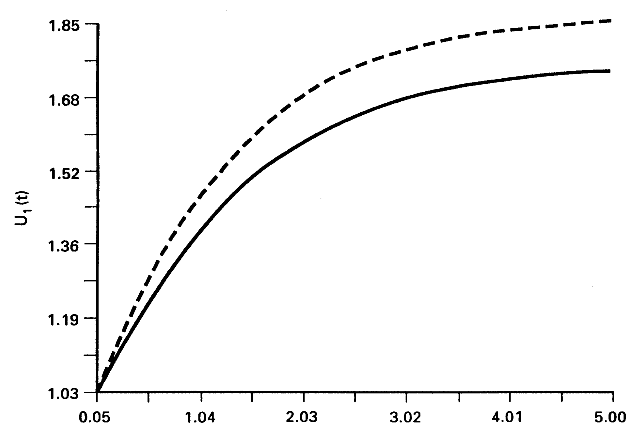

FIG. 2. Deterministic time dependence of $U_1(t)$. Solid curve represents numerical integration [Eq. (10)]; dashed curve represents the analytic approximation [Eqs. (11) and (12)]. Same parameters as in Fig. 1.

attractor, although very local, for $J_{11}^2 R_1 R_2 > 1$ as is shown in Fig. 1. It has the advantage that the integral may be easily performed. Figures 1 and 2 show the results for two neurons. The effective one-dimensional potential is shown in Fig. 1 and a comparison of the time-dependent solutions is shown in Fig. 2. Here we have set $(R_1 C_1, c, R_2) \equiv (1, 4, 0.125)$. The solid curve indicates the numerical integration results of Eq. (10) and the other curve has been obtained using the approximation (11).

III. STOCHASTIC EFFECTIVE NEURON

Noise is important in the modeling of neural networks.[6,10,22] For biological modeling the inclusion of noise sources is essential in the description. This has also lead to the fruitful use of (Ising-like) spin-glass analogies in this area.[3,7–9]

Let us first introduce noise into a two-neuron system (the reason for this apparent limitation will become clear) and carry out the stochastic counterpart of the deterministic adiabatic elimination.[15–17] In Eq. (1) we allow the connectivity of the neurons to fluctuate:

$$J_{12}(t) = J + \delta J_2(t) , \quad J_{21}(t) = J + \delta J_1(t) , \tag{14}$$

where $\delta J_1(t)$ and $\delta J_2(t)$ are taken to be white noise having zero mean and uncorrelated:

$$\langle \delta J_1(t) \delta J_2(0) \rangle = 0 , \quad \langle \delta J_1(t) \delta J_1(0) \rangle = \langle \delta J_2(t) \delta J_2(0) \rangle = \sigma^2 \delta(t) , \tag{15}$$

$\delta(t)$ being the Dirac delta function. In addition, an additive (i.e., Langevin) white background current fluctuation $F(t)$ having zero mean, variance σ_a^2, and uncorrelated with the multiplicative fluctuations is assumed:

$$\langle F(t) \rangle = 0 = \langle F(t) \delta J_i(t) \rangle, \quad i = 1,2 \quad \langle F(t) F(0) \rangle = \sigma_a^2 \delta(t) . \tag{16}$$

The two-neuron coupled stochastic differential equations now take the form

$$C_1 \dot{U}_1 = -\frac{U_1}{R_1} + [J + \delta J_2(t)] \tanh U_2 + F(t) , \quad C_2 \dot{U}_2 = -\frac{U_2}{R_2} + [J + \delta J_1(t)] \tanh U_1 + F(t) . \tag{17}$$

In the Ito interpretation[17] the corresponding two-dimensional Stratonovich-Fokker-Planck equation[17,19,23] for the probability density function $P \equiv P(U_1, U_2, t)$ is

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial U_1}[F_1(U_1, U_2) P] - \frac{\partial}{\partial U_2}[F_2(U_1, U_2) P] + \tfrac{1}{2} B_1(U_2) \frac{\partial^2 P}{\partial U_1^2} + \tfrac{1}{2} B_2(U_1) \frac{\partial^2 P}{\partial U_2^2} + \frac{\sigma_a^2}{C_1 C_2} \frac{\partial^2 P}{\partial U_1 \partial U_2} , \tag{18}$$

with

$$F_1(U_1, U_2) \equiv -\frac{U_1}{R_1 C_1} + \frac{J}{C_1} \tanh U_2 , \quad F_2(U_1, U_2) \equiv -\frac{U_2}{R_2 C_2} + \frac{J}{C_2} \tanh U_1 , \tag{19}$$

and

$$B_1(U_2) \equiv \frac{\sigma^2}{C_1^2} \tanh^2 U_2 + \frac{\sigma_a^2}{C_1^2} \quad B_2(U_1) \equiv \frac{\sigma^2}{C_2^2} \tanh^2 U_1 + \frac{\sigma_a^2}{C_2^2} . \tag{20}$$

We assume neuron "2" to be statistically rapidly varying and "slaved" by neuron "1."[15,16] Let

$$P(U_1, U_2, t) = h(2|1,t) g(1,t) , \tag{21}$$

with

$$\int_{-\infty}^{\infty} h(2|1,t) dU_2 = 1 = \int_{-\infty}^{\infty} g(1,t) dU_1 .$$

Here $h(2|1,t) \equiv h(U_2|U_1,t)$ is to be interpreted as a conditional probability density function to find U_2 given U_1. Substituting (21) into the original Fokker-Planck equation (18), one may obtain (the procedure is outlined in Ref. 15) the separate equations

$$\frac{\partial}{\partial t} h(2|1,t) = -\frac{\partial}{\partial U_2}[F_2(U_1, U_2) h(2|1,t)] + \frac{1}{2} B_2(U_1) \frac{\partial^2}{\partial U_2^2} h(2|1,t) \tag{22}$$

and

$$\frac{\partial}{\partial t} g(1,t) = -\frac{\partial}{\partial U_1}[\bar{F}_1(U_1) g(1,t)] + \frac{1}{2} \frac{\partial^2}{\partial U_1^2}[D_1(U_1) g(1,t)] , \tag{23}$$

where we introduce the quantities

$$\bar{F}_1(U_1) \equiv -\frac{U_1}{R_1 C_1} + \frac{J}{C_1} G(U_1) , \tag{24a}$$

$$D_1(U_1) \equiv C_1^{-2}[\sigma_a^2 + \sigma^2 H(U_1)] \equiv \frac{\sigma^2}{C_1^2} B_1(U_1) , \tag{24b}$$

$$H(U_1) \equiv \int_{-\infty}^{\infty} h(2|1) \tanh^2 U_2 dU_2 \tag{24c}$$

$$G(U_1) \equiv \int_{-\infty}^{\infty} h(2|1) \tanh U_2 dU_2 . \tag{24d}$$

In the above integrals, $h(2|1)$ represents the long-time solution obtained by setting the left-hand side of (22) equal to zero (the variable U_1 is treated as a constant when obtaining this solution, since U_2 relaxes on a far shorter time scale). This solution is readily seen to be a Gaussian in U_2 (assuming vanishing probability flux at the boundaries $U_2 = \pm\infty$):

$$h(2|1)=K^{-1}\exp\left[\frac{2C_2^2}{\sigma^2\tanh^2 U_1+\sigma_a^2}\times\left\{-\frac{U_2^2}{2R_2C_2}+\frac{JU_2}{C_2}\tanh U_1\right\}\right], \quad (25)$$

K being the normalization constant. The above solution is used in evaluating the integrals appearing on the right-hand side of (23), thereby reducing the latter to an effective-one-neuron Fokker-Planck equation. This procedure will be carried out below. The diffusion coefficient is positive but not constant. This is due to the multiplicative noise and may be lead to qualitatively interesting results.[12,18]

To integrate the terms containing $h(2|1)$ in (23), we complete the square in (25) and expand the hyperbolic functions in the integrands, about the steady-state value

$$\bar{U}_2=JR_2\tanh U_1 , \quad (26)$$

which coincides with the maximum of the Gaussian distribution in U_2. The steady-state value (26) may also be obtained by equating the drift term F_2 in (22) to zero. The integration procedure is equivalent (there is, however, some subtlety involved) to the method of steepest descents.[24] The scaling $R_2 \ll R_1$, which was used in Sec. II in connection with the deterministic calculation, is here invoked to justify the approximation to the integrals. Carrying out the procedure outlined above, we obtain, to the order $(U_2-\bar{U}_2)^2$ in the Taylor expansion, the expressions

$$\bar{F}_1(U_1)=-\frac{U_1}{R_1C_1}+\frac{J}{C_1}\left[\tanh\bar{U}_2-\frac{1}{2A}\tanh\bar{U}_2\operatorname{sech}^2\bar{U}_2\right] \quad (27)$$

and

$$D_1(U_1)=\frac{\sigma_a^2}{C_1^2}+\frac{\sigma^2}{C_1^2}\left[\tanh^2\bar{U}_2+\frac{1}{2A}\operatorname{sech}^2\bar{U}_2\times(\operatorname{sech}^2\bar{U}_2-2\tanh^2\bar{U}_2)\right], \quad (28)$$

where

$$A\equiv\frac{C_2/R_2}{\sigma^2\tanh^2U_1+\sigma_a^2} . \quad (29)$$

Consistent with Sec. II, we take

$$\sigma^2R_2 \ll C_2 . \quad (30)$$

In this case, the higher-order terms in the above expansion increase as powers of σ^2R_2/C_2 and may be neglected. We also observe that setting $\tanh\bar{U}_2\approx\bar{U}_2$ as in Sec. II leads to the simplified expressions

$$\bar{F}_1(U_1)=-\frac{U_1}{R_1C_1}+\frac{J^2R_2}{C_1}\tanh U_1 \quad (31)$$

and

$$D_1(U_1)=\frac{\sigma_a^2}{C_1^2}+\frac{\sigma^2}{C_1^2}J^2R_2^2\tanh^2U_1 . \quad (32)$$

In the expression (27) for $\bar{F}(U_1)$, the lowest term in the steepest descents expansion [this term is the second term on the right-hand side of (27)] dominates. In the expression for $D_1(U_1)$, however, higher-order terms may need to be retained in order to improve the accuracy of the approximation. We will return to this point later.

The equivalent single-neuron Stratonovich stochastic differential equation which would lead to the Fokker-Planck equation (23) is[17,19,25]

$$\frac{dU_1}{dt}=\bar{F}(U_1)-\frac{1}{4}\frac{d}{dU_1}D_1(U_1)+[D_1(U_1)]^{1/2}\xi(t) , \quad (33)$$

$\xi(t)$ being white noise having zero mean and unit variance. To this order, Eq. (33), with $D_1(U_1)$ given by (32), has the *form* of the stochastic differential equation assumed by Bulsara, Boss, and Jacobs[12] in their construction of a stochastic generalization to the single-neuron model of Babcock and Westervelt.[11] It is important to point out that in the work of Ref. 12, a fluctuating self-coupling term $J_{ii}(t)$ was assumed *a priori*, leading to steady-state distribution functions that were dependent on the strength of the (multiplicative) fluctuations in $J_{ii}(t)$. Such self-coupling terms have been excluded from the current analysis. We see, from (28), that there are important additional terms in the effective-one-neuron "self-diffusion." This will be examined below. Also, the term of $O(\sigma^4)$ and the explicit form of the coefficients were not known in this approach.

Numerical integrations of Eqs. (27) and(28) were performed (on an Apollo DN4500 work station) and compared with the analytic approximations developed in this section. In Figs. 3–5 we plot (as a function of R_2) the in-

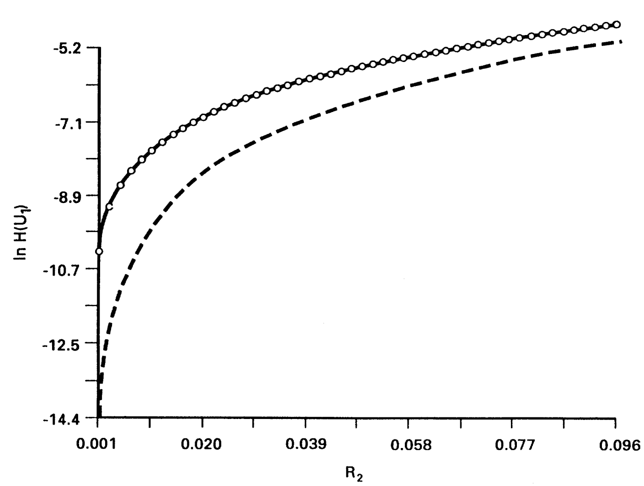

FIG. 3. The integral $H(U_1)$ defined in (24c) as a function of R_2 for $U_1=1.0$. Solid curve represents exact (i.e., numerical evaluation of the integral), data points represent full steepest descents approximation (28), dashed curve represents lowest-order steepest descents approximation (32). $(C_2,J,\sigma_a^2,\sigma^2)\equiv(1,1,0.01,0.1)$.

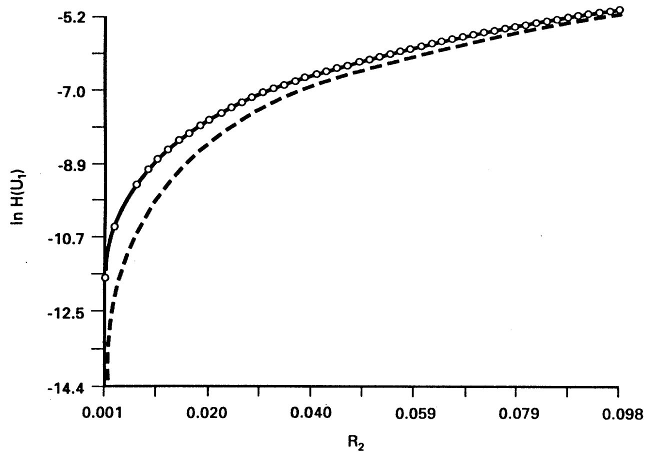

FIG. 4. Same as Fig. 3 with $\sigma^2=0.01$.

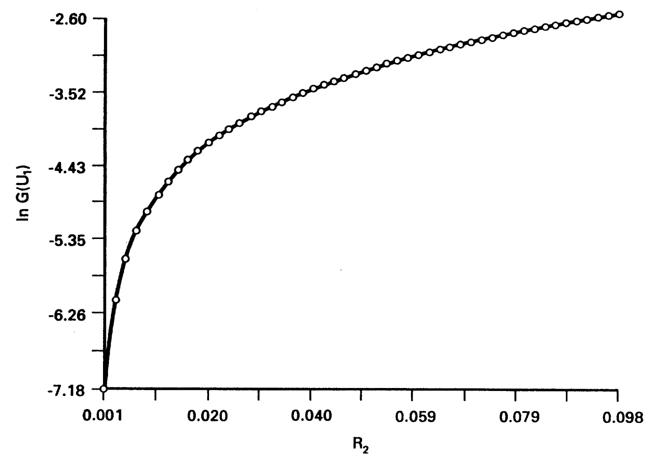

FIG. 6. The integral $G(U_1)$ defined in (24d) as a function of R_2 for $U_1=1.0$. Solid curve represents numerical integration and data points represent the steepest descents approximation (27). $(C_2,J,\sigma_a^2,\sigma^2)\equiv(0.1,1,0.01,0.01)$.

tegral $H(U_1)$ defined in (24c); the multiplicative noise variance σ^2 is varied in these plots. The solid curves show the results of numerically evaluating the integral $H(U_1)$, for a fixed value of U_1. The full steepest descents approximation of Eq. (28) (shown as large data points) agrees very well with the numerical calculation, however, the approximation (32), shown as the dotted curves, does not appear to be very good. Hence the diffusion term $D_1(U_1)$ is well represented by retaining two significant orders in the expansion, as has been done in (29). However, the drift term $\bar{F}_1(U_1)$ is well approximated by the first order in the steepest descents expansion [i.e., the second term on the right-hand side of (31)]. This is apparent in Fig. 6 where we have plotted the integral $G(U_1)$ defined in (24d), together with the steepest descents approximation (27) (large data points). On the scale of this figure the curve corresponding to the lowest-order approximation, given by the second term on the right-hand side of (31), cannot be separated from the solid curve. The effects of varying R_2 and C_2 are seen in Figs. 7–11. In Figs. 7 and 8 we plot the integrals $H(U_1)$ and $G(U_1)$, respectively, as functions of the multiplicative noise variance σ^2. Note the scale of Fig. 8; the drift term is constant as a function of σ^2 on the scale of the figure. In Figs. 9–11, we plot the numerically evaluated integral $H(U_1)$ together with the approximation obtained by representing $H(U_1)$ by the second term within the large parentheses on the right-hand side of (28), i.e., we set

$$H(U_1)\approx\frac{1}{2A}\operatorname{sech}^4\bar{U}_2\equiv\bar{H}(U_1)\ .$$

This expression is plotted (dotted curve) in Figs. 9–11. In these figures, the complete steepest descents expression [obtained by retaining all of Eq. (28)] coincides with the solid curve and is not shown. It is apparent that, for a

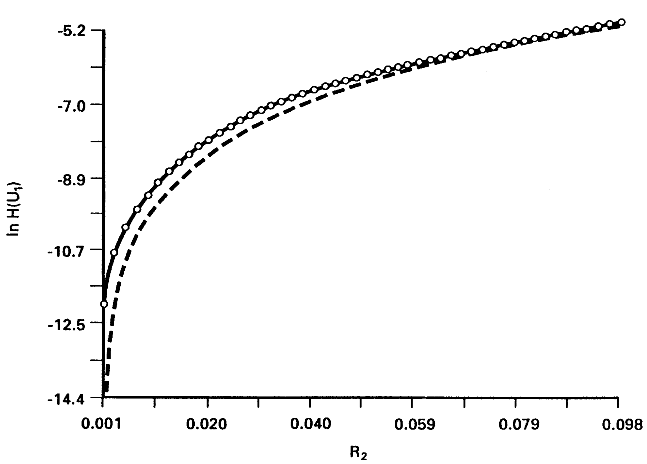

FIG.5. Same as Fig. 3 with $\sigma^2=0.001$.

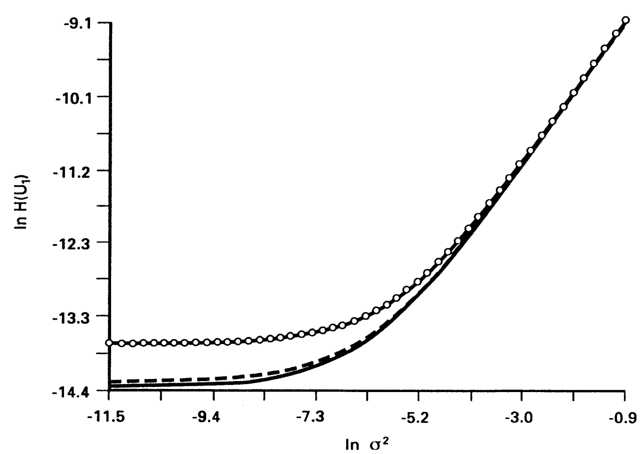

FIG. 7. The integral $H(U_1)$ as a function of the multiplicative nosie variance σ^2. $(C_2,R_2,U_1,J)\equiv(1,0.001,1,1)$ and $\sigma_a^2=0$ (solid curve); 0.0001 (dashed curve); and 0.001 (data points).

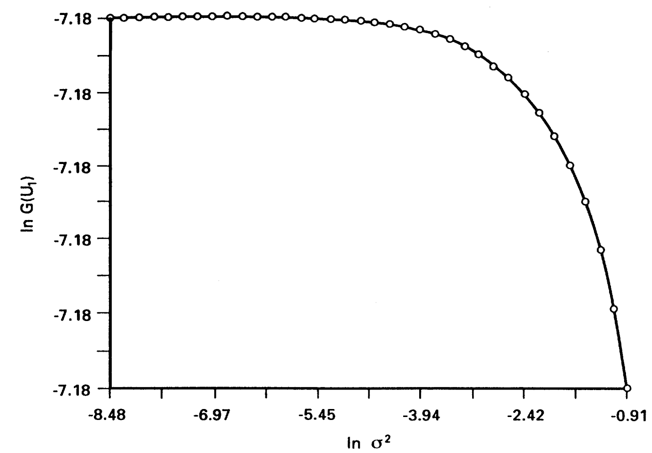

FIG. 8. The integral $G(U_1)$ as a function of the multiplicative noise variance σ^2 for $\sigma_a^2=0.001,0.0001$. The two curves are not separable on the scale of the figure (note the scale on vertical axis). Other parameters are the same as in Fig. 7.

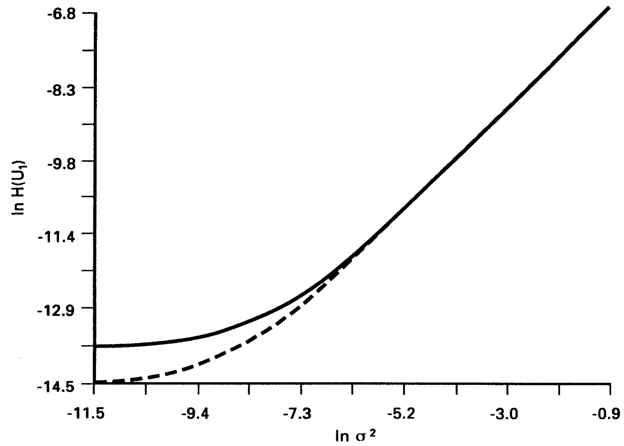

FIG. 10. Same as Fig. 9 with $R_2=0.001$.

given R_2, increasing the additive noise variance σ_a^2, improves the agreement between the function $\bar{H}(U_1)$ and the exact integral $H(U_1)$ (solid curve).

The procedure discussed above for two neurons can, in principle, be carried forward to three or more neurons. However, there is a serious, well-known problem, namely that the Fokker-Planck equation for higher dimensions cannot be guaranteed to have a steady solution.[16,17,23] The well-known detailed balance conditions for a stationary solution of the Fokker-Planck equation describing the fast variables are cumbersome. Even an attempt to prove detailed balance in three dimensions using MACSYMA has not been enlightening.

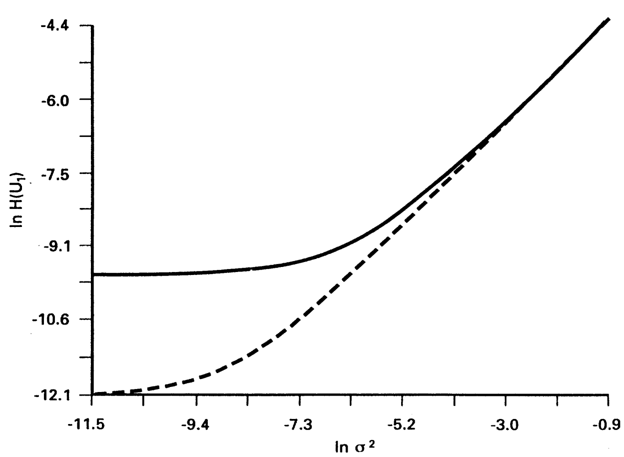

FIG. 9. The integral $H(U_1)$ as a function of multiplicative noise variance σ^2. $(C_2,R_2,U_1,J,\sigma_a^2)\equiv(0.1,0.01,1,1,0.0001)$. Solid curve represents numerical integration and dashed curve represents the approximation $\bar{H}(U_1)\equiv(2A)^{-1}\text{sech}^4\bar{U}_2$. The complete steepest descents expression [obtained from Eq. (28)] coincides with the solid curve.

As an alternative, we have adopted a local Gaussian approximation procedure,[19,26,27] which effectively assumes a steady-state solution of the potential form in the neighborhood of the elliptic points of the single-neuron potential. With this assumption, the results are, as we shall see, similar to the above discussion for two neurons and the generalization to N neutrons becomes transparent.

Let us outline the procedure for three neurons. We take $i=2,3$ to be the slaved neurons, $i=1$ being the slow neuron (i.e., $R_{2,3}\ll R_1$). The multiplicative noise terms in the dynamics are defined, for $i,j=1,2,3$, according to

$$\begin{aligned}&J_{ij}=\bar{J}_{ij}+\delta J_{ij},\quad \bar{J}_{ij}=\bar{J}_{ji}\ ,\\ &\langle \delta J_{ij}(t)\rangle=0\ ,\\ &\langle \delta J_{ij}(t)\delta J_{kl}(0)\rangle=\delta_{ik}\delta_{jl}\sigma_{ij}^2\delta(t).\quad \sigma_{ij}^2=\sigma_{ji}^2\ ,\end{aligned}\tag{34}$$

where δ_{ab} is the Kronecker delta and the Langevin noise terms $F(t)$ are defined in a manner analogous to (16)

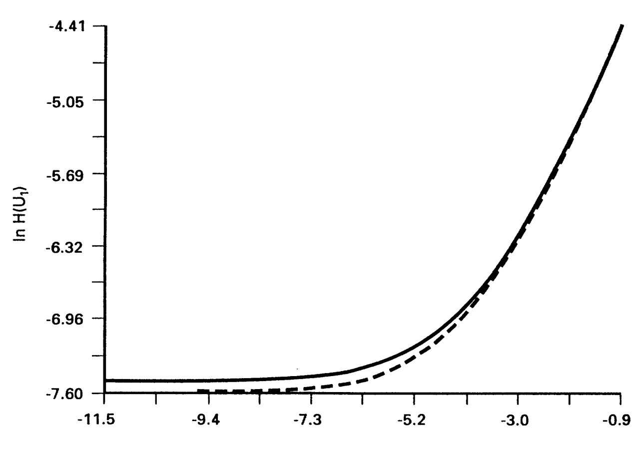

FIG. 11. Same as Fig. 9 with $\sigma_a^2=0.01$.

(they are assumed to be the same in each neuron). The above restrictions are not essential to the calculation; however, they do simplify it considerably. The three-dimensional Fokker-Planck equation for the probability density function $P \equiv P(U_1, U_2, U_3, t)$ may be written in the form

$$\frac{\partial P}{\partial t} = -\sum_i \frac{\partial}{\partial U_i}[F_i(U_1,U_2,U_3)P] + \frac{1}{2}\sum_i B_i(U_{j\neq i})\frac{\partial^2 P}{\partial U_1^2} + \sigma_a^2 \sum_{\substack{ij \\ i\neq j}} (C_i C_j)^{-1}\frac{\partial^2 P}{\partial U_i \partial U_j}, \quad (35)$$

where

$$F_i(U_1,U_2,U_3) = -\frac{U_i}{R_i C_i} + \frac{1}{C_i}\sum_{\substack{ij \\ i\neq j}} \bar{J}_{ij}\tanh U_j ,$$
$$B_i(U_{j\neq i}) = \frac{1}{C_1^2}\left[\sum_{\substack{ij \\ i\neq j}} \sigma_{ij}^2 \tanh^2 U_j + \sigma_a^2\right] . \quad (36)$$

As in the two-neuron case we assume a decomposition of the probability density function of the form

$$P(U_1,U_2,U_3,t) = h(2,3|1,t)g(1,t),$$

where the conditional density function $h \equiv h(2,3|1,t)$ may be shown to satisfy a Fokker-Planck equation of the form

$$\frac{\partial h}{\partial t} = -\frac{\partial}{\partial U_2}[F_2(U_1,U_2,U_3)h] - \frac{\partial}{\partial U_3}[F_3(U_1,U_2,U_3)h] + \frac{1}{2}B_2(U_1,U_3)\frac{\partial^2 h}{\partial U_2^2} + \frac{1}{2}B_3(U_1,U_2)\frac{\partial^2 h}{\partial U_3^2} + \frac{\sigma_a^2}{C_2 C_3}\frac{\partial^2 h}{\partial U_2 \partial U_3} , \quad (37)$$

and the single-neuron Fokker-Planck equation may be written as

$$\frac{\partial}{\partial t}g(1,t) = -\frac{\partial}{\partial U_1}\left[\left[\frac{-U_1}{R_1 C_1} + \bar{F}_{12}(U_1) + \bar{F}_{13}(U_1)\right]g(1,t)\right] + \frac{1}{2}\frac{\partial^2}{\partial U_1^2}\left[\left[\frac{\sigma_a^2}{C_1^2} + \frac{\sigma_{12}^2}{C_1^2}B_{12}(U_1) + \frac{\sigma_{13}^2}{C_1^2}B_{13}(U_1)\right]g(1,t)\right] , \quad (38)$$

where $(j=2,3)$

$$\bar{F}_{1j}(U_1) \equiv \bar{J}_{1j} C_1^{-1} \int_{-\infty}^{\infty} h(2,3|1)\tanh U_j \, dU_2 dU_3 , \quad (39)$$

and

$$B_{1j}(U_1) \equiv \int_{-\infty}^{\infty} h(2,3|1)\tanh^2 U_j \, dU_2 U_3 . \quad (40)$$

As in the two-neuron calculation, the above integrals are to be evaluated with the stationary solution $h(2,3|1)$ obtained by solving (37) in the $t\rightarrow\infty$ limit with U_1 held constant. However, as discussed above, such a solution cannot be obtained with the same facility as in the 1D case. Accordingly, we assume that, *in the neighborhood of the steady states* $\bar{U}_2$ *and* $\bar{U}_3$, the following Gaussian potential solution to (37) exists:

$$h(2,3|1) = K^{-1}\exp(-Z) , \quad (41a)$$

where the potential function Z is defined to be a two-dimensional Gaussian:

$$Z \equiv a(U_2-\bar{U}_2)^2 + b(U_2-\bar{U}_2)(U_3-\bar{U}_3) + c(U_3-\bar{U}_3)^2 , \quad (41b)$$

K being a normalization constant. Such a solution is formally obtained by a Taylor-series expansion of (37) (in the steady state) to second order, about the deterministic steady states $\bar{U}_2$ and $\bar{U}_3$ determined from the drift terms in the Fokker-Planck equation. Then, the coefficients a,b,c are obtained by equating the coefficients of the second-order derivatives evaluated at the steady states.[16,19,27,28] We will evaluate below the integrals in (39) and (40) for given a,b,c; the computation of the coefficients themselves is outlined in the Appendix. The form (41) of the solution is certainly reasonable since we have, throughout this work, assumed that the fast neurons relax to their steady states on a time scale that is much shorter that that which governs the slow neuron dynamics.

The deterministic three-neuron steady-state equations are given by Eqs. (3b) and (3c) with $\tanh\bar{U}_2$ and $\tanh\bar{U}_3$ given by (4). Alternatively, we may find the deterministic steady states by equating to zero, the drift terms F_2 and F_3 in the Fokker-Planck equation (37). It is important to notice here that because of our choice of correlation statistics [Eqs. (34)], the stochastic problem admits of the same steady states as the deterministic one. In general, however, the stochastic steady states, in the presence of multiplicative noise, are functions of the noise variance and do not coincide with the deterministic ones. Neglecting products of the form $R_i\bar{J}_{ij}$ for $i,j\neq 1$ [this is equivalent to assuming weak coupling between the fast neurons; the assumption is not necessary for the analysis to proceed, but does permit one to write down an analytic expression for the steady state $\bar{U}_j$ analogous to the two-neuron result (26)] we readily obtain

$$\bar{U}_j = R_j \bar{J}_{1j}\tanh U_1, \quad j=2,3 . \quad (42)$$

The integrals in (39) and (40) are done, as earlier, by introducing the expansions $(j=2,3)$

$$\tanh U_j = \tanh\bar{U}_j + (U_j-\bar{U}_j)\text{sech}^2\bar{U}_j - (U_j-\bar{U}_j)^2\text{sech}^2\bar{U}_j\tanh\bar{U}_j$$

and

$$\tanh^2 U_j = \tanh^2\bar{U}_j + 2(U_j-\bar{U}_j)\text{sech}^2\bar{U}_j\tanh\bar{U}_j + (U_j-\bar{U}_j)^2(\text{sech}^4\bar{U}_j - 2\,\text{sech}^2\bar{U}_j\tanh^2\bar{U}_j) . \quad (43)$$

The integrals in (39) and (40) now become

$$\bar{F}_1(U_1)=\frac{\bar{J}_{1j}}{C_1}(\tanh\bar{U}_j - A_j^{-1}\tanh\bar{U}_j\operatorname{sech}^2\bar{U}_j) \quad (44a)$$

and

$$B_{1j}(U_1)=\tanh^2\bar{U}_j + A_j^{-1}(\operatorname{sech}^4\bar{U}_j - 2\operatorname{sech}^2\bar{U}_j\tanh^2\bar{U}_j)\ , \quad (44b)$$

where the stationary quantities $\bar{U}_j$ are expressed in terms of the slow neuron variable U_1 by (42) and

$$A_2^{-1}=2c(4ac-b^2)^{-1}\ ,$$
$$A_3^{-1}=2a(4ac-b^2)^{-1}\ . \quad (45)$$

The coefficients a,b,c have been evaluated in the appendix. The conditional probability density function (40a) then assumes the same form as (25) for the two-neuron case, with Z being a local "potential" for this case, in the sense of (25) for the two-neuron case.

A calculation similar to the above may be carried out for the case of four neurons. In this case one obtains expressions similar to (44) for the integrals $\bar{F}_{1j}(U_1)$ and $B_{1j}(U_1)$ $(j=2,3,4)$ with additional correction terms that are of higher order in σ^2R/C and may be neglected. The local equilibrium solution analogous to (41) now contains three additional unknown parameters which may be computed in a manner analogous to the calculation (described in the Appendix) for the three-neuron case. This calculation is, however, quite tedious and will not be reproduced here.

The Fokker-Planck equation (39) for $g(1,t)$ now contains the explicit forms (39) and (40) in the drift and diffusion terms. Corresponding to it, one may write down the Stratonovich stochastic differential equation in the form used in (33) for the two-neuron case. However, rather than do so, we will write down by inspection the stochastic differential equation corresponding to the N-neuron case (the $i-1$ neuron is assumed to be the slow neuron in this case):

$$\dot{U}_1=-\frac{U_1}{R_1C_1}+C_1^{-1}\sum_{j=2}^{N}\bar{J}_{1j}A_{1j}(U_1) - \frac{1}{4C_1^2}\sum_{j=2}^{N}\sigma_{1j}^2\frac{\partial}{\partial U_1}B_{1j}(U_1) + \frac{1}{C_1}\left(\sigma_a^2+\sum_{j=2}^{N}\sigma_{1j}^2B_{1j}(U_1)\right)^{1/2}\xi(t)\ , \quad (46)$$

where, once again, $\xi(t)$ is white noise having zero mean and unit variance, and we have defined

$$A_{1j}(U_1)\equiv\int h(2,3,\ldots,N|1)\tanh U_j\,dU_2dU_3\cdots dU_N\ ,$$
$$B_{1j}(U_1)\equiv\int h(2,3,\ldots,N|1)\tanh^2 U_j\,dU_2dU_3\cdots dU_N\ . \quad (47)$$

These coefficients are given, for the three-neuron case, by (44a) and (44b). For the general case, expressions of the form (44) may be computed for the integrals above [although the coefficients $a,b,c,\ldots$ in the $(N-1)$-body steady-state solution may not be easy to obtain, if all orders in σ^2R/C are required].

IV. SUMMARY AND DISCUSSION

In this work, the deterministic effective-single-neuron equation has been obtained by adiabatically eliminating the fast coordinates. The result is Eqs. (7) and (8), which are of the form assumed by Babcock and Westervelt[11] and others. The self-connection term, J_{11} depends on the synaptic connections J_{1j} for $j>1$ and resistances of the *other* neural elements. It is positive. In a sense, the single neuron must be understood as the *dominant mode* of relaxation of the coupled neurons, much like a mode of a lattice oscillation or an effective electron in a semiconductor. With the assumptions $R_{j\neq 1}\ll R_1$, we have identified this dominant mode within the framework of our theory. Of course, other methods might be used, e.g., an alternate approximate diagonalization via nonlinear transformations of the coupled nonlinear equations (1). This would lead to a discrete eigenvalue spectrum with the lowest (nonzero) eigenvalue defining the dominant longtime relaxing mode, the effective single neuron. If we interpret the single neuron in this fashion, then the addition of inertial terms and possible "external" sinusoidal driving to achieve "exotic" nonlinear dynamic effects, such as chaos, is premature. If, on the other hand, in Eq. (1) we were to include by assumption a J_{ii} term initially (as suggested by Hopfield[2] and carried out by Bulsara, Boss, and Jacobs[12]), then the strong coupling added terms in (8) would act as a "renormalization" of that self-coupling. The precise nature of this renormalization of the self-coupling term for the general case in which it is allowed to fluctuate is under investigation.

If both additive and multiplicative noise terms are included, as we believe natural, the resulting effective-single-neuron stochastic differential equation is given by (20) for two neurons and the generalization to N neurons has been given by (46). The adiabatic elimination for the higher-dimension stochastic case is hampered by the inability to find steady-state solutions to Fokker-Planck equations of the form (37) in two or more dimensions. With the local Gaussian assumption, we have obtained solutions in terms of the coefficients a,b,c, which may be readily obtained (see the Appendix) for the three-neuron case. The extension of this procedure to N neurons may be carried forth in principle; in practice, considerable difficulty may be encountered (in the absence of any further simplifying assumptions on the noise and other neuron parameters) in evaluating these coefficients.

The new stochastic differential equation (46) for the single-neuron dynamics is significantly different from the intuitive effective equation[12] written down as the stochastic generalization of the deterministic model.[11] The principle difference may be seen in a comparison of Eqs. (28) and (32); in general, when evaluating the integrals in the diffusion term the second-order steepest descents contribution must be retained. For the drift term, the lowest-order contribution suffices. Figures 9–11 show this difference. It has been shown, however, that the *form* of the stochastic differential equation considered by Bulsara, Boss, and Jacobs[12] may be obtained from the theory of this paper under certain approximations; these were spelled out in Sec. III. In a later publication, the impact of multiplicative noise, and, specifically, the steady-state solutions to the general one-neuron stochastic differential equation (46) will be examined in detail. Comments regarding the physical meaning of the single stochastic neuron may be made in a manner completely analogous to the deterministic case discussed above. We reiterate that, due to the choice of correlation statistics for the multiplicative noise adopted in this work, as well as the conditions that are necessary for the adiabatic elimination, the Fokker-Planck equations (22) and (37) describing the *fast* neurons admit of steady-state solutions that correspond to their deterministic counterparts. This is not the case if the statistics (34) are made more general; the stochastic steady states $\overline{U}_{j\neq 1}$ will then depend on the multiplicative noise and may have to be determined numerically.

Finally, we wish to point out that the additive noise (having variance σ_a^2) plays an important role in the theory. It has previously been observed[12,29–32] that pure multiplicative noise (i.e., zero additive noise) can lead to non-normalized (i.e., unphysical) probability density functions. In some electronic systems (e.g., the rf superconducting quantum interference device) external Langevin noise introduces multiplicative fluctuations into the system dynamics; such a mechanism might reasonably be expected to provide one of the sources for the multiplicative nosie discussed in this work. Under these conditions, it might well be unphysical to consider the system as influenced by purely multiplicative fluctuations.

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APPENDIX

We discuss the evaluation of the coefficients a,b,c of Sec. III. To the quadratic order[19,28] we have the condition $(\alpha,\beta=2,3)$,

$$\sum_{\sigma=2}^{3}(a_{\alpha\sigma}V_{\sigma\beta}+a_{\beta\sigma}V_{\sigma\alpha}=-\{B_{\alpha\beta}\}_{\rm ss}\ . \qquad \text{(A1)}$$

Here we define

$$u_{ij}=\left\{\frac{\partial^2 Z(U_i,U_j)}{\partial U_i\partial U_j}\right\}_{\rm ss}\ ,$$

Z being the potential function (41b) and the subscript "ss" denoting that the corresponding quantity is evaluated in the steady state. The matrix V is defined by

$$V=u^{-1}\equiv\Delta^{-1}\begin{bmatrix}2c & -b\\ -b & 2a\end{bmatrix}\ , \qquad \text{(A2)}$$

where $\Delta\equiv 4ac-b^2$. The matrix $a_{\alpha\sigma}$ is $\{\partial F_\alpha/\partial U_\sigma\}_{\rm ss}$ with F_α defined in (36). We now evaluate the condition (A1) for the cases $(\alpha,\beta)\equiv(2,2)$, (2,3), and (3,3). This leads to a linear system in the variables $(2a/\Delta, b/\Delta, 2c/\Delta)$:

$$\begin{aligned} &a_1\frac{2a}{\delta}+b_1\frac{b}{\Delta}=A\ ,\\ &b_2\frac{b}{\Delta}+c_1\frac{2c}{\Delta}=B\ ,\\ &a_2\frac{2a}{\Delta}+b_3\frac{b}{\Delta}+c_2\frac{2c}{\Delta}=C\ , \end{aligned} \qquad \text{(A3)}$$

where we have defined

$$\begin{aligned} &a_1=-\frac{2}{R_3C_3},\quad b_1=\frac{2J_{23}}{C_3}\ ,\\ &b_2=-\frac{2J_{23}}{C_2},\quad c_1=-\frac{2}{R_2C_2}\ ,\\ &a_2=\frac{J_{23}}{C_2},\quad b_3=\frac{1}{R_2C_2}+\frac{1}{R_3C_3},\quad c_2=\frac{J_{23}}{C_3}\ ,\\ &A=-C_3^{-2}[(\sigma_{13}^2+\sigma_{23}^2R_2^2\overline{J}_{23}^{\,2})\tanh^2U_1+\sigma_a^2]\ ,\\ &B=-C_2^{-2}[(\sigma_{12}^2+\sigma_{23}^2R_3^2\overline{J}_{23}^{\,2})\tanh^2U_1+\sigma_a^2]\ ,\\ &C=-\frac{\sigma_a^2}{C_2C_3}\ . \end{aligned} \qquad \text{(A4)}$$

In writing down the above coefficients, we have replaced U_2 and U_3 by their steady-state values given by (42). Furthermore, we have assumed that $\text{sech}^2\overline{U}_j\approx 1$ in keeping with the conditions of the adiabatic elimination utilized throughout this work. The system (A3) is readily solved:

$$\frac{2a}{\Delta}=\Delta_1^{-1}\Delta_a,\quad \frac{b}{\Delta}=\Delta_1^{-1}\Delta_b,\quad \frac{2c}{\Delta}=\Delta_1^{-1}\Delta_c\ , \qquad \text{(A5)}$$

where we define the determinants,

$$\Delta_1\equiv\begin{vmatrix}a_1 & b_1 & 0\\ 0 & b_2 & c_1\\ a_2 & b_3 & c_2\end{vmatrix},\quad \Delta_a\equiv\begin{vmatrix}A & b_1 & 0\\ B & b_2 & c_1\\ C & b_3 & c_2\end{vmatrix}\ ,$$

$$\Delta_b=\begin{vmatrix}a_1 & A & 0\\ 0 & B & c_1\\ a_2 & C & c_2\end{vmatrix},\quad \Delta_c\equiv\begin{vmatrix}a_1 & b_1 & A\\ 0 & b_2 & B\\ a_2 & b_3 & C\end{vmatrix}\ .$$

In order for the solution (41) to be normalizable, the elliptic condition $\Delta>0$ must be satisfied. In terms of the above solutions, one readily writes this condition in the form

$$\Delta_a\Delta_c-\Delta_b^2>0\ . \qquad \text{(A6)}$$

A detailed proof of the inequality (A6) may be carried out. For the purpose of this paper, we wish to point out that, for the limiting special case $C_2=C_3=C$, $A=B=C=-\sigma_a^2/C^2$, the condition (A6) reduces to the condition

$$\frac{R_2+R_3}{2} > (R_2 R_3)^{1/2} .$$

This inequality is always satisified except for the special case $R_2 = R_3$. The elliptic condition (A6) thus holds for the simple case considered here.

From the system (A5) we may now calculate the coefficients a, b, c:

$$2a = \frac{\Delta_1 \Delta_a}{\Delta_a \Delta_c - \Delta_b^2} ,$$
$$b = \frac{\Delta_1 \Delta_b}{\Delta_a \Delta_c - \Delta_b^2} , \qquad \text{(A7)}$$
$$2c = \frac{\Delta_1 \Delta_c}{\Delta_a \Delta_c - \Delta_b^2} .$$

Chandrasekhar[27] has solved a two-dimensional Fokker-Planck equation that is somewhat simpler than our Eq. (37). Although he does not make the assumptions leading to the solution (41) (his Fokker-Planck equation admits of a potential solution), the final form of his solution bears a striking resemblance to our solution (41) with the coefficients a, b, c given by (A7). A calculation along similar lines may be carried for the four- (one slow and three fast) neuron case. In this case, the potential function Z introduced in (41b) contains terms in $(U_4 - \overline{U}_4)$ and three additional coefficients must be evaluated following the procedure outlined above. The details of this calculation (which may be extended to the case of N neurons) are not reproduced here.

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