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Exact nonequilibrium potential for the FitzHugh-Nagumo model in the excitable and bistable regimes

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We obtain an analytically exact nonequilibrium potential for the space-independent FitzHugh-Nagumo model, valid in the excitable and bistable regimes (in the limit of small noise). This potential allows us to characterize the nature of the barrier in the excitable regime and, after subjecting the system to a modulated weak signal that rocks the potential inducing the phenomenon of stochastic resonance, to calculate the signal-to-noise ratio in the bistable regime. [S1063-651X(98)08506-7]

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I. INTRODUCTION

The past decade has seen a considerable increase in the research of nonequilibrium phenomena in macroscopic systems, in order to explain the plethora of phenomena observed in experiments in physical, chemical, and biological systems, instabilities in fluids, etc. [1]. Particular attention has been paid to the search for extremal principles allowing one to characterize the stationary probability distribution of macroscopic variables, in order to understand pattern selection in self-organizing systems and other related phenomena [2–5]. For nonvariational systems, where the dynamics cannot be entirely deduced from the existence of a Lyapunov function, it is a nontrivial task to determine stationary probability densities.

It is now well known that the interplay between deterministic nonlinear dynamics and noise can lead to nontrivial phenomena such as purely noise-induced *phase* transitions [6] and *stochastic resonance* (SR) [7,8]. The last phenomenon is characterized by the enhancement of the signal-to-noise ratio (SNR) caused by the injection of an optimal amount of noise into a periodically modulated nonlinear system. The increase in the noise intensity from small initial values induces an increase in the SNR until it reaches a maximum, beyond which there is a decay of the SNR for large noise values. SR phenomena have been reported in monostable, multistable, and excitable systems [9]. Several recent proceedings and reviews show the wide interest of these phenomena and the state of the art [10].

One aspect that recently has attracted considerable interest is related to SR in extended or coupled systems [11,12]. The characterization of the SR phenomena is one of the issues that require the knowledge of the stationary probability densities, in this case in order to evaluate the ensemble-averaged escape rates from local attractors [7].

In a series of remarkable papers, Graham and collaborators developed and exploited in several contexts the notion of *nonequilibrium potential* (NEP), defined as a coarse-grained Boltzmann-like H function, and provided explicit procedures for its calculation in exact form (in the limit of small noise) or at least in a perturbative way [3,13–15]. The knowledge of such nonequilibrium potentials gives a direct access to that of the stationary probability distribution and allows one to address questions such as the identification of the globally stable states, the calculation of the height of the barrier that separates local attractors, the characterization of nontrivial thresholds in excitable dynamics, and the quantitative analysis of noise-induced transitions [16].

In this paper we obtain an exact nonequilibrium potential for the FitzHugh-Nagumo (FHN) model (for the nonextended system), which is a two-component nonlinear oscillator of the Bonhoffer–van der Pol type. The FHN model has been considered in physiologically motivated SR investigations [17], because its dynamics provides a simple representation of the firing dynamics of sensory neurons. Being a typical two-component dissipative system, it lacks a cherished feature of one-component ones, namely, being variational. The search for an exact NEP for the FHN model had been unfruitful up to now: At most, approximate expressions had been given in slaving approximations [18,19]. Here we consider the zero-dimensional *stochastic* FHN system

$$\dot{u}=\epsilon^{-1}[u(u-a)(1-u)-v+A(t)]+r_1\xi_1(t)+r_2\xi_2(t),$$

$$\dot{v}=\beta u-v+r_3\xi_1(t)+r_4\xi_2(t), \tag{1}$$

where ϵ is the ratio of the relaxation rates of u and v, $A(t)$ is an external periodic subthreshold activation signal [8]

$$A(t)=A_0+\delta A\ \cos(\Omega t+\phi),$$

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A_0 being a constant (tonic) signal, $\delta A \ll A_0$, and the r_i ($i=1,\ldots,4$) are real positive constants. The $\xi_i(t)$ ($i=1,2$) are statistically independent sources of Gaussian white noise

$$\langle \xi_i(t)\rangle = 0, \quad \langle \xi_i(t)\xi_j(t')\rangle = \eta\delta_{ij}\delta(t-t').$$

Whereas in the excitable regime the nullclines of the deterministic version of Eq. (1) have one root, the stable attractor, in the bistable regime they have three: two stable roots (local attractors) and one unstable one (repeller). We should emphasize that the deterministic version of the original set of equations (1) is *nonvariational* as long as β is positive [1].

In the following sections we present a brief review of the notion of the nonequilibrium potential, the derivation of that potential for Eq. (1), an analysis of the ''topography'' of the nonequilibrium potential landscape in the excitable regime, and an analysis of the stochastic resonance phenomenon in the bistable regime.

II. THE NONEQUILIBRIUM POTENTIAL

A. A brief review

In order to introduce the nonequilibrium potentials, we consider in this section a more general form of nonlinear stochastic equations, which admit the possibility of *multiplicative noises*. In particular, we consider equations of the form

$$\dot{q}^{\nu} = K^{\nu}(q) + g_i^{\nu}(q)\xi_i(t), \qquad \nu = 1,\ldots,n, \tag{2}$$

where repeated indices are summed over. Equation (2) is stated in the sense of Itô. Again, the $\xi_i(t)$ ($i=1,\ldots,m \leqslant n$) are mutually independent sources of Gaussian white noise with typical strength η. It is clear that Eq. (1) is a particular case of Eq. (2). The Fokker-Planck equation corresponding to Eq. (2) takes the form

$$\frac{\partial P}{\partial t} = -\frac{\partial}{\partial q^{\nu}}K^{\nu}(q)P + \frac{\eta}{2}\frac{\partial^2}{\partial q^{\nu}\partial q^{\mu}}Q^{\nu\mu}(q)P, \tag{3}$$

where $P(q,t;\eta)$ is the probability density to observe $q=(q_1,\ldots,q_n)$ at time t for noise intensity η and $Q^{\nu\mu}(q) = g_i^{\nu}(q)g_i^{\mu}(q)$ is the matrix of transport coefficients of the system, which is symmetric and non-negative. In the long-time limit ($t\to\infty$), the solution of Eq. (3) tends to the stationary distribution $P_{stat}(q)$. According to Ref. [4], the nonequilibrium potential $\Phi(q)$ associated with Eq. (3) is then defined by

$$\Phi(q) = -\lim_{\eta\to 0}\eta \ln P_{stat}(q,\eta) \tag{4}$$

or, equivalently,

$$P_{stat}(q)d^n q = Z(q)\exp\left[-\frac{\Phi(q)}{\eta} + O(\eta)\right]dV_q,$$

where $\Phi(q)$ is the nonequilibrium potential of the system and $Z(q)$ is defined as the limit

$$\ln Z(q) = \lim_{\eta\to 0}\left[\ln P_{stat}(q,\eta) + \frac{1}{\eta}\Phi(q)\right].$$

Here $dV_q = d^n q/\sqrt{G(q)}$ is the invariant volume element in q space and $G(q)$ is the determinant of the contravariant metric tensor (for the Euclidean metric it is $G=1$). In the stationary case, Eq. (3) can be written in the form $\partial J^{\nu}(q,\eta)/\partial q^{\nu} = 0$, J^{ν} being the stationary probability current density

$$J^{\nu}(q,\eta) = -K^{\nu}(q)P_{stat}(q,\eta) + \frac{\eta}{2}\frac{\partial}{\partial q^{\mu}}Q^{\nu\mu}(q)P_{stat}(q,\eta).$$

As it was shown by Graham [4], $\Phi(q)$ is the solution of

$$K^{\nu}(q)\frac{\partial\Phi}{\partial q^{\nu}} + \frac{1}{2}Q^{\nu\mu}(q)\frac{\partial\Phi}{\partial q^{\nu}}\frac{\partial\Phi}{\partial q^{\mu}} = 0$$

and $Z(q)$ is the solution of a linear first-order partial differential equation depending on $\Phi(q)$

$$\left(\frac{\partial K^{\nu}}{\partial q^{\nu}} + \frac{\partial Q^{\nu\mu}}{\partial q^{\mu}}\frac{\partial\Phi}{\partial q^{\mu}} + \frac{1}{2}Q^{\nu\mu}\frac{\partial^2\Phi}{\partial q^{\nu}\partial q^{\mu}}\right)Z + \left(K^{\nu} + Q^{\nu\mu}\frac{\partial\Phi}{\partial q^{\mu}}\right)\frac{\partial Z}{\partial q^{\nu}} = 0 \tag{5}$$

(note that both equations are independent of η, as they should be). Following Ref. [4], we introduce the streaming velocity $R^{\nu}(q,\eta)$ of the probability flow in the steady state

$$R^{\nu}(q,\eta) = \frac{J^{\nu}(q,\eta)}{P_{stat}(q,\eta)},$$

which in the limit of small noise takes the form

$$R^{\nu}(q) = \lim_{\eta\to 0}R^{\nu}(q,\eta) = K^{\nu}(q) + \frac{1}{2}Q^{\nu\mu}(q)\frac{\partial\Phi}{\partial q^{\mu}}.$$

As in Ref. [4] we split the drift $K^{\nu}(q)$ into two parts $R^{\nu}(q)$ and $d^{\nu}(q)$,

$$K^{\nu}(q) = d^{\nu}(q) + R^{\nu}(q),$$

in such a way that $R^{\nu}(q)$ conserves the potential $\Phi(q)$,

$$R^{\nu}(q)\frac{\partial\Phi(q)}{\partial q^{\nu}} = 0, \tag{6}$$

while the other part $d^{\nu}(q)$ may be written in the limit $\eta\to 0$ as

$$d^{\nu}(q) = -\frac{1}{2}Q^{\nu\mu}(q)\frac{\partial\Phi(q)}{\partial q^{\mu}}. \tag{7}$$

If the inverse $Q_{\nu\mu}$ of the transport matrix $Q^{\mu\nu}$ exists, we may express $\Phi(q)$ by a quadrature

$$\Phi(q) = \Phi(q_0) - 2\int_{q_0}^{q}dq^{\nu}Q_{\nu\mu}(q)d^{\mu}(q).$$

Equation (4) and the normalizability condition ensure that Φ is bounded from below. Furthermore, from Eqs. (6) and (7) it follows that

$$\frac{d\Phi(q)}{dt}=K^{\nu}(q)\frac{\partial\Phi(q)}{\partial q^{\nu}}=-\frac{1}{2}Q^{\nu\mu}(q)\frac{\partial\Phi}{\partial q^{\nu}}\frac{\partial\Phi}{\partial q^{\mu}}\leqslant 0,$$

i.e., Φ is a *Lyapunov* function for the dynamics of the system. Under the deterministic dynamics $\dot{q}^{\nu}=K^{\nu}(q)$, Φ decreases monotonically and takes a minimum value on attractors. In particular, Φ must be constant on all extended attractors (like limit cycles or strange attractors) since for $t\to\infty$ there are ω-limit sets describing steady states of $\dot{q}^{\nu}=K^{\nu}(q)$ (in which $\dot{\Phi}=0$) [4,14].

B. The FHN model

In the case of Eq. (1), the transport matrix adopts the form

$$Q^{\nu\mu}=\begin{pmatrix}\lambda_1 & \lambda\\ \lambda & \lambda_2\end{pmatrix}=\begin{pmatrix} r_1^2+r_2^2 & r_1r_3+r_2r_4\\ r_1r_3+r_2r_4 & r_3^2+r_4^2\end{pmatrix}.$$

Here we consider only those situations in which the inverse of the transport matrix exists [i.e., $\det\|Q^{\mu\nu}\|=(r_1r_3-r_2r_4)^2\neq 0$]. For that case, the nonequilibrium potential associated with Eq. (1) is

$$\Phi(u,v)=\frac{v^2}{\lambda_2}-\frac{2\beta}{\lambda_2}uv+\frac{2\lambda\beta}{\lambda_1\lambda_2}u^2-\frac{2}{\lambda_1\epsilon}\left[-\frac{u^4}{4}+\frac{1+a}{3}u^3-\frac{a}{2}u^2+Au\right], \tag{8}$$

where, in order to obtain the original drift, we have considered the expression

$$R^{\nu}(q)=-\frac{1}{2}A^{\mu\nu}\frac{\partial\Phi(q)}{\partial q^{\mu}}$$

and the matrix

$$A^{\nu\mu}=\begin{pmatrix}0 & \lambda\\ -\lambda & 0\end{pmatrix}.$$

By symmetry, R^{ν} satisfies Eq. (6). The following equation relates the parameters of the system with the transport matrix coefficients and can be interpreted as an integrability condition:

$$2\lambda-\lambda_1\beta=\lambda_2. \tag{9}$$

By solving Eq. (5), $Z(q)$ can be obtained in terms of the nonequilibrium potential, the transport matrix, and the drift. For the FHN system (1), it results in a positive constant. The stationary probability current density adopts the form

$$J^{\nu}=\frac{1}{2}A^{\mu\nu}\frac{\partial\phi}{\partial q^{\mu}}Z\exp(-\phi/\eta).$$

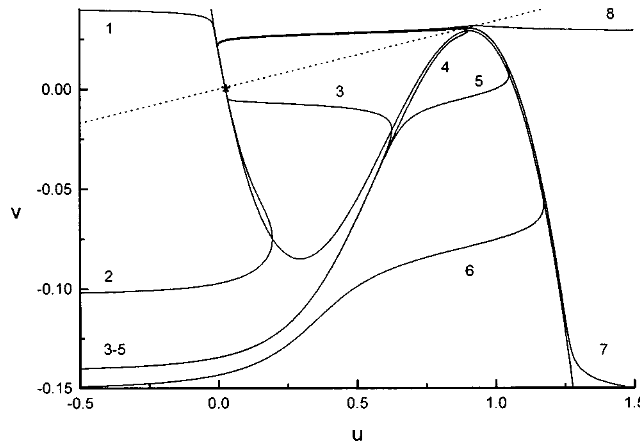

FIG. 1. Time evolution in (u,v) space for deterministic excitable dynamics. The curve denoted 4 indicates the separatrix between nonexcitable and excitable behaviors. The initial conditions used here are (1) $u=-0.8, v=0.04$; (2) $u=-0.8, v=-0.1025$; (3) $u=-0.25, v=-0.138\,711$; (4) $u=-0.5068, v=-0.1402$; (5) $u=-0.25, v=-0.138\,712$; (6) $u=-0.8, v=-0.15$; (7) $u=1.5, v=-0.15$; (8) $u=1.7, v=0.029$; and (9) $u=1.5, v=0.05$. The values of the parameters are $A_0=0.02$, $\delta A=0$, $\beta=0.034$, $a=0.8$, and $\epsilon=0.0341$, which configure a neatly defined excitable regime.

Equation (8) is the exact expression for the nonequilibrium potential we shall work with.

III. EXCITABLE AND BISTABLE REGIMES

A. Nature of the threshold

Here we analyze the time evolution of the FHN system in the excitable regime in terms of the nonequilibrium potential given by Eq. (8). We consider a parametric regime in which $u(t)$ is a fast variable and $v(t)$ is a slow (recovery) variable. For completeness, we show in Fig. 1 the evolution from several initial conditions in (u,v) space for the following values of the parameters: $\beta=0.034$, $a=0.8$, $A=0.02$, $\delta A=0$, and $\epsilon=0.0341$. We verify that a subthreshold perturbation decays to the stable attractor (indicated by a small circle in the figure). On the other hand, above-threshold initial conditions experience a large excursion in the configuration space before decaying. The curve labeled 4 denotes the limit trajectory (threshold) between nonexcitable and excitable decays.

In Fig. 2 we show, for the same parameters as in Fig. 1, the structure of the nonequilibrium potential. Associated with curve 4 in Fig. 1 (and denoted by the same label 4) is an *extended* potential barrier that is *not* a saddle point. In fact, it corresponds to a *nonconstant* potential line that separates the excitable from nonexcitable behaviors. In Fig. 3 we show the time evolution of the nonequilibrium potential for subthreshold and above-threshold initial conditions. It can be appreciated that $\dot{\Phi}\leqslant 0$. In both cases, the slow time variations are associated with the evolutions along the null clines. We have used a finite-difference scheme with a time step $\Delta t=2.5\times 10^{-6}$ in order to simulate the excitable dynamics.

The NEP given in Eq. (8) can be written in the form

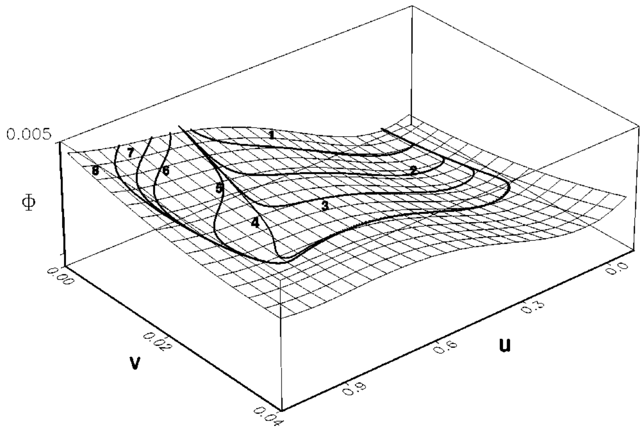

FIG. 2. Nonequilibrium potential in (u,v) space for the noise parameters $r_1=29.3147$, $r_2=0.7943$, $r_3=0.9982$, and $r_4=0.0270$ (the remaining parameters are the same as in Fig. 1) and the projected time evolution of the initial conditions $v=0$ and (1) $u=0.7$, (2) $u=0.7164$, (3) $u=0.7172$, (5) $u=0.7176$, (6) $u=0.75$, (7) $u=0.8$, and (8) $u=0.9$. The curve labeled 4 corresponds to curve 4 in Fig. 1, i.e., the separatrix (barrier) between nonexcitable and excitable behaviors.

$$\Phi(u,v)=\frac{(v-\beta u)^2}{\lambda_2}+\frac{\beta}{\lambda_1\epsilon}u^2-\frac{2}{\lambda_1\epsilon}\left[-\frac{u^4}{4}+\frac{1+a}{3}u^3-\frac{a}{2}u^2+Au\right]. \tag{10}$$

The first term in Eq. (10) is lost when an adiabatic elimination is done in order to estimate the NEP. In fact, the NEP given in Eq. (10) tends to the NEP obtained by adiabatic elimination of the fast variable (with $r_2=r_3=r_4=0$) [18]. However, the derivation presented here for the NEP is not valid for this singular transport matrix.

B. Stochastic resonance

Let us now consider the *bistable regime* of the FHN model as given by Eq. (1): We shall use the NEP given in Eq. (8) to obtain the SNR within the framework of a two-state description [7]. For bistable systems, the mean first-passage time associated with the escape from a local attractor q_{meta} adopts the Kramers-like form

$$\langle\tau\rangle=\tau_0\exp\left[\frac{\Delta\Phi}{\eta}\right],$$

where q_{unst} is the nondegenerate saddle point that confines the attractor in the configuration space and $\Delta\Phi=\Phi(q_{unst})$ $\Delta\Phi$=Φ(qunst)$-\Phi(q_{meta})$ [20]. The prefactor

$$\tau_0=\sqrt{2\pi\eta}\,\frac{Z(q_{meta})}{Z(q_{unst})}\,\frac{\sqrt{|H(q_{unst})|}}{\sqrt{H(q_{meta})}}$$

is essentially determined by the curvature of Φ at its extrema

$$H(q_k)=\det\left(\frac{\partial^2\Phi}{\partial q^\nu\partial q^\mu}\right)_{q=q_k}$$

and is typically several orders of magnitude smaller than the average time $\langle\tau\rangle$. The inverse of $\langle\tau\rangle$ gives us the transition probability W for the escape from q_{meta}. In order to analyze the SR phenomenon, we consider a situation in which we have a well-defined bistable regime, i.e., we consider numerical values for the parameters of the system in which (for $\delta A=0$) both stable attractors have the same value of the nonequilibrium potential and the same value of the corresponding Hessian. In that case, the transition probabilities for the two possible noise-assisted transitions adopt the same value and the effect of introducing the weak periodic component of the signal is to produce a small change in the relative stability between the local attractors. To proceed with the calculation of the correlation function, we need to evaluate the transition probabilities

$$W_\pm=\tau_0^{-1}\exp\left[-\frac{\Delta\Phi}{\eta}\right]$$

when the periodic signal is activated. The expansion of $\Delta\Phi(q,A)$ in powers of δA up to first order

$$\Delta\Phi(q,A)=\Delta\Phi(q,A_0)+\left.\frac{\partial\Delta\Phi(q,A)}{\partial A}\right|_{A=A_0}\delta A\,\cos(\Omega t+\phi)+\cdots,$$

yields, for the transition probabilities,

$$W_\pm=\frac{1}{2}[\alpha_0\mp\alpha_1\delta A\,\cos(\Omega t+\phi)],$$

where

$$\alpha_0=\frac{2}{\tau_0}\exp[-\Delta\Phi(q,A_0)/\eta],\qquad \alpha_1=\frac{\alpha_0}{\eta}d\Delta\Phi/dA|_{A_0}.$$

In the adiabatic limit (i.e., Ω much less than the mean threshold-crossing rate), the stochastic stationarity can be continously achieved because the probability densities adjust adiabatically to the changing nonequilibrium potential. Within the framework of a two-state description (the corresponding theory was developed by McNamara and Wiesen-

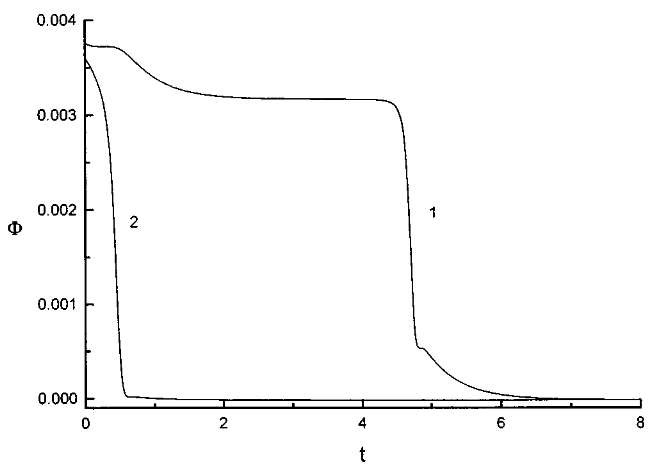

FIG. 3. Time evolution of the nonequilibrium potential Φ for an excitable behavior (curve A) and for a nonexcitable one (curve B). The values of the parameters are the same as in Fig. 2.

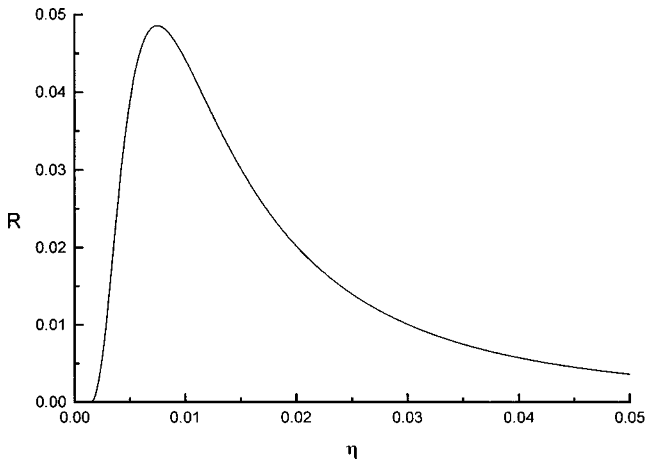

FIG. 4. Signal-to-noise ratio R vs noise strength η for a bistable regime. The maximum indicates the stochastic resonance. Here $A_0 = 0.02$, $\delta A = 0.002$, $\beta = 0.039$, $a = 1/2$, $\epsilon = 1$, $r_1 = 1$ and $r_2 = r_3 = r_4 = 0.02$.

feld in Ref. [7] and exploited in Refs. [12,21]) we can use those transition probabilities to evaluate the autocorrelation function and through its Fourier transform the power spectrum $S(\omega)$. In terms of the output signal power spectrum, the SNR (indicated by R) takes the standard form for bistable systems

$$R(\alpha_0,\alpha_1) = \frac{\pi \alpha_1^2 (\delta A)^2}{4\alpha_0} \left[1 - \frac{\alpha_1^2 (\delta A)^2}{2(\alpha_0^2 + \Omega^2)} \right]^{-1}. \qquad (11)$$

In Fig. 4 we plot R vs η for the system corresponding to Eq. (1). The enhancement of the SNR with increasing η is apparent. The existence of a maximum in this curve is the identifying characteristic of the stochastic resonance phenomenon.

IV. CONCLUSIONS

Summarizing, we have derived, by means of a quadrature, an exact nonequilibrium potential for the zero-dimensional FitzHugh-Nagumo model in the limit of small noise, thus obtaining results that are valid in the excitable and the bistable regimes. Then, using this potential, we have discussed the nature of the barrier in the excitable regime and the stochastic resonance in the bistable case, within the framework of a two-state description, when an external subthreshold periodic signal is injected.

The relevance of the present results for technological applications in signal detection is apparent, as well as their biological implications. Many electronic circuits can be regarded as nonlinear oscillators (for instance, of the related Bonhoffer–van der Pol type). This schematic model has also been used to discuss numerous problems: pattern formation and propagation in simplified activator-inhibitor models [1,16], experimental and theoretical descriptions of processes involving stochastic resonance in neuronal systems [17,18,22], as well as in a theoretical description of the influence of the spatial coupling on SR [12]. It is also expected that it can provide a useful framework to discuss some recent experimental results regarding SR in several chemical reactions done under good-stirring conditions [23], as well as other recent experiments on resonant pattern formation in a chemical system [24]. We are now considering the extension of this approach to stochastic-resonant media [21], and its possible connection with spatiotemporal synchronization phenomena [25].

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