PHYSICAL REVIEW E, VOLUME 65, 041915

Noise-induced resonances in the Hindmarsh-Rose neuronal model

J. P. Baltanás
Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Tulipán s/n, 28933 Móstoles, Spain

J. M. Casado
Área de Física Teórica. Universidad de Sevilla, Apartado Correos 1065, 41080 Sevilla, Spain

(Received 24 October 2001; published 3 April 2002)

The behavior of neurons under stimulation is often described by means of dynamical systems having bifurcations from fixed points to limit cycles. In these models, the presence of noise can induce irregular crossings of the bifurcation threshold leading to intrinsic oscillations of the system variables that describe the detection of the otherwise subthreshold signals by the neuron. In this paper, the response of the Hindmarsh-Rose neuronal model to noisy signals is investigated and a variety of noise-induced resonances are described.

DOI: 10.1103/PhysRevE.65.041915 PACS number(s): 87.10.+e, 05.20.−y, 05.40.Ca

I. INTRODUCTION

From a functional point of view, sensory neurons are mainly transducers, i.e., devices that operate by converting signals from the external world into trains of stereotyped action potentials or spikes that flow along the neural pathways to the central processing centers in the brain. The detection and coding of external signals by neuronal cells have become the subject of intense research in the last decades both from an experimental and a theoretical point of view. Some time ago, it was suggested by Longtin, Bulsara, and Moss that the stochastic resonance (SR) scenario could be of importance in neurobiology as it provides a basis for understanding the effect of noise in the process of transduction/coding of information by sensory neurons [1]. Those authors argued that, in some well defined sense, the response of a stimulated neuron could be described by the dynamics of a particle in a bistable potential under the combined action of forcing and noise and showed that some aspects of this dynamics reproduce the experimental behavior found in certain neurons of the sensory system. The suggestion that the SR phenomenology could be relevant to the efficient detection and coding of information by sensory neurons produced a huge flow of publications aiming to explore the response of neuronal models to the cooperative action of periodic (mostly monochromatic) forcing and noise [2].

The detection of external signals by neurons occurs basically through a threshold process. Each time the signal crosses some activation threshold the neuron fires a spike and then returns to its resting state after a refractory period. The importance of SR phenomenology to the detection of signals by neurons lies mainly in the so-called subthreshold regime, in which noiseless stimuli delivered to the cell are unable to elicit neuronal responses. In presence of a finite amount of noise, however, a subthreshold signal becomes able to cross from time to time the activation threshold and thus spike trains are produced by the neuron signaling the detection of the stimulus. In fact, it has been shown both experimentally [3] and theoretically [4] that the addition of noise enhances the ability of sensory neurons to process weak input signals.

Some years ago, Sigeti and Horsthemke [5] and later Gang *et al.* [6] showed that in dynamical systems having saddle-node bifurcations coherent motion can be stimulated by adding a finite amount of noise. Later on, Longtin tackled the same problem, this time by using the FitzHugh-Nagumo (FHN) neuronal model [7]. This author showed that a finite level of noise enhances the coherence of the system's response and termed this phenomenon autonomous stochastic resonance (ASR). On the other hand, Pikovsky and Kurths coined the term coherence resonance (CR) to describe the noise-induced enhancement of coherence in the behavior of excitable systems [8]. Since then, CR has been found in the Hodgkin-Huxley model of spike generation [9], in a model of oscillatory pattern formation under the effect of environmental noise [10] and in an excitable electronic circuit [11].

The excitable dynamics of the Hindmarsh-Rose (HR) model comes from the existence of a Hopf bifurcation giving rise to a limit cycle past an activation threshold [12]. Besides, it has been shown that the HR model presents a selective sensitivity to the forcing frequency: signals with frequency within the range of 15–60 Hz have been found to induce spiking at weaker amplitudes than those outside this range [13]. The aim of this paper is to analyze the response of the HR model to a periodic forcing term embedded in noise. In Sec. I, the basic features of this model are presented in order to stress its potentialities for the study of signal transduction by neurons. In the following sections, we use a stochastic version of the model to analyze the noise-induced enhancement of coherence in its response. Some conclusions are drawn at the end of the paper.

II. THE HINDMARSH-ROSE MODEL

Let us consider a dynamical system described by the set of equations

$$\dot{x}=y-ax^3+bx^2-z+I_0+I_1\cos(\omega t),$$

$$\dot{y}=c-dx^2-y,$$

$$\dot{z}=r[s(x-x_0)-z], \tag{1}$$

©2002 The American Physical Society

where a, b, c, d, r, s, and x_0 are parameters. We have fixed the values of these constants to $a=1$, $b=3$, $c=1$, $d=5$, $r=0.006$, $s=4$, and $x_0=-1.6$ in order to compare our results with previous studies on the same model [13,14]. In these equations, the variable $x(t)$ represents the difference of electrical potential across the neuron's membrane and $y(t)$ describes the dynamics of the resetting mechanism that restores the polarity of the membrane after the firing of each action potential. The additional variable $z(t)$ allows the precise tuning of the interspike interval. The parameter I_0, giving the intensity of a constant (tonic) signal that is delivered to the neuron from the external world, is usually considered in the SR scenario as the bifurcation parameter of the dynamical system. The original Hindmarsh-Rose model, i.e., the system (1) with $I_1=0$, was introduced by those authors in a slightly different form in an attempt to describe accurately the firing pattern produced by a particular class of neurons [12]. Since then, it has been extensively studied by a number of people, which have found that it displays a rather rich dynamics that include chaotic behavior. When a sinusoidal forcing term is applied to the right of Eq. (1), the HR model displays a wide variety of different behaviors that have been studied by Wang and co-workers [14].

The linear stability analysis of the HR model with $I_1=0$ shows that, for the values of the parameters stated above, the stable fixed point interchanges its stability with a limit cycle solution through a supercritical Hopf bifurcation occurring at $I_0=I_0^{(1)}=1.32$. The period of the limit cycle just beyond the bifurcation point is $T_{LC}\approx 153$ ms, thus producing an intrinsic oscillation frequency of $\omega_{LC}=40.9$ Hz. The coherent spike train emitted by the system as a result of this oscillation is presented in panel A of Fig. 1. If we increase the strength of the external signal, the system develops a cascade of bifurcations leading to chaos, each one of its stages representing a different type of bursting.

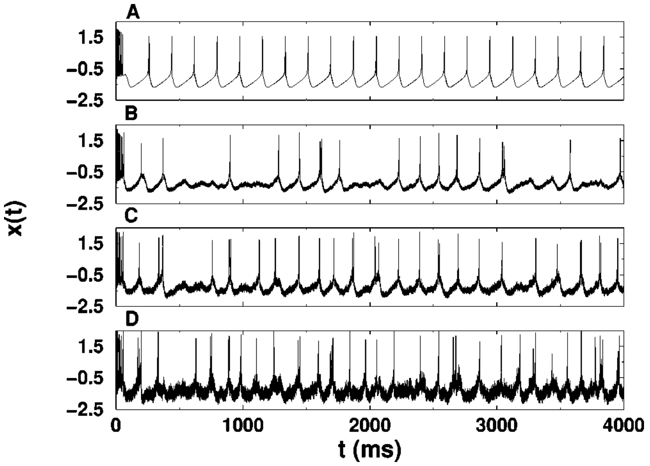

FIG. 1. Some spike trains generated by the HR system with $a=1$, $b=3$, $c=1$, $d=5$, $r=0.006$, $x_0=-1.6$, and $I_1=0$. In panel A, the response from the purely deterministic case to a tonic signal just beyond the bifurcation point ($I_0=1.32$) is presented showing a completely regular spike train generated by the intrinsic oscillatory behavior of the system. In panels B, C, and D, sections of the noise-induced spike train generated by a noisy subthreshold signal ($I_0=1.31$) are plotted for three different values of the noise intensity ($D=0.05$, $D=0.15$, and $D=0.6$ for panels B, C, and D, respectively) to show graphically the existence of an optimal value of D that makes the system to fire more coherently ($D=0.15$).

The response of the HR system to a sinusoidal signal of frequency ω and amplitude I_1 clearly shows frequency sensitivity, that is, the minimum value of I_1 to provoke limit cycle behavior depends on the forcing frequency $I_1^{\min}=f(\omega)$. In fact, this is not an exclusive characteristic of the HR model; a very similar relation between the forcing frequency and I_1 can also be found, for example, in the FHN model, although in this case frequency sensitivity is not as evident as in the HR model. For this case, this behavior is showed in the diagram displayed in Fig. 2. In the parameter space ω-I_1, the upper boundary of region A corresponds to the frequency-sensitivity relationship for $I_0=0.8$ [13]. Values of I_1 within region A do not drive the system to the oscillatory regime. On the other hand, within regions B and C, periodic firings take place at the same frequency (region C) or at half the frequency of the forcing signal (region B). Region E is a transition zone where a periodic response of the system does not take place. In physical terms, the boundaries AC and AB describe the enhancement of the system's sensitivity to monochromatic signals with frequencies within a rather broad interval around the intrinsic frequency of the system ω_{LC}. Observe that the minimum of the sensitivity curve occurs at a frequency $\omega_M\neq\omega_{LC}$. In Fig. 3, a smaller portion of the ω-I_1 plot is displayed in order to show that the frequency of the noise-induced spike train ω_{out} as revealed, for instance, by the position of the first peak of the interspike interval histogram (ISIH), is clearly dependent on the forcing frequency. In region C, the frequency of firing closely matches the value of the forcing frequency, the response of the system thus being synchronized 1:1 to the external signal. On the other hand, in region B, the system ceases to be

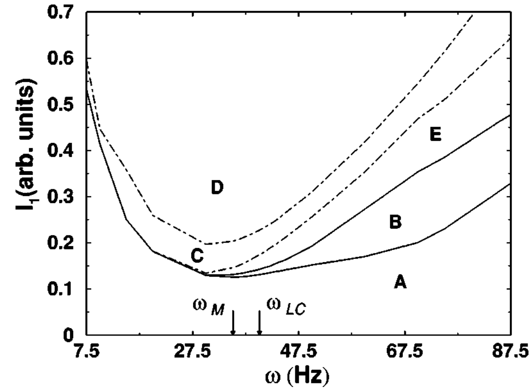

FIG. 2. The response of the forced HR model in the vicinity of the Hopf bifurcation. The continuous line between zones A and C and zones A and B describes the frequency sensitivity of the system to a sinusoidal signal. Region D corresponds to bursting behavior, whereas in region E the system fires nonperiodically. There is a narrow region just near the main boundary AB where the firing is irregular. This region is not depicted here for the sake of clarity. The arrows mark the frequencies of the limit cycle (ω_{LC}) and of the maximum sensitivity (ω_M).

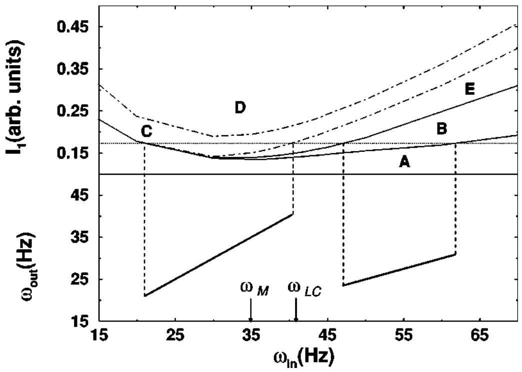

FIG. 3. Relationship between the frequency of the forcing signal ω_{in} and that of the spike train ω_{out}. When we consider the frequency of the response to different values of ω along the dotted line (i.e., at a fixed value of I_1), we obtain that in region *A* the system's response follows the forcing and fires with the same frequency. In region *B*, however, the system is unable to follow the forcing and is obliged to halve the frequency of firing. In region *E* the system no longer responds periodically to the external signal.

able to follow the external forcing and it halves its frequency by skipping one of each two firings. In region *E*, the analysis of the spike train clearly reveals that there is not a definite frequency in the response of the system after the onset of the external signal.

Returning to the diagram displayed in Fig. 2, it is worth discussing the nature of the response when the amplitude of the sinusoidal signal is increased so that the system leaves the frequency-locked regime. At every forcing frequency, if the forcing amplitude is increased, there appears a second boundary separating the region of spike trains with a single frequency from a region where bursting takes place (region D).

III. THE STOCHASTIC HR MODEL

Let us now turn our attention to a stochastic version of the sinusoidally forced HR model, namely,

$$\dot{x}=y-ax^3+bx^2-z+I_0+I_1\cos(\omega t)+\xi(t),$$

$$\dot{y}=c-dx^2-y,$$

$$\dot{z}=r[s(x-x_0)-z], \tag{2}$$

where $\xi(t)$ is a Gaussian white process with

$$\langle \xi(t)\rangle=0, \quad \langle \xi(t)\xi(s)\rangle=D\delta(t-s). \tag{3}$$

Let us consider first the case with $I_1=0$. For $I_0<I_0^{(1)}$, the action of noise renders unstable from time to time the otherwise stable fixed point by driving the system to cross the bifurcation threshold. It can be said, then, that the presence of noise activates the system's intrinsic oscillation associated with the limit cycle. In fact, this is the origin of the subthreshold detection capabilities of this neuronal model and the scenario associated with terms such as CR or ASR. Clear evidence of this intrinsic oscillation can be obtained from the presence of the broad peak in the noise-induced spectrum depicted in Fig. 4. The precise location of this peak also makes clear that this noise-induced oscillation virtually coincides with ω_{LC}.

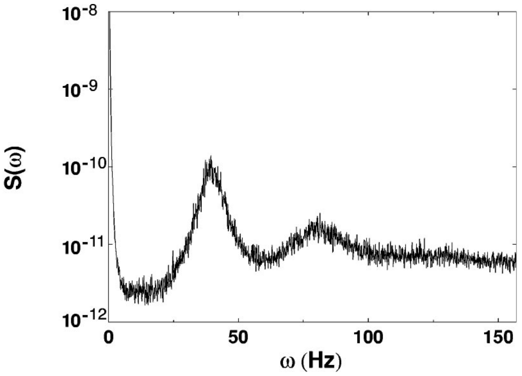

FIG. 4. Power spectrum of the noise-induced spike train. The broad peak near ω_{LC} indicates the existence of a periodic component of the noise-induced firing.

If in addition to noise, we introduce a sinusoidal signal of subthreshold intensity into the system, a resonance must take place between this signal and the noise-induced intrinsic oscillation, leading to an entrainment of the system's response to the signal. This resonance, which will take place when the frequency of the external signal matches that of the noise-induced limit cycle

$$\omega=\omega_{LC}, \tag{4}$$

has been studied in Ref. [15] for the FHN model. Under these circumstances, the temporal structure of the spike train, as shown, for example, by the signal-to-noise ratio (SNR) or by the ISIH, will reflect the periodic character of the dynamics beyond the bifurcation threshold. Thus, as pointed out in Refs. [15,16] this resonant process is closely related to the CR and ASR scenarios. Characteristically, this resonance occurs always at the frequency of the limit cycle, which has a weak dependence on the noise intensity. In fact, the enhancement of coherence in the spike train does not follow in this case the usual stochastic resonance phenomenology; it is rather a purely mechanical resonance induced by the presence of noise. As long as the noise allows the subthreshold signal to cross the bifurcation threshold, a resonance takes place producing an optimal stimulation of the system's response at the frequency of its limit cycle. Furthermore, the change of the noise intensity does not lead to a corresponding change in the location of the resonant peak. In order to illustrate the characteristic feature of this noise-induced resonance we have computed the SNR for several values of the forcing frequency around ω_{LC} and two different values of D. Figure 5 clearly shows that the location of the maximum of the SNR does not depend on the noise strength. It should be noticed, however, that those maxima are obtained at a frequency that is close, but not equal to ω_{LC}. This result is due to the difference between the frequencies ω_M and ω_{LC}.

There exists a completely different scenario in the interaction of noisy sinusoidal signals of subthreshold intensity

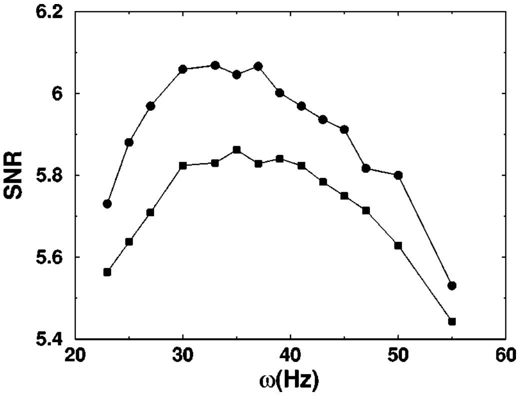

FIG. 5. Mechanical resonance induced by noise in the HR model. Circles correspond to $D=0.2$ and squares to $D=0.4$. The location of the peak of the SNR curves is independent on the noise intensity as discussed in the text.

with the dynamics of excitable systems like the FHN or the HR models. It arises at frequencies far below that of the limit cycle and gives rise to the true SR phenomenology in this kind of dynamical systems. Here, the two time scales that play a role are the mean time needed by the noisy signal to reach the bifurcation point (a kind of Kramers' time), and the period of the external forcing term. The important point is that the SR scenario does not involve the time scale associated with the period of the intrinsic limit cycle of the system. In fact, it is now well known that the occurrence of SR in excitable systems only needs the conjunction of a sinusoidal signal with a noise and a threshold. When a weak (subthreshold) signal is applied to the system, the noise makes the system to cross the threshold from time to time so that the firings are to some degree coherent with the signal. When the noise intensity is too small, there are too few firings to sample a cycle of the signal, thus allowing a very poor transduction of the signal by the excitable system. By contrast, when the noise intensity is too large, the firings become too random and again the timing of the spikes will reflect very poorly the spectral characteristics of the sinusoidal signal. The SR marks the existence of an optimal noise intensity at which the transduction process is maximized. The characteristic feature of the SR in excitable systems is the matching between the mean escape time from its resting state to the threshold $\tau(D)$ and half the period of the external signal

$$\tau(D)\approx\frac{\pi}{\omega}. \tag{5}$$

Thus, for a given value of I_0, this matching occurs at a frequency that depends on the intensity of noise. As for moderate values of the tonic signal τ grows rapidly when D decreases, the SR will usually take place at small frequencies with respect to the frequency of the system's limit cycle

$$\omega\ll\omega_{LC}, \tag{6}$$

i.e., in the adiabatic regime. The dependence of the position of the resonant peak on the noise intensity is shown in Fig. 6. We have computed the SNR for the same two values of D used previously, and for several different frequencies verifying Eq. (6). This time each value of D leads to a different location of the SNR peak in accordance with Eq. (5). It is worth noticing that the behavior of the SNR curves for different values of D is inverted with respect to that of the previous case; there SNR values computed for $D=0.2$ were higher than the corresponding ones for $D=0.4$, whereas now the opposite is found. This is a clear evidence of the different roles played by the noise in both cases. In the SR scenario, the noise plays a constructive role leading to an increase of the SNR as the noise intensity is increased (up to a certain limit). For the purely mechanical resonance induced by noise, the increase of the noise intensity only degrades the response of the system.

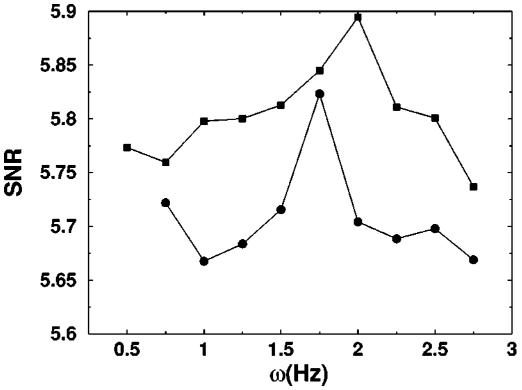

FIG. 6. Stochastic resonance in the HR model. The frequency at which the SNR peaks is now a function of D. Circles stand for $D=0.2$ and squares for $D=0.4$.

IV. CR IN THE HR MODEL

In this section, we will consider how the presence of a finite amount of noise can force the system to behave more coherently in absence of a forcing signal. Noise-induced coherence enhancement will appear when some noise $\xi(t)$ is added to a subthreshold tonic signal ($I_0<I_0^{(1)}$) so that the full stimulus $s(t)=I_0+\xi(t)$ becomes able to cross occasionally the bifurcation point. Then, the response of the system to this stimulus will be a train of irregularly spaced spikes, each one of them lasting approximately the period of the limit cycle (excursion time t_e) and being separated from the preceding one by the time of escape from I_0 to the threshold $I_0^{(1)}$ (activation time t_a). The full duration of each process t_s will be the sum of these two times $t_s=t_a+t_e$ and the spike train will have some temporal structure reflecting the competition of these two time scales.

To quantify the structure of the spike train we will start using the coefficient of variation of the ISIH as given, for example, by [8]

$$R(D)=\frac{\sqrt{\mathrm{Var}\,(t_s)}}{\langle t_s\rangle}. \tag{7}$$

To calculate the distribution functions for t_a, t_e, and t_s we have solved the system of stochastic equations (2) for $I_1=0$ by means of a stochastic Runge-Kutta algorithm [17],

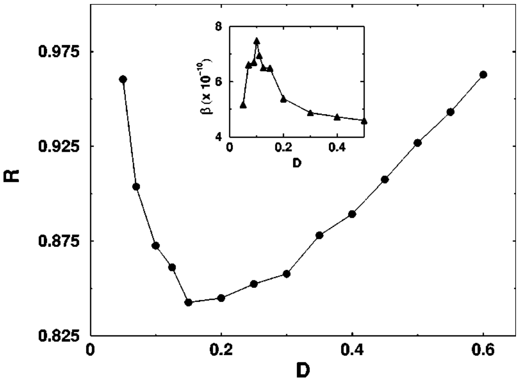

FIG. 7. Coherence resonance in the HR model. The coefficient of variation R and the parameter β are plotted as functions of D for $I_0=1.31$, showing a minimum and maximun, respectively, at the optimal noise intensity $D_c=0.15$.

thus producing a number of spike trains allowing the calculation of the statistics of activation and excursion times. Typically, we have used $N=50$ spike trains, each one having a very big number of firings.

The CR arises from the different dependence on the noise strength D of the statistical properties of the activation and excursion times. For weak enough noise strength, the activation time decreases rapidly with D according to the Kramers formula $\langle t_a\rangle \sim \exp D^{-1}$ and, besides, $\mathrm{Var}(t_a) \approx \langle t_a\rangle^2$. Thus, in the limit of small noise, $t_a \gg t_e$, and the system will spend large intervals of time around the fixed point before being able to fire a spike. Thus, the temporal structure of the spike train will be dominated by the large activation time and $R\sim 1$.

For large noise intensity, the signal will cross the threshold many times during the performing of a single limit cycle and so, the time between succesive spikes will be dominated by the relative fluctuations of the excursion time. Between those asymptotic regimes there is a crossover where R reaches its minimum. Near the optimal noise intensity each time (in mean) the signal reaches the threshold, it finds the system variable completing a limit cycle and ready to start another one and, then, the coherence of the resulting spike train will be maximal. This implies that CR will occur to a sufficiently large noise strength so that excursion time dominates the temporal structure of the spike train but not very large so that its fluctuations remain small.

In Fig. 7, a plot of R as a function of the noise strength D is presented for the stochastic HR model. It is apparent that there exists an optimum value of noise D_c at which the coherence of the spike train is maximal. When comparing this curve with those obtained for the FHN model [8] we can appreciate that both models behave analogously, a fact that is not surprising given that their firing mechanism is associated with the same type of bifurcation.

The temporal structure of the spike train can also be analyzed by means of spectral techniques. The existence of a more or less defined time scale will be associated with the presence of a peak in the spectrum because the inverse of a noise-induced period should be a noise-induced frequency. Thus, another measure of coherence can be defined as the product of the height of the peak H to its quality factor Q

$$\beta = HQ, \qquad Q=\frac{\omega_p}{\Delta\omega}, \tag{8}$$

where ω_p is the frequency of the peak and $\Delta\omega$ is its width at half maximun amplitude [6]. In the inset appearing in Fig. 7, a plot of β is presented to show its dependence on the noise intensity. Here, too, an optimum value of noise appears which coincides roughly with the one determined by using Eq. (7).

V. CONCLUSIONS

In this paper we have investigated the response of an excitable system to monochromatic signals and noise by means of a model of relevance in neurobiology. The use of the Hindmarsh-Rose model has allowed us to study the frequency sensitivity of the response to noise. We have found that the sensitivity curve has some features that have remained undetected in previous studies. In addition, we have made a distinction between the different possible scenarios in the interaction of noise and subthreshold monochromatic signals in this model, which to our knowledge was lacking in the literature. For a system subjected to noise alone, we have found the existence of a noise strength that optimally enhances the coherence in the response.

ACKNOWLEDGMENTS

J.M.C. acknowledges the Dirección General de Investigación Científica y Técnica (DG-ICYT) of Spain (Project No. PB98-1120) for support. J.P.B. thanks the Spanish Ministry of Science and Technology (Project No. BFM2000-0967) for financial support.

---

[1] A. Longtin, A. Bulsara, and F. Moss, Phys. Rev. Lett. **67**, 656 (1991).
[2] L. Gammaitoni, P. Hängii, P. Jung, and F. Marchesoni, Rev. Mod. Phys. **70**, 223 (1998).
[3] H.A. Braun, H. Wissing, K. Schäfer, and M.C. Hirsh, Nature (London) **367**, 270 (1994); J.K. Douglass, L. Wilkens, E. Pantazelou, and F. Moss, *ibid.* **365**, 337 (1993).
[4] K. Wiesenfeld, D. Pierson, E. Pantazelou, C. Dames, and F. Moss, Phys. Rev. Lett. **72**, 2125 (1994); A. Longtin, J. Stat. Phys. **70**, 309 (1993).
[5] D. Sigeti and W. Hortsthemke, J. Stat. Phys. **54**, 1217 (1989).
[6] H. Gang, T. Ditzinger, C.Z. Ning, and H. Haken, Phys. Rev. Lett. **71**, 807 (1993).
[7] A. Longtin, Phys. Rev. E **55**, 868 (1997).
[8] A.S. Pikovsky and J. Kurths, Phys. Rev. Lett. **78**, 775 (1997).
[9] S.G. Lee, A. Neiman, and S. Kim, Phys. Rev. E **57**, 3292 (1998).
[10] S. Katsev and I. L'Heureux, Phys. Rev. E **61**, 4972 (2000).

[11] D.E. Postnov, S.K. Han, T.G. Yim, and O.V. Sosnovtseva, Phys. Rev. E **59**, R3791 (1999).
[12] J.L. Hindmarsh and R.M. Rose, Nature (London) **296**, 162 (1982); Proc. R. Soc. London, Ser. B **221**, 87 (1984); **225**, 161 (1985).
[13] F. Liu, J.F. Wang, and W. Wang, Phys. Rev. E **59**, 3453 (1999).
[14] W. Wang, Y. Wang, and Z.D. Wang, Phys. Rev. E **57**, R2527 (1998).
[15] S.R. Massanés and C.J. Pérez Vicente, Phys. Rev. E **59**, 4490 (1999).
[16] J.R. Pradines, G.V. Osipov, and J.J. Collins, Phys. Rev. E **60**, 6407 (1999).
[17] H.S. Greenside and E. Helfand, Bell Syst. Tech. J. **60**, 1927 (1981); E. Helfand, *ibid.* **58**, 2289 (1979).