PHYSICAL REVIEW E

STATISTICAL PHYSICS, PLASMAS, FLUIDS, AND RELATED INTERDISCIPLINARY TOPICS

THIRD SERIES, VOLUME 55, NUMBER 6 PART A — JUNE 1997

RAPID COMMUNICATIONS

The Rapid Communications section is intended for the accelerated publication of important new results. Since manuscripts submitted to this section are given priority treatment both in the editorial office and in production, authors should explain in their submittal letter why the work justifies this special handling. A Rapid Communication should be no longer than 4 printed pages and must be accompanied by an abstract. Page proofs are sent to authors.

Aperiodic stochastic resonance with chaotic input signals in excitable systems

C. Eichwald and J. Walleczek*

Bioelectromagnetics Laboratory, Department of Radiation Oncology, School of Medicine, AO38, Stanford University, Stanford, California 94305-5124

(Received 5 March 1997)

A model of two relaxation-type nonlinear oscillators is investigated. The chaotic spike sequence generated by the first system is used as a subthreshold input signal for the second system. When also exposed to noise, the latter behaves as a detector of temporal patterns in the chaotic input signal. Calculation of dynamic correlation measures shows that the information transfer between the two systems is optimized by intermediate noise levels. This behavior represents an interesting class of aperiodic stochastic resonance (ASR) with deterministic chaotic input signals. Results show that ASR is not restricted to slowly varying input signals. [S1063-651X(97)50206-6]

PACS number(s): 05.40.+j, 05.45.+b, 87.10.+e

The phenomenon of stochastic resonance (SR) characterizes a behavior wherein the response of a nonlinear system to a weak periodic input signal is optimized by intermediate noise levels [1]. Recently the original definition of SR has been generalized into cases involving slowly varying aperiodic input signals [2,3]. Theoretical studies showed that under the appropriate conditions the response of certain nonlinear systems can be enhanced by a nonzero level of noise. For this type of behavior the term aperiodic stochastic resonance (ASR) has been introduced [2]. In theoretical studies of ASR one usually investigates the response of excitable systems exhibiting an activation threshold, where both the subthreshold aperiodic stimulus and the noise are applied to a single nonlinear element. With regard to biological applications, these nonlinear elements often consist of neuronal models like the FitzHugh-Nagumo equations or the Hodgkin-Huxley equations. These two models were also integrated into summing networks of elements coupled in parallel [3]. Studies showed that the signal detection performance in response to aperiodic stimuli can be enhanced by noise. ASR has also been demonstrated experimentally in biological sensory systems [4].

In this paper, ASR is studied with deterministic chaotic instead of stochastic input signals. Specifically, input signals varying on a time scale that is comparable to the characteristic time of the responding system are investigated. Motivation for this work is twofold. Deterministic chaotic behavior has been observed in a wide range of biological systems including periodically stimulated squid giant axons, the crayfish caudal photoreceptor as well as electrically excitable cell assemblies in cardiology and neuroscience [5,6]. However, evidence regarding a functional role of chaotic behavior in biological systems still remains elusive. Theoretical studies suggest that ASR may be a widespread phenomenon, because the conditions leading to ASR are relatively general. Biological systems such as neurons, ion channels, and enzymes often exhibit the appropriate nonlinearities, i.e., they operate as threshold devices [7,8]. Because of the inevitable presence of fluctuations in biological systems, noise enhancement may likely have a functional role in the detection of subthreshold input signals including chaotic ones. These aspects suggest studying the signal processing capabilities of nonlinear systems to different kinds of input signals in the presence of noise.

*Author to whom correspondence should be addressed. Electronic address: jan.walleczek@forsythe.stanford.edu

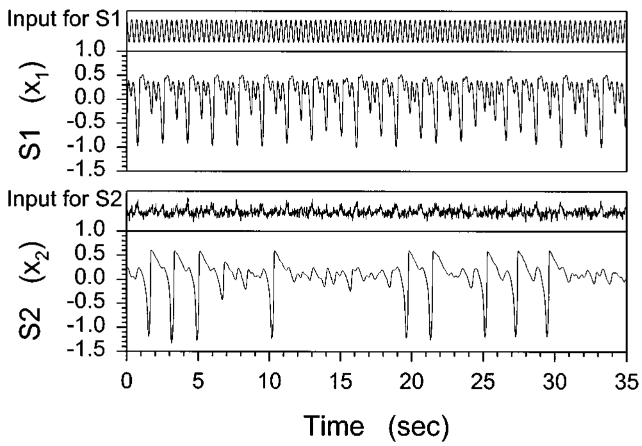

FIG. 1. Time series of the two oscillators, Eqs. (1)–(4). The first oscillator ($S1$) is driven into a chaotic state by harmonic forcing. The two top traces depict the harmonic driver (y-axis scaling ± 1.75) and the resulting chaotic oscillations of the variable x_1. The chaotic signal is coupled into the second oscillator ($S2$). The latter is also exposed to noise. In the simulations exponentially correlated noise, with zero mean and Gaussian-distributed amplitudes, is used (variance: $\langle \xi^2 \rangle = \sigma^2$; correlation time: τ). The two bottom traces depict the total input signal for $S2$ (y-axis scaling ± 0.75) and the resulting oscillations of the variable x_2. Parameters: $\varepsilon = 0.01$, $\alpha = 0.1$, $\mu = -0.25$, $A = 1$, $\omega = 18\ \mathrm{s}^{-1}$, $\sigma = 0.1$, and $\tau = 0.01$ s. Integration stepsize: $\Delta t = T_P/1000$ ($T_P = 2\pi/\omega \approx 0.349$ s).

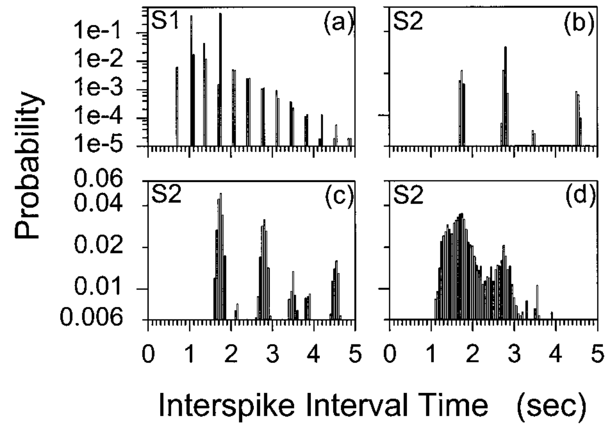

FIG. 2. Interspike interval histograms (ISIH's). (a) ISIH of the chaotic oscillations of $S1$. (b)–(d) ISIH's for the resulting oscillations of the coupled system $S2$ at three noise intensity levels. The ISIH's were calculated from the time series of the variables $x_{1,2}$. All deflections that exceeded the threshold $x_{1,2}^{\mathrm{th}} = -0.5$ in the negative direction were counted as spikes, and the interval between successive spikes was calculated. The binsize of the ISIH's was set equal to $\Delta T = 0.05$. Results do not change qualitatively if a different value for $x_{1,2}^{\mathrm{th}}$ or a different binsize is used. The ISIH of the chaotic oscillations in (a) was calculated on the basis of $N_1 = 52\,560$ interspike intervals. For the ISIH's of the coupled system in (b)–(d) $N_2 = 5000$ intervals were counted. The y-axis scaling is the same for diagrams (b)–(d). Parameters are the same as in Fig. 1, except (b) $\sigma = 0.03$, (c) $\sigma = 0.1$, and (d) $\sigma = 0.3$.

The following system of two coupled relaxation-type nonlinear oscillators is investigated [9]:

$$\varepsilon \frac{dx_1}{dt} = y_1 - \frac{x_1^2}{2} - \frac{x_1^3}{3}, \tag{1}$$

$$\frac{dy_1}{dt} = -x_1 + \alpha + A\cos(\omega t), \tag{2}$$

$$\varepsilon \frac{dx_2}{dt} = y_2 - \frac{x_2^2}{2} - \frac{x_2^3}{3}, \tag{3}$$

$$\frac{dy_2}{dt} = -x_2 + \alpha + \mu x_1 + \xi(t), \tag{4}$$

where $0 < \varepsilon \ll 1$. In the following the system consisting of Eqs. (1) and (2) [Eqs. (3) and (4)] is referred to as $S1$ ($S2$). Simulations revealed that the oscillator exhibits a great variety of dynamical kinds of behavior when driven by weak periodic forces [9]. Therefore the model provides a broad dynamical spectrum for further investigations.

Equations (1) and (2) exhibit a single steady state (stable focus for $\alpha > 0, \alpha(1+\alpha) < 2\sqrt{\varepsilon}$, Hopf bifurcation at $\alpha = 0$). In the following the parameters are adjusted to yield a stable focus for both systems. $S1$ is driven into a chaotic state by harmonic forcing, and the resulting oscillations are used as the input signal for $S2$. The coupling constant $\mu < 0$ is adjusted to yield a subthreshold input signal. A negative value of μ is chosen, because the relaxation oscillations exhibit negative deflections and mainly occur in phase with the positive cycle of the cosine function (see Fig. 1 below). $S2$ responds with relaxation oscillations (''firing sequences'') when also exposed to a noise source $\xi(t)$. In the simulations exponentially correlated noise is used with zero-mean and Gaussian-distributed amplitudes of variance $\langle \xi^2 \rangle = \sigma^2$ [10]. The random lifetimes of the fluctuations are calculated as $t_N = -\tau \ln(R)$, where R is a random number ($0 < R < 1$), and τ is the correlation time. The latter is much smaller than all other time scales. Application of nonwhite noise is preferred, because it provides a more realistic description for biological systems.

Figure 1 depicts the resulting oscillation patterns at an intermediate noise intensity level. Note that the aperiodic input signal ($S1$) varies on a time scale that is comparable to the characteristic time of the responding system ($S2$). This is opposite to the models studied so far from the perspective of ASR [2].

$S1$ exhibits a chaotic sequence of spike events that mainly occur in phase with the positive cycle of the cosine function. Consequently, the spike events are phase locked with the external drive, and the interspike intervals are nearly integer multiples of the driver's period T_P. This can also be recognized in the structure of the interspike interval histogram (ISIH) [Fig. 2(a)]. Almost nine-tenths of the intervals are located within $\Delta T = 0.05$ of integer multiples of the driver's period, including main contributions at three and five times T_P. This kind of behavior has been observed in similar relaxation-type systems before [6,11]. Examples include experimental investigations with periodically stimulated squid giant axons and numerical simulations of the FitzHugh-Nagumo model [6]. The specific distribution of the peaks in the ISIH of $S1$ enables a quantitative comparison with the activity of $S2$. The response pattern of $S2$ (Fig. 1, bottom diagram) exhibits dynamic filtering characteristics, because the fast variations of $S1$ are not reproduced. $S2$ does not respond to every input spike but rather to sequences of spikes. Figures 2(b)–2(d) depict ISIH's for $S2$ at three different noise intensity levels. At lower noise intensity levels the ISIH's display a distinct pattern of spike intervals incor-

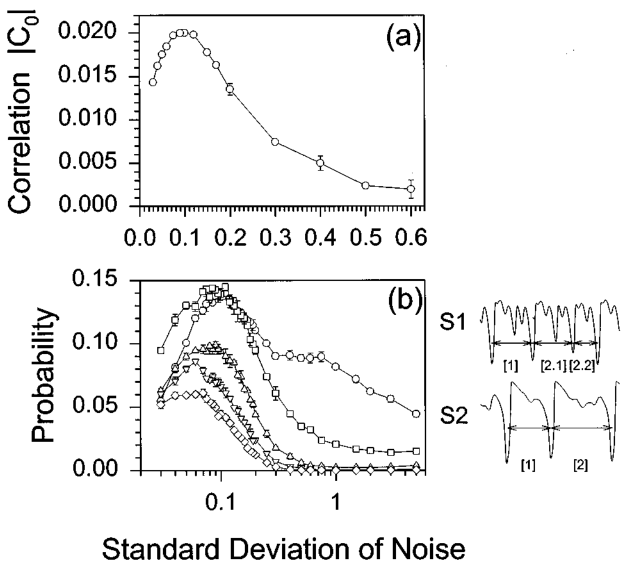

FIG. 3. Correlation between the chaotic input signal and the response pattern. (a) The power norm defined by Eq. 5 as a function of increasing noise intensity. Data points were obtained in duplicate by averaging over $N_P = 20\,000$ periods of the harmonic driver of $S1$. (b) Correlation between the mean interspike interval of a sequence of spikes in the chaotic input signal producing a response spike, and the interspike interval of the response. Each sequence of spikes in the chaotic input signal is compared with the response spike it produces. The procedure is illustrated in the scheme on the right side of the figure, showing a part of the time series depicted in Fig. 1. In this example the interspike interval {1} of $S1$ is compared with {1} of $S2$, and the mean of the interspike intervals {2.1} and {2.2} of $S1$ is compared with {2} of $S2$. The diagram depicts the probability that the interspike interval of the detector response is located within $\Delta T = \pm 0.05$ of an integer multiple of the mean interspike interval of the sequence of spikes in chaotic input signal producing the response. The symbols represent multiples $n = 1-5$ (circles: $n = 1$, squares: $n = 2$, triangles: $n = 3$, upside-down triangles: $n = 4$, diamonds: $n = 5$). The probability was estimated by averaging over $N_2 = 5000$ response spikes and calculating the mean interspike interval producing each response spike. Data points were obtained in triplicate. For every data point shown in (a) and (b), a different sequence of the chaotic attractor and different sets of random numbers for calculating the noise amplitudes and correlation times were used. Error bars represent standard deviations. Parameters are the same as in Fig. 1.

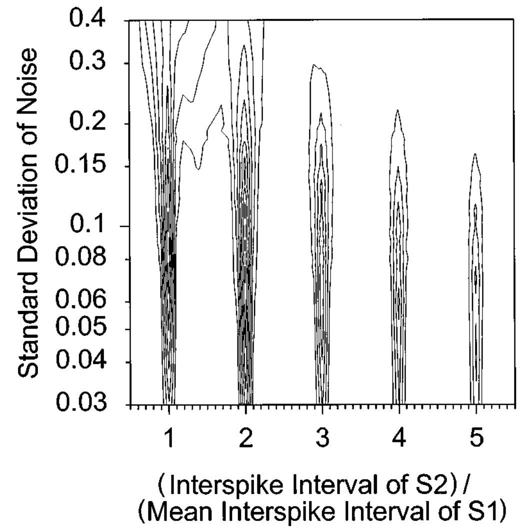

FIG. 4. Contour plot showing the probability for the occurrence of a specific ratio between the interspike interval of the detector ($S2$) and the mean interspike interval of the chaotic signal ($S1$) producing the response [see Fig. 3(b) for details]. The outermost lines represent a probability of $P = 0.02$. The probability increases in increments of $\Delta P = 0.02$ between lines. Parameters are the same as in Fig. 1.

porating characteristics of the chaotic input signal as well as specific properties determined by the coupling of the systems [Figs. 2(b) and 2(c)]. For example, in the ISIH in Fig. 2(c) one can recognize sequences of peaks that are separated by the two main interspike intervals present in the chaotic input signal (the first sequence around $T = 1.75$, 2.80 and 3.85; the second around $T = 3.50$ and 4.55). The individual peaks within the two sequences are separated by an interval corresponding to the second largest peak at $T = 1.05$ in the ISIH of the chaotic input signal. Furthermore, the two series are shifted against each other by an interval corresponding to the largest peak at $T = 1.75$.

The preceding discussion suggests regarding $S2$ as a temporal pattern detector that is capable of responding to patterns in the interspike interval distribution of the input signal. There is no linear relationship between the spike pattern of the chaotic input and the response pattern. Rather the response pattern combines characteristics of the chaotic input signal and dynamic properties of the detector given by its excitability.

Information processing is made possible by the presence of noise, because the chaotic input signal is subthreshold. Therefore the possibility exists that the information transfer is optimized at an intermediate noise intensity level. Intuitively one may conclude that the characteristics of the ISIH's already reflect this behavior. At lower noise intensities the spectrum is flat, and contains only a few distinct peaks [Fig. 2(b)]. On the other hand, at very high noise levels the resulting spectrum is concentrated around a single broad peak that reflects the minimum response time of the detector to any kind of perturbations [Fig. 2(d)]. In this case the ISIH contains only a small amount of information about the chaotic input signal. These observations suggest that there is an intermediate noise intensity range where the information transfer is maximally enhanced by noise. This property can be demonstrated by calculating simple correlation measures [12]. For example, the correspondence between the ISIH's of the two systems is defined by $\langle P_1 P_2 \rangle / \langle P_1 P_1 \rangle$. Here P_i denotes the probability for the occurrence of a specific interspike interval and averaging extends over all bins within the ISIH's. A second method is to estimate the squared difference between the ISIH's by calculating $\langle (P_1 - P_2)^2 \rangle$. This method allows for an interesting comparison to neural network theory. The ''Hamming distance'' is defined as the mean-square deviation between an input pattern and a stored pattern in a neural network [13]. This function exhibits a minimal value for the stored pattern that most closely resembles the input pattern. Indeed, in the present case one can show that the squared difference between the ISIH's of the chaotic input signal and the response signal exhibits a minimal value at intermediate noise intensity levels around $\sigma = 0.1$. In the same range the correspondence between the ISIH's is maximal.

Although the two correlation measures defined above already reveal a behavior that can be identified as SR, these functions only compare long-term-averaged properties between the input and output patterns. Because the input signal is a dynamic one, it is more meaningful to estimate the correlation between the two systems on a dynamical basis. For

ASR it has been suggested to use the power norm C_0 [2]. In the present case this is written in the following way:

$$C_0 = \langle (x_1 - \langle x_1 \rangle_t)(x_2 - \langle x_2 \rangle_t) \rangle_t, \tag{5}$$

where $\langle\ \rangle_t$ denotes time averaging. In Fig. 3(a) the absolute value of C_0 is shown as a function of increasing noise intensities. The absolute value is used to allow for an easier comparison with results obtained in other studies. The actual value of C_0 is negative, because the variables $x_{1,2}$ exhibit negative deflections, and there is a time delay between a sequence of spikes in the chaotic input signal and the response of the detector. Figure 3(a) reveals that there is an intermediate noise intensity range around $\sigma = 0.1$, where the correlation between the oscillation patterns of the two systems is maximal. In this range the response sensitivity of the detector is optimized with regard to the chaotic input signal. In contrast at lower noise intensity levels the propability for spiking activity of $S2$ is low, whereas at high levels the system mainly responds to the noise input.

Another way of quantifying the correlation between the two systems is to compare directly each sequence of spikes in the chaotic input signal with the response spike it produces. This can be achieved by calculating the mean interspike interval of the sequence of spikes in the chaotic input signal producing the response spike, and comparing it with the interspike interval of the response. Figure 3(b) depicts the probability that the interspike interval of the detector response is located within $\Delta T = \pm 0.05$ of an integer multiple of the mean interspike interval of the sequence in the chaotic input signal producing the response. In Fig. 4 the global behavior is shown. One finds that for multiples $n = 1-5$ the probability exhibits a maximal value at intermediate noise intensity levels. The maximal probability for multiples $n = 1$ and 2 is observed around $\sigma = 0.1$, corresponding to the same noise intensity range where the absolute value of the power norm exhibits a maximal value. At higher order muliples $n = 3,4,5, \ldots,$ the maximum of the probability is shifted toward lower noise intensity levels. This behavior results because at lower noise intensity levels the spiking probability of $S2$ decreases thus leading to prolonged interspike intervals.

The results presented in this paper demonstrate that the excitable focus $S2$ is capable of detecting temporal patterns in the chaotic input signal. The information transfer is enabled by the presence of noise, and is optimized at an intermediate noise intensity level. This phenomenon can be regarded as a noise-induced coherence between the two oscillators. Because the input signal is aperiodic, the behavior can be interpreted as a form of ASR. However, in the original definition the aperiodic input signal fluctuates stochastically on a time scale that is slower than the characteristic time of the responding system [2]. In contrast, in the present case the deterministic chaotic input signal varies on a time scale that is comparable to the characteristic time of the responding system. The results reveal that the signal-processing capabilities of the responding system are optimized at an intermediate noise level. This shows that the phenomenon of ASR is not restricted to slowly varying input signals [14].

In a recent experimental study it was observed that the reliability of spike timing in neocortical neurons is enhanced by fluctuating input signals in comparison with constant stimuli [15]. This suggests that cortical neurons respond reliably to fluctuating input signals. These observations exhibit some similarities with the present investigations. In both cases the performance of the excitable system's information processing capabilities is enhanced by aperiodic input signals.

C.E. acknowledges financial support from the Fetzer Institute. Work at the Bioelectromagnetics Laboratory was supported by the Fetzer Institute and the U.S. Department of Energy.

[1] F. Moss, D. Pierson, and D. O'Gorman, Int. J. Bifurcation Chaos Appl. Sci. Eng. **4**, 1383 (1994); K. Wiesenfeld and F. Moss, Nature (London) **373**, 33 (1995).
[2] J. J. Collins, C. C. Chow, and T. T. Imhoff, Phys. Rev. E **52**, R3321 (1995); **54**, 5575 (1996).
[3] J. J. Collins, C. C. Chow, and T. T. Imhoff, Nature (London) **376**, 236 (1995); X. Pei, L. Wilkens, and F. Moss, Phys. Rev. Lett. **77**, 4679 (1996).
[4] J. E. Levin and J. P. Miller, Nature (London) **380**, 165 (1996); J. J. Collins, T. T. Imhoff, and P. Grigg, J. Neurophysiol. **76**, 642 (1996).
[5] N. Takahashi, Y. Hanyu, T. Musha, R. Kubo, and G. Matsumoto, Physica D **43**, 318 (1990); W. J. Freeman, Int. J. Bifurcation Chaos Appl. Sci. Eng. **2**, 451 (1992); T. Elbert, W. J. Ray, Z. J. Kowalik, J. E. Skinner, K. E. Graf, and N. Birbaumer, Physiol. Rev. **74**, 1 (1994); X. Pei and F. Moss, Nature (London) **379**, 618 (1996).
[6] D. T. Kaplan, J. R. Clay, T. Manning, L. Glass, M. R. Guevara, and A. Shrier, Phys. Rev. Lett. **76**, 4074 (1996).
[7] H.-S. Hahn, A. Nitzan, P. Ortoleva, and J. Ross, Proc. Natl. Acad. Sci. USA **71**, 4067 (1974); A. Arkin and J. Ross, Biophys. J. **67**, 560 (1994); D. Bray, Nature (London) **376**, 307 (1995).
[8] For many biological systems like enzymes, for example, the threshold is not a sharp, steplike function, but rather there is a gradual transition [7]. Recently, it has been shown that such systems are also capable of exhibiting stochastic resonance [S. M. Bezrukov and I. Vodyanoy, Nature (London) **385**, 319 (1997)].
[9] B. Braaksma and J. Grasman, Physica D **68**, 265 (1993).
[10] K. Binder, in *Monte Carlo Methods in Statistical Physics,* edited by K. Binder (Springer, Berlin, 1986), p. 1; C. Eichwald and F. Kaiser, Bioelectromagnetics **16**, 75 (1995).
[11] A. Longtin, A. Bulsara, and F. Moss, Phys. Rev. Lett. **67**, 656 (1991); A. Longtin, J. Stat. Phys. **70**, 309 (1993).
[12] The characterization of SR in threshold systems by correlation functions and (more recently) by information measures is discussed in a number of contributions [Z. Gingl, L. B. Kiss, and F. Moss, Europhys. Lett. **29**, 191 (1995); L. B. Kiss, in *Proceedings of the Third Technical Conference on Nonlinear Dynamics (Chaos) and Full Spectrum Processing,* edited by R. Katz (AIP, New York, 1996), p. 382; A. R. Bulsara and A. Zador, Phys. Rev. E **54**, R2185 (1996); C. Heneghan, C. C. Chow, J. J. Collins, T. T. Imhoff, S. B. Lowen, and M. C. Teich, *ibid.* **54**, R2228 (1996)].
[13] B. Müller, J. Reinhardt, and M. T. Strickland, *Neural Networks* (Springer, Berlin, 1995).
[14] During the review stage of this paper, another paper was published that contains a critical discussion of ASR with slowly varying input signals. It was anticipated that it should be possible to obtain "true SR" for aperiodic signals with a higher frequency content [D. R. Chialvo, A. Longtin, and J. Müller-Gerking, Phys. Rev. E **55**, 1798 (1997)].
[15] Z. F. Mainen and T. J. Sejnowski, Science **268**, 1503 (1995).