Stochastic Resonance in Ensembles of Nondynamical Elements: The Role of Internal Noise

Paul C. Gailey,[1] Alexander Neiman,[2,3] James J. Collins,[4] and Frank Moss[2]
[1]*Oak Ridge National Laboratory, P.O. Box 2008, Oak Ridge, Tennessee 37831-6070*
[2]*Center for Neurodynamics, University of Missouri at St. Louis, St. Louis, Missouri 63121*
[3]*Department of Physics, Saratov State University, Saratov 410073, Russia*
[4]*Department of Biomedical Engineering, Boston University, 44 Cummington Street, Boston, Massachusetts 02215*
(Received 30 June 1997)

While many examples of noise-induced signal enhancement have been reported, the role of internal noise has received little attention. Here we study aperiodic stochastic resonance in parallel arrays of nondynamical elements with internal noise. Ensembles of both threshold and threshold-free elements are studied, and the model is applied to two-state ion channels. In finite systems where the input signal controls the probability of discrete events, we demonstrate that the internal noise is modulated by both the applied signal and the external noise. We also show that the internal noise plays a constructive role in information transfer through such systems via an increase in external noise. [S0031-9007(97)04777-7]

PACS numbers: 87.10.+e, 05.40.+j

Internal noise occurs in some form in all information-processing systems. The presence of this intrinsic noise complicates the analysis of such systems, especially when nonlinear processes such as stochastic resonance (SR) [1–3] are considered. Not least among the obstacles to understanding the role of internal noise is the fact that its sources and properties are often unknown. However, it is widely appreciated that the role of internal noise in information-processing systems is generally negative. One method for reducing internal fluctuations is to use an array of elements instead of a single element. In such an ensemble, all elements have a common input and their outputs are summed. If the number of elements in such an array is large enough, the internal fluctuations, being statistically independent in each element, can be decreased due to averaging at the summed center, so that the signal-to-noise ratio (SNR) at the summed output is increased in proportion to the number of elements [4]. An array of information-processing elements acting in parallel is also an appropriate model for some biological systems, such as ion channels and sensory neurons. This model applied to a parallel array of stochastic resonators exhibits the important effect of SR without tuning [5]: the collective response of the array to a small input signal can be optimized for a range of *internal noise* intensities larger than some small value. An experimental observation of SR in an array of ion channels was recently reported by Bezrukov and Vodyanoy [6].

In real information-processing systems, the internal noise is generally assumed to be difficult to control, while applied information signals are always contaminated by external noise that is more accessible for control and measurement. However, here we demonstrate that in finite arrays of stochastic, two-state elements, the intensity of the internal noise is a function of both the applied input signal and external noise. As we show, this external modulation of internal noise can play an important role in information processing. We study SR in a simple but generic model of an ensemble of nonlinear nondynamical elements, each of which exhibit internal noise, and we concentrate on the role that these internal fluctuations play. We consider both threshold elements and threshold-free elements, as have been studied recently in Ref. [7]. In the latter case, we apply the model to two-state ion channels and show that internal noise can play a constructive role in the sense that external noise added to the input signal can improve the information transfer through the system, while this effect is absent when the internal noise is not taken into account.

SR has been experimentally demonstrated in a variety of biological systems [8], for which nondynamical theory has been usefully applied [7,9–11]. We use a nondynamical approach here, describing the process as a nonlinear transformation of the applied input signal and external noise. To simplify our theoretical analysis, both the input signal and the external noise are taken to be statistically independent Gaussian processes. We thus study *aperiodic stochastic resonance* (ASR) as introduced by Collins *et al.* in Ref. [12]. Recently in Ref. [13] it was shown that ASR can be viewed as conventional SR by using linear response theory. Instead of calculating the threshold-crossing rate, as has been done in previous studies of nondynamical SR [7,9–11], we use the classical theory of nonlinear transformation of a Gaussian process [14–16] to obtain cross-correlation measures. To demonstrate this technique, we consider first an ensemble of N threshold elements, each of which is characterized by the Heaviside unit-step transfer function, $y_k(t) = \Theta[x(t) - b] + \xi_k(t)$, where x and y_k are the input and output, respectively, of kth element, $\xi_k(t)$ mimics an internal noise generated by the kth element, and b is a constant (see [10] for a single element). All elements are subjected to the same input $x(t)$, which is the sum of the signal $s(t)$ and the external noise $n(t)$. We also suppose that the input signal, the external noise, and the internal fluctuations ξ_k are statistically independent zero-mean Gaussian stationary processes with variances q^2, σ^2, and r^2, respectively. The outputs of the elements are summed giving the collective response $Y(t)$:

$$Y(t) = N\Theta[x(t) - b] + \sum_{k=1}^{N} \xi_k(t), \quad x(t) = s(t) + n(t), \tag{1}$$

$$\langle s^2 \rangle = q^2, \qquad \langle n^2 \rangle = \sigma^2, \qquad \langle \xi^2 \rangle = r^2. \tag{2}$$

The quantities of interest, which characterize the information transfer through the array, are the covariance, c, and the correlation coefficient, ρ, between input signal and the summed output:

$$c = \langle Y \cdot s \rangle, \qquad \rho = \frac{\langle Y \cdot s \rangle}{\sqrt{\langle Y^2 \rangle \langle s^2 \rangle}}, \tag{3}$$

where the cumulant brackets $\langle \cdot \rangle$ denote averaging over the ensembles of stochastic processes s, n, and ξ. These quantities have been used recently to study ASR in Ref. [12]. For the unit-step function, all cumulants can be calculated analytically [14,16], giving for the covariance and the correlation coefficient the following expressions:

$$\frac{c}{N} = \frac{q^2}{\sqrt{2\pi(q^2 + \sigma^2)}} \exp\left[-\frac{b^2}{2(q^2 + \sigma^2)}\right], \tag{4}$$

$$\rho = \frac{c/N}{q\sqrt{\frac{1}{2}\{1 - \mathrm{erf}[b/\sqrt{2(q^2 + \sigma^2)}]\} + \frac{r^2}{N}}}, \tag{5}$$

where $\mathrm{erf}(x)$ is the error function.

Both the covariance and the correlation coefficient display bell-shaped curves reaching maxima at some optimal levels of external noise, thereby demonstrating ASR [see Fig. 1(a)]. For the covariance c, the optimal magnitude of external noise can be obtained exactly, $\sigma_{\mathrm{opt}} = \sqrt{b^2 - q^2}$. The correlation coefficient reaches its maximum for lower values of σ. In the limit $N \to \infty$, the last term in the denominator of Eq. (5), representing the internal noise, vanishes. This limit also gives the upper value for the correlation coefficient. In Fig. 1(b), a larger signal magnitude q is considered. For a large enough signal magnitude [Fig. 1(b), $N \to \infty$ case], the dependence $\rho(\sigma)$ becomes monotonic, i.e., the SR effect vanishes. However, in systems with a finite number of elements [Fig. 1(b), e.g., $N = 10$ case], an SR effect is again observed, even when the signal magnitude is large. As N is reduced, the internal noise of the system increases and the absolute value of the correlation coefficient decreases, indicating that finite systems with internal noise do not transmit information as effectively as systems without internal noise. If one is constrained to a finite system, however, these results [Fig. 1(b)] indicate that the presence of internal noise permits the optimization of the correlation coefficient as a function of external noise. Internal noise can thus play a constructive role in determining the information-processing properties of the system.

Let us now examine the model when each element in the array is characterized by a nonlinear voltage-

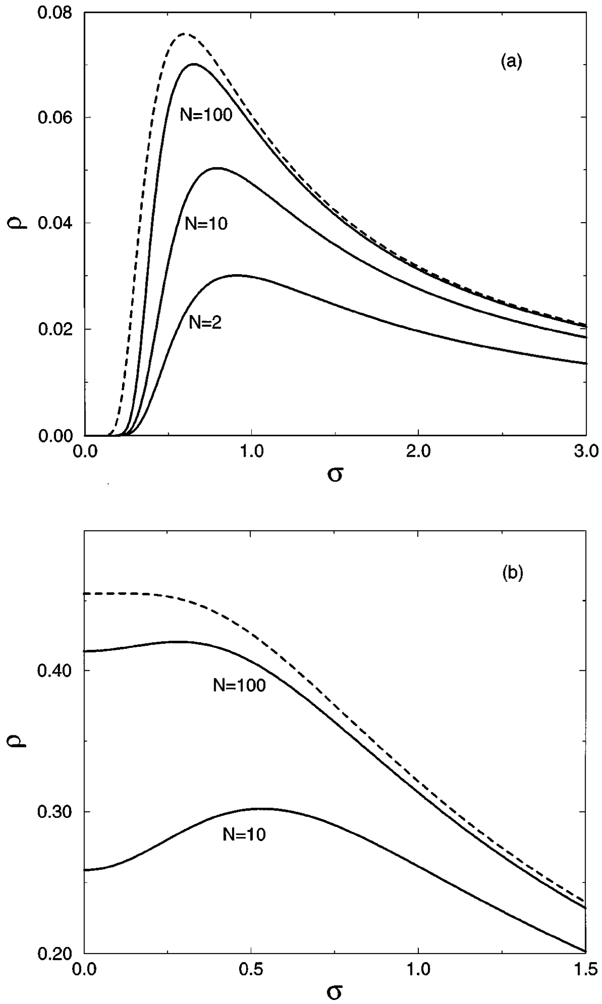

FIG. 1. The correlation coefficient, ρ, [Eq. (4)] as a function of external noise variance, σ, for different numbers of elements in an array of threshold elements. The dashed line corresponds to the limit $N \to \infty$. The parameters are $b = 1.0$, $r = 1.0$, $q = 0.1$ (a) and $q = 0.58$ (b).

dependent conductance $p(V)$. We introduce the internal fluctuations in the kth element via fluctuations of its conductance, as $\tilde{p}_k(V) = p(V) + g(V)\xi_k(t)$. A nonlinear function $g(V)$ is included because in the general case the internal fluctuations may be influenced by the input voltage V. The current through the kth element is $i_k = V[p(V) + g(V)\xi_k(t)]$. The whole current through the array is therefore

$$I(t) = NVp(V) + Vg(V) \sum_{k=1}^{N} \xi_k(t). \tag{6}$$

It is important to note that Eq. (6) also describes the current through an array of two-state ion channels which can exist in either a ground (closed) state or an excited (open) state [17]. The expectation value for the fraction of elements in the excited state (or expectation number of open channels) is $Np(V)$, where $p(V)$ represents the open probability, while the fluctuations around this expectation value have intensity $Np(V)[1 - p(V)]$. The latter term describes the fluctuations that will occur in any two-state (binomial) process, and reveals explicitly how the intensity of these fluctuations is modulated by the applied input signal and external noise, V, through the open probability, $p(V)$. The current through this ensemble is given by Eq. (6) with the specified function $g(V) = \sqrt{p(V)[1 - p(V)]}$. We take the nonlinear function $p(V)$ in the generic form of a Boltzmann relation as

$$p(V) = \frac{1}{1 + \exp[\Delta(W - V)]}, \tag{7}$$

where Δ is the constant determining the width (or slope) of the distribution associated with kT, and W refers to the energy barrier that must be overcome to open a closed channel. The structure of this model, while simple, is somewhat general in the sense that many natural processes are governed by Boltzmann relations [Eq. (7)] (e.g., lasers, semiconductors, and ion channels). In contrast to the previous case of an ensemble of threshold elements, elements of this model are threshold-free. Because of the finite width of the function $p(V)$, the output current can be obtained for arbitrarily small input voltages. We again suppose that the applied voltage contains the input signal and external noise, which are Gaussian, statistically independent processes $V(t) = s(t) + n(t)$ [e.g., see Eq. (2)]. We also assume that the internal-noise terms $\xi_k(t)$ are statistically independent from $V(t)$. This assumption is valid, in particular, in the adiabatic limit, when the input voltage varies much more slowly than any time scale of the system. The quantity of interest, the correlation coefficient, is

$$\rho = \frac{\langle I \cdot s \rangle}{\sqrt{(\langle I^2 \rangle - \langle I \rangle^2)\langle s^2 \rangle}}. \tag{8}$$

To calculate ρ, we use known rules for the opening of cumulant brackets. In particular, for two arbitrary zero-mean Gaussian processes $x(t)$ and $y(t)$ and a nonlinear function $f(x)$, the following formula is valid [16]: $\langle x f(y) \rangle = \langle f'(y) \rangle \langle xy \rangle$. Using this rule, we obtain

$$\langle I \rangle = N\langle p' \rangle D, \qquad \langle I \cdot s \rangle = Nq^2[\langle p \rangle + D\langle p'' \rangle],$$
$$\langle I^2 \rangle = ND\{N[\langle p^2 \rangle + D\langle (p^2)'' \rangle] + r^2[\langle g^2 \rangle + D\langle (g^2)'' \rangle]\}, \tag{9}$$

where $D = \langle V^2 \rangle = \sigma^2 + q^2$, and the averaged nonlinear functions are given by integrals over the Gaussian distribution of the input voltage, for example,

$$\langle p \rangle = \int_{-\infty}^{\infty} p(V) G(V)\, dV,$$
$$\langle p' \rangle = \int_{-\infty}^{\infty} \frac{dp}{dV} G(V)\, dV, \tag{10}$$
$$G(V) = \frac{1}{\sqrt{2\pi D}} \exp\left(\frac{-V^2}{2D}\right).$$

Unfortunately, some of these integrals cannot be taken analytically and must be calculated numerically. The covariance monotonically increases with σ. This behavior is similar to the monotonic increase of the output signal observed in ion channels [6] and calculated for threshold-free systems [7]. The dependence of the correlation coefficient on the external noise variance is shown in Fig. 2(a). The limit $N \to \infty$, which also refers to the case of no internal noise, is shown by the dashed line. These results differ markedly from the results presented earlier for threshold devices: for small external noise, the correlation coefficient decreases, reaches its minimum, and then passes through a maximum. This behavior is similar to that of the output SNR for conventional SR in an overdamped bistable system [18] and has the same origin. The presence of internal noise removes this part of the SR curve as is shown in Fig. 2(a).

Let us now consider the practical and important case of very small values of open probability $p(V) \ll 1$ as studied experimentally by Bezrukov and Vodyanoy [6]. This situation occurs for $V \ll W$. In this case, the presence of internal noise can also lead to qualitative changes. As

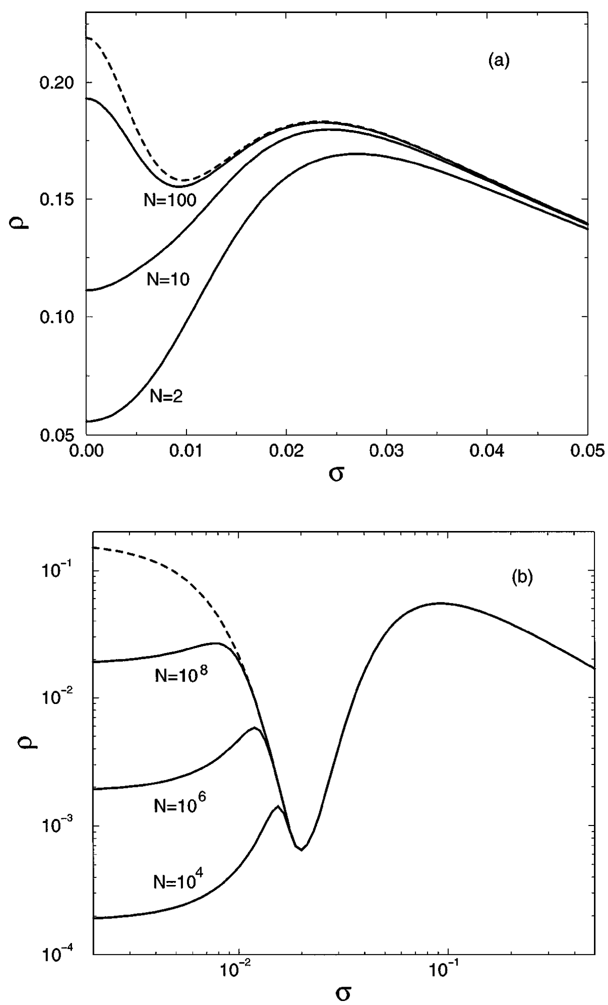

FIG. 2. The correlation coefficient, ρ, as a function of external noise variance, σ, for an array of two-state ion channels. The dashed line corresponds to the limit $N \to \infty$. The parameters are $\Delta = 200$, $r = 1.0$, $q = 0.01$, $W = 0.05$ (a) and $W = 0.15$ (b).

shown in Fig. 2(b), for a certain number of elements in the ensemble (i.e., for a certain level of internal noise), the SR curves possess two maxima. The new maximum appears for smaller values of σ as the result of competition between growing covariance and variance of the output current. The first peak in the correlation coefficient (and the SNR) occurs at an external noise value similar to the experimentally observed value [6]. We note that in experimental studies, it is possible that only the first maximum can be observed because the second maximum may occur for such large noise voltages that it is outside the working limits of the system. Note that for $V \ll W$, the open probability can be approximated as $p(V) \approx \exp[\Delta(V - W)]$ and $g(V) \approx [p(V)]^{1/2}$, so that the correlation coefficient can be calculated in closed form:

$$\rho = \frac{qP(1 + \Delta^2 D)}{\sqrt{D[Q - \Delta^2 DP^2 + 4\Delta^2 DQ + (r^2/N)P(1 + \Delta^2 D)]}},$$
$$P = \exp[\Delta(\Delta D - 2W)/2], \qquad Q = \exp[2\Delta(\Delta D - W)], \qquad D = \sigma^2 + q^2. \tag{11}$$

The correlation coefficient given by Eq. (11) reveals the same behavior as in Fig. 2(b), except that the second maximum cannot be observed for large values of σ.

In conclusion, we have studied ASR in ensembles of nondynamical elements acting in parallel. We considered both threshold and threshold-free elements. The latter case was applied to an array model of two-state ion channels. For such a model, we showed that the internal noise is modulated by the applied input signal and external noise, and that it can play a crucial role in changing the qualitative behavior of the system's input-output correlation coefficient as a function of the externally applied noise. For the case of a small probability of open channels, the internal noise results in the appearance of a new maximum in the plot of the correlation coefficient versus the external noise level. We note that qualitatively similar results can be obtained for conventional SR, when the applied input signal is periodic in nature. Indeed, our results agree with experimental findings for ion channels where both the monotonic increase in covariance and maximum in SNR predicted by our model were observed [6].

This work was supported in part by the U.S. Office of Naval Research Physics Division, the U.S. Department of Energy, and the National Science Foundation. A. N. is supported by a U.S. National Academy of Science COBASE grant.

[1] R. Benzi, A. Sutera, and A. Vulpiani, J. Phys. A **14**, L453 (1981); R. Benzi, G. Parisi, A. Sutera, and A. Vulpiani, Tellus **34**, 10 (1982); C. Nicolis, Tellus **34**, 1 (1982).

[2] *Proceedings of the NATO Advanced Research Workshop on Stochastic Resonance in Physics and Biology,* edited by F. Moss, A. Bulsara, and M. F. Shlesinger [J. Stat. Phys. **70**, 1 (1993)]; *Proceedings of the International Workshop on Fluctuations in Physics and Biology: Stochastic Resonance, Signal Processing and Related Phenomena,* edited by R. Mannella and P. V. E. McClintock [Nuovo Cimento Soc. Ital. Fis. **17D**, 653 (1995)].

[3] F. Moss, in *Some Contemporary Problems in Statistical Physics,* edited by G. Weiss (SIAM, Philadelphia, 1994), p. 205; F. Moss, D. Pierson, and D. O'Gorman, Int. J. Bifurcation and Chaos **4**, 1383 (1994); K. Wiesenfeld and F. Moss, Nature (London) **373**, 33 (1995); A. R. Bulsara and L. Gammaitoni, Phys. Today **49**, No. 3, 39 (1996); a full bibliography can be found at WWW site http://www.pg.infn.it/sr/.

[4] J. S. Bendat and A. G. Piersol, *Random Data* (John Wiley & Sons, New York, 1986).

[5] J. J. Collins, C. C. Chow, and T. T. Imhoff, Nature (London) **376**, 236 (1995).

[6] S. M. Bezrukov and I. Vodyanoy, Nature (London) **378**, 362 (1995).

[7] S. M. Bezrukov and I. Vodyanoy, Nature (London) **385**, 319 (1997).

[8] J. K. Douglass, L. Wilkens, E. Pantazelou, and F. Moss, Nature (London) **365**, 337 (1993); 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); R. P. Morse and E. F. Evans, Nature Medicine **2**, 928 (1996); P. Cordo, J. T. Inglis, S. Verschueren, J. J. Collins, D. M. Merfeld, S. Rosenblum, S. Buckley, and F. Moss, Nature (London) **383**, 769 (1996); F. Y. Chiou-Tan, K. N. Magee, L. R. Robinson, M. R. Nelson, S. S. Tuel, T. A. Krouskop, and F. Moss, Int. J. Bifurcation Chaos **6**, 1389 (1996); B. J. Gluckman, T. I. Netoff, E. J. Neel, W. L. Ditto, M. L. Spano, and S. J. Schiff, Phys. Rev. Lett. **77**, 4098 (1996).

[9] K. Wiesenfeld, D. Pierson, E. Pentazelou, C. Dames, and F. Moss, Phys. Rev. Lett. **72**, 2125 (1994); Z. Gingl, L. Kiss, and F. Moss, Europhys. Lett. **29**, 191 (1995).

[10] P. Jung, Phys. Rev. E **50**, 2513 (1994).

[11] P. Jung, Phys. Lett. A **207**, 93 (1995).

[12] J. J. Collins, C. C. Chow, and T. T. Imhoff, Phys. Rev. E **52**, R3321 (1995); J. J. Collins, C. C. Chow, A. C. Capela, and T. T. Imhoff, Phys. Rev. E **54**, 5575 (1996).

[13] A. Neiman, L. Schimansky-Geier, and F. Moss, Phys. Rev. E **56**, R9 (1997).

[14] S. O. Rice, in *Selected Papers on Noise and Stochastic Processes,* edited by N. Wax (Dover, New York, 1954), pp. 133–294.

[15] R. L. Stratonovich, *Topics in the Theory of Random Noise* (Gordon and Breach, New York, London, 1963), Vol. 1.

[16] A. N. Malakhov, *Cumulant Analysis of Random Non-Gaussian Processes and Their Transformations* (Sov. Radio, Moscow, 1978) (in Russian).

[17] L. J. DeFelice, *Introduction to Membrane Noise* (Plenum Press, New York, London, 1981).

[18] B. McNamara and K. Wiesenfeld, Phys. Rev. A **39**, 4854 (1989).