Information measures quantifying aperiodic stochastic resonance

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(Received 1 May 1996)

Aperiodic stochastic resonance (ASR) is a phenomenon in which the response of a nonlinear system to a subthreshold information-bearing signal is optimized by the presence of noise. We have previously characterized this effect by the use of cross-correlation-based measures. Here we apply a measure (transinformation) that directly quantifies the rate of information transfer from stimulus to response and show that the presence of noise optimizes the information-transfer rate. By considering a nonlinear system (the FitzHugh-Nagumo model) that captures the functional dynamics of neuronal firing, we demonstrate that sensory neurons could, in principle, harness ASR to optimize the detection and transmission of weak stimuli. [S1063-651X(96)51309-7]

PACS number(s): 87.10.+e, 87.22.−q, 05.40.+j

Stochastic resonance (SR) is a phenomenon in which the response of a nonlinear system to a weak periodic input signal is optimized by a particular level of additive noise [1]. Theories of SR have been developed for multistable [2,3], monostable [4], and excitable [5] systems, as well as threshold-crossing detectors [6]. Many of these studies were restricted to cases with periodic input signals, which is somewhat limiting from a practical standpoint as many systems of interest are driven by nonperiodic inputs. Previous work has considered also the possibility of aperiodic input signals consisting of stationary stochastic processes for SR studies in a bistable system [3,7]. Recently, we have shown that the notion of SR can be readily extended to cases with aperiodic (arbitrary) inputs [8,9]. We coined the term *aperiodic stochastic resonance* (ASR) to describe this phenomenon.

It is implicitly assumed that both SR [10,11] and ASR [8,9] indicate some maximum in the rate of *information transfer* between system input and output. This issue has been addressed explicitly only recently [12–14]; previous results inferred a maximum in information transfer from a maximum in coherence or cross-correlation measures between the input and output. In this paper, we establish that the cross-correlation measures employed for ASR [8,9] are indeed accompanied by a maximum in the information-transfer rate for the model at hand.

We employ the FitzHugh-Nagumo (FHN) construct [15] as the model system for investigating ASR. This system has been used in a number of physiologically motivated SR investigations [5,8–10,16] because it provides a compact representation of the firing dynamics of sensory neurons driven by an external signal. In particular, for sufficiently strong (i.e., suprathreshold) input signals, the FHN model exhibits excursions (firings) from a fixed point, followed by a deterministic return to that point within a short period of time (i.e., the dead time), similar in character to action potential activity observed on nerve fibers. A subthreshold input signal, by contrast, cannot cause firing; however, addition of a noise component allows the possibility of occasional firings arising from random noise-induced excursions across the threshold. This firing behavior of the FHN model provides a prototypical environment for numerical SR experiments, since it forms a type of nonlinear response, a fundamental component of an SR system.

In this paper, we consider the FHN model under the influence of a subthreshold aperiodic signal $s(t)$ to which Gaussian white noise $\xi(t)$ has been added:

$$\epsilon\dot{v} = -v(v^2 - \tfrac{1}{4}) - w + A_T - B + s(t) + \xi(t), \qquad (1)$$

$$\dot{w} = v - w,$$

where $v(t)$ is a fast (voltage) variable, $w(t)$ is a slow (recovery) variable, A_T is the threshold voltage which must be exceeded for firings to occur, B is the signal-to-threshold distance, $s(t)$ is an arbitrary input signal, and $\xi(t)$ is a white, zero-mean Gaussian noise term with an autocorrelation function $\langle \xi(t)\xi(s)\rangle = 2D\delta(t-s)$. The angular brackets $\langle\ \rangle$ denote ensemble averaging over the distribution of ξ.

The exact form of $s(t)$ is unimportant in demonstrating ASR, as long as its variations occur on a time scale slower than the slowest characteristic time of the nonlinear system under study. In the numerical simulations reported in this paper, $s(t)$ was formed by convolving Gaussian correlated noise (with a correlation time $1/\alpha = 20$ s), with a 10-s unit-area Hanning-window filter. The state variables $v(t)$ and $w(t)$ exhibit dynamics on different time scales, since the parameter ϵ is chosen such that $\epsilon \ll 1$ (see Fig. 1 caption), while both vary on time scales faster than that of $s(t)$. Without loss of generality, $s(t)$ is taken to be zero mean, since otherwise its mean can be subsumed into B, the signal-to-threshold distance. Conventionally, $v(t)$ is taken as modeling the membrane voltage of a neuron, and an event (spike) occurs when $v(t)$ makes a positive crossing through some chosen threshold. Typical event rates for the parameters used here are 0.1–2.0 events per second. A time-varying firing rate $r(t)$, defined as the number of spikes per second, can be

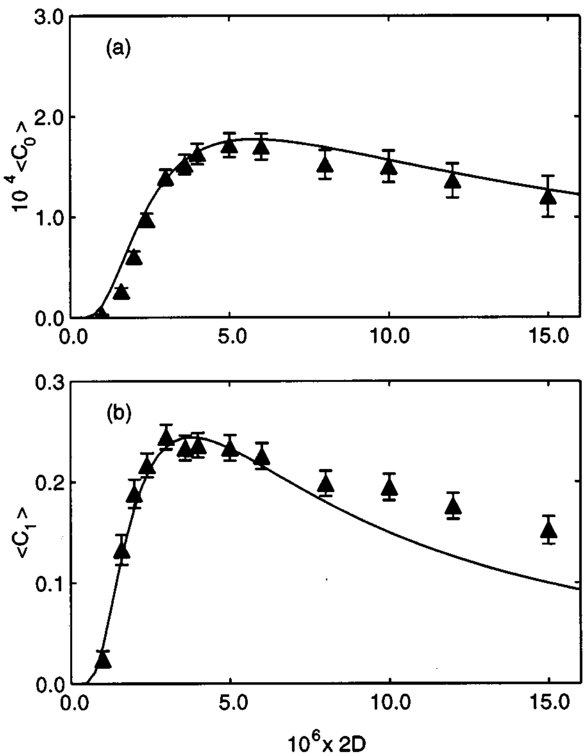

FIG. 1. Ensemble-averaged values (triangles) and standard errors (bars) of (a) the power norm C_0 and (b) the normalized power norm C_1 vs $2D$, where D is the intensity of the input Gaussian white noise, for the FHN model with a subthreshold aperiodic input signal $s(t)$. The parameter values used in Eq. (1) were $\epsilon=0.005$, $A_T=-5/(12\sqrt{3})$, and $B=0.07$. The input signal $s(t)$ was Gaussian noise with a correlation time of 20 s followed by a 10-s Hanning filter. The same input signal $s(t)$, with variance $\sigma_s^2=1.5\times10^{-5}$ and total time length = 300 s was used for all results presented. The theoretical predictions for C_0 and C_1 from Ref. [8] are shown as solid curves. C_0 and C_1 were computed for each trial and then averaged over 200 trials using different seeds to generate the Gaussian white noise. These curves differ slightly from those shown in Ref. [8] because a dead time of 0.25 s is now assumed between firings of the FHN model.

formed by convolving the output spike train with a time-averaging window [17]. The phenomenon of ASR, as reported in Ref. [8], describes the way in which the cross-correlation between this firing rate $r(t)$ and the original input signal $s(t)$ reaches a peak for some level of the input noise $\xi(t)$.

We begin with a review of the cross correlation measures used in Ref. [8]. The first measure considered was the power norm C_0 [18], defined as

$$C_0=\overline{s(t)r(t)}, \tag{2}$$

where $s(t)$ is the zero-mean aperiodic input signal, $r(t)$ is the firing rate at the output of the FHN model, and the overbar denotes a time average. This definition is suitable under the assumption that the firing rate contains information about $s(t)$, rather than $\dot{s}(t)$ or some more complex measure of $s(t)$ (as considered in Ref. [19]). However, for the FHN model, where $s(t)$ directly affects the probability of crossing the threshold, it seems appropriate to proceed on the assumption that $s(t)$ is the relevant transmitted quantity. The second cross-correlation measure considered was the normalized power norm C_1 given by

$$C_1=\frac{C_0}{[\overline{s^2(t)}]^{1/2}[\overline{\{r(t)-\overline{r(t)}\}^2}]^{1/2}}. \tag{3}$$

The numerical results [20] for the FHN model with a subthreshold aperiodic signal $s(t)$ are shown in Fig. 1. The ensemble-averaged values (and standard errors) of C_0 and C_1 are shown as a function of the input noise intensity D. A single realization of $s(t)$ was used in calculating these curves. The solid curves are theoretical results presented in Ref. [8], and show reasonable agreement with the numerical simulations, especially for smaller noise intensities, as expected. Both C_0 and C_1 exhibit clear maxima for specific values of D, although they provide slightly different estimates of the optimal noise intensity.

While these cross-correlation measures are intuitively satisfying in describing the system's behavior, information theory provides a means to quantify directly the information-transfer rate (transinformation) of the system from input to output. First, we evaluate an upper bound for the source information rate, by invoking a relation proposed by Shannon [21]:

$$W\log_2\left(\frac{P_e}{N_1}\right)\leqslant I\leqslant W\log_2\left(\frac{P_s}{N_1}\right), \tag{4}$$

where W is the bandwidth of the source signal $s(t)$, $P_e=2^{2H}/2\pi e$ is a quantity defined as the entropy power, with H the source entropy (see below), N_1 is the maximum tolerable mean-square error in a received version of $s(t)$, I is source information rate in bits per second, and P_s is the stimulus power. The source entropy H is defined as

$$H=\lim_{n\to\infty}-\frac{1}{n}\int\int\ \dots\int p(s_1,s_2,\dots,s_n) \times\log_2 p(s_1,s_2,\dots,s_n)ds_1ds_2\dots ds_n, \tag{5}$$

where s_i represent samples of $s(t)$ and $p(s_1,s_2,\dots,s_n)$ is their joint probability density over n samples. Assuming a bandwidth $W=0.8$ Hz (i.e., 99.5% of the energy in the stimulus lies below this frequency) and a mean-square error $N_1=0.05P_s$, an upper limit of approximately 3.5 bits/s can be inferred from Eq. (4). If the transinformation exceeds this figure, then the signal is being transmitted with a mean-square error smaller than 5%; conversely, a lower transinformation means a higher mean-square error.

Different approaches for estimating information transfer in neuronal systems exist [22]. We concentrate on an approach used recently by other investigators [12,19]. In this method, neural coding is viewed as a process in which reliable estimates $s_{\rm est}(t)$ of the input stimulus are made by filtering the neural spike train with filters chosen subject to an optimization criterion, such as minimizing $|s_{\rm est}(t)-s(t)|^2$. In general, these filters can be either linear or nonlinear. (Calculating a rate function from a neural spike train is a special case of linear filtering.) Since, in many cases, nonlinear fil-

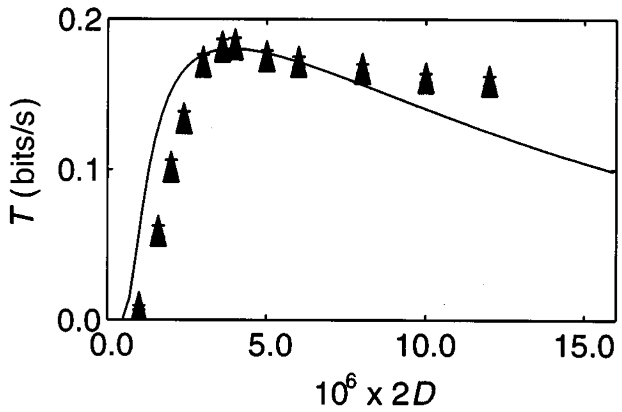

FIG. 2. Ensemble-averaged values (triangles) and standard errors of the transinformation T (in bits per second) calculated by applying Shannon's formula to the same 200 trials as used in Fig. 1. The theoretical prediction for T from Eq. (11) as a function of the input noise intensity D is shown as the solid curve, with parameters as in Fig. 1, and $K_1=1$.

tering provides little extra benefit over linear filtering [19], we choose $r(t)$ as a possible estimate of $s(t)$ and use this assumption in calculating the transinformation theoretically and analytically. (The interevent interval between neural spikes, or some other measure, could also serve as the information-carrying symbol [13,23].)

To do this, both stimulus and response rate are divided into contiguous segments $s_i(t)$ and $r_i(t)$, which are assumed to be related by

$$\hat{r}_i(\omega)=\hat{g}(\omega)[\hat{s}_i(\omega)+\hat{n}_i(\omega)], \tag{6}$$

where $\hat{r}_i(\omega)$ and $\hat{s}_i(\omega)$ are representations of the rate and signal segments in the Fourier domain, $\hat{g}(\omega)$ models the effect of any filtering in the neural coding and rate-formation process, and $\hat{n}_i(\omega)$ is an effective noise level referred to the input level. Given enough segments of stimulus and response, a reasonable estimate of $\hat{g}(\omega)$ can be obtained, allowing calculation of $n_i(t)$, the noise waveform, for each segment. Simulations have shown that for the present case the resultant effective input noise is approximately Gaussian, so that Shannon's formula for the transinformation T across a memoryless channel applies [19,21]:

$$T=\frac{1}{2\pi}\int_0^\infty \log_2[1+S(\omega)/N(\omega)]d\omega, \tag{7}$$

where $S(\omega)$ and $N(\omega)$ are the power spectral densities of $s(t)$ and $n(t)$, respectively. Figure 2 shows the estimated transinformation (in bits/s) as a function of the input noise intensity D for the same set of simulations used in Fig. 1. This measure exhibits a resonant peak at $D\approx 2\times 10^{-6}$. The estimated transinformations lie well below the available source bit rate, as expected for the driving signals (i.e., subthreshold broadband signals plus noise) used in this study.

We can analytically estimate the transinformation from Eq. (7) using results from Ref. [8]. The firing rate $r(t)$ obtained by filtering the spike train with a time-averaging window is the convolution of the instantaneous firing rate with the windowing function. In Ref. [8], we adopted the ansatz that the instantaneous firing rate was equal to the ensemble-averaged Kramers's escape rate plus some noise term $p(t)$. This ansatz leads to an overall expression for $r(t)$:

$$r(t)=\int f(t-u)[\langle r(u)\rangle+p(u)]du, \tag{8}$$

where the angular brackets denote ensemble averaging over ξ, $f(t)$ is the time-averaging window, and

$$\langle r(t)\rangle=K_0\exp[-\Theta+\Delta s(t)], \tag{9}$$

with $K_0=2\sqrt{3}B\pi\epsilon$, $\Theta=\sqrt{3}B^3\epsilon/D$, and $\Delta=3\sqrt{3}B^2\epsilon/D$ [8]. [Note that Eq. (8) is an amended version of Eq. (15) in [8].] Expanding Eq. (9) to linear order in $s(t)$ yields $\langle r(t)\rangle\simeq r_0[1+\Delta s(t)]$, where $r_0=K_0\exp(-\Theta)$. Generally, we consider the zero-mean rate $r(t)$, so we take instead $\langle r(t)\rangle\simeq\Delta r_0 s(t)$. Substituting this rate into Eq. (8) and Fourier transforming yields $\hat{r}(\omega)\simeq\hat{f}(\omega)[K_0\Delta r_0\hat{s}(\omega)+\hat{p}(\omega)]$, from which we can identify $\hat{g}(\omega)\simeq K_0\Delta r_0\hat{f}(\omega)$.

The power spectral density $N(\omega)$ is the Fourier transform of the autocorrelation function $G_n(\tau)$, which is obtained by ensemble and segment averaging of $n_i(t)=p_i(t)/(K_0\Delta r_0)$, i.e., $G_n(\tau)=\overline{\langle n(t)n(t-\tau)\rangle}$, where the bar denotes segment average and $\overline{n(t)}=\langle n(t)\rangle=0$. We assume that $G_n(\tau)$ will be of the form $G_n(\tau)\simeq\sigma_n^2 z_1(\tau)$, for some integrable function $z_1(\tau)$. The variance σ_n^2 will comprise two terms. One is from the variance of the noise term $p(t)$. Assuming that the output spike train is approximately Poisson in nature, $\langle p(t)\rangle=0$, and the variance of the instantaneous firing rate will be proportional to the rate itself [24], giving $\langle p(t)^2\rangle=K_1\overline{\langle r(t)\rangle}\simeq K_1 r_0$, where K_1 is a constant approximately equal to unity. The second term is a subtle effect due to the averaging over segments, and arises from the nonlinear variation of the rate with the input signal $s(t)$, and is given by $\overline{(\langle r(t)\rangle-\overline{\langle r(t)\rangle})^2}\simeq r_0^2\Delta^2\sigma_s^2\exp(\Delta^2\sigma_s^2)/K_0^2$ where $\sigma_s^2=\overline{s^2(t)}$ [8,25]. Combining these two terms yields

$$N(\omega)\simeq\frac{K_1 r_0+r_0^2\Delta^2\sigma_s^2\exp(\Delta^2\sigma_s^2)/K_0^2}{(K_0\Delta r_0)^2}\hat{z}_1(\omega), \tag{10}$$

which can be substituted into Eq. (7). Assume that the input signal is drawn from an ensemble of filtered correlated noise source and has the spectrum $S(\omega)=\sigma_s^2\hat{z}_2(\omega)$, where $\hat{z}_2(\omega)$ is an integrable function. For $S(\omega)/N(\omega)<<1$ we can expand the logarithm in Eq. (7) to obtain

$$T\simeq\frac{1}{2\pi\ln 2}\left[\frac{\sigma_s^2K_0^4\Delta^2 r_0}{K_0^2K_1+r_0\Delta^2\sigma_s^2\exp(\Delta^2\sigma_s^2)}\right]\int_0^\infty\frac{\hat{z}_2(\omega)}{\hat{z}_1(\omega)}d\omega. \tag{11}$$

The integral will contribute a constant. In this form, the Shannon transinformation is directly proportional to the square of C_1 [8,25]. The transinformation as a function of D, calculated in this manner, is shown in Fig. 2 as a solid curve. This estimate predicts both the presence of a maximum in the transinformation, and the noise intensity value at which that maximum occurs. The discrepancy between the theoretical and realized values of transinformation, can be attributed to several factors, the main one likely being the non-Poisson behavior of the spike train. A superior model is the dead-time modified Poisson process [26]. This deviation will become more pronounced with increasing D, as is apparent in Fig. 2. Errors may also arise from the breakdown of the Kramers's rate for large values of D and the use of a delta function to approximate the correlation of $p(t)$, which was an assumption used in obtaining the ensemble-averaged rate. Nevertheless, our estimate carries the key elements of the behavior of the transinformation.

This analysis confirms that the peak in the cross-correlation measures C_0 and C_1 for a particular level of input noise is matched by a peak in the transinformation, complementing the results contained in Ref. [13]. In particular, the shape of the normalized power norm C_1 curve matches the shape of the transinformation curve quite well. This result was not unexpected, given that C_1 incorporates stimulus-response coherence effects. Our transinformation findings are also consistent with experimental results obtained from the cricket cercal sensory system [12], for which a form of ASR was observed, albeit with a quasi-white-noise stimulus rather than a slowly varying stimulus.

This work clearly shows that for cases with subthreshold aperiodic input stimuli, the addition of noise can optimize the information-transfer rate, as well as second-order coherence measures, in the FHN model. From a neurophysiological standpoint, this finding suggests that sensory neurons could, in principle, harness ASR to optimize the detection and transmission of weak stimuli. Further experiments on sensory neurons are needed to test this hypothesis. Our results also raise other related, interesting lines of inquiry. For instance, it is intriguing to consider whether other factors, such as nonwhite input noise and/or optimal neural decoding strategies [19], provide an enhanced ASR effect. Such work could provide further insight into the functioning of neurophysiological sensory systems.

We thank A. Bulsara and A. Zador for helpful discussions. This work was supported by the Office of Naval Research under Grant No. N00014-92-J-1251, the Whitaker Foundation under Grant No. CU01455801, and the National Science Foundation.

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