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Aperiodic stochastic resonance in excitable systems

J. J. Collins,[1,2] Carson C. Chow,[1] and Thomas T. Imhoff[1]
[1]NeuroMuscular Research Center, Boston University, 44 Cummington Street, Boston, Massachusetts 02215
[2]Department of Biomedical Engineering, Boston University, 44 Cummington Street, Boston, Massachusetts 02215
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Stochastic resonance (SR) is a phenomenon wherein the response of a nonlinear system to a weak periodic input signal is optimized by the presence of a particular level of noise. Here we present a method and theory for characterizing SR-type behavior in excitable systems with aperiodic inputs. These developments demonstrate that noise can serve to enhance the response of a nonlinear system to a weak input signal, regardless of whether the signal is periodic or aperiodic.

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Stochastic resonance (SR) is a phenomenon wherein the response of a nonlinear system to a weak periodic input signal is optimized by the presence of a particular level of noise [1]. SR was originally proposed as a possible explanation for the observed periodicities in global climate dynamics [2]. Since then, SR has been examined experimentally in several systems, including an electronic Schmitt trigger [3], a bidirectional ring laser [4], a magnetoelastic ribbon [5], and sensory neurons [6,7]. Moreover, theories of SR have been developed for multistable [8,9], monostable [10], and excitable [11] systems. All of the aforementioned work, however, has been limited to the treatment of systems with periodic inputs. This focus has served to limit the applicability of SR to practical situations, given that real-world external signals are often not periodic. Here we present a method and theory for characterizing SR-type behavior in excitable systems with aperiodic inputs. For this general type of behavior, we coin the term *aperiodic stochastic resonance* (ASR).

Wiesenfeld *et al.* [11] developed a theory of SR for excitable systems by considering a simple system made up of three major components: a threshold (or potential barrier), a subthreshold periodic signal (i.e., one which is insufficient for the system's state point to cross or surmount the barrier), and zero-mean Gaussian white noise. In particular, they studied the FitzHugh-Nagumo (FHN) neuronal model, which is a two-dimensional limit-cycle oscillator. The FHN model has been utilized in a number of physiologically motivated SR investigations [11–13] because its dynamics provide a simple representation of the firing dynamics of sensory neurons.

Here we also consider the FHN model, with the exception that we study its dynamics under the influence of a subthreshold aperiodic signal, as opposed to a periodic one. In particular, we consider the following system:

$$\epsilon\dot{v}=v(v-a)(1-v)-w+A+S(t)+\xi(t),$$
$$\dot{w}=v-w-b, \tag{1}$$

where $v(t)$ is a fast (voltage) variable, $w(t)$ is a slow (recovery) variable, A is a constant (tonic) activation signal, $\epsilon=0.005$, $a=0.5$, $b=0.15$, $\xi(t)$ is Gaussian white noise with zero mean and autocorrelation $\langle\xi(t)\xi(s)\rangle=2D\delta(t-s)$, the brackets $\langle\cdot\rangle$ denote an ensemble average, and $S(t)$ is an aperiodic signal. [Without loss of generality, $S(t)$ is taken to have zero mean.] For ASR, the exact form of $S(t)$ is unimportant, provided its variations occur on a time scale which is slower than the characteristic time(s) of the system under study. For a subthreshold activation signal A, the FHN model has deterministically resettable dynamics, i.e., after the barrier threshold has been crossed [e.g., due to the effects of the time-varying inputs of Eqs. (1)], the system's state point is returned deterministically (within some refractory period) to its starting point (i.e., a stable fixed point).

In general, the phenomenon of SR indicates that the flow of information through a system (i.e., the coherence between the input stimulus and the system response) is optimized by the presence of a particular level of noise [1,12,14]. In line with this operational definition, SR in excitable systems has been characterized by examining (a) the output signal-to-noise ratio (SNR), which is computed from the power spectrum and defined as the ratio of the strength of the signal peak (i.e., its area) to the mean amplitude of the background noise at the input signal frequency [7,11,12], and/or (b) the modes in the interspike interval histograms [15] located at integer multiples of the input signal period [6,7,13]. Both of these methods assess the coherence of the response of the system (i.e., its spiking activity) with the input signal frequency. Thus, these techniques are clearly inappropriate for systems with aperiodic inputs.

We propose an SR measure—the power norm—which is appropriate for characterizing ASR. For the above FHN model, we define the power norm C_0 [16] as

$$C_0=\overline{S(t)R(t)} \tag{2}$$

where $S(t)$ is the aperiodic (zero-mean) input signal, $R(t)$ is the mean firing rate signal constructed from the output of the FHN model [17], and the overbar denotes an average over time. This measure is based on the assumption that information is transmitted by the system (e.g., a sensory neuron) via temporal changes in its firing rate [18]. We also consider the normalized power norm C_1 given by

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

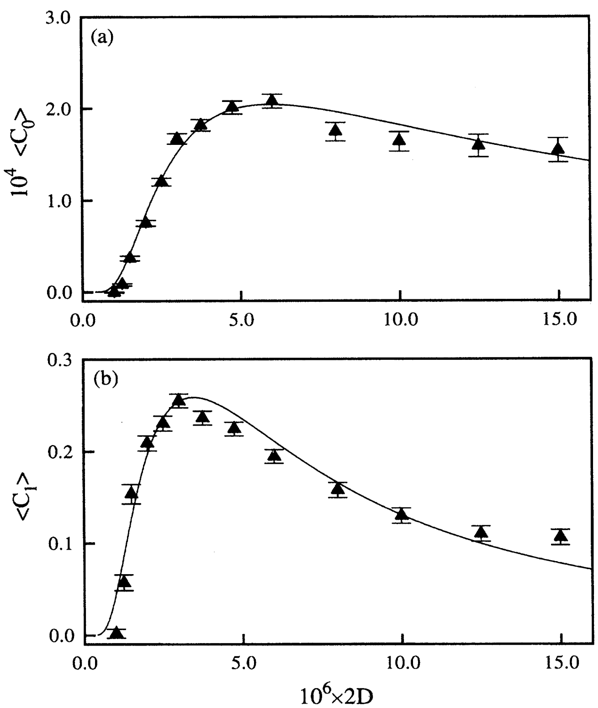

FIG. 1. Ensemble-averaged values (triangles) and standard errors of the (a) power norm C_0 and (b) normalized power norm C_1 versus $2D$, where D is the intensity of the input Gaussian white noise, for the FHN model with a subthreshold aperiodic input signal $S(t)$. The theoretical predictions (solid curves) from Eqs. (14) and (21) are given in (a) and (b), respectively. The signal-to-threshold distance B was 0.07. $S(t)$ was formed by convolving Gaussian correlated noise (with correlation time=20 s) with the filter described in Ref. [17]. The same input signal $S(t)$, with variance $=1.5\times 10^{-5}$ and total time length $=300$ s, was used for all results presented. C_0 and C_1 were computed for each trial and then averaged over 300 trials using different seeds to generate the Gaussian white noise. For the theoretical predictions in (b), we used $\sigma(D)=1.7\times 10^4 D+3.5\times 10^9 D^2$.

From a signal-processing perspective, maximizing C_1 corresponds to maximizing the shape matching between the input stimulus $S(t)$ and the system response $R(t)$, whereas maximizing C_0 corresponds to taking account of both signal amplification and shape matching. These measures thus enable one to quantify the two noise-induced effects associated with SR, i.e., the original notion of signal amplification [2] and the later notion of optimal stimulus-response coherence [1,4,8,12,14].

The numerical results [19] for the FHN model with a subthreshold aperiodic signal $S(t)$ are given in Fig. 1. Shown are the ensemble-averaged values (and standard errors) of C_0 and C_1 as a function of the input noise intensity D. (The solid curves are from the theory to be described below.) These results show characteristic signatures of SR-type behavior: a rapid rise to a clear peak, and then a slow decrease for higher values of noise intensity. (For smaller signal-to-threshold distances and/or for subthreshold input signals with larger variance, it was possible to obtain peak C_1 values of ~ 0.9.)

We have developed a theory to account for the numerical results. This theory will be applicable to ASR in other excitable systems. We compute the mean firing rate $R(t)$ and from that the two power-norm measures, C_0 and C_1. We calculate $R(t)$ for the FHN model by formulating the problem as a barrier-escape problem. This allows the use of Kramers's formula for the escape rate [20] to determine $R(t)$.

For a subthreshold activation signal A, the FHN model has a stable fixed point. Input Gaussian noise, such as that in Eqs. (1), "kicks" the system away from the fixed point. If the system is kicked over the threshold, it "fires" and subsequently returns to the stable fixed point after a refractory period. Using a particle analogy, the particle is kicked out of a stable well (fixed point) by thermal noise, and then it returns to the stable well through another degree of freedom. Thus, to calculate the mean firing rate $R(t)$, which is proportional to the probability of escaping from the stable fixed point, we need to determine the location of the fixed point and the form of the potential well.

For $a=0.5$, the FHN model can be transformed to a simpler form with $v=v'+1/2$, $w=w'-b+1/2$, and $A=A'-b+1/2$. With these changes, Eqs. (1), without the time-varying inputs, become

$$\epsilon\dot{v}=-v(v^2-\tfrac{1}{4})-w+A, \quad \dot{w}=v-w, \tag{4}$$

where the primes have been dropped. The location of the fixed point is given by the intersection of a cubic nullcline, $w=v(v^2-0.25)+A$, coming from $\dot{v}=0$, with a linear nullcline, $w=v$, coming from $\dot{w}=0$. This requires the solution of a cubic polynomial. The calculation can be simplified by expanding around the threshold of stability. By inspection of the (v,w) phase plane, it can be seen that threshold occurs when the minimum of the cubic nullcline [i.e., when $w'(v)=0$] intersects the linear nullcline, i.e., when the minimum is a fixed point [21]. For a smaller activation signal A, the fixed point is stable; for a larger A, the fixed point becomes unstable and the orbit flows to a stable limit cycle. The minimum of the cubic nullcline occurs at $v_-=-1/(2\sqrt{3})$. Using $\dot{w}=\dot{v}=0$ with $w=v\equiv v_-$ yields the threshold voltage $A_T=-5/(12\sqrt{3})$. In the original coordinates of Eqs. (1), this corresponds to a threshold of ~ 0.11, which matched the numerical result.

We now rewrite Eqs. (4) taking account of the threshold voltage and the time-varying inputs of Eqs. (1):

$$\epsilon\dot{v}=-v(v^2-\tfrac{1}{4})-w+A_T-\gamma+\xi(t), \quad \dot{w}=v-w, \tag{5}$$

where $\gamma(t)=B-S(t)$, and B is a constant parameter which corresponds to the signal-to-threshold distance. When $\gamma>0$, the fixed point is stable (i.e., the system is subthreshold). To determine the fixed-point location for $\gamma>0$, we expand around the result for $\gamma=0$ (threshold). We need to solve

$$-v(v^2-\tfrac{1}{4})-v+A_T-\gamma=0. \tag{6}$$

For $\gamma\ll 1$, we expect the root to be near v_-. Let v_1 be the root, where (to quadratic order) $v_1 \sim v_-+a\gamma+b\gamma^2$. Substituting v_1 into Eq. (6) and solving order by order in γ yields $a=-1$ and $b=\sqrt{3}/2$.

For $\epsilon \ll 1$, v is a fast variable and w is a slow variable. Therefore, the escape from the fixed point is "quasi"-one-dimensional along v. The problem thus can be recast as an escape from a one-dimensional double well. Assuming $\dot{w} \sim 0$ and $w \sim v = v_1$, Eqs. (5) reduce to

$$\epsilon \dot{v} \sim -V'(v) + \xi(t) \quad (7)$$

where

$$V(v) = Cv - \frac{v^2}{8} + \frac{v^4}{4}, \quad (8)$$

$$C = v_- - A_T + \frac{\sqrt{3}}{2}\gamma^2. \quad (9)$$

This is a double-well barrier-escape problem, where C controls the "tilt" of the potential well $V(v)$ [8].

In the double-well regime, $V'(v)$ has three roots v_1, v_2, v_3. By analogy, the particle (i.e., the state point) is caught in well v_1 (i.e., the stable fixed point). It needs to surmount v_2 to get to v_3 (i.e., in order for the system to fire). Once at v_3, it returns to v_1 through the w degree of freedom and gets caught in the well again. Using Kramers's formula [20], the ensemble-averaged rate of escape from v_1 is given by

$$\langle R(t) \rangle \propto \exp(-U_0/T), \quad (10)$$

where $T = D/\epsilon$ and the barrier height $U_0(t) = V(v_2) - V(v_1)$. To determine the barrier height, we need the location of v_2. (The location of v_1 was determined above.) To do so, we solve for $V'(v) = 0$. Again we expand around v_- and solve to first order in γ. This yields $v_1 = v_- - \gamma$ (as expected) and $v_2 = v_- + \gamma$. It then can be shown that $U_0 = \sqrt{3}\gamma^3$. For $[\overline{S^2(t)}]^{1/2} \ll B$,

$$\gamma^3 = [B - S(t)]^3 \sim B^3 - 3B^2 S(t). \quad (11)$$

Equation (10) then takes the form

$$\langle R(t) \rangle \propto \exp\{-\sqrt{3}[B^3 - 3B^2 S(t)]\epsilon/D\}. \quad (12)$$

This rate formula matches the form proposed in Ref. [11] for computing the SNR for SR in excitable systems.

The aperiodic signal $S(t)$ is not altered by the noise so the ensemble-averaged power norm in Eq. (2) is

$$\langle C_0 \rangle = \langle \overline{S(t)R(t)} \rangle \equiv \overline{S(t)\langle R(t) \rangle}. \quad (13)$$

By substituting Eq. (12) into Eq. (13) and expanding to first order in $3\sqrt{3}B^2 \epsilon \overline{S(t)^2}/D$, we obtain

$$\langle C_0 \rangle \propto \frac{1}{D} \exp\left(\frac{-\sqrt{3}B^3 \epsilon}{D}\right) \overline{S^2(t)}. \quad (14)$$

From Eq. (14), it can be seen that the maximum value of $\langle C_0 \rangle$ should occur at $D \simeq \sqrt{3}B^3 \epsilon$. A curve based on Eq. (14) is shown in Fig. 1(a), where only the amplitude has been adjusted to fit the data. The theory matches the data, predicting the location of the maximum. The theory also fit the numerical results for other barrier heights. (The numerical results have a "dip" just after the maximum that is not accounted for by the theory. This is likely to be due to "return hopping" where the particle once in well v_3 hops back to well v_1 instead of proceeding to v_1 through the w degree of freedom. This will be investigated in a future study.)

The calculation of C_1 requires $\overline{R^2(t)}$ in the normalization factor of Eq. (3). For this, we use the ansatz that $R(t)$ will be given by

$$R(t) = \langle R(t) \rangle + \eta(t), \quad (15)$$

where $\langle R(t) \rangle$ is proportional to Kramers's escape rate [given by Eq. (12)] and $\eta(t)$ is a stochastic component which arises from the input noise. We assume $\overline{\eta(t)} = 0$ and $\overline{\eta^2(t)} \equiv \sigma(D)$ is a monotonically increasing function of D. [The stochastic component $\eta(t)$ does not affect the computation of $\langle C_0 \rangle$.] Consider the normalization factor

$$N^2 = \overline{[R(t) - \overline{R(t)}]^2}. \quad (16)$$

Substituting Eq. (15) into Eq. (16) yields

$$N^2 = \overline{\langle R(t) \rangle^2} - \langle \overline{R(t)} \rangle^2 + \overline{\eta^2(t)}. \quad (17)$$

(Note that the averaging operations commute.)

Consider the situation where $S(t)$ has Gaussian statistics. Then by using Eq. (12) and applying Wick's theorem, it can be shown that

$$\langle \overline{R(t)} \rangle^2 = \exp[\Theta + \Delta^2 \overline{S^2(t)}], \quad (18)$$

$$\overline{\langle R(t) \rangle^2} = \exp[\Theta + 2\Delta^2 \overline{S^2(t)}], \quad (19)$$

where $\Theta = -2\sqrt{3}B^3 \epsilon/D$ and $\Delta = 3\sqrt{3}B^2 \epsilon/D$. Equation (17) thus becomes

$$N^2 = \exp[\Theta + 2\Delta^2 \overline{S^2(t)}] - \exp[\Theta + \Delta^2 \overline{S^2(t)}] + \sigma(D). \quad (20)$$

The normalized power norm is constructed as

$$\langle C_1 \rangle \simeq \left\langle \frac{C_0}{N[\overline{S^2(t)}]^{1/2}} \right\rangle \simeq \frac{\langle C_0 \rangle}{N[\overline{S^2(t)}]^{1/2}}, \quad (21)$$

where N is given by Eq. (20). For $S(t)$ obeying Gaussian statistics, $\langle C_0 \rangle$ can be computed explicitly from Eq. (12) using Wick's theorem to obtain

$$\langle C_0 \rangle \simeq \Delta \exp\left(\frac{-\sqrt{3}B^3 \epsilon}{D} + \frac{27B^4 \epsilon^2 \overline{S^2(t)}}{2D^2}\right) \overline{S^2(t)}. \quad (22)$$

[Note that the numerator of the prefactor Δ was omitted in Eq. (14).] Equation (22) is then used in Eq. (21) to obtain a formula for $\langle C_1 \rangle$. Assuming $\sigma(D)$ to be quadratic in D, the prediction for $\langle C_1 \rangle$ matched the numerical results, as shown in Fig. 1(b). It should be noted that $\langle C_1 \rangle$ is only weakly sensitive to the form of $\sigma(D)$.

This work clearly shows that SR-type behavior is not limited to systems with periodic inputs. Thus, in general, noise can serve to enhance the response of a nonlinear system to a weak input signal, regardless of whether the signal is periodic or aperiodic. These developments open up a number of potential applications. For instance, this work suggests that it may be possible to introduce noise artificially into sensory neurons in order to improve their abilities to detect arbitrary subthreshold signals. With "smart" transducers, it may be possible to modulate the input noise intensity systematically as a function of the changing nature of the signal to be detected. For this sort of application, we note that the proposed power-norm measures can also be used to characterize SR in systems with periodic inputs, provided the period of the input signal is slower than the characteristic time(s) of the system under study.

The techniques and theory of ASR are not limited in their applications to biological systems. For instance, as noted in Refs. [11,12], a number of physical systems, such as subthreshold Josephson junctions and semiconductor lasers, can also be represented as excitable systems with deterministically resettable dynamics. It is also important to point out that the methods and theory presented above can be extended to other general classes of systems, such as double-well systems and integrate-and-fire neuronal models. This will be addressed in a future paper.

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