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
(Received 23 January 1995)

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.

PACS number(s): 05.40.+j, 87.22.Jb

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 magnetoelectric 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 model 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 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:

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

(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

\[ C_0 = \frac{S(t)R(t)}{S^2(t)} \]  

(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

\[ C_1 = \frac{C_0}{[S^2(t)]^{1/2}[\langle (R(t)-\bar{R})^2 \rangle]^{1/2}}. \]  

(3)
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

$$\epsilon \dot{v} = -v(v^2 - \frac{1}{3}) - w + A, \quad w = v - w,$$

(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 $v = 0$, with a linear nullcline, $w = v$, coming from $w = 0$. 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 $w = v = v_-$ yields the threshold voltage $A_T = -5/(12\sqrt{3})$. In the original coordinates of Eqs. (1), this corresponds to a threshold of $\sim 0.11$, which matched the numerical result.

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

$$\epsilon \dot{v} = -v(v^2 - \frac{1}{3}) - w + A_T - \gamma - \xi(t), \quad w = v - w,$$

(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

$$-v(v^2 - \frac{1}{3}) - w + A_T - \gamma = 0.$$

(6)

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

![Graphical representation of the ensemble-averaged values](image-url)
For $\epsilon=1$, $v$ 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 $\dot{w}=0$ and $w-v=v_1$, Eqs. (5) reduce to

$$\epsilon \dot{v} = -V'(v) + \xi(t)$$  \hspace{1cm} (7)

where

$$V(v)=Cv-\frac{v^2}{8}+\frac{v^4}{4}$$  \hspace{1cm} (8)

$$C=v_-A_\tau+\frac{\sqrt{3}}{2} \gamma^2.$$  \hspace{1cm} (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' formula [20], the ensemble-averaged rate of escape from $v_1$ is given by

$$\langle R(t) \rangle \propto \exp(-U_0/T),$$  \hspace{1cm} (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 $\gamma$. This yields $v_1=v_- - \gamma$ (as expected) and $v_2=v_- + \gamma$. It then can be shown that

$$U_0=\frac{3\sqrt{3}}{4} \gamma^2.$$  \hspace{1cm} (11)

Equation (10) then takes the form

$$\langle R(t) \rangle \propto \exp(-\sqrt{3}[B-S(t)]^2/4D).$$  \hspace{1cm} (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

$$\langle C_0 \rangle = \langle S(t) R(t) \rangle = S(t) \langle R(t) \rangle.$$  \hspace{1cm} (13)

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

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

From Eq. (14), it can be seen that the maximum value of $\langle C_0 \rangle$ should occur at $D=\sqrt{3}B^2\epsilon$. 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 fits 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 $\tilde{R}^2(t)$ in the normalization factor of Eq. (3). For this, we use the ansatz that $R(t)$ will be given by

$$R(t) = \langle R(t) \rangle + \eta(t),$$  \hspace{1cm} (15)

where $\langle R(t) \rangle$ is proportional to Kramers’ escape rate [given by Eq. (12)] and $\eta(t)$ is a stochastic component which arises from the input noise. We assume $\eta(t)=0$ and $\tilde{\eta}^2(t)=\sigma(D)$ 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

$$N^2=\frac{[R(t)-\langle R(t) \rangle]^2}{\langle R(t) \rangle^2-\langle R(t) \rangle^2+\tilde{\eta}^2(t)}.$$  \hspace{1cm} (16)

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

$$N^2=\langle R(t) \rangle^2-\langle R(t) \rangle^2+\tilde{\eta}^2(t).$$  \hspace{1cm} (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

$$\langle R(t) \rangle^2=\exp[\Theta+\Delta^2 S^2(t)],$$  \hspace{1cm} (18)

$$\langle \tilde{R}(t) \rangle^2=\exp[\Theta+2\Delta^2 S^2(t)],$$  \hspace{1cm} (19)

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

$$N^2=\exp[\Theta+2\Delta^2 S^2(t)]-\exp[\Theta+2\Delta^2 S^2(t)]+\sigma(D).$$  \hspace{1cm} (20)

The normalized power norm is constructed as

$$\langle C_1 \rangle=\frac{\langle C_0 \rangle}{N[\langle S^2(t) \rangle]^{1/2}} \approx \frac{\langle C_0 \rangle}{N[\langle S^2(t) \rangle]^{1/2}},$$  \hspace{1cm} (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

$$\langle C_0 \rangle=\Delta \exp \left(-\frac{\sqrt{3}B^2\epsilon}{D} + \frac{27B^4\epsilon^2 S^2(t)}{2D^2} \right) S^2(t).$$  \hspace{1cm} (22)

[Note that the numerator of the prefactor $\Delta$ 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.

We thank Z. Erim for helpful discussions. This work was supported by the National Science Foundation.

[16] In the present study, the peak in the cross-correlation function formed between the input signal and the constructed output signal always occurred at a time lag of zero, and, thus, the power norm was a suitable measure. However, for certain systems, there may be a lag between the stimulus and the response. For ASR, one should, in general, utilize a measure which quantifies the peak in the input-output cross-correlation function.
[17] The time-varying mean firing rate, defined as the number of spikes per second produced by the FHN model, was computed by passing a 10.0 s unit-area symmetric Hanning window filter over an impulse train corresponding to the firings of the model [C.J. De Luca, R.S. LeFever, M.P. McCue, and A.P. Xenakis, J. Physiol. 329, 113 (1982)]. (The firings of the FHN model were determined using the method described in Ref. [13].)
[18] This is a valid assumption for many types of sensory neurons [e.g., see G.M. Shepherd, Neurobiology, 2nd ed. (Oxford University Press, Oxford, 1988)].
[19] The FHN equations were solved numerically using an algorithm developed for stochastic differential equations [R. Mannella and V. Palleschi, Phys. Rev. A 40, 3381 (1989)]. An integration step size of 0.001 s was used. The reported results did not change for smaller step sizes.
[21] This applies equally and symmetrically to the maximum.