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Stochastic Resonance on a Circle

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We describe a new realization of stochastic resonance, applicable to a broad class of systems, based on an underlying excitable dynamics with deterministic reinjection. A simple but general theory of such "single-trigger" systems is compared with analog simulations of the Fitzhugh-Nagumo model, as well as experimental data obtained from stimulated sensory neurons in the crayfish.

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Following the introduction of a modern theory [1], and its demonstration in a wide variety of experiments [2], there has been a great deal of continued interest in stochastic resonance (SR) [2-4]. However, all theoretical treatments, including the original discovery of SR as a dynamical aspect of a global climate model [5], as well as all experimental realizations reported to date, have explored its existence in systems exclusively based on the classical motion of a particle confined in a monostable or multistable potential. A weak periodic signal is applied, for example, to the bistable potential, in such a way as to cause the wells to alternately be raised and lowered with respect to the barrier. The amplitude of the signal alone is insufficient to cause the particle to surmount the barrier and to switch wells, but, with the addition of noise, usually Gaussian and white, a nonzero probability of switching from either well to the other appears which varies with the period of the signal. The resulting motion is a train of switching events which occur at more-or-less random times but with some degree of coherence with the signal. Recent and interesting experimental examples, one wherein this type of motion was induced by purely thermal noise [6], and the other employing optical bistability [7], have been reported.

There is an interpretation of SR based on noisy information transmission. In this view, an interwell switching event is interpreted as the transmission through the system of one bit of information about the frequency of the

signal. In this view, the intrawell particle motion is ignored or filtered out, since it conveys virtually no information about the signal. The signal-to-noise ratio (SNR) of the system response is obtained from the power spectrum of the interwell motion. The signature of SR is that the SNR passes through a maximum at an optimal value of the input noise intensity [1,8]. The details of the behavior depend on the specific dynamical properties of the system, for example, the unperturbed barrier height, the inertia of the particle (unless infinitely damped), the damping properties of the medium in which the particle moves, and the details of the shape of the potential barrier and wells.

Here we explore SR with a different class of dynamical systems based not on bistability but rather on an excitable dynamics [9]. Our proposed system consists only of a potential barrier, a weak coherent (periodic) signal $\epsilon \sin \omega t$ whose amplitude is insufficient to cause the state point to surmount the barrier, and a Gaussian white noise $\xi(t)$ with zero mean. A key ingredient here, in contrast to previously studied SR systems, is a deterministic reinjection: Upon crossing the barrier, the state point returns to its "rest state" deterministically, within a certain refractory time. This view is appealing, since it represents a simple dynamical process based on a single potential well, for which SR can be observed. It has the additional advantage that, in the present context, it is believed to represent the fundamental *dynamical* process which ac-

counts for action potential (firing) events in sensory neurons [10]. SR has recently been observed in experiments with hydrodynamically sensitive hair mechanoreceptors in the crayfish *Procambarus clarkii* [11]. (We note that other "single-state" versions of SR have been reported, which while interesting in their own right are, however, rather different: Gitterman and Weiss define SR as a minimum in the escape time from a single well [12]; Stocks, Stein, and McClintock describe "nonconventional" SR where inertia plays a central role [13].)

To fix ideas, consider the simplest realization of this picture, as illustrated in Fig. 1(a), which depicts a one-dimensional circular phase space. The state point, driven by a weak signal and noise, jiggles about its nominal rest state (stable fixed point); there is also a barrier threshold (corresponding to the unstable fixed point). For example, a specific realization of this situation is given by

$$d\phi/dt + \sin\phi = A + \varepsilon \sin\omega t + \xi(t), \quad A < 1, \quad (1)$$

which describes a Josephson junction biased in its zero voltage state, or a rigid charge density wave below its depinning threshold. Whenever the barrier is crossed, the dynamics automatically returns the state point to the stable fixed point. Each time the barrier is crossed, the system executes one circuit, returning to the neighborhood of the fixed point after the refractory time Δt . Each trip around the circle is represented by a single pulse of height V_0 and width Δt in the time series $V(t)$; see Fig. 1(b). The time series $V(t)$ is partially coherent with the signal, resulting in the sharp peaks at the signal frequency and its harmonics in the power spectrum, as illustrated in Fig. 2(a). For rectangular pulses, the broadband noise background in the power spectrum is a squared sinc function whose zeros are determined by the width of the pulses Δt .

Though Fig. 1(a) depicts perhaps its simplest incarnation, this sort of excitable dynamics with deterministic reinjection occurs in a broad range of systems. Motivated

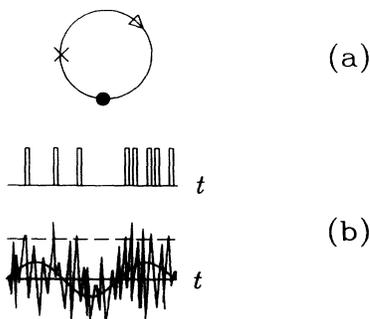


FIG. 1. (a) Dynamical motion on a circle driven by a sinusoidal function plus noise. The cross (dot) represents an unstable (stable) fixed point; (b) time series generated by successive escapes (bottom): each crossing results in a standard pulse added to the time series (top).

by the crayfish neuron experiments, we chose to study another example, namely, the Fitzhugh-Nagumo (FN) neuron model [10]:

$$\begin{aligned} \tau_r \dot{v} &= v(v-0.5)(1-v) - w, \\ \tau_w \dot{w} &= v - w - b + \varepsilon \sin\omega t + \xi(t), \end{aligned} \quad (2)$$

where $v(t)$ is the fast variable representing the action potential, $w(t)$ is the slow, or recovery, variable which establishes the refractory time, and τ_r and τ_w are the fast and slow characteristic times, respectively. We constructed an electronic circuit model of Eqs. (2); the output $v(t)$ was converted into a time series of standard pulses $V(t)$ with $V_0=1.0$ V and $\Delta t=2.5$ ms. The power spectrum shown in Fig. 2(a) was generated from this model.

We now turn to a theoretical analysis of this generic threshold-plus-reinjection dynamics, to demonstrate that it leads to SR. Our approach is quite different from previous SR theories; we do not proceed from any particular

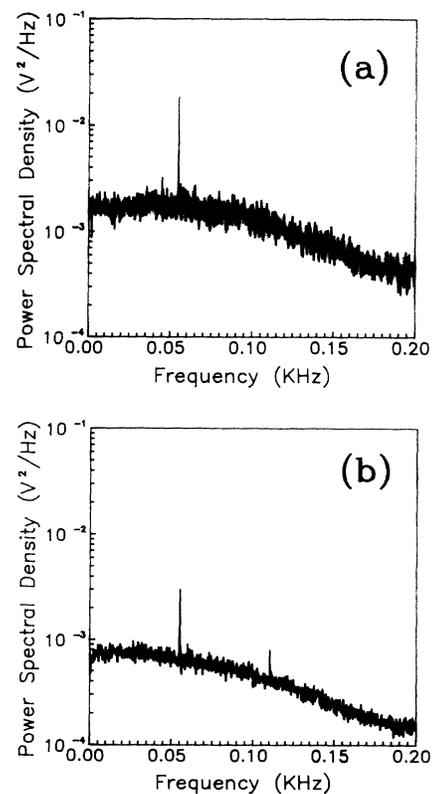


FIG. 2. (a) A power spectrum generated by the electronic FN model for $b=0$, noise voltage of $0.34 V_{rms}$, $\varepsilon=0.03$ V, and $\omega=55$ Hz. The threshold for firing is $b_c=0.15$ V. The characteristic times were $\tau_r=10 \mu s$ and $\tau_w=1$ ms which resulted in action potential widths ($\approx 200 \mu s$) and refractory times (≈ 2.5 ms) in good agreement with those obtained from the crayfish neuron experiments. (b) A power spectrum obtained from the mechanoreceptor cell.

stochastic differential equation model. Rather, we formulate the problem as a modified version of the "shot effect."

In the classic shot effect [14], one assumes a constant rate of events (threshold crossings) α_0 , each event gives rise to a single pulse $F(t)$, and successive events at times t_1, t_2, \dots , are statistically independent. The total response is simply $V = \sum_K F(t - t_K)$. The probability that K events occur in the time interval $(0, T)$ is given by the Poisson distribution

$$P_K(T) = (\alpha_0 T)^K \exp(-\alpha_0 T) / K!. \quad (3)$$

From the resulting series of pulses $V(t)$, one calculates the autocorrelation function $C(\tau) = \langle V(t)V(t+\tau) \rangle$, where $\langle \dots \rangle$ denotes an ensemble average, with the result [14]

$$C(\tau) = \alpha_0 \int_0^\infty F(t)F(t+\tau)dt + \left(\alpha_0 \int_0^\infty F(t)dt \right)^2. \quad (4)$$

This formulation corresponds to the signal-free ($\varepsilon=0$) version of our problem. The effect of the signal is to periodically modulate the event rate. We thus want to adapt the calculation to the case of a time-periodic rate $\alpha(t)$. Of course, it is insufficient to simply substitute $\alpha(t)$ for α_0 in Eq. (4); rather, we must rederive the expression for the correlation function. Most importantly, we want to preserve the feature of statistically independent events. To this end, we modify the Poisson distribution by taking $\alpha_0 T \rightarrow \int_0^T \alpha(t)dt$ in Eq. (3); physically, we demand that the rate $\alpha(t)$ is non-negative. Since $\alpha(t)$ is periodic, we can expand it in a Fourier series,

$$\alpha(t) = \alpha_0 + \sum_{q=1}^{\infty} \alpha_q \cos(q\omega t + \psi_q). \quad (5)$$

The calculation is now repeated: Since the process is no longer stationary, we additionally average over the phase of $\alpha(t)$. The resulting correlation function is the sum of expression (4), plus oscillations at each frequency $\omega, 2\omega, \dots$. In the limit where the pulse width is small, $\omega\Delta t \ll 1$, the expression becomes

$$\{C(\tau)\} = \alpha_0 (V_0 \Delta t)^2 \delta(\tau) + (\alpha_0 V_0 \Delta t)^2 + \frac{1}{2} (V_0 \Delta t)^2 \sum_{q=1}^{\infty} \alpha_q^2 \cos(q\omega\tau), \quad (6)$$

where $\{\dots\}$ denotes the phase average, and V_0 is the pulse height. The last term in Eq. (6) leads to the signal feature, a series of δ -function spikes, in the power spectrum with the strength $\alpha_q^2 V_0^2 \Delta t^2 / 2$, while the $\delta(\tau)$ term yields the broadband noise. The SNR is then the ratio of the strength of the $q=1$ spike to the noise background evaluated at the signal frequency

$$\text{SNR} = 10 \log_{10} (\alpha_1^2 / 2\alpha_0). \quad (7)$$

The last step is to relate our rate $\alpha(t)$ to the noise strength D . As an example, we consider the Kramers-type formula

$$\alpha(t) = \exp[-(U/D)(1 - \eta \cos \omega t)], \quad (8)$$

where η need not be small, and U is a constant. Using Eqs. (5) and (7) we obtain

$$\text{SNR} = 10 \log_{10} \left(\frac{4I_1^2(z)}{I_0(z)} \exp(-U/D) \right), \quad (9)$$

where $z = \eta U/D$ and I_n is the modified Bessel function of order n . Equation (9) displays the characteristic signature of stochastic resonance over a wide range of parameter values η and U , namely, a peak as a function of D . For small z , this reduces to

$$\text{SNR} = 10 \log_{10} \left(\frac{U^2 \eta^2}{D^2} \exp(-U/D) \right). \quad (10)$$

This result differs from the well-known result for a bistable system [1] by a factor of 2 in the denominator of the exponent, a result which can be understood physically since transitions are made only "to one side" in the present case [clockwise as depicted in Fig. 1(a)] as compared with the two "back and forth" transitions in bistable systems. Equation (10) is compared to data from the FN model and from experiments on the crayfish mechanoreceptor as shown by the solid curve in Fig. 3.

We turn now to the experiment. We have chosen a simple sensory neuron, the hair mechanoreceptor cell in the tailfan of the crayfish *Procambarus clarkii*, in order to demonstrate this simple model for SR. In this system, a hair located in the tailfan senses water motions which

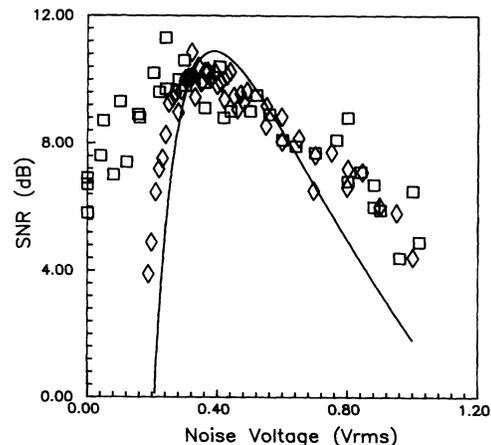


FIG. 3. The SNR measured on the crayfish mechanoreceptor (squares) compared to similar measurements made on the electronic Fitzhugh-Nagumo model neuron (diamonds) and the theory, Eq. (10), with $U=0.15$ and $\eta=4.76$ (solid curve). Note that we have defined the rms noise voltage $\sqrt{\langle \xi^2 \rangle} = \sqrt{2D}$. Both data sets were obtained for a stimulus frequency of 55 Hz. In the case of the crayfish, the stimulus strength was adjusted to be just barely detectable in the absence of external noise. For the electronic model, the signal strength was smaller than the value necessary for spontaneous firing.

are transduced into a train of action potentials (firing events) in the sensory neuron connected to the abdominal ganglion. In our experiment, a piece of the tailfan containing the hair, nerve, and abdominal ganglion was excised and mounted on a motion transducer in a bath of saline solution. A neuron with low internal noise, i.e., low spontaneous firing rate, was chosen in order to emphasize the effects of the externally applied noise. A combination of periodic and random motions was applied to the hair relative to the solution. Extracellular recordings from the nerve were made using standard techniques. The action potentials were converted into rectangular pulses of 1.0 V amplitude and width 3.0 ms, digitized, and processed with a program identical to the simulations. The experimental details have been described elsewhere [11]. An example power spectrum is shown in Fig. 2(b), and compares favorably with the one generated by the FN model. The SNR's were obtained from a series of power spectra measured at differing external noise intensities in a manner identical to the simulations. The squares in Fig. 3 show the crayfish SNR's measured from one cell [15].

We have chosen the FN model as an example excitable system governed by the dynamics defined in Fig. 1, which is also familiar to neuroscientists. A detailed description of this simulation will be published elsewhere; however, some data are shown by the diamonds in Fig. 3. One notable difference between these two data sets is that the crayfish SNR's do not fall rapidly as the noise approaches zero, but instead asymptotically approach some nonzero value on the vertical axis. We believe this is due to the residual internal noise which, even in a neuron selected for low spontaneous rate, cannot be avoided. We have noticed that this zero noise asymptotic value is larger for neurons with larger internal noise, and the maximum disappears entirely for neurons which are too spontaneously noisy. Efforts are currently under way to quantitatively relate the parameter values used in the simulations and the theory to the voltages input to the motion transducer and to the FN model.

While our simple theory captures the broad features of the data, it is clear that detailed agreement is lacking. Of course, one reason is that the Kramers-type formula (8) is not expected to be correct in detail for these two systems. Another is that our model neglects a relevant time scale, namely, the refractory period. Physically, this means that during the deterministic reinjection, firing events are impossible; our model neglects this effect because we assumed statistical independence. This effect is especially important when the firing rate becomes comparable to the reinjection rate Δt^{-1} , that is, at high noise levels. As expected, Fig. 3 shows that the high- D limit in particular seems to deviate from the theoretical fit: The experimental data lie above the theory for large D where more threshold crossings, which in this range contribute to the randomization of the output, are missed during the refractory period. Work is currently under way to include the statistical correlations induced by the presence

of a finite refractory time.

We can compare our results with earlier discussions of SR in single-well systems. The monostable SR discussed by Stocks *et al.* is rooted in inertial effects in the underdamped-oscillator limit [13]; in contrast, our single-trigger SR is dominated by large superthreshold events, and the only important "oscillation" is the deterministic reinjection to the rest state. Meanwhile, Gitterman and Weiss [12] focused on the statistics of single escape events, without any reinjection mechanism. Thus, their study is relevant to a more careful modeling of the escape rate $\alpha(t)$, while we used a simpler adiabatic Kramers-type formula in our example.

Finally, although we have focused on the crayfish neuron, we emphasize that single-trigger dynamics is also encountered in settings more familiar to physicists. These include Josephson junctions biased below the critical current and semiconductor lasers pumped below the lasing threshold. [The latter obeys rate equations very similar to Eq. (2).] Since the "modified shot effect" theory applies equally well to any system having excitable dynamics and deterministic reinjection, we expect SR to be observable in these systems as well.

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- [15] We have detected evidence for SR using external noise in a total of 11 cells out of the 12 tested. Cells with too large an *internal* noise, as noted from the spontaneous firing rate, seldom show evidence for SR. In these cells the SNR's simply decrease monotonously with increasing external noise. We speculate that such cells are already operating at the optimum (internal) noise level, and consequently the addition of external noise cannot improve signal detection.