

Stochastic resonance in a neuron model that transmits spike trains

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Numerical simulation of a classic integrate-and-fire neuron model, driven by a periodic spike train and a Poisson noise train, demonstrates that stochastic resonance is a property that is available in neural transmission of spike trains. Beyond peripheral sensory neurons that process analog stimuli, our study extends to central neurons that process spike trains, the possibility of noise-enhanced signal transmission. Also, it enlarges the scope of stochastic resonance to the transmission of signals formed by trains of discrete pulses.

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The phenomenon of stochastic resonance can be described as an increase of the signal-to-noise ratio on the output of certain nonlinear systems, that is obtained through an increase of the noise level on the input. This paradoxical property was first introduced over a decade ago, in the context of climate dynamics [1]. It has since been observed in a large variety of both model systems and natural ones [2]. Stochastic resonance has now gained the status of a central paradigm that demonstrates the possibility of extracting signal from noise, or order from disorder, in complex (nonlinear) systems.

For a while, after its introduction, stochastic resonance was essentially recognized and theorized in dynamical systems of a bistable type [3]. Only recently has stochastic resonance been extended to monostable systems [4], and, of this kind, to threshold or excitable devices [5]. An important experimental prototype that is very often suggested for this class of systems is the neuron [5]. Neurons in the brain are engaged in complex and very efficient signal-processing operations, that are currently the object of intense investigations. In this respect, it is quite important to elucidate whether, and how, stochastic resonance in neuron transmission is a property that is indeed available for the brain function.

To date, this issue has been considered only for the case of peripheral sensory neurons. In those investigations, the neuron is submitted to analog signals: a coherent input that is usually a sine wave, and a noise input that is a continuous, usually Gaussian white, noise. These two inputs are interpreted as analog signals from the external world that impinge on the sensory neuron. Such conditions have been studied in model neurons with a monostable excitable character [5], and also in other models where it is shown that a bistable system can reproduce some properties of a neuron [6]. The possibility of stochastic resonance was established, in these models, for the response to continuous periodic forcing in the presence of continuous noise. An experimental demonstration of stochastic resonance in sensory neurons was also obtained recently, on the hair mechanoreceptor neural cell of the crayfish, stimulated by a combination of periodic and random motions [7].

Beyond the case of peripheral sensory neurons that are submitted to analog stimuli because of their direct con-

tact with the external world, it is known that most neurons process signals under the form of trains of (discrete) spikes. These spike trains convey the information involved in cognitive processes. In other circumstances, spike trains can also have the status of a noise, which results from stochastic stages that can dominate in the neural response or in the endogenous activity of pacemaker neurons [8]. Both informative, coherent spike trains, and noise spike trains can thus be envisaged in the nervous system. In the following, we demonstrate through the simulation of a simple neuron model that stochastic resonance can occur in the transmission of spike trains by a neuron.

We consider a classic integrate-and-fire neuron model. The neuron membrane, of time constant τ_m , has its electric potential $V(t)$ governed by

$$\tau_m \frac{dV}{dt} = -V(t) + ws(t) + w\eta(t). \quad (1)$$

As input signals on $V(t)$, there is the coherent component $s(t) = \sum_n \delta(t - nT_s)$ with n integer, that represents a periodic spike train with period T_s . There is also the noise component $\eta(t) = \sum_k \delta(t - t_k)$, where the t_k 's are Poisson-distributed random instants of density $1/T_\eta$, with autocorrelation function $R_{\eta\eta}(\tau) \equiv \langle \eta(t)\eta(t+\tau) \rangle = D\delta(\tau) + D^2$, and power spectral density $S_{\eta\eta}(\nu) = D^2\delta(\nu) + D$, with $D = 1/T_\eta$ [9]. w is a synaptic coupling, which could be different for the noise and the coherent input pathways, but which we suppose the same here to limit the number of parameters.

If the membrane potential V reaches the threshold $V_{th} > 0$, a spike is fired by the neuron, and then V is reset to zero, from where the variation of V resumes according to Eq. (1). The signal $y(t)$ on the neuron output thus evolves according to the following:

$$\begin{aligned} \text{If } V(t) = V_{th} \text{ then } y(t) = \delta(t' - t), \quad V(t) = 0; \\ \text{else } y(t) = 0. \end{aligned} \quad (2)$$

The response of Eq. (1) to a single input spike at t_0 is, for $t > t_0$,

$$V(t) = \left[V(t_0^-) + \frac{w}{\tau_m} \right] \exp \left[-\frac{t - t_0}{\tau_m} \right]. \quad (3)$$

In standard stochastic resonance, the coherent input alone is not sufficient to induce a transition of the output. Accordingly, here, the synaptic coupling w is chosen so that the coherent signal $s(t)$ alone is not sufficient to drive $V(t)$ to V_{th} . But we allow two sufficiently close input spikes to elicit an output spike. For the neuron that starts from $V(t_0^-) = 0$, a second input spike after the one at t_0 has to occur before $t_0 + T_h$, with

$$T_h = -\tau_m \ln \left[\frac{V_{th}}{w/\tau_m} - 1 \right], \quad (4)$$

in order to generate an output spike.

Thus, in the absence of the noise $\eta(t)$, the coherent signal $s(t)$ alone is insufficient to trigger the output. As the noise power density D is gradually increased from 0 (or equivalently as T_η is reduced), there will be a possibility for a noise spike to occur close enough to a coherent spike on the input. The cooperative effect of two such input spikes is able to elicit an output spike, which will be correlated with the coherent spike on the input. As D is increased, this outcome will first get more and more probable, leading to a reinforcement of the correlation between the output train and the coherent input train. For D still stronger, the possibility of two noise spikes occurring close enough to elicit by themselves an output spike will begin to matter, and from then on will gradually destroy the correlation of the output train with the coherent input train. Due to this nonmonotonic influence of the input noise power, one can thus expect a stochastic resonance effect.

This property has been verified by means of a numerical simulation of the neuron model. A Euler discretization with time step $\Delta t = 10^{-2}\tau_m$ has been used for Eq. (1). The autocorrelation function $R_{yy}(\tau) \equiv \langle y(t)y(t+\tau) \rangle$ of the output spike train $y(t)$ has been computed; for any value of τ , in the averaging process, $t \bmod T_s$ uniformly covers the interval $[0, T_s[$. A Fourier transform of $R_{yy}(\tau)$ then yielded the output power spectral density $S_{yy}(\nu)$. At the signal frequency $\nu = 1/T_s$, the magnitude of the strong peak $S_{yy}(1/T_s)$ has been measured on the output power spectral density (PSD), together with $N(1/T_s)$, the level of the broadband noise background at $1/T_s$. This served for the standard definition of the signal-to-noise ratio (SNR): $10 \log_{10}[S_{yy}(1/T_s)/N(1/T_s)]$. The variation of the SNR was then examined as a function of the input noise power density D .

Stochastic resonance was observed for a large range of the neural parameters. For illustration we chose a situation where it is clearly visible, with $T_s = 5\tau_m$ and $w/\tau_m = 0.8V_{th}$, which gives $T_h = 0.28T_s$ in Eq. (4). Figure 1 shows the normalized output autocorrelation function $R_{yy}(\tau)$ at $T_\eta = 0.5T_s$ which is the location observed for the resonance; and Fig. 2 the corresponding PSD $S_{yy}(\nu)$. The variation of the SNR as a function of the input noise power density $D = 1/T_\eta$ is given in Fig. 3(a). The curve of Fig. 3(a) displays a nonmonotonic evolution of the SNR with the noise level, with a maximum, here at $D = 2/T_s$, that is the signature of stochastic resonance. We have observed that the SNR at higher-order harmon-

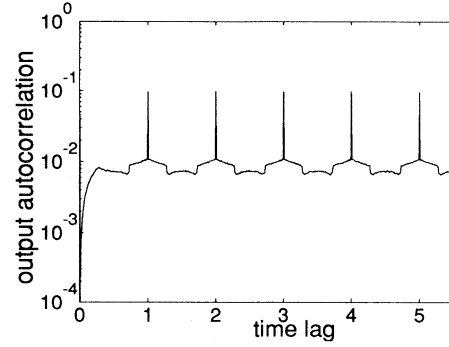


FIG. 1. Normalized output autocorrelation function $R_{yy}(\tau)$ as a function of the time lag τ/T_s , with a noise parameter $T_\eta = 0.5T_s$ which is the location observed for the resonance.

ics of the signal frequency $1/T_s$ also resonates in the same region of D , although not strictly at the same value. We have tested the harmonics up to $10 \times 1/T_s$, and all were found to resonate. Figure 3 also shows the SNR at $2 \times 1/T_s$ and at $4 \times 1/T_s$, which yielded, in this order, the strongest resonance after the fundamental $1/T_s$.

We observed that the value of T_η at the resonance is dependent upon both T_s and the interval T_h of Eq. (4), and T_η increases as T_s or T_h increases. We found that, given T_s , if the system operates at the value of T_h that yields the strongest resonant peak (it is the case in Figs. 1–3), then the resonance takes place when $T_\eta \approx 0.5T_s$. This behavior can be related to stochastic resonance in symmetric bistable systems, where there is a maximum in the response to the periodic signal when its period approximately matches twice the mean first passage time. We also observed with our system that, in the region of the resonance, on the output autocorrelation function $R_{yy}(\tau)$, as illustrated in Fig. 1, around each sharp peak at integer multiples of T_s there is a small symmetric plateau whose radius is approximately T_h . The parameter T_h has a direct influence on the characteristics of the resonance, since it represents the time scale over which strong correlation between a coherent input spike and an output spike

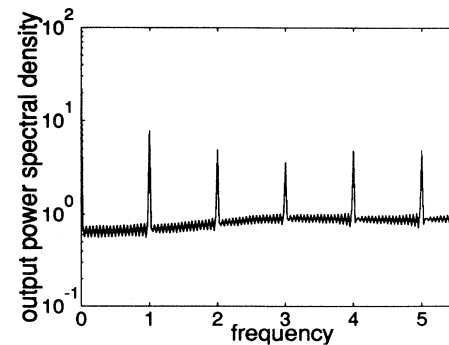


FIG. 2. Output power spectral density $S_{yy}(\nu)$ resulting from a Fourier transform of $R_{yy}(\tau)$ of Fig. 1, as a function of the frequency $\nu/(1/T_s)$.

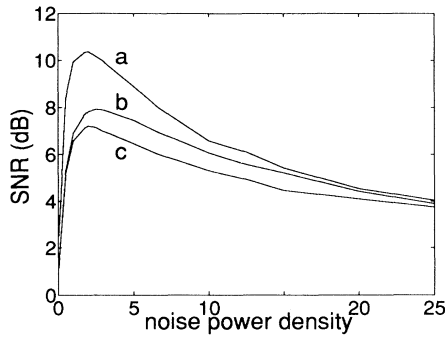


FIG. 3. Signal-to-noise ratio SNR on the output, as a function of the input noise power density $D/(1/T_s)$, at the fundamental frequency $1/T_s$ in (a), and at harmonics $2/T_s$ in (b) and $4/T_s$ in (c). The nonmonotonic variation of the SNR, which passes through a maximum for a specific noise level, is the signature of stochastic resonance.

can be preserved.

The present study extends the scope of stochastic resonance beyond the case of analog signals to the transmission of a new class of signals under the form of trains of discrete pulses. Our model can be categorized in the class of threshold-crossing models such as those reported in [5]. The main differences from the stochastically reso-

nant models of [5] are that our model uses (1) a different kind of noise (shot noise instead of continuous noise), and (2) a different kind of coherent signal (a pulse train instead of a sine wave). We are currently working on the theoretical description of the results reported here. However, modeling strategies previously applied to stochastic resonance, like rate-equation approaches or level-crossing theory or linear-response theory, do not seem to transpose directly here, as we abandon the domain of continuous signals for that of discrete pulses, yet still in a nonstationary context.

Our study also extends, beyond the case of peripheral sensory neurons that process analog stimuli, to central neurons that process spike trains, the possibility of noise-enhanced signal transmission. Whether real neurons actually exploit stochastic resonance in spike transmission is still an unproven matter; however, the present results demonstrate that this possibility is authorized by the basic neural mechanisms of spike transmission. The neuron model we have used carries, in a schematized way, the most essential features of neural transmission of spike trains (capacitive integration followed by a threshold response). We are now considering the evolution of the effect when more detailed elements are taken into account in the description of the neuron, and also when neurons interact in networks, in order to gain broader assessment of a property that may have important implications in neural information processing.

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