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# Stochastic resonance in neural systems: Effect of temporal correlation in the spike trains

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We consider here the effect of temporal correlations on the transmission of spike trains in an integrate-and-fire neuron. We find that if the noisy input spike train is variable enough, the signal-to-noise ratio can display more than one peak as a function of the noise strength. This result is analyzed in terms of a simple probabilistic description of the problem. [S1063-651X(98)08407-4]

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## I. INTRODUCTION

Stochastic resonance (SR) is a nonlinear effect in which noise can enhance the detection of weak signals. It was originally proposed to explain the recurrences of Earth's ice ages [1,2], and later applied to a variety of systems such as electronic circuits, lasers, superconducting devices, and neurons [3,4].

The concept was first applied to bistable systems. A weak signal could be too small to induce a transition from one minimum to the other, but adding noise will allow the system to overcome the barrier. If the level of noise is too high the state of the system will become uncorrelated to the signal. Therefore one can expect the existence of a value of the noise that optimizes the detection of signals.

The phenomenon has also been found in different kinds of systems, such as single potential wells [5] and integrate-and-fire (IF) dynamics [6]. The latter is a common model for neural dynamics. It consists of a linear differential equation for the subthreshold dynamics and a resetting of the membrane potential when it reaches a given threshold value [7]. The output of the system is, in this case, a ''pulse'' each time the membrane potential of the neuron crosses the threshold.

The noise-enhanced transmission of spike trains in IF neurons has been investigated in [8]. In this work the signal is taken as a series of periodic spike trains, while the noise consists of random spike trains. The latter ones are assumed to be independent Poisson processes. The strength of the noise is controlled by changing the number of random spike trains (that is equivalent to changing the mean value of the Poisson process), while the size of the postsynaptic potential generated by each spike is kept constant. Let us note that this does not affect the mean value of the noise only, but also its variance. In fact, in the limit of an infinite number of noisy spike trains, the ratio between the variance and the mean value of the intervals goes to zero. Another possibility is to keep the number of noisy inputs in a given time interval constant and change the size of the postsynaptic potential generated by each individual spike. In this way we can increase the mean value of the noisy input without decreasing the relative variance of the interspike intervals.

An interesting point that is not usually addressed in the context of neural dynamics is the influence of temporal correlations in the spike trains. Noisy spike trains are usually assumed to be Poissonian, as in [8]. However, experimental measurements of activity do not agree with this assumption. For instance, in [9], it is found that the ratio between the variance of the number of spikes observed in a given interval and the mean value of the number of spikes is 1.9, while for a Poissonian distribution it should be 1. Even higher ratios have also been observed [10,11]. This non-Poissonian behavior indicates that there must be correlations in the timing of the spikes, i.e., the probability of having a spike in a given time interval is a function of the timing of the previous spikes.

In this work we address the question of the influence of temporal correlations in the timing of the spikes on SR. To do this we will simulate an IF neuron that receives as inputs two spike trains: one is periodic and the other is noisy with a distribution of interspike intervals having a given variability. The plan of the paper is as follows. In Sec. II we introduce the model for the neuron and for the generation of the noisy spike trains. In Sec. III we describe the results of the simulations. In Sec. IV we analyze the problem in terms of a simple probabilistic description of the system [12,13]. In Sec. V we discuss the results and possible extensions.

## II. MODEL

The subthreshold dynamics is given by

$$\tau \frac{dV}{dt} = -V(t) + G(t)[V_{\text{rev}} - V(t)], \tag{1}$$

where $V(t)$ is the membrane potential, $\tau$ is the membrane time constant, $G(t)$ is the synaptic conductance, and $V_{\text{rev}}$ is the reversal potential of the interaction. If $V(t)$ reaches the threshold value $\theta$ then it is reset instantly to 0. The output of the neuron is given by the function

$$O(t) = \sum_{t_{\text{spikes}}} \delta(t - t_{\text{spikes}}), \tag{2}$$

where $t_{\text{spikes}}$ are the times where $V(t)$ has reached the threshold.

The evolution of the synaptic conductance is given by

$$\tau_G \frac{dG}{dt} = -G(t) + E(t), \tag{3}$$

where $\tau_G$ is the characteristic decay time of the interaction and $E(t)$ represent the input spike trains:

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$$E(t)=w_{\mathrm{signal}}\sum_k \delta(t-t_k^{\mathrm{signal}})+w_{\mathrm{noise}}\sum_k \delta(t-t_k^{\mathrm{noise}}), \quad (4)$$

where $w_{\mathrm{signal}}$ and $w_{\mathrm{noise}}$ are the strength of the signal and noise spike trains and $t_k^{\mathrm{signal}}$ and $t_k^{\mathrm{noise}}$ are the times of the $k$th spike in each one of the trains.

For the periodic spike train the spike times are given by $t_k^{\mathrm{signal}}=kT$, where $T$ is the period. For the noisy spike train

$$t_k^{\mathrm{noise}}=t_{k-1}^{\mathrm{noise}}+u_k \quad (5)$$

for $k>0$ and $t_1^{\mathrm{noise}}=0$. The interspike intervals $u_k$ are independent random variables with a probability density function given by

$$P(u)=\frac{\lambda^{\mu}u^{\mu-1}e^{-\lambda u}}{\Gamma(\mu)}. \quad (6)$$

This probability density function has a mean value $\langle u\rangle=\mu/\lambda$ and a variance $\sigma_u^2\equiv\langle u^2\rangle-\langle u\rangle^2=\mu/\lambda^2$. Therefore the coefficient of variability is

$$c_v\equiv\frac{\sigma_u}{\langle u\rangle}=\frac{1}{\mu^{1/2}}. \quad (7)$$

For $\mu=1$ we recover an exponential distribution of the interspike intervals and a Poisson distribution for the number of spikes in a given time interval. For $\mu>1$ we have a less variable process, leading to a periodic spike train in the limit of very large $\mu$. For $\mu<1$ the process is more variable than Poisson. In this case the spikes have a tendency to ''cluster'' because the distribution of interspike intervals has a divergence at $u=0$.

## III. SIMULATION RESULTS

We solved Eqs. (1) and (3) numerically using an Euler discretization scheme with a time step of 0.1 ms (much smaller than the time constants of the problem). We choose $\tau=10$ ms, $\tau_G=3$ ms, $V_{\mathrm{rev}}=70$ mV above rest, and a threshold $\theta=20$ mV. The strength of the periodic spike train is chosen as $w_{\mathrm{signal}}=6$ ms. Let us remark that because of the form of Eq. (1), the synaptic conductance is dimensionless while $w_{\mathrm{signal}}$ and $w_{\mathrm{noise}}$ have units of time. For this strength of the periodic input the neuron will have no output if there is no noise present.

The noisy spike trains are generated using Eqs. (5) and (6). The output function $O(t)$ is Fourier transformed in order to evaluate its power spectrum. The value of the peak at the frequency of the periodic train is identified as the signal $S$, and the background value is the noise $N$. The signal-to-noise ratio is defined by

$$R=10\log_{10}\frac{S}{N}. \quad (8)$$

In Figs. 1 (a)–1(e) we show the results for the signal-to-noise ratio as a function of the noise strength $w_{\mathrm{noise}}$ for different values of $\mu$: 3, 2, 1, 0.5 and 0.25. The most interesting feature of these results is the appearance of a double peak in the signal-to-noise ratio for small values of $\mu$. The first peak appears at a value of $w_{\mathrm{noise}}$ that is approximately 1/2 of the second peak. This suggests that pairs of spikes arriving in a small time window are contributing to the response of the system. This pairing is more probable for smaller values of $\mu$, because for this case the probability density function of the interspike intervals is maximum at 0. In the next section we will formulate this argument in a more quantitative form.

## IV. PROBABILISTIC DESCRIPTION

A simple argument by Gammaitoni [12] can be used to obtain an estimation of the output signal from the probability density function of the noise in a threshold system.

We denote the average firing rate for a constant input $A$ with $\langle O(A)\rangle$. Let us suppose that the signal is not a train of spikes but it is alternating periodically between the values $A-B$ and $A+B$ with frequency $\omega_0$. The signal, that is, the power spectrum at frequency $\omega_0$, will be proportional to the square of the difference of the *output* firing rate of the $A-B$ period $[\langle O(A-B)\rangle]$ minus the *output* firing rate of the $A+B$ period $[\langle O(A+B)\rangle]$. If the value of $B$ is small the signal will be [13]

$$S\propto\left[\frac{\partial}{\partial A}\langle O(A)\rangle\right]^2. \quad (9)$$

For a fixed value of the input $A$ the average firing rate will be proportional to the probability that the noise becomes equal to or larger than the difference between the signal and the threshold. If the probability density function of the noise is $P(\xi)$, then

$$\langle O(A)\rangle\propto\int_{\theta-A}^{\infty}P(\xi)d\xi. \quad (10)$$

Replacing this result in Eq. (9) we find that the signal is proportional to the square of the probability density function of the noise evaluated at $\theta-A$.

In this approximation the problem is reduced to evaluating the probability density function of the noise from the distribution of the interspike intervals. The calculation is quite simple in the case $\tau_G\ll\tau$. In this limit each spike in the noisy train generates a post-synaptic potential with an exponential time evolution:

$$V_{\mathrm{noise}}(t)=V_{\max}\sum_k \exp[-(t-t_k^{\mathrm{noise}})/\tau]\Theta(t-t_k^{\mathrm{noise}}), \quad (11)$$

where

$$V_{\max}=\frac{w_{\mathrm{noise}}V_{\mathrm{rev}}}{\tau} \quad (12)$$

and $\Theta$ is the Heaviside function.

The potential at a given time is determined by the timing of all the spikes previous to this time. However, there will be one predominant contribution coming from the last spike in the train previous to that time. If we take into account the effect of this spike only, neglecting the contribution of the

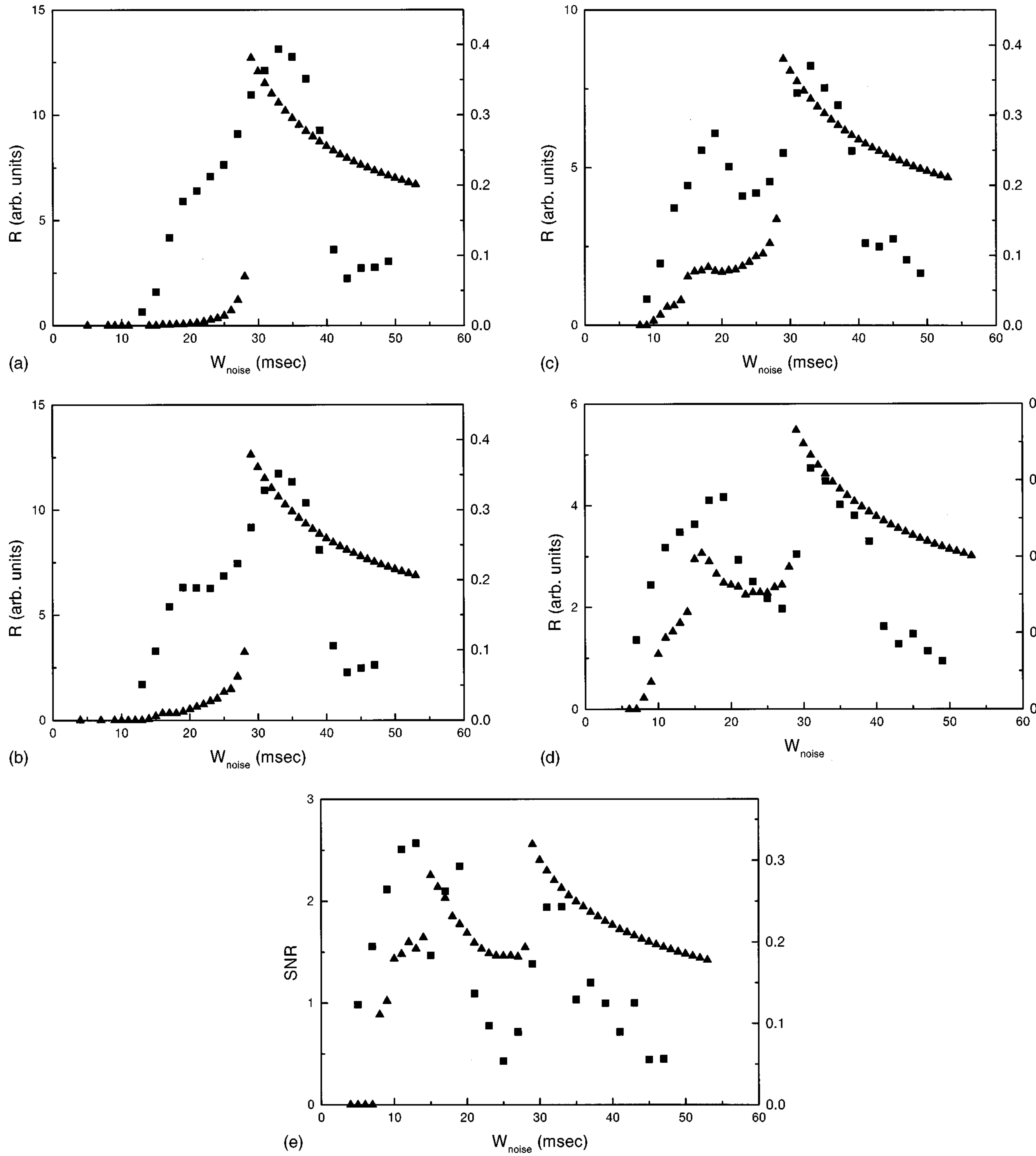

FIG. 1. Signal-to-noise ratio as a function of the noise strength $w_{\rm noise}$ for (a) $\mu=3$, (b) $\mu=2$, (c) $\mu=1$, (d) $\mu=0.5$, and (e) $\mu=0.25$. Squares: simulation results. Triangles: estimation from the probabilistic description.

others, the probability density function of finding a value of the potential between $V_{\rm noise}$ and $V_{\rm noise}+dV$ inside an interspike of length $T$ would be

$$P(V_{\rm noise})=\frac{\tau}{TV_{\rm noise}}, \tag{13}$$

where $V_{\rm noise}$ is in the range $[V_{\max},V_{\max}e^{-T/\tau}]$. Averaging over all the possible interspike intervals (and taking into account that it is more probable to find longer interspike intervals than shorter ones) we obtain

$$P_{w_{\rm noise}}(V_{\rm noise})=\frac{\tau\lambda}{V_{\max}}\,\frac{\Gamma(\mu,\tau\lambda\ln[V_{\max}/V_{\rm noise}])}{\Gamma(\mu+1)}\times\Theta(V_{\max}-V_{\rm noise}), \tag{14}$$

where $\Gamma(a,x)=\int_x^\infty e^{-t}t^{a-1}dt$ is the incomplete gamma function.

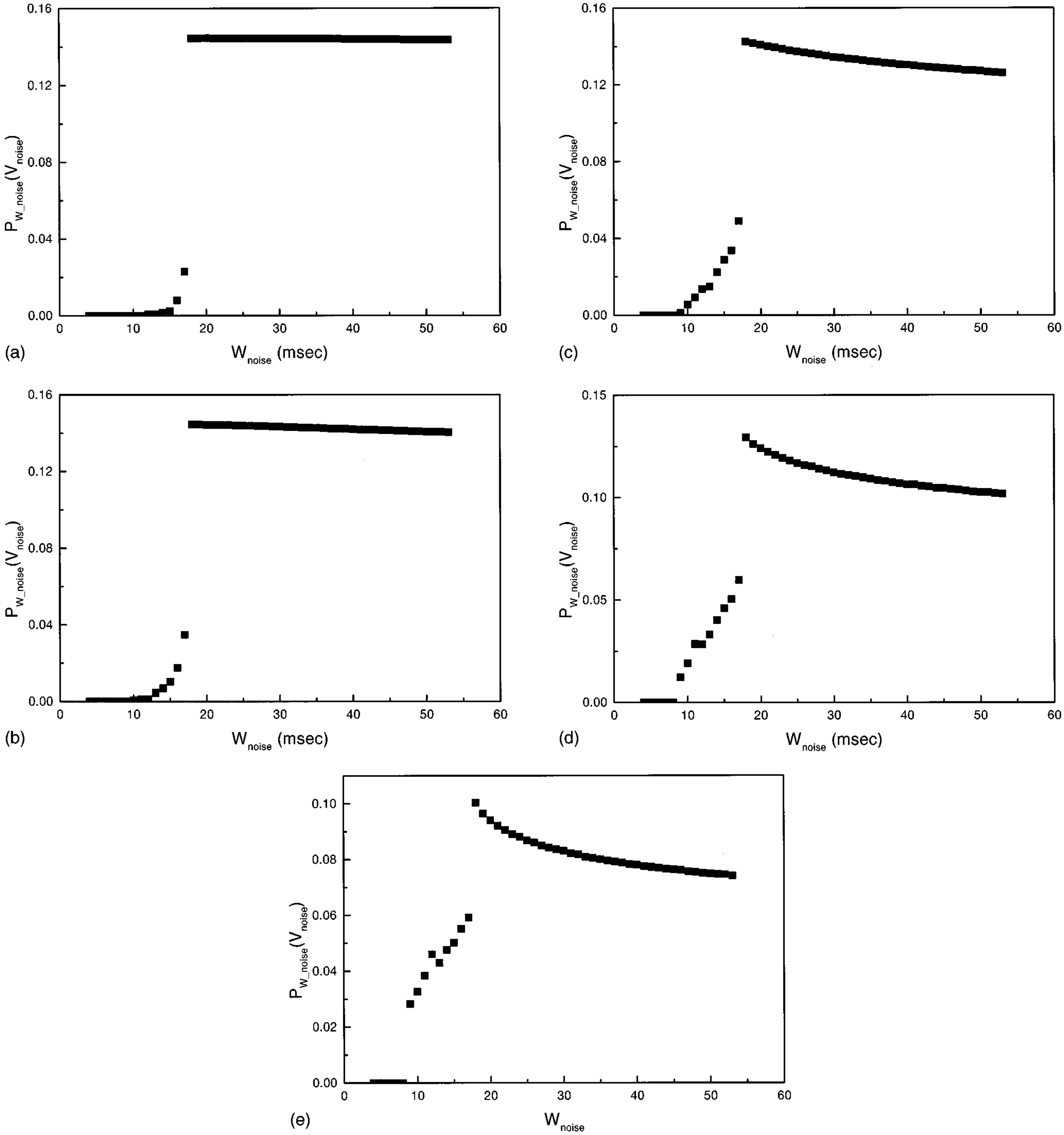

FIG. 2. Probability density function of the noise $P_{w_{\rm noise}}(V_{\rm noise})$ for $V_{\rm noise}=5$ as a function of $w_{\rm noise}$, for the same values of $\mu$ as in Fig. 1: (a) $\mu=3$, (b) $\mu=2$, (c) $\mu=1$, (d) $\mu=0.5$, and (e) $\mu=0.25$.

If we also take into account the previous spikes (with interspike intervals $T_1$, $T_2$, etc.), the probability density function of $V_{\rm noise}$ for a given value of $V_{\rm max}$ is

$$P_{w_{\rm noise}}(V_{\rm noise})=\left\langle \frac{\tau\lambda}{V_{\rm max}} \frac{\Gamma(\mu,\tau\lambda\ln[V_{\rm max}(1+e^{-T_1/\tau}+e^{-(T_1+T_2)/\tau}+\cdots)/V_{\rm noise}])}{\Gamma(\mu+1)}\right\rangle, \tag{15}$$

where the brackets $\langle\cdots\rangle$ denote an average over $T_1$, $T_2$, etc. with the distribution of Eq. (6).

In Figs. 2(a)–2(e) we show $P_{w_{\rm noise}}(V_{\rm noise})$ as a function of $w_{\rm noise}$ for a fixed value of $V_{\rm noise}$, and several values of $\mu$. These functions display a peak at the value $V_{\rm max}=V_{\rm noise}$. This corresponds to the contribution of one spike, as shown in Eq. (14). The part of the curve to the left of this peak corresponds to contributions from the previous spikes. This contribution becomes more important for smaller values of $\mu$ because in those cases it is more probable to have small values of $T_1$, $T_2$, etc. The number of spikes of the most important contribution will depend on the value of $\mu$, but independently of this number an expansion of the incomplete $\Gamma$ function leads for this contribution to

$$P_{w_{\rm noise}}(V_{\rm noise})\approx(V_{\rm max}-V^0_{\rm max})^{\mu}, \qquad (16)$$

where $V^0_{\rm max}$ is the minimum possible value for $V_{\rm max}$ for the largest contribution.

In order to estimate the signal-to-noise ratio we now have to divide the result of Eq. (15) by the fluctuation of the firing rate. It is not possible to evaluate this number in the framework of the present theory, because Eq. (10) gives us only the average number of spikes in a given time but not the variance. However, the numerical simulations indicate that the fluctuations of the firing rate are of the same order as the firing rate itself. The coefficient of variability of the *output* spike train goes from 0.8 for $\mu=3$ to 1.2 for $\mu=0.8$ (the output spike train is more Poissonian than the input ones). Neglecting the corrections to Poisson statistics in the output spike train, we can replace the fluctuation of the firing rate by the firing rate itself. This quantity can be evaluated using Eqs. (10) and (15).

The estimated values of the signal-to-noise ratio for the different values of $\mu$ are shown in Figs. 1(a)–1(e). We can see that for small values of $\mu$ the signal-to-noise ratio indeed has two peaks. The right-hand-side peak falls on the peak of the signal, and corresponds to an output generated by one noisy spike in the input, while the other peak corresponds to the contributions of the accumulation of two or more spikes.

## V. DISCUSSION

In this work we have shown that pulsed noise can lead to interesting new behavior in the framework of stochastic resonance, such as the appearance of multiple peaks in the signal-to-noise ratio as a function of the noise strength. These peaks appear even in the case of spikes generated with a Poisson statistics, but the relative sizes of the peaks can be controlled by changing the correlation of the input spike train.

The pulsed characteristics of the noise are essential to obtain this result. Previous works have addressed the question of colored noise, for instance, in [14,15] using exponentially correlated noise or in [16] studying a threshold system with a band limited $1/f$ noise. But in these cases the correlation does not induce multiple peaks in the signal-to-noise ratio.

A simple probabilistic description of the system is enough to understand qualitatively the appearance of the peaks, and its dependence on the correlation characteristics of the spike trains. This description is independent of the details of the dynamics of the neuron. Therefore it is very probable that the results are valid even for more complex dynamics, such as conductance based models.

As mentioned in [17] it is important to elucidate the relevance of SR for brain function. The precise nature of the neural code is widely debated (see [18] for a review.) If the precise spike times are relevant, then there is no ‘‘noise’’ in the system. Every spike carries some information. On the other hand, if the information is conveyed in firing rates, a noisy input can help to detect changes of the signal and stochastic resonance can be a way to enhance information processing.

We have shown that the variability of the noisy spike trains (and not only the strength of the interactions) can control the response of the system. In this sense we are showing that there are additional degrees of freedom that can be useful to control information processing. In nervous systems the variability is a consequence of the dynamical properties of the network (synaptic time constants, synaptic efficacies, intrinsic properties of the neurons). One important point to be studied is the relation between these factors and the variability of the spike trains.

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