STOCHASTIC RESONANCE IN NONLINEAR TRANSMISSION OF SPIKE SIGNALS: AN EXACT MODEL AND AN APPLICATION TO THE NEURON

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Nonlinear transmission of trains of pulses enhanced by noise addition through stochastic resonance is studied. First, an exact model is presented which describes stochastic resonance in the transmission of a periodic train of pulses by a threshold system in the presence of arbitrarily distributed white noise. Second, a simulation demonstrates a novel possibility of stochastic resonance in the neuron, in the nonlinear transmission of spike trains assisted by noise. Third, it is shown that the exact model can provide a satisfactory approximation of stochastic resonance in the neuron, as the reported effect is mainly sensitive to correlations at a dominant time scale formed by the coherent period, and to the overall input signal amplitude relative to the threshold of the nonlinearity. The present results enlarge the scope of the effect of noise-enhanced transmission of signals through stochastic resonance, and also of the possible mechanisms for neural information processing.

1. Introduction

Stochastic resonance is a nonlinear phenomenon consisting of an enhancement of the transmission of a periodic coherent signal by certain nonlinear systems, that is obtained through an increase of the noise applied to the system [Moss *et al.*, 1993, 1994; Wiesenfeld & Moss, 1995]. This paradoxical nonlinear effect has been reported in various physical systems including lasers [Vemuri & Roy, 1989], electronic circuits [Fauve & Heslot, 1983; Gong *et al.*, 1991; Anishchenko *et al.*, 1992, 1994], neurons [Bulsara *et al.*, 1991, 1993, 1994; Douglass *et al.*, 1993; Longtin, 1993; Longtin *et al.*, 1994; Jung, 1994; Wiesenfeld *et al.*, 1994; Pei *et al.*, 1995; Chapeau-Blondeau *et al.*, 1996a].

Theoretical analyses of stochastic resonance have to cope with a nonlinear and nonstationary context which usually hinders exact treatments. To date, very few stochastically resonant systems are known that are amenable to an exact description.

The available theoretical treatments developed for stochastically resonant systems usually resort to various approximations [McNamara & Wiesenfeld, 1989; Jung & Hänggi, 1991; Stocks *et al.*, 1993; Wiesenfeld *et al.*, 1994; Gingl *et al.*, 1995; Gammaitoni, 1995a, 1995b]. A frequent one is that of a slow and small periodic coherent signal. Also, the hypothesis of a Gaussian noise is often crucial, and the focus placed on a sinusoidal coherent input. In contrast, we present here a simple nonlinear system which transmits a periodic train of pulses as the coherent input, instead of a sinusoid. Furthermore this system operates with white, but arbitrarily distributed, noise, not restricted to the Gaussian. We then show that this system exhibits a stochastic resonance that lends itself to an exact theoretical description. Especially, the treatment offers an exact model in which the influence of the noise distribution on the resonance can be directly examined.

An important embodiment of stochastically resonant systems is the neuron. For the neuron, stochastic resonance has been demonstrated in both theoretical models [Bulsara *et al.*, 1991, 1993, 1994; Longtin, 1993; Longtin *et al.*, 1994; Jung, 1994; Wiesenfeld *et al.*, 1994; Pei *et al.*, 1995; Collins *et al.*, 1995] and experimental preparations [Douglass *et al.*, 1993; Levin & Miller, 1996]. These studies consider the case of a neuron directly exposed to the external world, what justifies the application of a coherent input under the form of an analog signal — most of the time a sinusoid. Beyond the case of analog stimuli from the external world, it is known that most neurons process signals under the form of trains of pulses or spikes (action potentials). The possibility of stochastic resonance in the transmission of spike trains by the neuron has been shown with a simulation in [Chapeau-Blondeau *et al.*, 1996a], in the presence of an external shot noise formed by an incoherent spike train which superposes to the coherent spike train. Further, we show here for the first time that stochastic resonance in a spike train (not sinusoid) transmission by the neuron, is also authorized in the presence of an internal continuous noise which originates in random channel gating in the neuron membrane. These results enlarge the useful role that can be assigned to neural noise in nonlinear information transfer by neurons.

Finally we examine the ability of the exact theoretical model we propose here, to provide a description of the stochastic resonance we observe in spike train transmission by the neuron.

2. An Exact Model of Stochastic Resonance in a Threshold System

Let $s(t)$ be a periodic signal with period T. Let $\eta(t)$ be a stationary white noise, with complementary distribution function $F_c(u) = \Pr\{\eta(t) > u\}$. In order to avoid difficulties attached to the idealized notion of a white noise, and also to have the possibility of a direct numerical evaluation of every relevant quantity, especially for the purpose of comparison with computer simulations, we choose to define the present model in the context of discrete-time signals. The time scale is thus discretized with a step $\Delta t \ll T$, and such that $T = N\Delta t$. Now in practice, the white noise $\eta(t)$ need only be a noise with a correlation length shorter than Δt.

The periodic signal $s(t)$ is now given in the form of a train of brief unit pulses described as

$$s(t = j\Delta t) = \sum_{m=-\infty}^{+\infty} h(t - mT), \qquad (1)$$

with m integer, and the discrete-time unit pulse $h(j\Delta t) = 1$ if $j = 0$ and $h(j\Delta t) = 0$ otherwise.

We consider a nonlinear system with threshold θ, which receives $s(t)$ and $\eta(t)$ as inputs, and produces unit pulses on its output $y(t)$ according to:

If $s(j\Delta t) + \eta(j\Delta t) > \theta$ then $y(j\Delta t) = 1$;
else $y(j\Delta t) = 0$. (2)

The present system can be categorized in the class considered in [Chapeau-Blondeau, 1996b]. Specifically here, the signals $s(t)$ and $y(t)$ are given in the form of trains of pulses, so as to give way, in the next section, to a neuronal interpretation.

We want to compute a statistical autocorrelation function for the output signal $y(t)$. Since y only assumes values 0 or 1, the expectation $E[y(t)y(t - \tau)]$, for fixed $\tau \neq 0$ and fixed t, can be expressed as the probability:

$$E[y(t)y(t - \tau)] = \Pr\{y(t) = 1 \text{ and } y(t - \tau) = 1\}, \qquad (3)$$

which is also:

$$E[y(t)y(t-\tau)] = \Pr\{s(t) + \eta(t) > \theta \text{ and } s(t-\tau) + \eta(t-\tau) > \theta\}. \qquad (4)$$

Since s is a deterministic signal and η a *white* noise, one can write

$$E[y(t)y(t-\tau)] = F_c[\theta - s(t)]F_c[\theta - s(t-\tau)]. \qquad (5)$$

And for $\tau = 0$, one has

$$E[y(t)y(t-\tau)] = \Pr\{y(t) = 1\} = F_c[\theta - s(t)]. \qquad (6)$$

Equations (5) and (6) can be combined into a single expression for all $\tau = k\Delta t$:

$$E[y(t)y(t - \tau)] = \{F_c[\theta - s(t)] - F_c^2[\theta - s(t)]\}\hat{\delta}(\tau) + F_c[\theta - s(t)]F_c[\theta - s(t - \tau)], \qquad (7)$$

with the discrete-time Dirac pulse $\hat{\delta}(k\Delta t) = 1$ if $k = 0$ and $\hat{\delta}(k\Delta t) = 0$ otherwise.

Both $F_c[\theta - s(t)]$ and $F_c[\theta - s(t - \tau)]$ are periodic in t and τ with period T. Because of the periodic coherent modulation introduced by $s(t)$, the random signal $y(t)$ is nonstationary, yet it is cyclostationary with period T [Papoulis, 1991]. It is possible to construct a "stationary" autocorrelation function $R_{yy}(\tau)$ for $y(t)$ through a proper time averaging of $E[y(t)y(t - \tau)]$ over an interval T, when t, or $t \bmod T$, uniformly covers $[0, T[$. We then define the "stationary" autocorrelation function of the output as

$$R_{yy}(\tau = k\Delta t) = \frac{1}{N} \sum_{t=0}^{(N-1)\Delta t} E[y(t)y(t - \tau)]. \quad (8)$$

Expressions (7) and (1) are used for an explicit evaluation of the average in Eq. (8) which gives

$$R_{yy}(k\Delta t) = R_0 \hat{\delta}(k\Delta t) + \tilde{R}_{yy}(k\Delta t), \quad (9)$$

with

$$R_0 = \frac{1}{N} F_c(\theta - 1)[1 - F_c(\theta - 1)] + \frac{N-1}{N} F_c(\theta)[1 - F_c(\theta)], \quad (10)$$

and $\tilde{R}_{yy}(k\Delta t)$ is a periodic component which verifies $\tilde{R}_{yy}(\tau = k\Delta t) = \tilde{R}_{yy}(\tau + T)$, and

$$\tilde{R}_{yy}(0) = \frac{1}{N} F_c^2(\theta - 1) + \frac{N-1}{N} F_c^2(\theta), \quad (11)$$

$$\tilde{R}_{yy}(k\Delta t) = \frac{2}{N} F_c(\theta - 1) F_c(\theta)$$

$$+ \frac{N-2}{N} F_c^2(\theta) \quad \text{for } 0 < k < N. \quad (12)$$

We now define the discrete Fourier transform of R_{yy}, over a time interval of an integer number $2M$ of periods T, as

$$\mathrm{DFT}[R_{yy}(k\Delta t)]$$

$$= \sum_{k=-MN}^{MN-1} R_{yy}(k\Delta t) \exp\left(-i2\pi \frac{k\ell}{2MN}\right), \quad (13)$$

what affords a frequency resolution $\Delta\nu = 1/(2MN\Delta t)$.

The autocorrelation function R_{yy} of Eq. (9) is formed by a pulse at the origin with magnitude R_0, superposed to the periodic component $\tilde{R}_{yy}$ with period T. The Fourier transform of R_{yy} defines the output power spectral density P_{yy}, which will then be formed by a constant background with magnitude R_0, superposed to a series of spectral lines at integer multiples of $1/T$. Application of Eq. (13) to Eq. (9) then yields

$$P_{yy}\left(\frac{n}{T}\right) = R_0 + \frac{2M}{N}[F_c(\theta - 1) - F_c(\theta)]^2. \quad (14)$$

This type of form for the power spectral density, with sharp coherent spectral lines sitting on a broad-band noise background, is typical for the output of a stochastically resonant system. We choose to define the signal-to-noise ratio, at frequency n/T on the output, as the ratio of the power contained in the spectral line alone to the power contained in the background in a frequency band of $1/(NT)$ around n/T. The corresponding expression of the SNR then follows as

$$SNR\left(\frac{n}{T}\right) = \frac{[F_c(\theta - 1) - F_c(\theta)]^2}{R_0}. \quad (15)$$

This theoretical description makes it possible to verify that many conditions lead to stochastic resonance in the model. For illustration we consider the case where $\eta(t)$ is a Gaussian noise of zero mean and variance σ_η^2, and with $\theta = 1.2$ and $N = 100$. Figure 1 (solid line) then represents the variation of the SNR of Eq. (15) as a function of the input noise variance σ_η^2. The non-monotonic variation of
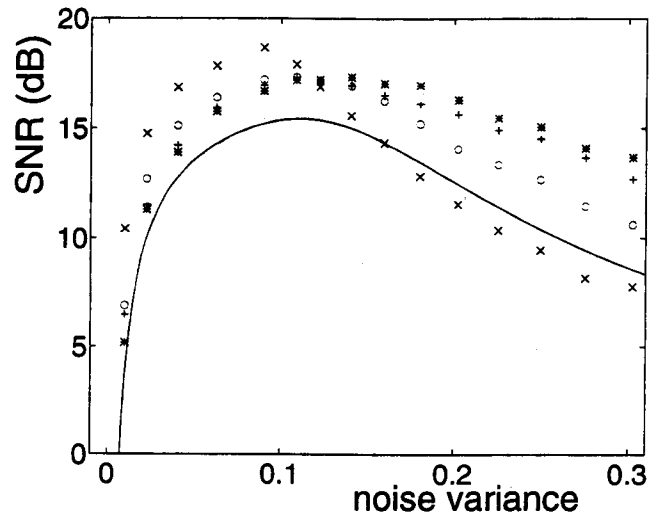

Fig. 1. Output SNR as a function of the variance of the noise on the input of the threshold nonlinearity. The solid line is the theoretical SNR from Eq. (15) of model 1. The four sets of experimental points are obtained from a simulation of the neuron model, with $T_0 = 1$ ms, $T_r = 3$ ms and $T = 300$ ms, and for: ($\times$) $\tau_m = 3$ ms, (o) $\tau_m = 10$ ms, (+) $\tau_m = 20$ ms and ($*$) $\tau_m = 30$ ms.

the *SNR* which passes through a maximum with σ_η^2, is a clear signature of stochastic resonance. With the present model, we also observed that other noise distributions lead to higher values of the exact *SNR* of Eq. (15), for the same noise variance, but we shall not go further, here, into the study of the influence of the noise distribution on the resonance.

The exact treatment we have developed relies on the hypothesis of a white noise. If the noise has a non-vanishing correlation time τ_c, this will translate into a peak of width $\sim \tau_c$ in the output autocorrelation function around the origin. Nevertheless, the magnitude of this peak in $\tau = 0$ will be correctly represented by Eq. (9), while its exact shape will not be described by Eq. (9). The exact shape of this peak of duration $\sim \tau_c$, will start to manifest its influence on the output power spectral density in the frequency range of order $1/\tau_c$. The stochastic resonance effect is sensitive to correlations that occur over a time scale of order T and that show up in the frequency range $1/T$. Consequently, if τ_c is sufficiently small compared to T, one can expect that the stochastic resonance effect in the range $1/T$ will be little affected by perturbations in the range $1/\tau_c$. Indeed, in the following we show that the present theoretical model can provide a description for a novel type of stochastic resonance in spike transmission by a neuron with colored noise impinging on its threshold nonlinearity.

3. Stochastic Resonance in Neural Transmission of Spike Signals

In neural signal transmission [Chapeau-Blondeau & Chambet, 1995], a presynaptic action potential or spike elicits the release of neurotransmitter molecules in the synaptic cleft. These molecules trigger the gating of ion channels which translates into electric conductance changes in the membrane of the postsynaptic neuron. The ion channels, which exist with high density in synaptic regions, are also capable of spontaneous random gating independent of neurotransmitter release. When both sources of membrane conductance changes are present, the electric potential above rest $V(t)$ of the postsynaptic neuron is varied according to

$$C_m \frac{dV}{dt} = - G_m V(t) + G_{\text{coher}}(t)[V_{\text{rev}} - V(t)]$$
$$+ G_{\text{noise}}(t)[V_{\text{rev}} - V(t)], \qquad (16)$$

where C_m and G_m are respectively the capacitance and conductance of the neuron membrane at rest, $G_{\text{coher}}(t)$ and $G_{\text{noise}}(t)$ are the membrane conductance variations induced respectively by presynaptic spikes and by spontaneous random channel gating. V_{rev} is the reversal potential of the ions that circulate through the gated channels; it is positive (i.e. above the resting potential) for excitatory channels, and negative (i.e. below the resting potential) for inhibitory channels.

When the potential $V(t)$ governed by Eq. (16) reaches the firing threshold V_{th}, an output spike is fired by the postsynaptic neuron and $V(t)$ is reset to zero.

For the purpose of studying stochastic resonance in the neural transmission of spikes, Eq. (16) is simplified into

$$\tau_m \frac{dV}{dt} = -V(t) + e(t) + \xi(t), \qquad (17)$$

with $\tau_m = C_m/G_m$, $e(t) = V_{\text{rev}} G_{\text{coher}}(t)/G_m$ and $\xi(t) = V_{\text{rev}} G_{\text{noise}}(t)/G_m$.

To obtain Eq. (17), we have performed a linearizing step which is frequently taken in neural modeling [Koch & Segev, 1989; Chapeau-Blondeau & Chambet, 1995], and in which $V_{\text{rev}} - V(t)$ is approximated simply by the constant V_{rev}. One assumes here that the excursion of $V(t)$, which can never exceed $V_{\text{th}} \approx 20$ mV above rest, remains sufficiently far from the value of V_{rev}. For instance, for typical excitatory channels one has $V_{\text{rev}} \approx 70$ mV above rest. This linearizing approximation introduces a small distorsion in the dynamics of $V(t)$, but which we think is non-critical for the observation of stochastic resonance in the neuron response.

The signal $e(t) = V_{\text{rev}} G_{\text{coher}}(t)/G_m$ of Eq. (17) reproduces the conductance changes, taken to be of an excitatory type ($V_{\text{rev}} > 0$), in response to presynaptic spikes. A presynaptic spike is a brief pulse of duration $T_0 \sim 1$ ms. Neurotransmitter release and channel gating are fast processes, and as a consequence, the conductance change $G_{\text{coher}}(t)$ in response to a single presynaptic spike is also a brief pulse of conductance which also lasts for a duration $\sim T_0$. For the observation of stochastic resonance, the exact form of such a conductance pulse is not critical. Accordingly, such a pulse is represented here as $E_0 \text{sq}(t)$, where E_0 is a constant which fixes the amplitude of the pulse, and $\text{sq}(t)$ is a unit square pulse of duration T_0, i.e. $\text{sq}(t) = 1$ for $0 \le t < T_0$ and $\text{sq}(t) = 0$ otherwise. The coherent input $e(t)$ is

now assigned the following form:

$$e(t) = \sum_{m=-\infty}^{+\infty} E_0 \text{sq}(t - mT), \qquad (18)$$

with m integer, which represents the effect of a periodic train of presynaptic spikes with period T.

The signal $\xi(t) = V_{\text{rev}} G_{\text{noise}}(t)/G_m$ of Eq. (17) reproduces the conductance changes induced by the random gating of the channels. Because channel kinetics can be assumed to be fast compared to the membrane potential dynamics governed by Eq. (17) with time constant τ_m, then in this equation $\xi(t)$ can be considered a white noise. Because the conductance changes described by $\xi(t)$ involve the gating of a large number of independent channels, then $\xi(t)$ can be considered a Gaussian noise. $\xi(t)$ is thus taken to be a stationary Gaussian white noise whose autocorrelation function is written as: $\langle \xi(t)\xi(t - \tau)\rangle = 2D\delta(\tau)$. The mean of $\xi(t)$ is taken to be zero, and this can be obtained by assuming two populations of random channels, one excitatory with $V_{\text{rev}} > 0$, one inhibitory with $V_{\text{rev}} < 0$. Again, these simple and plausible hypotheses concerning the neural noise, are not critical for the observation of stochastic resonance in the neuron response.

Equation (17) represents a first-order low-pass linear filtering of the input $e(t) + \xi(t)$. The solution of Eq. (17) can then be expressed analytically under the form $V(t) = e_f(t) + \xi_f(t)$. The term $e_f(t)$ is the filtered version of the input $e(t)$:

$$e_f(t) = \sum_m E_0 \text{sq}_f(t - mT), \qquad (19)$$

with the exponential pulse $\text{sq}_f(t)$ which is the filtered version of the square pulse $\text{sq}(t)$:

$$\text{sq}_f(t) = 1 - \exp(-t/\tau_m) \qquad \text{for } 0 \leq t < T_0,$$
$$\text{sq}_f(t) = [1 - \exp(-T_0/\tau_m)]$$
$$\cdot \exp[-(t - T_0)/\tau_m] \qquad \text{for } t \geq T_0. \qquad (20)$$

And the term $\xi_f(t)$ is the filtered version of $\xi(t)$: It is a colored Gaussian noise with autocorrelation function $\langle \xi_f(t)\xi_f(t-\tau)\rangle = D\tau_m^{-1}\exp(-|\tau|/\tau_m)$, and variance $D\tau_m^{-1}$.

To complete the description of signal transmission by the neuron, we complement Eq. (17) by the specification that when the membrane potential $V(t) = e_f(t) + \xi_f(t)$ exceeds the threshold V_{th} then an output spike is emitted on the neuron output $S(t)$, and $V(t)$ is reset to zero:

If $V(t) = e_f(t) + \xi_f(t) > V_{\text{th}}$

then $S(t) = \delta(t' - t)$,

$$V(t) \leftarrow 0 \text{ frozen during } T_r;$$

$$\text{else} \quad S(t) = 0. \qquad (21)$$

After the emission of a spike, V remains frozen at zero during a refractory period T_r, after which the evolution of V resumes according to Eq. (17).

The neuron model of Eqs. (17)–(21) has been numerically simulated, with a Euler discretization of the equations, with a time step much smaller than the relevant time constants τ_m, T_0 and T_r. When the coherent signal $e_f(t)$ remains below the firing threshold V_{th}, addition of the noise $\xi_f(t)$ can bring the neuron to fire. In such a regime, the *SNR* at the neuron output can be evaluated with the same definition as in Sec. 2, and the results showed that stochastic resonance takes place in the neuron response, for a broad range of parameter values.

Further, we want to examine to what extent the theoretical model of Sec. 2 (let us call it model 1), can provide a description for stochastic resonance in the neuron response. Because of the refractory period, the neuron can update its output only every T_r. It is thus natural to identify Δt of model 1 to T_r. In this way, both model 1 and the neuron model experience a periodic train of pulses surperposed to a continuous noise which impinge on their threshold nonlinearity, and their output is updated every $\Delta t \equiv T_r$ with the emission of an output spike each time the threshold is exceeded. A visible difference between model 1 and the neuron model is the presence of the low-pass filter with time constant τ_m of Eq. (17) on the neuron input. The effect of this filter is to distort and lengthen the coherent input pulses, and to broaden the correlation time of the noise to a range of order τ_m. The amplitude of the filtered pulses which form $e_f(t)$ is $E_0[1 - \exp(-T_0/\tau_m)]$ according to Eqs. (19) and (20); this amplitude has to be taken as the unit of amplitude in the neuron model, since model 1 operates with coherent pulses of amplitude unity. To summarize, the correspondence between the neuron model and model 1 is, for the time scale $T_r \equiv \Delta t$, and for the signal amplitudes $E_0[1 - \exp(-T_0/\tau_m)] \equiv 1$.

Once this correspondence is performed, it remains that the neuron nonlinearity has to operate with (a) a colored noise $\xi_f(t)$ of correlation length $\sim \tau_m$ which stays finite (of order 10 ms) in a plausible neuron, and (b) coherent pulses whose amplitude is correctly modeled but whose shape is distorted on the time scale $\sim \tau_m$. In addition, to conform with the situation of model 1, the

correlation length $\sim \tau_m$ of the noise should remain large relative to T_0 (the amplitude of the noise should not change much over the duration of a coherent pulse). This, altogether, imposes severe temporal constraints which hinder the neuron model to exactly superpose to model 1. Nevertheless, for the reasons anticipated at the end of Sec. 2, it can be expected that if τ_m remains sufficiently below the coherent period T, and also sufficiently above T_0, then the stochastic resonance effect occuring in the neuron will be correctly approximated by model 1. This expectation is verified by the results presented in Fig. 1.

For the comparison of Fig. 1 between model 1 and the neuron, we have taken the following plausible typical values for the neuronal parameters: $T_0 = 1$ ms, $T_r = 3$ ms, $\tau_m = 3$ to 30 ms, together with $T = 300$ ms, and $V_{th} = 1.2$ relative to the unit of signal amplitude $E_0[1 - \exp(-T_0/\tau_m)]$. The curves of Fig. 1 reveal an overall satisfactory agreement between model 1 and the neuron. As anticipated, the overall agreement between model 1 and the neuron, both in the resonance region and on both sides of it, is best for intermediate values of τ_m ($\tau_m \approx 10$ ms), and it degrades when τ_m increases toward T or decreases toward T_0. We observe in Fig. 1, that the value of the noise variance for the maximum of the SNR in the neuron, is satisfactorily predicted by model 1, especially for the best condition $\tau_m = 10$ ms. This outcome may be attributed to the fact that this resonant value of the variance is essentially determined by the amplitude of the coherent pulse plus noise relative to the threshold, and is little sensible to the exact shape of the coherent pulse and to the correlation structure of the noise. The magnitude of the SNR in the neuron, which usually exceeds the SNR in model 1, especially in the region of the resonance, might be attributed to a higher degree of coherence or correlation in the neuron output, that would originate in the correlation present in the colored neural noise compared to the white noise of model 1, and also in the longer duration of the coherent pulses impinging on the neuron nonlinearity.

4. Discussion and Conclusion

First, we have introduced a nonlinear threshold system which was shown capable of stochastic resonance in the transmission of a periodic train of pulses with white noise. This model offers an example of a conceptually very simple stochastically

resonant system, and it lends itself to an exact treatment in the presence of an arbitrarily distributed white noise. Especially, the present treatment provides an exact expression for the SNR, and it authorizes direct examination of the influence of the noise distribution on the resonance (although this study has not been carried out here).

Other recent studies have also considered stochastic resonance in threshold systems of various kinds [Bulsara *et al.*, 1994; Jung, 1994, 1995; Wiesenfeld *et al.*, 1994; Gingl *et al.*, 1995; Pei *et al.*, 1995; Gammaitoni, 1995a, 1995b]. A large majority of these studies have considered the transmission of a sinusoid with Gaussian noise [Bulsara *et al.*, 1994; Jung, 1994, 1995; Wiesenfeld *et al.*, 1994; Gingl *et al.*, 1995; Pei *et al.*, 1995], while our present study considers the transmission of a periodic train of pulses with arbitrarily distributed noise. The study in [Gammaitoni, 1995a, 1995b] also considers arbitrary noise distributions, but it only offers an approximate treatment, especially with only an approximate expression for the SNR. Also in [Gammaitoni, 1995a, 1995b] the transmission of pulse trains is not considered, and no application to the neuron is proposed. An interesting study in [Kiss, 1995] considers the transmission of pulse trains, but with a noise restricted to the Gaussian case, and no application to the neuron.

Second, here, we have demonstrated, with a numerical simulation, a novel possibility of stochastic resonance in the neuron, in the transmission of spike trains. This is the first study of this kind to report stochastic resonance in the transmission of an input spike train, in the presence of an internal continuous neural noise originating in random channel gating in the membrane. Special care has been devoted here to render visible the origin of the neural noise, instead of an *ad hoc* introduction of a noise signal in the model. Other models dealing with neurons [Bulsara *et al.*, 1991, 1993, 1994; Longtin, 1993; Longtin *et al.*, 1994; Jung, 1994; Wiesenfeld *et al.*, 1994; Pei *et al.*, 1995; Collins *et al.*, 1995; Douglass *et al.*, 1993; Levin & Miller, 1996] have reported stochastic resonance in the transmission of an analog stimulus, usually a sinusoid, and not a spike train as we report here. Whether this property of noise-enhanced spike train transmission is actually used by actual neurons remains an unproven issue, which would require experimental examination. Yet, without further evidence, the present study demonstrates with theoretical arguments that this possibility is at least authorized by the

basic neural mechanisms of spike train transmission, making it available for information processing by neurons.

Finally, we have shown that the exact model we propose, can provide a satisfactory approximation for stochastic resonance in the neuron.

The system of Eq. (2) only describes the peak level of an output spike, and does not include a description of its shape with the rising and falling parts of the spike. If output spikes were emitted at the very high rate of one spike every Δt, then the output y of Eq. (2) would appear as a constant level 1.

However, when the system of Eq. (2) responds to the input spike train $s(t)$ of Eq. (1), output spikes are emitted at a repetition interval of order T much larger than the elementary time step Δt. In this condition, an output spike can be emitted with appreciable probability only when an input spike is present, and consequently a level 1 occurring on the output will almost invariably be preceded and succeeded by the 0 level, restoring a spike nature for the output in response to an input spike train with repetition $T \gg \Delta t$.

The simple nature of the output y of Eq. (2) which only produces levels 0 or 1 is a key feature to allow the development of an exact treatment of the system. It is also appropriate to approximate the output spike train responding to an input spike train with a repetition interval $T \gg \Delta t$. Individual spikes in the trains, both in model 1 and in the neuron model, are represented in a schematized way. Yet this conforms with a general assumption in neural modeling which admits that the exact (almost invariant) shape of every individual spike in not significant for the coding of information, but rather the temporal organization of these spikes assembled in trains.

The ability that we have shown, of our exact model 1 to provide an approximation for stochastic resonance in the neuron, can essentially be attributed to the fact that the resonance effect is mainly sensitive to correlations at a dominant time scale formed by the coherent period T, and to the overall input signal amplitude relative to the threshold of the nonlinearity. Other parameters, that describe additional details in the signals over time scales sufficiently smaller than T, have comparatively minor influence.

The present study with a simple and (rare of its kind) exact model system, added to novel results on spike train transmission by neurons,

enlarge the scope of stochastic resonance and also of the possible mechanisms for neural information processing.

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