

Noise enhancement of signal transduction by parallel arrays of nonlinear neurons with threshold and saturation

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Abstract

A classic model neuron with threshold and saturation is used to form parallel uncoupled neuronal arrays in charge of the transduction of a periodic or aperiodic noisy input signal. The impact on the transduction efficacy of added noises is investigated. In isolated neurons, improvement by noise is possible only in the subthreshold and in the strongly saturating regimes of the neuronal response. In arrays, improvement by noise is always reinforced, and it becomes possible in all regimes of operation, i.e. in the threshold, in the saturation, and also in the intermediate curvilinear part of the neuronal response. All the configurations of improvement by noise apply equally to periodic and to aperiodic signals. These results extend the possible forms of stochastic resonance or improvement by noise accessible in neuronal systems for the processing of information.

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1. Introduction

Neurons interconnected in networks are very efficient for signal and information processing, through detailed modalities and mechanisms which are still under intense investigation. Neurons are intrinsically nonlinear devices. It is now known that in nonlinear processes, the presence or even the injection of noise, can play a beneficial role for signal and information processing. This type of useful-noise phenomena have been widely investigated under the denomination of stochastic resonance [15,1]. Many forms of stochastic resonance or improvement by noise have been reported in various nonlinear systems involved in diverse signal processing operations. Several forms of stochastic resonance have been reported in neural processes (see for instance [14,12] for early experimental demonstrations, and [21] for a recent overview). At the level of the nonlinear neuron, many reported instances of stochastic resonance essentially rely on the threshold or excitable dynamics inherent to the neuron. In such situations, there is usually a

small information-carrying signal, which is by itself too weak to elicit an efficient response from the threshold or excitable dynamics. The noise then cooperates constructively with the small signal, in such a way as to elicit a more efficient neuronal response.

Recently, a new mechanism of stochastic resonance has been exhibited when threshold or excitable nonlinearities are assembled into an uncoupled parallel array. This new form has been introduced under the name of suprathreshold stochastic resonance in [25,26], because in the array, addition of noise can improve the transmission of an input signal with arbitrary amplitude, not necessarily a small subthreshold signal. A parallel array is a common architecture for neuron assemblies, especially in sensory systems in charge of the transduction of noisy signals from the environment. Stochastic resonance has been shown possible in neuronal parallel arrays, with various models for the threshold or excitable nonlinear dynamics of the neuron. In neuronal arrays, Collins et al. [11], Chialvo et al. [9], and Hoch et al. [18,19] show stochastic resonance essentially with a subthreshold input signal, while Stocks [24], Stocks and Mannella [27], and Hoch et al. [17] show the novel form of suprathreshold stochastic resonance.

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In the neuronal arrays, suprathreshold stochastic resonance is shown in [24,17] with simple threshold binary neurons, meanwhile Collins et al. [11], and Stocks and Mannella [27] for this investigate an excitable FitzHugh–Nagumo model in its subthreshold and suprathreshold regimes.

For isolated nonlinear systems, it has recently been shown that stochastic resonance can also operate in threshold-free nonlinearities with saturation, where the noise has the ability to reduce the distortion experienced by a signal because of the saturation [23], with an extension to arrays of threshold-free sensors with saturation given in [8]. Saturation is also a feature present in the neuronal response, and this effect of stochastic resonance at saturation has been shown to occur [22] in the transmission by a nonlinear neuron in its saturating region. More detailedly, Rousseau and Chapeau-Blondeau [22] demonstrate that in signal transmission by an isolated neuron, improvement by noise can take place both in the region of the threshold and in the region of the saturation; in between, when the neuron operates in the intermediate region avoiding both the threshold and the saturation, then improvement by noise does not take place. In the present paper, we shall consider the same type of neuron model with saturation as in [22]; we shall assemble these neurons into a parallel array, and investigate the impact of added noise in the array. We shall exhibit that different occurrences of stochastic resonance take place in the array. We shall show in the array that stochastic resonance is present in the threshold and in the saturation regimes of the neuronal response, just like in the case of an isolated neuron, but always with an increased efficacy brought in by the array. In addition, we shall show that in the array, stochastic resonance also takes place in the intermediate regime of operation that avoids both the threshold and the saturation of the neuron. Stochastic resonance does not arise in isolated neurons in this regime, but the property becomes possible in neuronal arrays through a truly specific array effect.

2. The model of neuronal array

We consider the neuron model of [22]. The input signal to the neuron, at time t , is taken as the total somatic current $I(t)$. This input current $I(t)$ may result from presynaptic neuronal activities, or also from an external stimulus of the environment for sensory neurons, a situation to which stochastic resonance effects are specially relevant. The output response of the neuron is taken as the short-term firing rate $f(t)$ at which action potentials are emitted in response to $I(t)$. A classic modeling of the integrate-and-fire dynamics of the neuron leads to an input–output firing function $g(\cdot)$, under the so-called Lapicque form [20,4]

$$f(t) = g[I(t)] = \begin{cases} 0 & \text{for } I(t) \leq I_{\text{th}}, \\ \frac{1/T_r}{1 - (\tau_m/T_r) \ln[1 - I_{\text{th}}/I(t)]} & \text{for } I(t) > I_{\text{th}}. \end{cases} \quad (1)$$

In the firing function of Eq. (1), a threshold current arises as $I_{\text{th}} = V_{\text{th}}/R_m$, with V_{th} the standard firing potential of the neuron, and R_m its total membrane resistance. Also in Eq. (1), τ_m is the membrane time constant, and T_r the neuron refractory period. We take the typical values as in [22]: $V_{\text{th}} = 10$ mV above the neuron resting potential, $R_m = 100$ M Ω leading to $I_{\text{th}} = 0.1$ nA, and $\tau_m = 10$ ms and $T_r = 1$ ms. The resulting neuron firing function of Eq. (1) is depicted in Fig. 1.

Although resulting from a very simplified description of the neuronal dynamics, the firing function of Eq. (1) is able to capture essential features of the neuron response [20,4] characterized by the presence of a threshold, a saturation, and in between a smooth curvilinear part.

A number N of identical neurons modeled as Eq. (1) and labeled with index $i = 1$ to N , are assembled into an uncoupled parallel array. Each neuron i in the array receives a common input signal $I(t)$. There is also, at the level of each neuron i , a local noise $\eta_i(t)$, independent of $I(t)$, which adds to $I(t)$ and leads to the response of neuron i as

$$f_i(t) = g[I(t) + \eta_i(t)], \quad i = 1, 2, \dots, N. \quad (2)$$

The N noises $\eta_i(t)$ are assumed white, mutually independent and identically distributed (i.i.d.) with probability density function $p_\eta(u)$. The response $y(t)$ of the array can be taken as the sum $\sum_{i=1}^N f_i(t)$ or as the average $N^{-1} \sum_{i=1}^N f_i(t)$ of the N neuron outputs, and both quantities would behave in the same way in the present study; for the sequel we will consider

$$y(t) = \frac{1}{N} \sum_{i=1}^N f_i(t). \quad (3)$$

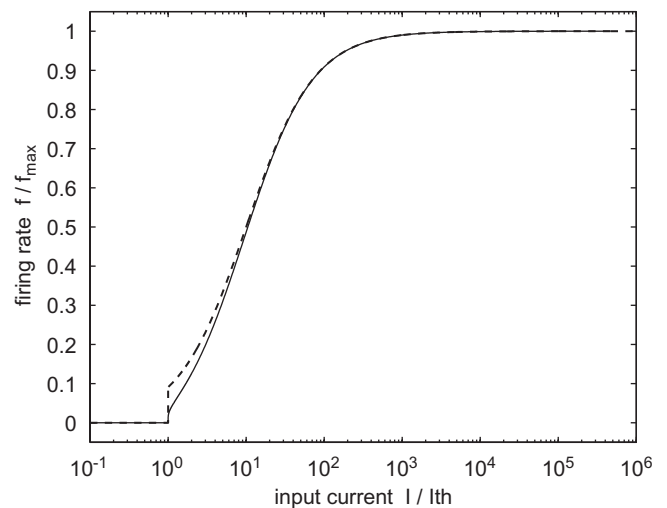


Fig. 1. Output firing rate $f(t)$ in units of $f_{\text{max}} = 1/T_r$, as a function of the input somatic current $I(t)$ in units of I_{th} , in typical conditions with $\tau_m = 10$ ms, $T_r = 1$ ms and $I_{\text{th}} = 0.1$ nA, according to the neuron firing function Eq. (1) (solid line) and its approximation Eq. (17) (dashed line).

3. Assessing nonlinear transmission by the array

To demonstrate a neuronal transmission aided by noise, we consider that the input current $I(t)$ to the array is formed as

$$I(t) = s(t) + \zeta(t). \quad (4)$$

In Eq. (4), $s(t)$ is our information-carrying signal, which will be successively considered to be a periodic and an aperiodic component. $s(t)$ conveys an image of the information coming from presynaptic neurons or from the external world for sensory cells. Also in Eq. (4), $\zeta(t)$ is a white noise, independent of $s(t)$ and of the $\eta_i(t)$, with probability density function $p_\zeta(u)$. This noise $\zeta(t)$ may have its origin in random activities of presynaptic neurons, or in the external environment. The input signal-plus-noise mixture $I(t) = s(t) + \zeta(t)$ is transmitted by the neuronal array to produce the corresponding output $y(t)$ via Eqs. (2)–(3). We will now study the impact of the array noises $\eta_i(t)$ on the efficacy of transmission of $s(t)$ by the array.

3.1. Periodic signal transmission

To assess the transmission efficacy, when $s(t)$ is a periodic signal with period T_s , a standard measure in stochastic resonance studies is the signal-to-noise ratio (SNR), defined in the frequency domain [5,15]. At the output, the SNR measures in $y(t)$ the power contained in the coherent spectral line existing at $1/T_s$ divided by the power contained in the noise background in a small frequency band ΔB around $1/T_s$, and reads [5]

$$\mathcal{R}_{\text{out}} = \frac{|\langle E[y(t)] \exp(-i2\pi t/T_s) \rangle|^2}{\langle \text{var}[y(t)] \rangle \Delta t \Delta B}. \quad (5)$$

In Eq. (5), a time average is defined as

$$\langle \dots \rangle = \frac{1}{T_s} \int_0^{T_s} \dots dt, \quad (6)$$

$E[y(t)]$ and $\text{var}[y(t)] = E[y^2(t)] - E^2[y(t)]$ represent the expectation and variance of $y(t)$ at a fixed time t ; and Δt is the time resolution of the measurement (i.e. the signal sampling period in a discrete time implementation), throughout this study we take $\Delta t \Delta B = 10^{-3}$.

At time t , for a fixed given value I of the input current $I(t)$, according to the linearity of Eq. (3), one has the conditional expectations

$$E[y(t)|I] = E[f_i(t)|I] \quad (7)$$

and

$$E[y^2(t)|I] = \frac{1}{N} E[f_i^2(t)|I] + \frac{N-1}{N} E^2[f_i(t)|I], \quad (8)$$

which are both independent of i since the $\eta_i(t)$, and therefore the $f_i(t)$, are i.i.d. From Eq. (2), one has for every i ,

$$E[f_i(t)|I] = \int_{-\infty}^{+\infty} g(I+u)p_\eta(u) du \quad (9)$$

and

$$E[f_i^2(t)|I] = \int_{-\infty}^{+\infty} g^2(I+u)p_\eta(u) du. \quad (10)$$

Since $I(t) = s(t) + \zeta(t)$, the probability density for $I(t)$ is $p_\zeta(I - s(t))$, and one obtains

$$E[y(t)] = \int_{-\infty}^{+\infty} E[y(t)|I] p_\zeta(I - s(t)) dI, \quad (11)$$

and

$$E[y^2(t)] = \int_{-\infty}^{+\infty} E[y^2(t)|I] p_\zeta(I - s(t)) dI, \quad (12)$$

which completes the relations needed for evaluation of the output SNR \mathcal{R}_{out} of Eq. (5).

3.2. Aperiodic signal transmission

When the information-carrying input signal $s(t)$ is aperiodic, a standard measure in stochastic resonance studies is the normalized input–output cross-covariance, which quantifies the similarity between input $s(t)$ and output $y(t)$ in a way which is insensitive to both scaling and offsetting in signal amplitude [10,23]. When $s(t)$ is a deterministic aperiodic signal existing over the duration T_s , we introduce the signals centered around their time-averaged statistical expectation,

$$\tilde{s}(t) = s(t) - \langle s(t) \rangle \quad (13)$$

and

$$\tilde{y}(t) = y(t) - \langle E[y(t)] \rangle, \quad (14)$$

with the time average again defined by Eq. (6). The normalized time-averaged cross-covariance is

$$C_{sy} = \frac{\langle E[\tilde{s}(t)\tilde{y}(t)] \rangle}{\sqrt{\langle E[\tilde{s}^2(t)] \rangle \langle E[\tilde{y}^2(t)] \rangle}}, \quad (15)$$

or equivalently, since $s(t)$ is deterministic,

$$C_{sy} = \frac{\langle s(t)E[y(t)] \rangle - \langle s(t) \rangle \langle E[y(t)] \rangle}{\sqrt{[\langle s(t)^2 \rangle - \langle s(t) \rangle^2][\langle E[y^2(t)] \rangle - \langle E[y(t)] \rangle^2]}}, \quad (16)$$

with $E[y(t)]$ and $E[y^2(t)]$ again given by Eqs. (11) and (12).

With the measures of performance \mathcal{R}_{out} of Eq. (5) and C_{sy} of Eq. (16), we are now in a position to quantify the impact of the array noises $\eta_i(t)$ on the efficacy of transmission of a periodic or an aperiodic $s(t)$ by the neuronal array.

4. Array transmission aided by noise

Direct numerical evaluations of \mathcal{R}_{out} and C_{sy} can be realized through numerical integration of the integrals of Eqs. (9)–(12). Alternatively, to push further the analytical treatment, it is possible to consider the following situation. The Lapicque function $g(\cdot)$ of Eq. (1) can be approximated for $I(t)$ sufficiently above the threshold I_{th} by using

$\ln(1 - I_{\text{th}}/I) \approx -I_{\text{th}}/I$, yielding the approximation

$$f(t) = g[I(t)] = \begin{cases} 0 & \text{for } I(t) \leq I_{\text{th}}, \\ \frac{1/T_r}{1 + (\tau_m/T_r)(I_{\text{th}}/I(t))} & \text{for } I(t) > I_{\text{th}}, \end{cases} \quad (17)$$

which is also depicted in Fig. 1. Eq. (17) constitutes an interesting approximation that only departs slightly from Eq. (1) for $I(t)$ immediately above the threshold I_{th} , and it preserves the qualitative features of the existence of a threshold, a saturation and an intermediate curvilinear part in the response. This approximation, when associated to a probability density $p_\eta(u)$ uniform over $[-a, a]$ authorizes an analytical evaluation of integrals (9)–(10), as

$$E[f_i(t)|I] = \begin{cases} 0 & \text{for } I \leq I_{\text{th}} - a, \\ \frac{1}{T_r 2a} I_{\text{th}} [\Phi_1(I+a) - \Phi_1(I_{\text{th}})] & \text{for } I_{\text{th}} - a < I < I_{\text{th}} + a, \\ \frac{1}{T_r 2a} I_{\text{th}} [\Phi_1(I+a) - \Phi_1(I-a)] & \text{for } I \geq I_{\text{th}} + a, \end{cases} \quad (18)$$

and

$$E[f_i^2(t)|I] = \begin{cases} 0 & \text{for } I \leq I_{\text{th}} - a, \\ \left(\frac{1}{T_r}\right)^2 \frac{I_{\text{th}}^2}{2a} [\Phi_2(I+a) - \Phi_2(I_{\text{th}})] & \text{for } I_{\text{th}} - a < I < I_{\text{th}} + a, \\ \left(\frac{1}{T_r}\right)^2 \frac{I_{\text{th}}^2}{2a} [\Phi_2(I+a) - \Phi_2(I-a)] & \text{for } I \geq I_{\text{th}} + a, \end{cases} \quad (19)$$

with the two functions

$$\Phi_1(u) = \frac{u}{I_{\text{th}}} - \frac{\tau_m}{T_r} \ln\left(\frac{u}{I_{\text{th}}} + \frac{\tau_m}{T_r}\right) \quad (20)$$

and

$$\Phi_2(u) = \frac{u}{I_{\text{th}}} - 2\frac{\tau_m}{T_r} \ln\left(\frac{u}{I_{\text{th}}} + \frac{\tau_m}{T_r}\right) - \frac{(\tau_m/T_r)^2}{(u/I_{\text{th}}) + (\tau_m/T_r)}. \quad (21)$$

To illustrate noise-aided transmission by the neuronal array, we choose as in [22], the periodic input

$$s(t) = I_0 + I_1 \sin(2\pi t/T_s) \quad \forall t, \quad (22)$$

to be assessed by the SNR \mathcal{R}_{out} of Eq. (5), and the transient aperiodic input

$$s(t) = \begin{cases} I_0 + I_1 \sin(2\pi t/T_s) & \text{for } t \in [0, T_s], \\ 0 & \text{otherwise,} \end{cases} \quad (23)$$

to be assessed by the cross-covariance C_{sy} of Eq. (16). The parameters I_0 (offset) and I_1 (amplitude) of the coherent input $s(t)$ of Eqs. (22) or (23) will be varied, in order to solicit the array in various operation ranges of the

nonlinearity of Fig. 1, successively the threshold region, the intermediate curvilinear part, and the saturation region.

4.1. Transmission at threshold

We consider here the situation of a small information-carrying signal $s(t)$ which permanently evolves, for every t , below the threshold I_{th} . The input noise $\xi(t)$ which adds to $s(t)$ is also small, in such a way that the input signal–noise mixture $I(t) = s(t) + \xi(t)$ practically never reaches the neuron firing threshold I_{th} . Thus $I(t)$ alone is unable to trigger an efficient response at the output, and consequently the measures of transmission efficacy \mathcal{R}_{out} and C_{sy} remain essentially at zero. From this situation, Fig. 2 shows the action of the added array noises $\eta_i(t)$ to enhance the transmission.

In an isolated neuron, at $N = 1$ in Fig. 2, the added noise $\eta_1(t)$ cooperates with the subthreshold input $I(t)$ to reach the firing threshold I_{th} and to induce variations at the neuron output that will be correlated with the information-carrying input $s(t)$. This cooperative effect is observed for both a periodic (Fig. 2A) and an aperiodic (Fig. 2B) input $s(t)$. For the efficacy of the transmission, measured by the output SNR \mathcal{R}_{out} in Fig. 2A and by the input–output cross-covariance C_{sy} in Fig. 2B, the effect gives rise to a nonmonotonic evolution culminating at a maximum for a nonzero level of the added noise $\eta_1(t)$. This is a standard effect of stochastic resonance in a threshold nonlinearity, also observed in the same model of a single isolated neuron in [22].

We next show here that the noise-aided transmission of a subthreshold $s(t)$, already present in a single neuron, is reinforced when the neurons are associated into a parallel array. This is visible in Fig. 2 at $N > 1$, where both measures of efficacy \mathcal{R}_{out} and C_{sy} are always enhanced by the action of the added array noises $\eta_i(t)$. With no noises $\eta_i(t)$ added in the array, i.e. at $\sigma_\eta = 0$ in Fig. 2, all the neurons respond in unison as a single one, and therefore the performance is the same at $\sigma_\eta = 0$ for any N . Addition of the array noises $\eta_i(t)$ then always entails an enhancement of the efficacy of the neural transmission compared to the efficacy of a single isolated neuron, and the enhancement gets more and more important as the array size N increases as seen in Fig. 2. At the limit of large arrays, $N = \infty$ in Fig. 2, both measures \mathcal{R}_{out} and C_{sy} reach a plateau at large values of the rms amplitude σ_η of the array noises $\eta_i(t)$. The behavior of the array with the added noises $\eta_i(t)$, and especially the presence of the plateau, is consistent with a similar behavior observed in [11] with arrays of Fitz-Hugh–Nagumo neuron models for an input–output correlation measure and an aperiodic noise-free input signal. Here, for the input signal–noise mixture $I(t) = s(t) + \xi(t)$, the input SNR defined according to Eqs. (5) and (22) is $\mathcal{R}_{\text{in}} = I_1^2 / (4\sigma_\xi^2 \Delta t \Delta B)$, while the normalized cross-covariance between $s(t)$ and $I(t)$ defined according to Eqs. (16) and (23) is $C_{sI} = 1 / [1 + 2\sigma_\xi^2 / I_1^2]^{1/2}$. Precisely, in Fig. 2 at $N = \infty$ and large σ_η , the plateau

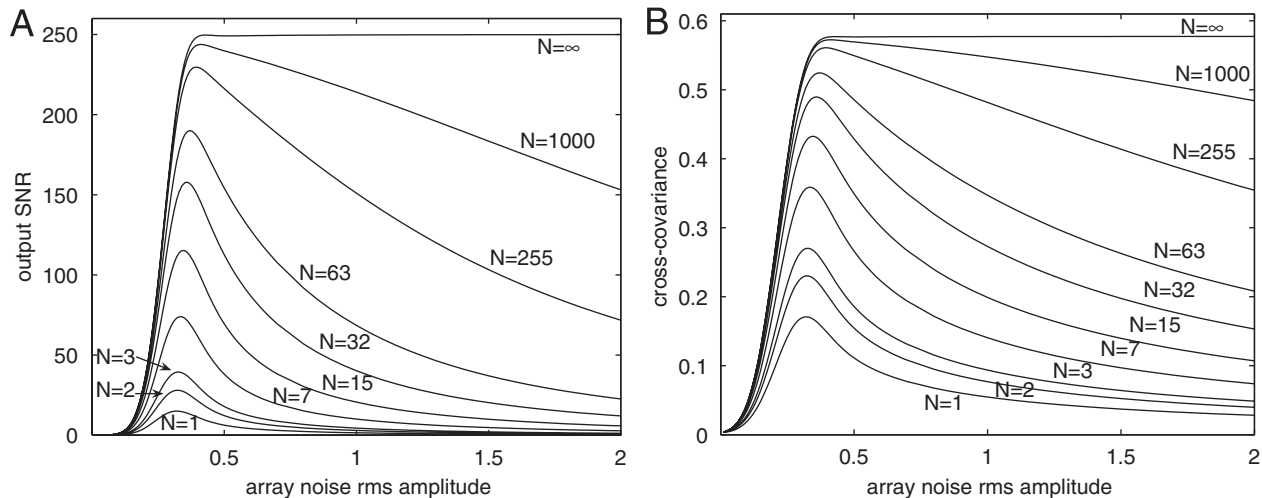


Fig. 2. Transmission at threshold by the neuronal array of size N , as a function of the rms amplitude σ_η/I_{th} of the array noises $\eta_i(t)$, with a zero-mean Gaussian input noise $\xi(t)$ of rms amplitude $\sigma_\xi = 0.1I_{th}$, and signal parameters $I_0 = 0.5I_{th}$ and $I_1 = 0.1I_{th}$: (A) output SNR \mathcal{R}_{out} of Eq. (5) for the T_s -periodic input $s(t)$ of Eq. (22); (B) input–output cross-covariance C_{sy} of Eq. (16) for the aperiodic input $s(t)$ of Eq. (23).

reached by the SNR \mathcal{R}_{out} is \mathcal{R}_{in} , and the plateau reached by the cross-covariance C_{sy} is C_{st} . This means that the arrays with added noises $\eta_i(t)$, which always enhance the transmission efficacy of an isolated neuron, have also the ability, at large size N , to restore the transmission efficacy as it would be if a direct observation of the input $I(t) = s(t) + \xi(t)$ were accessible instead of its observation by neurons with inherent thresholds.

A complementary point of view on the improvement by noise in the array is provided by Fig. 3 in the time domain. Fig. 3 considers a large array whose input is the same subthreshold sinusoid in noise as in Fig. 2. For the array output $y(t)$, Fig. 3 which depicts the mean $E[y(t)]$ and standard deviation $\text{std}[y(t)]$, shows that the beneficial effect of adding noise in the array is two-fold. When moving from Fig. 3A to B by addition of the array noises $\eta_i(t)$: (i) on average the output $y(t)$ resembles more the input sinusoid, (ii) the fluctuation $\text{std}[y(t)]$ relative to $E[y(t)]$ is reduced. In short, the output signal is less noisy and resembles more the input sinusoid. These aspects are properly quantified by the measures of Fig. 2, and can be visually appreciated in Fig. 3.

4.2. Transmission at medium range

Another interesting capability of the noisy arrays arises in the transmission of an input signal $s(t)$ which is large enough (but not too large) to permanently evolve, for every t , above the neuron firing threshold I_{th} , while at the same time avoiding to operate the neuron characteristic of Fig. 1 in its saturation region. In this situation of a medium signal $s(t)$, the behavior of the neuronal array is presented in Fig. 4.

In an isolated neuron, at $N = 1$ in Fig. 4, enhancement by noise of the transmission efficacy does not occur, as expressed by the monotonic decay of the SNR \mathcal{R}_{out} and of the cross-covariance C_{sy} when the level of noise σ_η grows.

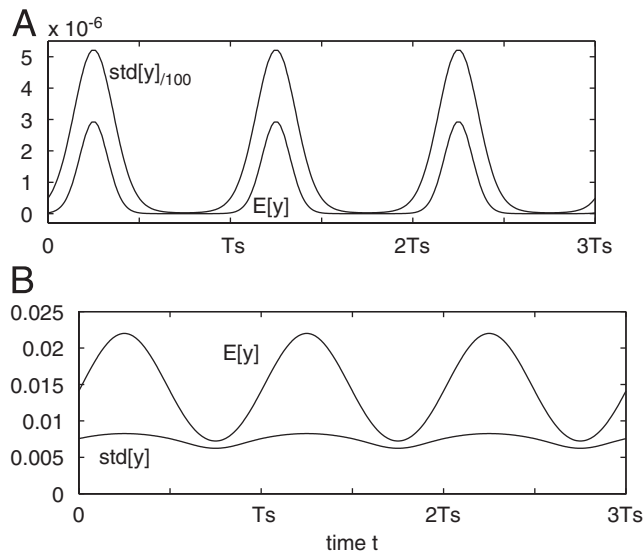


Fig. 3. For the array output $y(t)$: its mean $E[y(t)]$ and standard deviation $\text{std}[y(t)]$, in units of $f_{max} = 1/T_r$. The input signal is the noisy sinusoid of Eq. (22) with the same parameter values as in Fig. 2, applied to a large array of size $N \rightarrow \infty$: (A) is at $\sigma_\eta = 0$, i.e. with no added noises $\eta_i(t)$ in the array; (B) is at $\sigma_\eta = 0.4I_{th}$, i.e. with a nonzero level close to the optimum for the added array noises $\eta_i(t)$. (In (A), $\text{std}[y(t)]$ is shown divided by 100, so that it fits nicely in the graph along with $E[y(t)]$.)

This is because a medium $s(t)$, permanently above the threshold and below the saturation, has the ability by itself to trigger an efficient response from an isolated neuron. No assistance by noise, for instance to overcome a threshold or be shifted away of a saturation, is needed by a medium $s(t)$. In this condition, addition of noise is felt as a pure nuisance and always degrades the transmission efficacy of an isolated neuron. This same behavior of no stochastic resonance was also observed in the same model of a single isolated neuron in [22].

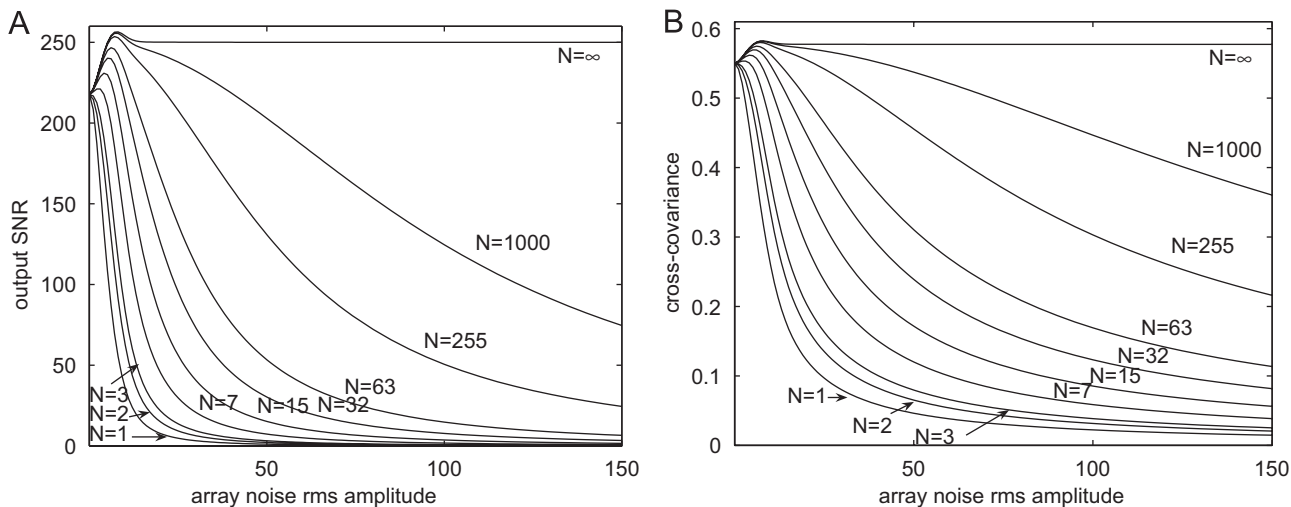


Fig. 4. Transmission at medium range by the neuronal array of size N , as a function of the rms amplitude σ_{η}/I_{th} of the array noises $\eta_i(t)$, with a zero-mean Gaussian input noise $\zeta(t)$ of rms amplitude $\sigma_{\zeta} = 5I_{th}$, and signal parameters $I_0 = 10I_{th}$ and $I_1 = 5I_{th}$: (A) output SNR \mathcal{R}_{out} of Eq. (5) for the T_s -periodic input $s(t)$ of Eq. (22); (B) input–output cross-covariance C_{sy} of Eq. (16) for the aperiodic input $s(t)$ of Eq. (23).

We demonstrate here that the picture is quite different when the neurons are assembled into a parallel array with added noises. In this case, Fig. 4 shows that with array sizes N sufficiently above 1, the array with added noises $\eta_i(t)$ always has the ability to improve the efficacy of transmission of a medium signal $s(t)$, compared to the efficacy achieved by an isolated neuron with no added noise $\eta_1(t)$. This constructive action of the added noises $\eta_i(t)$ in the array is again expressed by a possibility of increasing \mathcal{R}_{out} in Fig. 4A and C_{sy} in Fig. 4B by raising the noise level σ_{η} . The constructive action of the noise is more and more pronounced as the array size N gets larger. In the limit of an infinite array $N = \infty$ in Fig. 4, the input performances $\mathcal{R}_{out} = \mathcal{R}_{in}$ and $C_{sy} = C_{sI}$ are again recovered, on the plateaus at large σ_{η} , as if the array of nonlinear neurons was turned into a purely linear device.

Moreover, sufficiently large arrays even have the possibility, in a small range of the noise level σ_{η} , of improving the measures of efficacy \mathcal{R}_{out} and C_{sy} above their values \mathcal{R}_{in} and C_{sI} at the input. This is a small effect here, as visible in Fig. 4, where \mathcal{R}_{out} and C_{sy} slightly peak above the large- σ_{η} plateaus. Yet, this proves, in principle, that some nonlinear sensors, possibly aided by noise, can outperform a putative purely linear system providing direct access to the input signal. Such a direct linear observation is not available to isolated sensory neurons which have to cope with their inherent threshold and saturation; but it becomes possible, as shown here, when neurons are assembled in arrays with added noises. But beyond, as shown by Fig. 4, the neuronal arrays with added noises can sometimes outperform the performance of a strict linearization of the process. It is a remarkable property that arrays of neuronal nonlinearities with threshold and saturation can amplify the efficacies \mathcal{R}_{out} and C_{sy} above

their input values \mathcal{R}_{in} and C_{sI} , because this property is shared by very few systems.

It is well known that linear systems, even dynamic systems of arbitrarily high order, are incapable¹ of amplifying the output SNR \mathcal{R}_{out} of Eq. (5) above the input SNR \mathcal{R}_{in} . Very few nonlinear systems are capable of amplifying the SNR of a sinusoid in broadband white Gaussian noise as in Fig. 4. SNR amplification is a problem which has been addressed very early for signal processing [13,2]. For the less stringent condition of a *narrowband* noise addressed in [13,2], maximum SNR gains of 2 are reported, and achieved with hard-threshold or Heaviside nonlinearities. In the more stringent condition of a *broadband white* noise, the SNR gains effectively reported are also modest: Hänggi et al. [16] report a maximum SNR gain of 1.2 achieved by an isolated bistable dynamic system, Casado et al. [3] report a maximum SNR gain of 1.25 achieved by a fully coupled network of bistable dynamic systems, Chapeau-Blondeau and Rousseau [7] report a maximum SNR gain of 1.4 achieved by an optimally tuned static nonlinearity with saturation. It seems that, in nonlinearities capable of amplifying the SNR, a moderate amount of saturation, as in the case of [7] and also of neuronal nonlinearities as considered here, might be an interesting feature, due to its clipping capability on the input signal–noise mixture that could reduce the noise more than the coherent signal. Beyond the uncoupled parallel arrays of Fig. 4, more efficient arrangements of neuronal nonlinearities could be tested to specifically amplify the SNR for instance. Yet, this is not

¹Any linear system leaves the SNR unchanged, because in the output spectrum it multiplies both the coherent line at $1/T_s$ and the noise background around $1/T_s$ by the same factor, the squared modulus of its transmittance.

precisely the scope of the present study, which rather aims at demonstrating a constructive impact of added noises in simple uncoupled parallel neuronal arrays in different regimes of operation (at threshold, at medium range and at saturation, with periodic or aperiodic signal).

Fig. 5 offers a complementary point of view, in the time domain, on the improvement by noise in the array. For the same medium-range input sinusoid in noise as in Fig. 4, Fig. 5 shows again a two-fold beneficial action of the noise. When moving from Fig. 5A to B by addition of the array noises $\eta_i(t)$, on average the output $y(t)$ resembles more (slightly here) the input sinusoid, and the fluctuation $\text{std}[y(t)]$ is reduced.

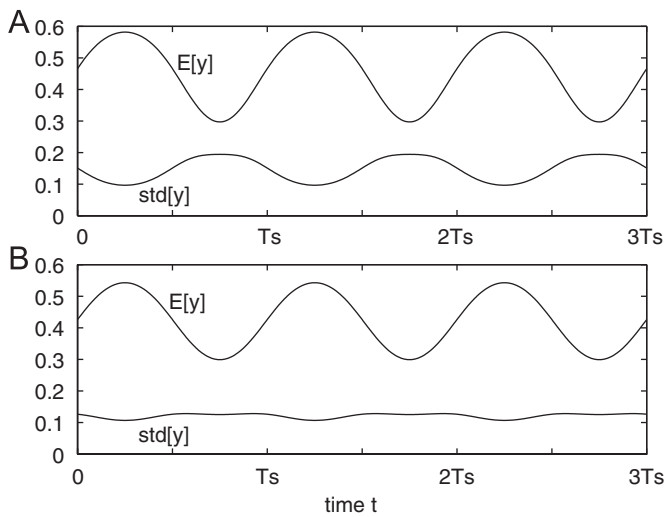


Fig. 5. For the array output $y(t)$: its mean $E[y(t)]$ and standard deviation $\text{std}[y(t)]$, in units of $f_{\max} = 1/T_r$. The input signal is the noisy sinusoid of Eq. (22) with the same parameter values as in Fig. 4, applied to a large array of size $N \rightarrow \infty$: (A) is at $\sigma_\eta = 0$, i.e. with no added noises $\eta_i(t)$ in the array; (B) is at $\sigma_\eta = 7I_{\text{th}}$, i.e. with a nonzero level close to the optimum for the added array noises $\eta_i(t)$.

4.3. Transmission at saturation

The conditions of Fig. 6 concern the operation of the array in the regime of strong saturation of the neuronal firing function. In an isolated neuron, at $N = 1$ in Fig. 6, the added noise $\eta_1(t)$ already is capable of inducing an improvement in the transmission efficacy of both a periodic and an aperiodic signal. A similar improvement at $N = 1$ was also present in Fig. 2 in the threshold region, but absent in Fig. 4 in the intermediate curvilinear region of the neuronal characteristic. This illustrates the ability of the added noise to bring some shift in the neuronal response, when needed, in order to displace it away of an unfavorable strongly nonlinear region (a threshold or a saturation) into a more favorable region (the curvilinear part) of the characteristic. Again, this behavior in a single isolated neuron was also observed in [22].

Next we show here that the noise-aided transmission in the saturation regime, already present in an isolated neuron at $N = 1$, is strongly enhanced when the neurons are assembled in an array at $N > 1$ in Fig. 6. The enhancement by noise applies to both periodic (Fig. 6A) and aperiodic (Fig. 6B) signals. Again the enhancement is more and more important as the array size N grows. At array sizes $N \rightarrow \infty$ and a sufficient amount of the added noises $\eta_i(t)$, the output of the nonlinear array recovers the performance as at the input.

Fig. 7 in the time domain shows again the two-fold beneficial action of the noises added to the array, for the large input sinusoid in noise of Fig. 6: on average the output $y(t)$ resembles more, with reduced saturation, the input sinusoid; and the fluctuation is decreased.

5. Discussion

The results presented here can be viewed as extensions concerning the various forms of stochastic resonance or

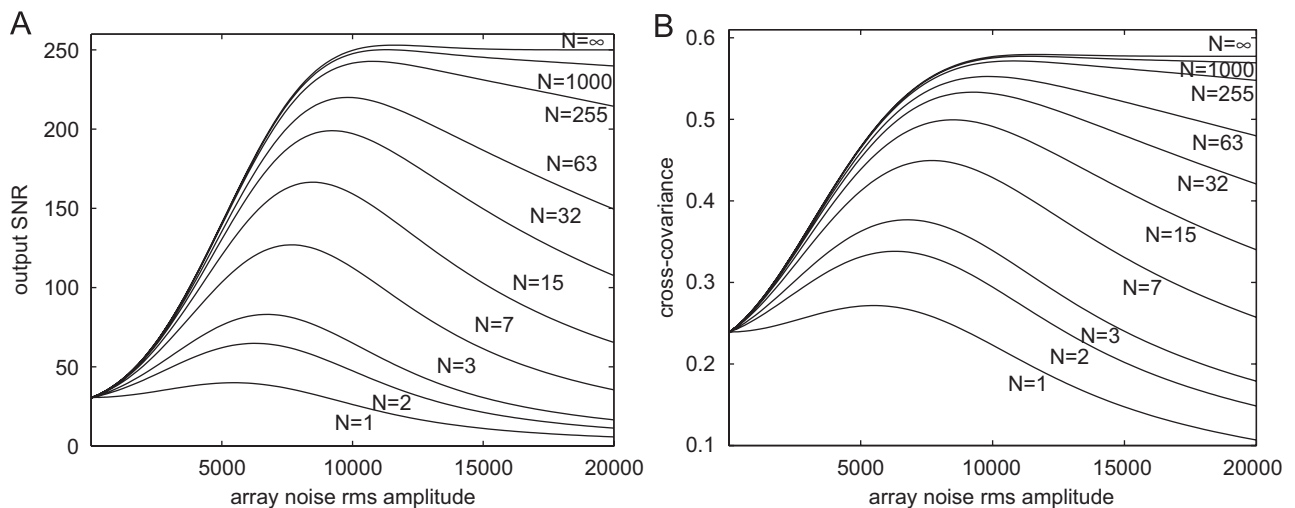


Fig. 6. Transmission at saturation by the neuronal array of size N , as a function of the rms amplitude $\sigma_\eta/I_{\text{th}}$ of the array noises $\eta_i(t)$, with a zero-mean Gaussian input noise $\zeta(t)$ of rms amplitude $\sigma_\zeta = 5 \times 10^3 I_{\text{th}}$, and signal parameters $I_0 = 10^4 I_{\text{th}}$ and $I_1 = 5 \times 10^3 I_{\text{th}}$: (A) output SNR \mathcal{R}_{out} of Eq. (5) for the T_s -periodic input $s(t)$ of Eq. (22); (B) input–output cross-covariance C_{sy} of Eq. (16) for the aperiodic input $s(t)$ of Eq. (23).

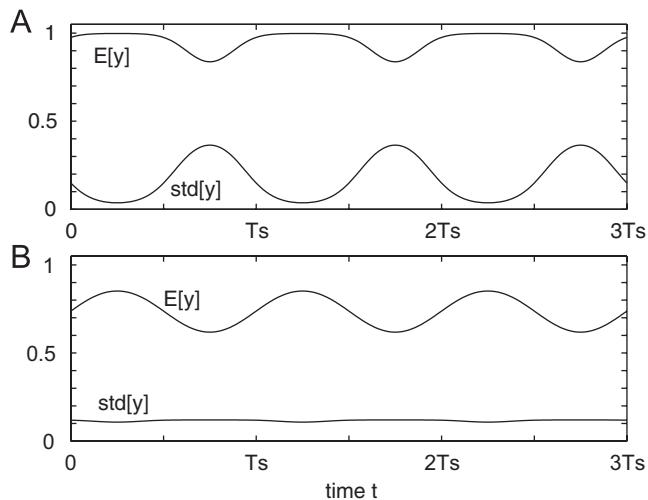


Fig. 7. For the array output $y(t)$: its mean $E[y(t)]$ and standard deviation $\text{std}[y(t)]$, in units of $f_{\max} = 1/T_r$. The input signal is the noisy sinusoid of Eq. (22) with the same parameter values as in Fig. 6, applied to a large array of size $N \rightarrow \infty$: (A) is at $\sigma_\eta = 0$, i.e. with no added noises $\eta_i(t)$ in the array; (B) is at $\sigma_\eta = 12 \times 10^3 I_{\text{th}}$, i.e. with a nonzero level close to the optimum for the added array noises $\eta_i(t)$.

improvement by noise in signal transduction by neurons. In this context, stochastic resonance has been widely studied for noise-enhanced signal transmission by neurons operating in the region of the threshold of activity. Here, by contrast, we have also investigated signal transmission away of the threshold, in the curvilinear part of the neuronal response, and beyond in the saturation region. For isolated neurons, we observed that improvement by noise of the transmission can occur both in the threshold and in the saturation of the response, but does not take place in the intermediate curvilinear part, as it was also found in [22]. Beyond, we have focused here on the situation of a common basic architecture for neuronal assemblies, i.e. parallel arrays of neurons, and the impact of independent noises injected in such arrays. We have observed that the stochastic resonance effect is always reinforced in the arrays with a sufficient amount of the added noises, compared to the situation of isolated neurons. Moreover, in arrays stochastic resonance becomes possible in the intermediate curvilinear part of the neuronal response, where it was not feasible in isolated neurons. Altogether in neuronal arrays, improvement by noise of signal transduction is possible for any regime of operation of the transmission, in the threshold, or in the intermediate, or in the saturation part of the neuronal response. This is afforded by the distinct mechanism of stochastic resonance in arrays, where the added noises force individual neurons to respond differently to a common input signal. This is the source of richer representation capabilities by the neuronal outputs that when collected over the array result in enhanced transduction of the input signal. This enhanced transduction obtained by gathering distinct nonlinear outputs, does not specifically require threshold-like or

saturation-like nonlinearities, and curvilinear nonlinearities also lend themselves to this effect as visible here. By contrast, in isolated neurons, the mechanism of improvement by noise can be interpreted as a form of biasing by noise, where the noise assists a signal hidden below a threshold or squeezed in a saturation to access a more favorable region of the characteristic. This mechanism, inherently, relies on threshold or saturation nonlinearities, and does not apply to smooth curvilinear ones. Both mechanisms of improvement by noise, in isolated neurons and in arrays, operate in conjunction in Figs. 2 and 6 at threshold and at saturation, while only one mechanism (the array one) operates in the intermediate condition of Fig. 4. Also here, all the configurations of improvement by noise have been verified, with standard measures of efficacy, to apply equally to periodic and to aperiodic signals. This illustrates the wide versatility of the forms of improvement by noise in neuronal structures.

An alternative interpretation of the constructive action of noise, which has been employed especially in threshold systems, resorts sometimes to a mechanism of linearization by noise of the input–output characteristic. First, a linearized characteristic may not be uniformly meaningful, nor even definable, for distinct time-varying signals as considered here. Second, clearly here there is more than a linearization, since the action of noise, as visible in Fig. 4, can increase the efficacy for signal transduction above that of a purely linear device. The present neuronal nonlinearities aided by noise, as also verified by other nonlinear systems [6,8], implement an “intelligent” preprocessing capable of reaching efficacies that no linear systems can achieve.

The various forms of neuronal transduction aided by noise in arrays, were shown here with a very simple neuron model based on Eq. (1). Yet, as it has been pointed out in many other neuronal studies [20], this model of Eq. (1) is able to capture essential features of the neuronal transmission, i.e. the presence of both threshold and saturation and in-between an intermediate curvilinear response. At the same time, it is known that stochastic resonance is usually a general and robust nonlinear phenomenon, which persists over many variations in the nonlinearities. More elaborate neuron models, with possibly couplings in the arrays, could next be tested to investigate how the basic properties exposed here are preserved or evolved, and how they could play a part in the highly efficient processing of information accomplished by neural systems.

References

- [1] B. Andò, S. Graziani, *Stochastic Resonance: Theory and Applications*, Kluwer Academic Publishers, Boston, 2000.
- [2] N.M. Blachman, The output signal-to-noise ratio of a power-law device, *J. Appl. Phys.* 24 (1953) 783–785.
- [3] J.M. Casado, J. Gómez Ordóñez, M. Morillo, Stochastic resonance of collective variables in finite sets of interacting identical subsystems, *Phys. Rev. E* 73 (2006) 011109, 1–8.

- [4] F. Chapeau-Blondeau, G. Chauvet, Dynamic properties of a biologically motivated neural network model, *Int. J. Neural Syst.* 3 (1992) 371–378.
- [5] F. Chapeau-Blondeau, X. Godivier, Theory of stochastic resonance in signal transmission by static nonlinear systems, *Phys. Rev. E* 55 (1997) 1478–1495.
- [6] F. Chapeau-Blondeau, D. Rousseau, Enhancement by noise in parallel arrays of sensors with power-law characteristics, *Phys. Rev. E* 70 (2004) 060101(R), 1–4.
- [7] F. Chapeau-Blondeau, D. Rousseau, Nonlinear SNR amplification of a harmonic signal in noise, *Electron. Lett.* 41 (2005) 618–619.
- [8] F. Chapeau-Blondeau, D. Rousseau, Noise-aided SNR amplification by parallel arrays of sensors with saturation, *Phys. Lett. A* 351 (2006) 231–237.
- [9] D.R. Chialvo, A. Longtin, J. Mullergerking, Stochastic resonance in models of neuronal ensembles, *Phys. Rev. E* 55 (1997) 1798–1808.
- [10] J.J. Collins, C.C. Chow, T.T. Imhoff, Aperiodic stochastic resonance in excitable systems, *Phys. Rev. E* 52 (1995) R3321–R3324.
- [11] J.J. Collins, C.C. Chow, T.T. Imhoff, Stochastic resonance without tuning, *Nature* 376 (1995) 236–238.
- [12] J.J. Collins, T.T. Imhoff, P. Grigg, Noise-enhanced information transmission in rat SA1 cutaneous mechanoreceptors via aperiodic stochastic resonance, *J. Neurophysiol.* 76 (1996) 642–645.
- [13] W.B. Davenport, Signal-to-noise ratios in band-pass limiters, *J. Appl. Phys.* 24 (1953) 720–727.
- [14] J.K. Douglass, L. Wilkens, E. Pantazelou, F. Moss, Noise enhancement of information transfer in crayfish mechanoreceptors by stochastic resonance, *Nature* 365 (1993) 337–340.
- [15] L. Gammaitoni, P. Hänggi, P. Jung, F. Marchesoni, Stochastic resonance, *Rev. Mod. Phys.* 70 (1998) 223–287.
- [16] P. Hänggi, M.E. Inchiosa, D. Fogliatti, A.R. Bulsara, Nonlinear stochastic resonance: the saga of anomalous output–input gain, *Phys. Rev. E* 62 (2000) 6155–6163.
- [17] T. Hoch, G. Wenning, K. Obermayer, Adaptation using local information for maximizing the global cost, *Neurocomputing* 52–54 (2003) 541–546.
- [18] T. Hoch, G. Wenning, K. Obermayer, Optimal noise-aided signal transmission through populations of neurons, *Phys. Rev. E* 68 (2003) 011911, 1–11.
- [19] T. Hoch, G. Wenning, K. Obermayer, The effect of correlations in the background activity on the information transmission properties of neural populations, *Neurocomputing* 65–66 (2005) 365–370.
- [20] C. Koch, *Biophysics of Computation: Information Processing in Single Neurons*, Oxford University Press, New York, 1999.
- [21] F. Moss, L.M. Ward, W.G. Sannita, Stochastic resonance and sensory information processing: a tutorial and a review of application, *Clin. Neurophysiol.* 115 (2004) 267–281.
- [22] D. Rousseau, F. Chapeau-Blondeau, Neuronal signal transduction aided by noise at threshold and at saturation, *Neural Process. Lett.* 20 (2004) 71–83.
- [23] D. Rousseau, J. Rojas Varela, F. Chapeau-Blondeau, Stochastic resonance for nonlinear sensors with saturation, *Phys. Rev. E* 67 (2003) 021102, 1–6.
- [24] N.G. Stocks, Optimizing information transmission in model neuronal ensembles: the role of internal noise, in: J.A. Freund, T. Poschel (Eds.), *Stochastic Processes in Physics, Chemistry and Biology*, Lecture Notes in Physics, vol. 557, Springer, Berlin, 2000, pp. 150–159.
- [25] N.G. Stocks, Suprathreshold stochastic resonance in multilevel threshold systems, *Phys. Rev. Lett.* 84 (2000) 2310–2313.
- [26] N.G. Stocks, Information transmission in parallel threshold arrays: suprathreshold stochastic resonance, *Phys. Rev. E* 63 (2001) 041114, 1–9.
- [27] N.G. Stocks, R. Mannella, Generic noise-enhanced coding in neuronal arrays, *Phys. Rev. E* 64 (2001) 030902, 1–4.



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