

Signal-to-noise ratio gain in neuronal systems

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We explore the possibility of a signal-to-noise ratio (SNR) gain both in a single neuron and a neuronal network. In the presence of a weak sinusoidal or pulse signal and Gaussian noise, the output SNR can exceed the input SNR over a wide range of noise intensities. The high output SNR and SNR gain can be acquired coincidentally at optimal noise levels. The results further verify that noise can play a constructive role in sensory processing in neuronal systems.

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The response of nonlinear systems to weak periodic stimuli and noise is known to exhibit cooperative effects, including stochastic resonance (SR). SR is a nonlinear phenomenon wherein the output signal-to-noise ratio (SNR) can be optimized by a particular level of noise [1]. SR has been investigated in a wide variety of nonlinear systems, especially in neuronal systems. It was demonstrated that noise can play an active role in signal processing. However, another significant issue has received less attention, namely, whether it is possible to make the signal detectability at the output exceed that at the input in a suitably optimized nonlinear system. This is important for practical applications of SR.

It was proven theoretically that the output SNR can never exceed the input SNR if nonlinear systems perform in the linear response limit (e.g., under the conditions where the signal amplitude is much smaller than the noise strength in bistable systems) [2]. On the other hand, a SNR gain has been observed in electronic analog circuits [3], an optically bistable element [4], a level-crossing detector [5], a rf superconducting quantum interference device loop [6], and a static nonlinear transfer [7], etc., all working in the nonlinear response regime. But to our knowledge, it has not been clarified whether it is possible to obtain enhanced signal detectability in neuronal systems in the presence of Gaussian noise. If a noisy signal can become less noisy after transduction by neurons, their signal-processing capability will be largely improved.

Motivated by the aforementioned considerations, we explore the possibility of SNR gain both in a single neuron and a neuronal network. It is demonstrated that the SNR improvement effect occurs in both cases, especially more remarkable in the network case, in the presence of a weak periodic signal and Gaussian noise.

We begin with the Hodgkin-Huxley (HH) neuronal model, whose dynamics is described as follows:

$$C_m \frac{dV}{dt} = -g_{Na} m^3 h (V - V_{Na}) - g_K n^4 (V - V_K) - g_l (V - V_l) + I_0 + s(t) + \eta(t), \quad (1)$$

$$\frac{dm}{dt} = \frac{m_\infty(V) - m}{\tau_m(V)}, \quad (2)$$

$$\frac{dh}{dt} = \frac{h_\infty(V) - h}{\tau_h(V)}, \quad (3)$$

$$\frac{dn}{dt} = \frac{n_\infty(V) - n}{\tau_n(V)}. \quad (4)$$

Here V , m , h , and n are the membrane potential, the activation and inactivation of the sodium current, and the activation of the potassium current, respectively. g_{Na} , g_K , and g_l are the maximal values of conductance of the sodium, potassium, and leakage currents; V_{Na} , V_K , and V_l are the corresponding reversal potentials. C_m is the capacity of the membrane. The parameter values [8] are $V_{Na} = 50$ mV, $V_K = -77$ mV, $V_l = -54.4$ mV, $g_{Na} = 120$ mS/cm², $g_K = 36$ mS/cm², $g_l = 0.3$ mS/cm², and $C_m = 1$ μ F/cm². The functions $m_\infty(V)$, $h_\infty(V)$, $n_\infty(V)$, $\tau_m(V)$, $\tau_h(V)$, and $\tau_n(V)$ are given by $x_\infty(V) = a_x / (a_x + b_x)$ and $\tau_x(V) = 1 / (a_x + b_x)$ with $x = m, h, n$. That is, $a_m = 0.1(V + 40) / (1 - e^{-(V+40)/10})$, $b_m = 4e^{-(V+65)/18}$, $a_h = 0.07e^{-(V+65)/20}$, $b_h = 1 / (1 + e^{-(V+35)/10})$, $a_n = 0.01(V + 55) / (1 - e^{-(V+55)/10})$, and $b_n = 0.125e^{-(V+65)/80}$.

We assume that the neuron is subject to a subthreshold signal, $s(t) = A \cos(2\pi f_s t)$ plus a constant bias I_0 , as well as a Gaussian noise $\eta(t)$ satisfying

$$\langle \eta(t) \rangle = 0, \quad \langle \eta(t_1) \eta(t_2) \rangle = D \lambda e^{-\lambda |t_1 - t_2|}. \quad (5)$$

Here D represents noise intensity and λ is the inverse of the correlation time. $\eta(t)$ is taken as the white noise (i.e., λ^{-1} equals to the integration step, 500/32 768 ms) throughout the paper, otherwise specified elsewhere. The numerical method for solving Eqs. (1)–(4) is based on a second-order algorithm proposed in Ref. [9]. An average over 100 different realizations of noise seeds is always taken to obtain final results.

Note that a spike occurs when $V(t)$ exceeds -20 mV. In our simulations the time course of $V(t)$ is converted into a time series of standard pulses $U(t)$ with $U_H = 1$ of width 2 ms and $U_L = 0$ corresponding, respectively, to the firing and nonfiring states. We use the fast Fourier transform to compute the power spectral density of signals. The SNR is defined as $10 \log_{10}(\Gamma/B)$ with Γ and B representing, respectively, the height of the signal peak and the mean amplitude of background noise at the input signal frequency f_s in the

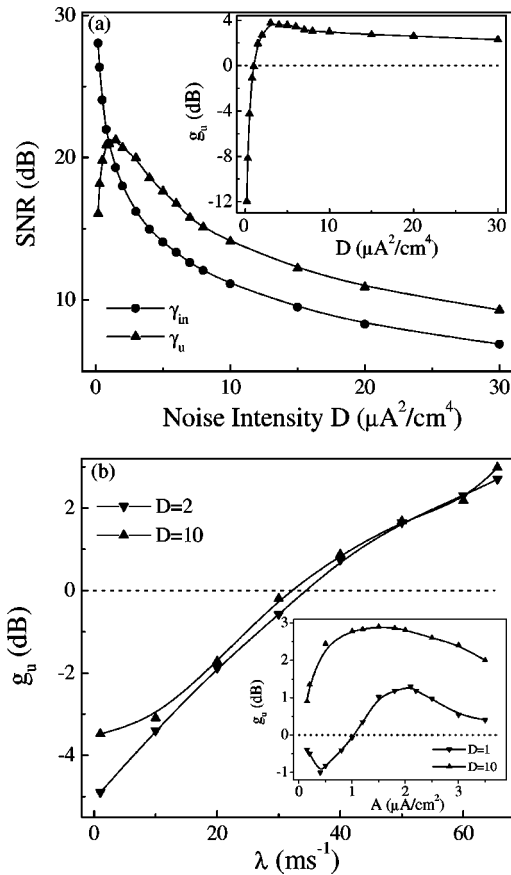


FIG. 1. (a) The SNR vs the noise intensity D for the case of $f_s = 70$ Hz and $A = 1$. The bias I_0 is taken as 1 throughout the paper. The inset is g_u vs D . (b) g_u vs λ for $D = 2$ and 10. The inset is g_u vs the signal amplitude A for $D = 1$ and 10.

power spectrum [10]. The SNR for the input $s(t) + \eta(t)$ and the output $U(t)$ is simply denoted as γ_{in} and γ_u . g_u represents $\gamma_u - \gamma_{in}$.

Figure 1(a) shows γ_{in} and γ_u versus the noise intensity D in the case of $f_s = 70$ Hz. Clearly, γ_{in} decreases monotonically with increasing D . Differently, γ_u first rises up to a maximum around $D_m = 1.5$ and then drops as D increases, exhibiting the typical characteristic of SR. In addition, γ_u is first smaller and then larger than γ_{in} , as seen in the inset of Fig. 1(a). g_u is negative when $D < 1$ and becomes positive if $D > 1$. g_u also first rises but then drops much more slowly with increasing D , with a maximum of 3.7 dB around $D_c = 3$. This indicates that the output SNR can exceed the input SNR over a wide range of noise intensities. Note that γ_u is larger at D_m than at D_c by 1.2 dB while g_u is larger at D_c than at D_m by 1.8 dB. Therefore, the neuron can acquire a large output SNR as well as a high SNR gain at optimal noise levels ($D_m \leq D \leq D_c$). This can largely contribute to weak signal detection and transduction in neuronal systems.

In the case of low noise level, the firings of the neuron are often separated by several driving cycles owing to the small effective stimulus strength. This leads to a small value of γ_u . As D rises, the firing rate increases and the correlation between the firing and the periodic signal is enhanced. The neuron discharges spikes around the maxima of the signal

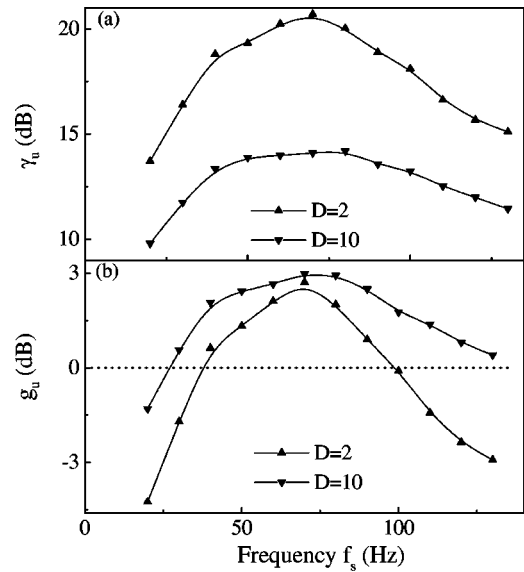


FIG. 2. (a) γ_u and (b) g_u vs the signal frequency for $D = 2$ and 10. For each frequency the signal amplitude is $A = 1$.

although there still exists the skipping in firing. Thus, γ_u quickly rises and reaches its maximum. As D further increases, while the neuron fires more frequently, the coherence of the firing with the signal decays gradually. γ_u thus drops remarkably. On the other hand, the increase of D always diminishes the order in the input since it is a linear summation of the signal $s(t)$ and the noise $\eta(t)$. Thus, γ_{in} drops monotonically with increasing D . But γ_{in} has a much larger value than γ_u for low noise level. In the case of high noise level, the periodic signal may be nearly submerged by the noise, whereas the output still contains prominent periodic components since the firing is modulated by the signal. As a result, γ_u is larger than γ_{in} over a wide range of noise intensities.

It is worth noting that the SNR gain is closely related to the correlation properties of input noise. Figure 1(b) depicts g_u versus λ for $D = 2$ and 10. Obviously, g_u rises with increasing λ but is negative when $\lambda \leq 30$. In fact, γ_{in} decreases remarkably while γ_u varies slightly as λ rises. γ_{in} drops monotonically with increasing λ because the correlation in the noise diminishes. For small λ the firing exhibits an evident coherence with the signal, while for large λ the firing rate rises slightly but the firing coherence with the signal becomes weak. This makes γ_u change slightly. The result implies that a high SNR gain can be obtained if the input noise has a high cutoff frequency. In addition, when the signal amplitude A increases (at fixed noise intensity), both γ_{in} and γ_u rise, while the SNR gain first rises and then drops. [For low noise level ($D < 2$), g_u first drops for weak signal driving before it increases.] This is clearly seen in the inset of Fig. 1(b). It is noted that g_u can also be positive for the suprathreshold signals (i.e., $A > A_{th} = 1.38$), although no SR effect occurs therein.

We also investigate the responses of the neuron to various sinusoidal signals with the identical amplitude. Figure 2(a) shows γ_u versus the signal frequency f_s for $D = 2$ and 10. Clearly, γ_u has relatively large values for signals with fre-

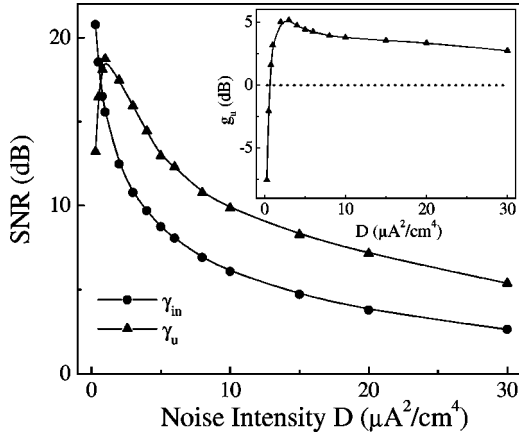


FIG. 3. The SNR vs the noise intensity D in the case of a pulse signal with a frequency of 70 Hz. The inset is g_u vs D .

quencies in the range of 40~90 Hz. That is, the neuron is more sensitive to these signals. Such frequency sensitivity is more remarkable for low noise level and results from the resonance between the periodic signal and the subthreshold intrinsic oscillation. The physical argument for this has been presented in Ref. [11]. Figure 2(b) plots g_u versus f_s . Obviously, for $D=2$, g_u takes a positive value for $40 \leq f_s < 100$ Hz, while for $D=10$, g_u is positive for each frequency considered here except for $f_s=20$ Hz. In the case of small noise level, the neuron fires rarely for high signal frequency, or the firing exhibits a weak coherence with the signal for low signal frequency. These lead to a small value of γ_u as well as a negative value of g_u for low and high signal frequency since γ_{in} is much larger. For high noise level γ_{in} becomes far smaller, while $U(t)$ still contains the periodic components and displays a coherent activity. Thus, g_u has a positive value. In addition, g_u also takes large values for signals with $40 \leq f_s \leq 90$ Hz. This indicates that the neuron exhibits a better detectability for these signals.

It is noted that the output SNR can exceed the input SNR not only in the presence of sinusoidal signals. Figure 3 shows γ_u and γ_{in} for the case wherein the neuron is subject to a periodic pulse signal with a frequency of 70 Hz. The duration of the pulse is 2 ms and the amplitude is 2 (as a subthreshold signal). Such a signal can model visual stimuli or the synaptic inputs from other neurons. Similar results to Fig. 1 can be observed here. As D increases, γ_{in} drops monotonically while γ_u first rises and then decreases with a maximum around $D_m=1$. The inset of Fig. 3 depicts g_u versus D . g_u is positive when $D > 0.8$ and reaches its maximum near $D_c=2$. Here the SNR gain can be as high as 5.1 dB since the firing can acquire a strong correlation with the pulse signal. These indicate that the SNR gain is robust to stimuli.

We have demonstrated that the detectability of a noisy signal after transduction by a neuron can be better than that of the incoming signal from the environment. This is of functional significance for sensory processing in neuronal systems. In fact, an important problem concerned with applicability of the SR effect is the potential possibility to increase the SNR of a noisy signal after information transfer. However, it was recently reported [12] that positive SNR gain can

be observed only for suprathreshold signals in a bistable system driven by a harmonic force and Gaussian noise. Although the response of a neuron to periodic stimuli plus noise can in some cases be approximated by periodically driven noisy underdamped dynamics [13], it cannot be simply viewed as an overdamped motion of a point particle in a bistable system [1]. For an underdamped bistable system, there exist multitimescales controlled separately by intrinsic damped oscillation, noise-induced transition between wells, and the input periodic stimulus. The cooperation of these effects results in the optimal response of the system, leading to the reported intrawell SR and interwell SR [13]. Differently, for an overdamped bistable system, there exists only interwell SR. That is, the optimal enhancement effect of switching results from the match between the noise-induced well-to-well transitions and the periodic signal. Therefore, for the HH model, its gain behavior is largely different from that of overdamped bistable systems [12] due to the coexistence of intrawell SR and interwell SR. Summarizing, when we consider a more realistic model of neurons, it is possible to observe the SNR improvement effect even in the presence of a sinusoidal signal. This also extends the observations in Ref. [5].

Finally, we explore the neuronal network case wherein the neurons are globally coupled with each other and subject to a common cosinusoidal signal and independent noise. Thus, a synaptic current item gets added on the right side of Eq. (1) as follows:

$$I_i^{syn}(t) = - \sum_{j=1, j \neq i}^N \frac{g_{syn}}{N} \alpha(t-t_j) (V_i - V_{syn}^{ij}) \theta(V_j - V_{th}), \quad (6)$$

with $\alpha(t-t_j) \equiv \alpha(t') = t' / \tau e^{-t'/\tau}$. t_j is the firing time of the j th neuron when its membrane potential exceeds the firing threshold $V_{th} = -20$ mV, $\tau = 2$ ms is the characteristic time of excitatory postsynaptic potential. V_{syn}^{ij} is the synaptic reversal potential between the i th and j th neurons, and its value is randomly taken as -80 or 0 mV corresponding, respectively, to the inhibitory and the excitatory coupling. g_{syn} is the coupling strength. $\theta(x)$ is the step function with $\theta(x) = 1$ if $x \geq 0$ and $\theta(x) = 0$ if $x < 0$. The number of neurons in the network is taken as $N = 100$. The average synaptic current is

$$A_{syn}(t) = \frac{1}{N} \sum_{i=1}^N I_i^{syn}(t). \quad (7)$$

The output of the network is defined as

$$I^{out}(t) = \frac{1}{N} \sum_{i=1}^N U_i(t). \quad (8)$$

The SNR for $I^{out}(t)$, $A_{syn}(t)$, and $U_1(t)$ is simply denoted as γ_o , γ_A , and γ_U . For $I^{out}(t)$ and $A_{syn}(t)$ the input SNR is obtained by taking an average over the input SNR of each neuron. g_o , g_A , and g_U are the corresponding output SNR minus the input SNR.

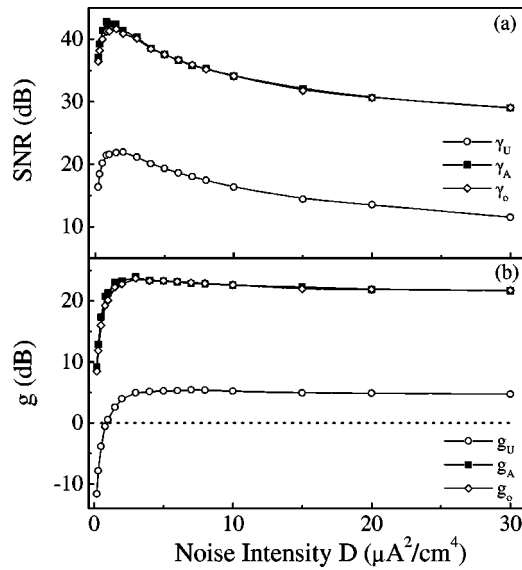


FIG. 4. For the neuronal network case. (a) The SNR vs the noise intensity D in the presence of a sinusoidal signal with $f_s = 70$ Hz and $A = 1$. (b) The SNR difference vs D . g_{syn} is set as 1 and the fraction of all the couplings being excitatory is 0.667.

Figure 4(a) shows the SNR versus the noise intensity D in the case of $f_s = 70$ Hz. All the curves exhibit the typical characteristic of SR: first a rise and then a drop. Compared with the single-neuron case, the value of γ_U rises slightly. As the mean of the responses of individual neurons can average out the uncorrelated parts and enhance the periodic components, γ_o and γ_A are much larger than γ_U . In addition, both the curves are basically overlapped except for low noise since $I^{out}(t)$ and $A_{syn}(t)$ exhibit nearly the same periodicity.

We have previously discussed the SR effects in a globally coupled neuronal network based on the Hindmarsh-Rose (HR) neuronal model [14]. Figure 4(b) displays the difference between the output and input SNRs. Clearly, the value of g_U also increases compared with the single-neuron case, although it still takes a large negative value for very low noise level. g_o and g_A are much larger than g_U and are always positive. They decrease much more slowly after the maximum is reached. Note that both γ_o (γ_A) and g_o (g_A) have large values for $1 < D \leq 3$. In other words, the high output SNR and SNR gain can be acquired at the same noise level. This implies that the signal-processing capability of neurons could be largely improved by an optimal noise level. The results also indicate that the information about input signal can be precisely conveyed by pooling of the individual responses.

In this paper we have investigated the possibility of SNR improvement both in the single neuron and the neural network cases. In the presence of a periodic sinusoidal or pulse signal, the output SNR can exceed the input SNR over a wide range of noise intensities, and such an effect is more remarkable in the network case. The high output SNR and SNR gain can be acquired coincidentally at optimal noise levels, and this largely contributes to signal processing. Such a discussion further verifies that noise can play a constructive role in weak signal detection and transduction of neurons. Finally, it is stressed that the conclusion obtained here also holds true for other neuronal models, such as the HR model.

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