

Effects of correlated and independent noise on signal processing in neuronal systemsFeng Liu,^{1,2} Bambi Hu,^{2,3} and Wei Wang¹¹*National Laboratory of Solid State Microstructure and Department of Physics, Nanjing University, Nanjing 210093, China*²*Department of Physics and Center for Nonlinear Studies, Hong Kong Baptist University, Hong Kong, China*³*Department of Physics, University of Houston, Houston, Texas 77204*

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Stochastic resonance has recently received considerable attention demonstrating that noise can play a constructive role in signal processing. We investigate the effects of input noise on sensory processing via numerical simulation when they are independent of each other or spatially correlated in a globally coupled neuronal network. The network exhibits a coherent behavior in the absence of stimulation. Such ongoing activity has a remarkable influence on neuronal responses to stimuli. In the presence of a subthreshold periodic signal, the activity averaged over neurons can convey precise information about the stimulus in the case of independent noise. On the other hand, when the noise is correlated among the neurons, the average response is nearly as noisy and variable as the responses of the individual neurons. Thus, the spatially correlated noise diminishes the beneficial effects of pooling, although it can evoke synchronous firings of neurons. These suggest that response variability in cortical activity may be closely related to the correlation in input noise.

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I. INTRODUCTION

Recently, stochastic resonance (SR) has attracted considerable attention and has been investigated both experimentally and theoretically in a large variety of nonlinear systems, especially in nervous systems [1]. It was demonstrated that the coherent responses of systems to input signals can be enhanced in the presence of an optimal level of noise. In particular, the coupling between neurons can strengthen the SR effect, improving their signal-processing capabilities [2–4]. These imply that noise can play a constructive role in signal processing. In most previous studies, however, the input noise for individual neurons was always considered to be independent of each other. A nontrivial question thus arises. What influence does the noise have on signal processing when it is correlated among a group of neurons, even highly correlated? Such an issue may be closely associated with the so-called response variability observed in cortical activity; that is, the neural responses to repeated presentations of the same stimulus vary largely from trial to trial [5].

Although the responses of single neurons in the visual cortex to a repeated visual stimulus are never the same, one often assumes that the response variability represents “neuronal noise” and that the averaged response over some populations of neurons may contain precise information about the stimulus [6]. Obviously, such population coding is based on a key hypothesis that the response variation in each neuron is more or less independent of that in its neighbors [5,7]. That is, while one neuron is responding poorly to the signal, others may be responding well. As a result, the averaged response of all the relevant neurons will yield reliable signals. However, a number of studies have recently displayed that neuronal populations in the visual cortex can exhibit significant covariance both in their spontaneous and visually evoked activity [8–10]. For example, Arieli *et al.* observed that the spontaneous activity of single neurons is highly correlated with the population activity [9]. Such a dynamically changing pattern of activity takes place both in the presence

and the absence of stimulation. Later, they further demonstrated that the evoked spatiotemporal firing patterns exhibit a large variability in response to the same stimulus, and argued that the observed activity is a linear summation of the reproducible response and the ongoing activity, which changes remarkably from trial to trial [10]. A stable and precise response pattern appears only when a large number of individual responses are averaged. These suggest that the response variability may result from the dynamics of the ongoing activity, which has a remarkable impact on neuronal responses. There have been a number of studies exploring the mechanisms underlying the response variability [11–13].

Despite the large fluctuations in response to sensory stimuli, cortical neurons can also exhibit reliable and temporally precise patterns of activity [14]. It was considered that both behaviors are related to the incidence of synchronous synaptic inputs onto the cortical neurons [11]. Clearly, such synaptic inputs are spatially correlated among the neurons. In addition, there has been the hypothesis that sensory processing is most efficient when neuronal activity is decorrelated so that it conveys independent messages in a nonredundant manner [15]. This is in part supported by the results obtained in Ref. [11]. On the other hand, it was suggested that, in the presence of correlation in response variation, one possible reason for the neurons to carry redundant messages may be to improve the temporal resolution in coding a dynamic variable that can vary rapidly [12].

Therefore, it is important to explore the conditions under which these two different kinds of neuronal activities occur and the characteristics of the involved signal processing. It is well known that there are numerous noise sources in nervous systems [16] and that neurons are subject to these noise inputs. Clearly, different intensities or natures of the noise will lead to various spatiotemporal firing patterns of the neurons. Thus, in order to interpret the aforementioned experimental phenomena, a dynamic modeling study considering various natures of input noise is needed. In particular, it is of interest to investigate what roles the spatially correlated or uncorre-

lated noise plays in signal processing within the context of the SR. Such a study may provide new insights into the effects of noise on signal transfer.

In the present paper, we investigate the cases wherein the input noise for each neuron is independent or spatially correlated in a globally coupled neuronal network subject to a subthreshold periodic signal. Both the cases exhibit the SR phenomena, that is, the output signal-to-noise ratio (SNR) first rises and then decreases as noise intensity increases. In the case of independent noise, the reliable signals can be conveyed by pooling the activity of neurons. On the other hand, in the case of spatially correlated noise, the averaged response is nearly as noisy and unreliable as the responses of the individual neurons, and thus the beneficial effect of pooling is diminished. These results imply that the response variability in cortical activity may be related to the correlation in input noise.

This paper is organized as follows. In Sec. II a model is described. The results for the cases wherein the neurons have an identical or independent noise input are presented in Sec. III, while those for the spatially correlated noise case are shown in Sec. IV. Finally, a conclusion is given in Sec. V.

II. MODEL

We construct a globally coupled neuronal network composed of the Hodgkin-Huxley (HH) model neurons. The dynamic equations for the network are described as follows:

$$C_m \frac{dV_i}{dt} = -g_{N_a} m_i^3 h_i (V_i - V_{N_a}) - g_K n_i^4 (V_i - V_K) - g_l (V_i - V_l) + I_0 + s(t) + \eta_i(t) + I_i^{syn}(t), \quad (1)$$

$$\frac{dm_i}{dt} = \frac{m_\infty(V_i) - m_i}{\tau_m(V_i)}, \quad (2)$$

$$\frac{dh_i}{dt} = \frac{h_\infty(V_i) - h_i}{\tau_h(V_i)}, \quad (3)$$

$$\frac{dn_i}{dt} = \frac{n_\infty(V_i) - n_i}{\tau_n(V_i)}, \quad i = 1, \dots, N. \quad (4)$$

Here V_i , m_i , h_i , and n_i are the membrane potential, the activation and inactivation of the sodium current, and the activation of the potassium current, respectively. g_{N_a} , g_K , and g_l are the maximal values of conductance of the sodium, potassium, and leakage currents V_{N_a} , V_K , and V_l are the corresponding reversal potentials. The capacity of the membrane is $C_m = 1 \mu\text{F}/\text{cm}^2$. The number of neurons is taken as $N = 100$. The auxiliary functions and the parameter values can be found in Ref. [17].

Here we assume that each neuron is subject to a common subthreshold signal $s(t) = A \cos(2\pi f_s t)$ with an amplitude A and frequency f_s . The noise term is chosen as $\eta_i(t) = \xi_i(t) + \chi(t)$ with

$$\langle \xi_i(t) \rangle = 0, \quad \langle \xi_i(t_1) \xi_j(t_2) \rangle = 2D_1 \delta_{ij} \delta(t_1 - t_2), \quad (5)$$

and

$$\langle \chi(t) \rangle = 0, \quad \langle \chi(t_1) \chi(t_2) \rangle = D_2 \lambda e^{-\lambda|t_1 - t_2|}. \quad (6)$$

That is, $\xi_i(t)$ is taken as the independent Gaussian white noise, while $\chi(t)$ is the Gaussian colored noise with a correlation time λ^{-1} . Therefore, there exists correlation in noise between the neurons,

$$\langle \eta_i(t_1) \eta_j(t_2) \rangle = 2D_1 \delta_{ij} \delta(t_1 - t_2) + D_2 \lambda e^{-\lambda|t_1 - t_2|}. \quad (7)$$

Here D_1 and D_2 represent the noise intensities. The above assumption can be interpreted as follows. There are numerous noise sources in nervous systems [16,18] such as thermal fluctuations, the variability of membrane parameters, and spontaneous opening or closing of ion channels. On the other hand, neurons have synaptic inputs from those beyond the system under consideration, which may also exhibit random-like behavior. For simplicity, all these effects can be considered together, and the total noise can be represented by $\eta_i(t)$ for a network consisting of a small number of neurons.

In fact, in order to compare different effects of various noise on neural activity, we discuss the following three cases.

Case I: identical noise. In this all the neurons are subject to an identical Gaussian white noise at any time, namely, $\eta_i(t) = \xi(t)$. This actually introduces a very strong correlation in noise among the neurons. It does not decay spatially, i.e., its correlation length in space is large enough. Such a consideration is for a system wherein the number of neurons is relatively small. Clearly, when no further on-site fluctuation is introduced (see Case III), the dynamics of the network will be reduced to the single-neuron case since each neuron has the same input.

Case II: Independent (or uncorrelated) noise. In this case the input noise for each neuron is assumed as an independent or uncorrelated Gaussian white noise, $\eta_i(t) = \xi_i(t)$. That is, at any time the noise is uncorrelated among the neurons. Although the same noise distribution on each neuron is assumed, the neurons have different values of noise at the same time.

Case III: Spatially correlated noise. When the input noise for each neuron is set as $\eta_i(t) = \xi_i(t) + \chi(t)$, we have spatially correlated noise. Similar to Case I, the term $\chi(t)$ is a common noise input to all the neurons and introduces a strong correlation in the noise. However, such a strong correlation becomes weak when the on-site fluctuation $\xi_i(t)$ is further included for each neuron. Thus, the total effect of $\eta_i(t) = \xi_i(t) + \chi(t)$ is to result in spatially correlated noise inputs. Nevertheless, this correlation is obviously weaker than that in Case I. The motivation for this case is based on the idea that there may be an incidence of correlated synaptic inputs from other neurons beyond the network under study. The simplest form for such inputs could be taken as an identical Gaussian colored noise. Similar common inputs have also been suggested in Ref. [11]. For the network with a small number of neurons, we may not need to assume that the noise correlation decays exponentially over the system, but rather that the correlation length is large enough. But for a large network with more number of neurons, a spatial cor-

relation length should be considered. Clearly, Case III is modulated by two noise intensities D_1 and D_2 . It is reduced to Case I if $D_1 \ll D_2$, since then the on-site fluctuation $\xi_i(t)$ is very small and cannot destroy the strong correlation in noise. On the other hand, for $D_1 \gg D_2$ Case III will be reduced to Case II as the on-site fluctuation $\xi_i(t)$ is very large. It is also worth noting that, for the sake of simplicity, here all the noise intensities are described by D_1 and D_2 and no further difference is made for the noise intensity on each neuron.

In Eq. (1) all the neurons are assumed to be globally coupled with any other, and the synaptic current is described as

$$I_i^{syn}(t) = - \sum_{j=1, j \neq i}^N \frac{g_{syn}}{N} \alpha(t-t_j) (V_i - V_{syn}^{ij}) \theta(V_j - V_{th}), \quad (8)$$

with $\alpha(t-t_j) = \alpha(t') = (t'/\tau)e^{-t'/\tau}$ [19]. 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. Here a fraction p is defined by the ratio of the number of excitatory couplings to that of the total couplings. It is assumed that each neuron has exactly the same fraction p of its couplings being excitatory. 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 average synaptic current is

$$A_{syn}(t) = \frac{1}{N} \sum_{i=1}^N I_i^{syn}(t). \quad (9)$$

The firings of each neuron are recorded and converted into a time series of standard pulses $U_i(t)$ with $U_A = 1$ of width 2 ms and $U_B = 0$ corresponding, respectively, to the firing and nonfiring states. The SNR is defined as $10 \log_{10}(\Gamma/B)$ with Γ and B representing the signal strength and the mean amplitude of the background noise at the input signal frequency f_s in the power spectrum, respectively [4]. The output of the network can be defined as

$$I^{out}(t) = \frac{1}{N} \sum_{i=1}^N U_i(t), \quad (10)$$

which is also regarded as the averaged activity over the neurons. Here we always take the output of the first neuron, denoted by $U(t)$, as a representative for the responses of the individual neurons within the network. The SNR for $I^{out}(t)$, $A_{syn}(t)$, and $U(t)$ is simply denoted by γ_o , γ_A , and γ_U .

The numerical integration of Eqs. (1)–(4) is done by using a second-order algorithm suggested in Ref. [20] and the integration step is taken as 0.03 ms. A long transient is discarded and the final result is obtained by taking an average over 50 different realizations of noise seeds.

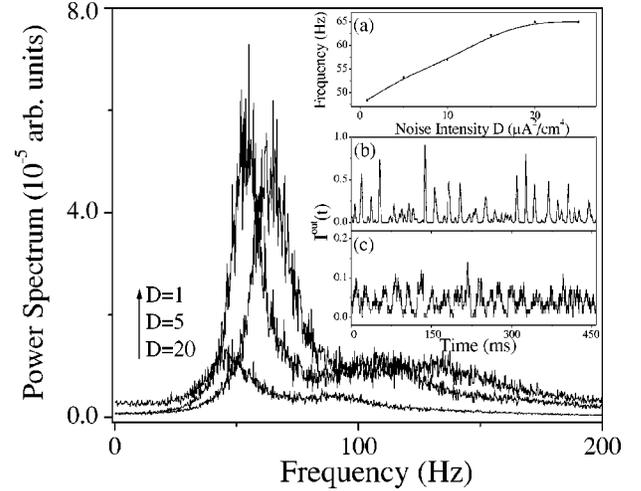


FIG. 1. The power spectrum of $I^{out}(t)$ for Case III with $D_1 = D_2 = D = 1, 5, 20$, respectively. The frequency corresponding to the peak vs D is shown in the inset (a). $I^{out}(t)$ vs time with $D = 2$ for Case III and II is shown, respectively, in the insets (b) and (c). It is assumed that $I_0 = 1$, $g_{syn} = 1$, and $\lambda = 5$ throughout the paper. The fraction of the couplings being excitatory is always 0.667, otherwise specified elsewhere.

Now let us present a general picture of the dynamics of the network in the absence of the input signal. It is noted that for a single neuron, in the presence of only a constant bias I_0 ($< I_c = 6.2$), the membrane potential can undergo a damping oscillation to the resting potential with a frequency of 50–85 Hz [21]. Such an intrinsic oscillation exerts an evident influence on the system's response to noise and/or external signal. In the presence of noise $\eta_i(t)$, the network can exhibit a coherent oscillatory activity as well as a SR-like effect called coherence resonance [22] due to this subthreshold intrinsic oscillation. Figure 1 depicts the power spectrum of $I^{out}(t)$. Obviously, there exists a small peak in each curve and the peak shifts rightward as the noise intensity D increases. This clearly demonstrates coherence resonance since the peak reflects the intrinsic oscillation, which can be activated by noise. Such noise-induced coherent activity has been found experimentally; for example, Ref. [9] demonstrated the coherent spatiotemporal patterns of the ongoing activity in the cat visual cortex, where the spontaneous activity of single neurons is not an independent process but is activated in a coherent fashion.

The inset (a) of Fig. 1 shows the frequency corresponding to the peak in the power spectrum. It lies within the range of 47–65 Hz, i.e., in the γ frequency band (30 - 70 Hz). The inset (b) of Fig. 1 displays the time course of $I^{out}(t)$, where a coherent activity can be seen. It is emphasized that the ongoing activity is closely related to the characteristics of the noise. To this end we also depict $I^{out}(t)$ versus time for the case of independent noise, i.e., $\eta_i(t) = \xi_i(t)$, in the inset (c) of Fig. 1. While there exists some periodicity in $I^{out}(t)$ as well, the firings of the neurons exhibit a weak correlation. As we shall see, the ongoing activity has a large influence on neuronal responses to stimuli.

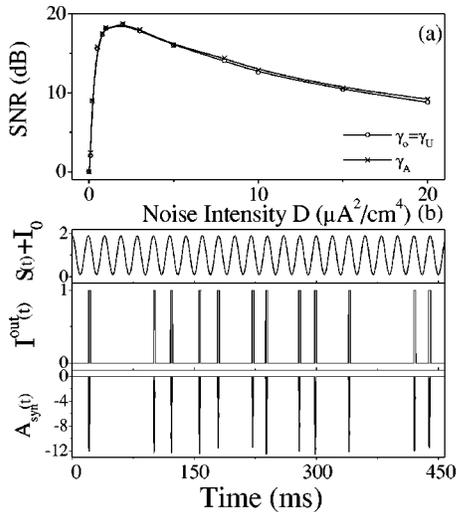


FIG. 2. For Case I with $\langle \xi(t_1)\xi(t_2) \rangle = 2D\delta(t_1 - t_2)$. (a) γ_o and γ_A vs the noise intensity D . (b) The input signal together with the bias $s(t) + I_0$, the output of the network $I^{out}(t)$, and the mean synaptic current $A_{syn}(t)$ vs time for $D=2$. The signal is always taken as $A=0.9$ and $f_s=50$ Hz, otherwise specified elsewhere.

III. IDENTICAL OR INDEPENDENT NOISE

Before discussing the spatially correlated noise case, we first consider two simple situations: Case I, *Identical noise* with $\eta_i(t) = \xi(t)$ and Case II, *Independent (or uncorrelated) noise* with $\eta_i(t) = \xi_i(t)$. Such a discussion enables us to distinguish different roles of $\xi_i(t)$ and $\chi(t)$ in signal processing.

Case I: Identical noise. Although this case appears somewhat trivial assuming that each neuron has the same value of the signal plus noise $s(t) + \xi(t)$ it is helpful to reveal some common effects of the correlated noise on signal transfer. When subject to a subthreshold signal, the neurons are evoked to fire only by noise. Here all the neurons fire simultaneously, and $I^{out}(t)$ is equal to $U(t)$. Thus, γ_U is also equal to γ_o . Figure 2(a) shows both γ_o and γ_A versus the noise intensity D . Both the curves basically overlap and exhibit a typical characteristic of the SR, that is, there exists an optimal noise level ($D_m=2$) at which the signal-detecting capability is maximally improved. Clearly, $I^{out}(t)$ and $A_{syn}(t)$ present the same periodicity as illustrated in Fig. 2(b). $I^{out}(t)$ takes a value of 1 and $A_{syn}(t)$ has a negative value [23] only when all the neurons fire synchronously, otherwise both take a value of zero. In the case of low noise level, since the effective stimulus strength is small, the firings of the neurons are often separated by several driving cycles, i.e., the so-called skipping phenomenon [24]. This results in a low value of the SNR. As D increases, the discharge rate increases and the firings are phase locked to the signal, although there still exists some skipping in firing. Therefore, the SNR rises quickly and reaches its maximum. For the case of high noise level, while the neurons nearly fire every stimulus cycle, the coherence of the firings with the signal is gradually degraded. The firing time with respect to the signal is widely distributed within one period of the signal. The SNR thus drops fast.

It is noted that the present case is in fact equivalent to the single neuron case, although there exist the couplings between neurons. As stated above, $A_{syn}(t)$ exhibits the δ -function like behavior with a nonzero value only when the neurons discharge spikes synchronously. This affects only the magnitude of the membrane potential after it exceeds the threshold. Thus, the firing dynamics of the network is the same as in the single unit case. Therefore, the averaged activity over the neurons is identical to the responses of the individual neurons, and contains no more information about the stimulus than the individual responses. If the white noise is replaced with the colored noise, i.e., $\eta_i(t) = \chi(t)$, a similar conclusion can be drawn. In brief, when all the neurons are evoked with an identical noise, the coupling does not improve the capability of sensory processing for the network and the averaged response is as noisy as the individual responses. Thus, it is generally assumed that the input noise for each neuron is not the same.

Case II: Independent (or uncorrelated) noise. In this case, since the input noise for each neuron is uncorrelated; the firings of the neurons are not synchronous in general. However, owing to the couplings between neurons, the firing behavior may be correlated and the system could exhibit some cooperative dynamical effects. Figure 3(a) plots the SNR versus the noise intensity. Apparently, these curves present a typical SR characteristic, i.e., first a rise and then a drop. The curves for γ_o and γ_A remain very close, implying that $I^{out}(t)$ and $A_{syn}(t)$ exhibit a similar periodicity. Note that γ_o is much larger than γ_U . This means that the coupling can enhance the signal processing as reported in Refs. [2–4]. On the other hand, it also implies that the average activity can better reflect the signal or contain more information about the stimulus when the noise in each neuron is independent. This can also be seen in Fig. 3(b).

In comparison with Fig. 2(b) (for the same noise intensity), the neurons fire spikes more frequently because of the increase in the effective stimulus strength, while there still exists the skipping phenomenon. Most firings occur near the maxima of the signal in each cycle, showing a high coherence with the signal. In contrast to skipping firings of the neurons, both $I^{out}(t)$ and $A_{syn}(t)$ vary nearly periodically with the same period as that of the signal. It is noted that there exists a finite width in the peaks of $I^{out}(t)$ meaning that the neurons discharge spikes with a phase difference owing to the independent noise inputs. Therefore, although the synchronization of firings in the network is weak, the average activity exhibits a strong correlation with the stimulus leading to a large value of γ_o . In other words, reliable signals can be conveyed by pooling the activities of many neurons. This is consistent with the typical population coding in which the pooling can average out the uncorrelated part among neuronal responses [5–7].

Previously, Inghiosa and Bulsara have studied the cooperative effects arising from the noise and coupling in an ensemble of nonlinear dynamic elements [3]. They demonstrated that the performance of the network can be improved by the coupling and speculated that the noise may play a constructive role in neural sensory processing, as shown here. Beyond these effects, in our case different phenomena

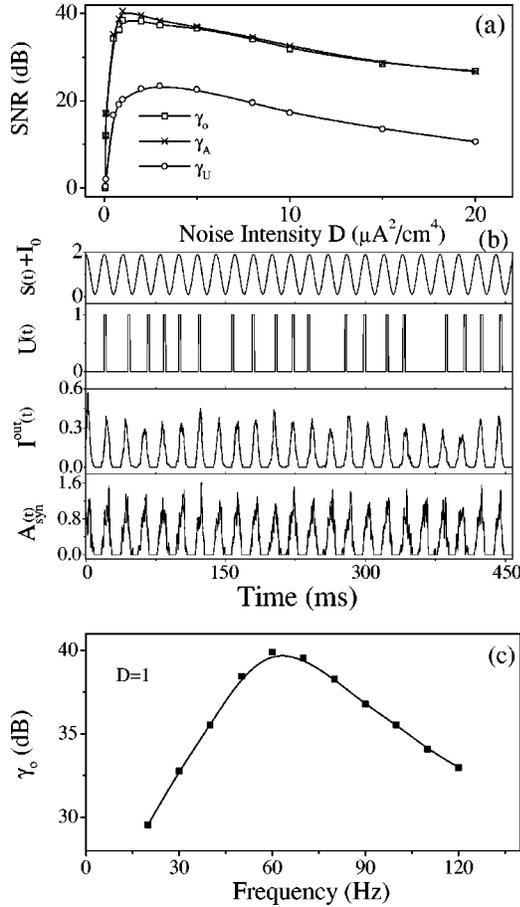


FIG. 3. For Case II with $\langle \xi_i(t_1) \xi_j(t_2) \rangle = 2D \delta_{ij} \delta(t_1 - t_2)$. (a) γ_o , γ_A , and γ_U vs the noise intensity D . (b) $s(t) + I_0$, the response $U(t)$ of the first neuron, $I^{\text{out}}(t)$, and $A_{\text{syn}}(t)$ vs time for $D=2$. (c) γ_o vs the signal frequency in the case of $D=1$ (all signals have the same amplitude).

can appear, such as frequency selection by a more realistic considering for the network. Owing to the excitability of the HH neurons, there exists subthreshold intrinsic oscillation, which can result in coherence resonance in the presence of noise. Therefore, the network is more sensitive to the input signal when its frequency is matchable with that of the ongoing oscillatory activity. This can be seen from Fig. 3(c) where γ_o has relatively large values for those signals with frequencies within the range of 40–100 Hz. We have also reported a similar frequency sensitivity in weak-signal detection based on the Hindmarsh-Rose (HR) neuronal model [4]. The results are consistent for both the models.

Comparing the results from Cases I and II, we see that whether the noise input to the neurons is identical or independent does have a substantial influence on the average activity and signal transfer.

IV. SPATIALLY CORRELATED NOISE

Now we consider a more general situation and explore the effects of spatially correlated noise on signal processing in the case of $\eta_i(t) = \xi_i(t) + \chi(t)$, i.e., the Case III.

We first assume $D_1 = D_2 = D$. Clearly, in the presence of

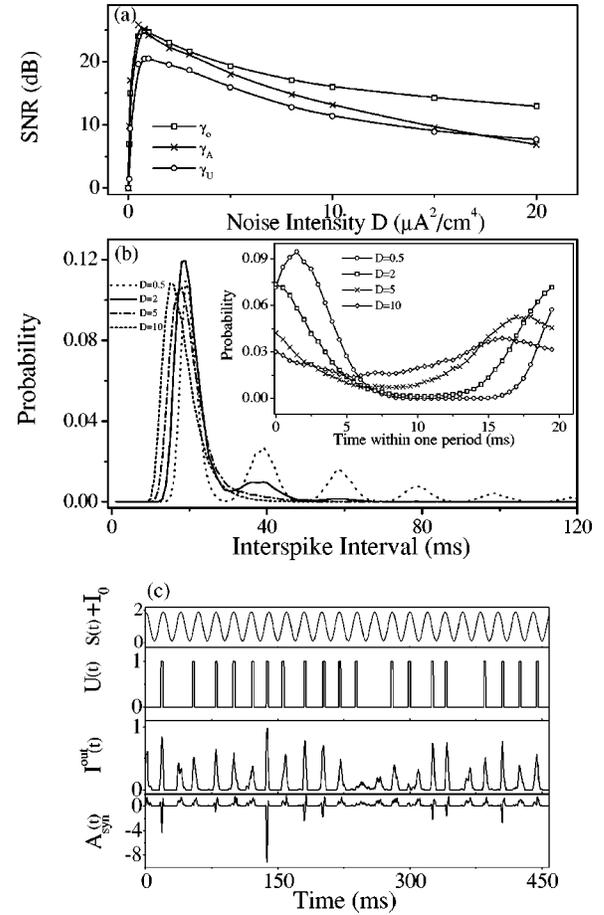


FIG. 4. For Case III with $D_1 = D_2 = D$. (a) γ_o , γ_A , and γ_U vs the noise intensity D . (b) The normalized number of spikes within the bins vs the interspike interval. The inset is the normalized number of spikes vs the firing time relative to the signal within one period of the signal. (c) $s(t) + I_0$, $U(t)$, $I^{\text{out}}(t)$, and $A_{\text{syn}}(t)$ vs time for $D=2$.

both the signal and the noise, there still exists SR as seen in Fig. 4(a). For low noise level, the firings of the neurons may be interrupted in several driving cycles. Thus there are many peaks located at multiple integers of the signal period in the interspike interval histogram (ISIH) as shown in Fig. 4(b). As D increases, more firings are induced and the number of peaks in the ISIH largely decreases, mainly located around the signal period. Therefore, the SNR rises quickly. At a noise level of $D_m = 1$ (for $I_0 = 1$), the firings of the neurons are phase locked to the signal and thus the SNR takes its maximum. However, as D further increases, the neurons fire randomly with the firing time extending to the whole period of the signal. Thus the SNR drops. The distribution of the firing time within one period of the signal is plotted in the inset of Fig. 4(b). Note that the distribution curve becomes flat when D is large.

It is noted that both γ_o and the difference in the SNR between the average activity and the responses of the individual neurons, i.e., $\gamma_o - \gamma_U$, become small compared to Case II. This can be interpreted as follows. Just as illustrated in Fig. 4(c), for $D=2$ most firings still occur around the maxima of the signal [here the discharge rate is slightly

higher than in Fig. 3(b)]. In the presence of correlation in noise, on one hand, the effect of synchronous firings of the neurons is enhanced and the value of $I^{out}(t)$ is sometimes close to 1 corresponding to the complete synchronization. This is also reflected in the narrow width of the peaks in $I^{out}(t)$. On the other hand, the peak values of $I^{out}(t)$ are very small within some driving cycles. This gives rise to the fluctuations in $I^{out}(t)$ between different driving cycles just resembling the skipping firings of the neurons. That is, the average activity is nearly as noisy as the responses of the individual neurons leading to a small value of γ_o . Thus, $I^{out}(t)$ may vary largely between different realizations of noise seeds and present the response variability. In addition, although $I^{out}(t)$ is closely related to $A_{syn}(t)$, there exists an evident difference in the SNR at high noise levels. While the neurons fire randomly in each cycle, the pooling can average out some random components and thus γ_o drops slowly with increasing D . Whereas, $A_{syn}(t)$ takes a relatively large negative value when a large number of neurons fire simultaneously and otherwise has a small or zero value. This makes the fluctuation in $A_{syn}(t)$ larger than that in $I^{out}(t)$, especially in the case of high noise levels where the neurons fire more frequently. This is why the difference between γ_o and γ_A becomes large as D increases. Comparing Fig. 4(c) with Fig. 3(b), we see that the response variability is related to the correlation in input noise.

Physically, the neurons have a tendency to discharge spikes synchronously in the presence of correlation in the noise. Once a large number of neurons fire synchronously, the mean synaptic current takes a relatively large negative value. This makes the effective stimulus strength become small [the time average of $A_{syn}(t)$ is equal to 0.21, 0.34, -0.35, corresponding, respectively, to the above described Cases I, II, III for $D=2$]. Thus, the neurons may need to take more spatiotemporal summation of inputs to fire and cannot even discharge spikes within some cycles. In addition, the ongoing activity preceding the stimulus exhibits a coherent behavior as stated above. The addition of the input signal is only to modulate the firing dynamics of the neurons [cf the inset (b) of Fig. 1 and Fig. 4(c)]. That is, the spontaneous activity exerts a large influence on the neuronal responses. Therefore, it is the spatially correlated noise that leads to the poor performance of the average activity.

Figure 5 shows the maximum C_m of the coefficient $c(\tau)$ of correlation between $I^{out}(t)$ and the input signal $s(t)$ versus the noise intensity D . Here $c(\tau)$ is defined as

$$c(\tau) = \frac{\overline{[s(t) - \bar{s}][I^{out}(t + \tau) - \bar{I}^{out}]}}{\overline{[s(t) - \bar{s}]^2}^{1/2} \overline{[I^{out}(t) - \bar{I}^{out}]^2}^{1/2}} \quad (11)$$

with the overbar denoting an averaging over time. Clearly, C_m also first rises and then decreases as D increases. This is consistent with the noise dependence of the SNR. In order to make a comparison, we have computed C_m for all three cases studied in this paper. For Case II the output shows a strong correlation with the input signal, indicating that the average activity can accurately convey the information about the stimulus. In contrast, for Cases I or III there clearly exists

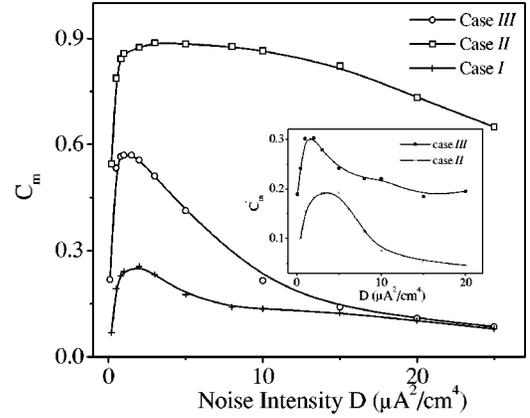


FIG. 5. The maximum C_m of the correlation coefficient vs the noise intensity for three cases. The inset is C'_m vs the noise intensity for both Case II and Case III.

weak correlation between the mean response and the signal, especially at high noise levels, e.g., for $D > 15$. In the inset of Fig. 5 is shown the maximum coefficient C'_m of correlation between the responses of two different neurons, say $U(t)$ and $U_{50}(t)$. Obviously, the neurons exhibit a larger correlation in their firing behavior for the case of spatially correlated noise than in the uncorrelated noise case. These results are in agreement with the SNR measure.

From the point of view of signal processing, the spatial correlation in the input noise diminishes the beneficial effects of pooling. (This has also been briefly mentioned in Ref. [25].) The correlated noise makes the neurons prone to behave synchronously, that is, most neurons may discharge spikes simultaneously within one driving cycle and not fire at all within another. Thus, the average activity presents large fluctuations and contains less information on the stimulus, or the information is buried in the large fluctuations. On the contrary, in the case of independent noise, while one neuron does not fire, others may discharge at the same time due to the independent noise inputs. As a consequence, pooling the activity of groups of neurons could yield reliable signals. In this sense the sensory processing might be more efficient when the input noise for the neurons is independent of each other. It could also be inferred that the key assumption that the averaging over the neuronal activity can contain precise information about the stimulus is definitely based on the hypothesis that the input noise on each neuron is uncorrelated.

We further investigate the effects of the noise by setting different values for D_1 and D_2 . Figure 6(a) depicts the values of γ_o and γ_U versus D_2 with a fixed value of D_1 . As the value of D_2 rises, the SNR decreases and the difference between γ_o and γ_U also becomes small as seen in the inset of Fig. 6(a). Obviously, the increase of D_2 is to enhance the correlation in the noise. For $D_2=0$, the peak values of $I^{out}(t)$ are small but it varies nearly periodically leading to a large value of γ_o (and also of γ_o/γ_U). As D_2 increases, both the discharge rate and the peak values of $I^{out}(t)$ rise. (For small D_1 this can give rise to a first increase in γ_U .) But this also reduces the coherence between the firings and the signal. Thus, γ_U drops slightly with increasing D_2 . On the other hand, no matter how small the value of D_2 is, it is possible

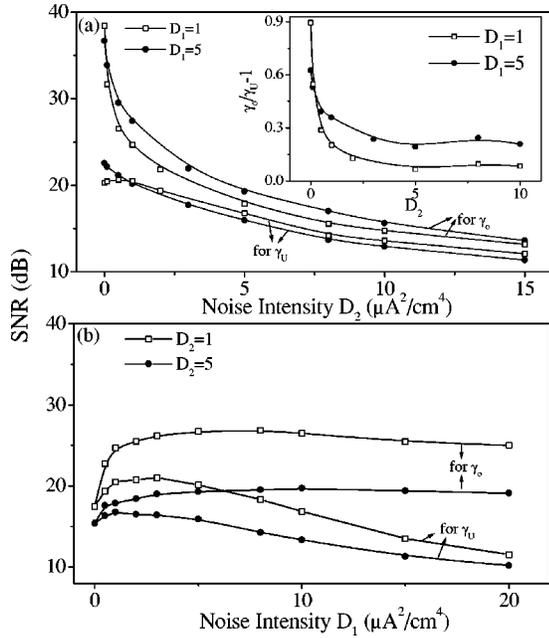


FIG. 6. (a) γ_o and γ_U vs the noise intensity D_2 with $D_1=1$ and 5, respectively. The inset is $\gamma_o/\gamma_U - 1$ vs D_2 . (b) γ_o and γ_U vs the noise intensity D_1 with $D_2=1$ and 5, respectively.

that only few neurons discharge within some driving cycles. As a result, $I^{out}(t)$ may vary remarkably between different cycles, and the fluctuations may become large as D_2 increases. In addition, the neurons fire randomly at high noise levels. These result in the fast drop of γ_o and the small difference between γ_o and γ_U .

Alternatively, when D_2 is kept unchanged and D_1 is increased, γ_o and γ_U first rise and then decrease but the change is much smaller than that shown in Fig. 6(a). This is clearly depicted in Fig. 6(b). We have mentioned that the firings of the neurons exhibit a remarkable skipping when $D_1=0$. As D_1 rises, the discharge rate increases and the correlation of firings with the signal is enhanced while the effect of synchronous firings becomes weak. Therefore, both γ_o and γ_U rise. As D_1 further rises, the neurons fire more frequently and the coherence of the firings with the signal is gradually degraded leading to the fall of γ_U . However, the pooling may average out some random components and γ_o still rises until there exists a large random component in $I^{out}(t)$. These results indicate that the SNR is more sensitive to the change in D_2 , which is related with the extent to which the noise is spatially correlated. This implies that the correlation in the input noise plays an important role in modulating the firing dynamics.

We also study the effects of the coupling and the number of neurons in the network on signal processing. Figure 7(a) shows the SNR versus the fraction p of the couplings being excitatory for the case of $D=1$. As p increases, the discharge rate increases and the correlation of firings with the signal is also improved giving rise to the increase in γ_U . For $I^{out}(t)$ since most firings occur near the maxima of the signal, only its peak values change as the value of p varies and thus γ_o varies slightly. At $p=0$ the value of $A_{syn}(t)$ is zero or nega-

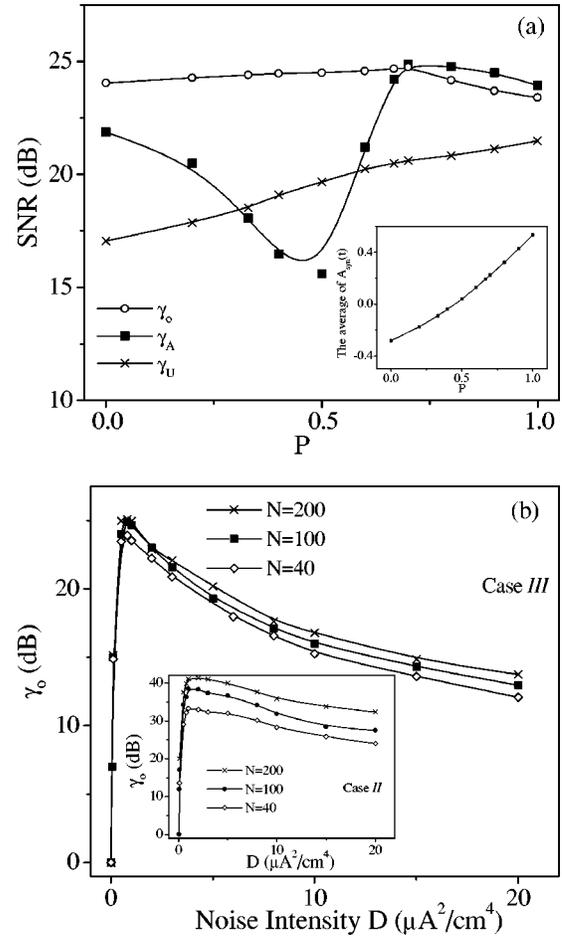


FIG. 7. (a) γ_o , γ_A , and γ_U vs the fraction p of the couplings being excitatory in the case of $D_1=D_2=D=1$. The inset is the time average of $A_{syn}(t)$ vs p . (b) γ_o vs the noise intensity D for the number of neurons $N=40$, 100, and 200, respectively, for Case III. The inset is that for Case II.

tive corresponding, respectively, to the nonfiring and firing states. As p rises, the neurons fire more frequently and the time average \bar{A} of $A_{syn}(t)$ also increases as seen in the inset of Fig. 7(a). But \bar{A} is less than zero when $p < 0.5$. This means that $A_{syn}(t)$ fluctuates around zero and such fluctuations become large as p further increases leading to the drop of γ_A . Therefore, there exists a minimum around $p=0.5$ with $\bar{A} \approx 0$. If $p > 0.5$, unless a large number of neurons are firing simultaneously, $A_{syn}(t)$ may be larger than zero and thus the periodicity in $A_{syn}(t)$ is improved. This gives rise to the increase in γ_A . It is noted that there appears a small local maximum of γ_A around $p=0.7$ implying that there exists an optimal coupling. Similar phenomena have been found in Ref. [26].

Figure 7(b) displays the influence of the number N of neurons in the network. Clearly, there exists a slight change in γ_o with N for Case III, whereas for Case II there is a relatively large difference, as seen in the inset of Fig. 7(b). For Case III, because of the strong correlation in the firing behavior, the neurons tend to behave synchronously. $I^{out}(t)$ exhibits a similar dynamical behavior while the pooling ef-

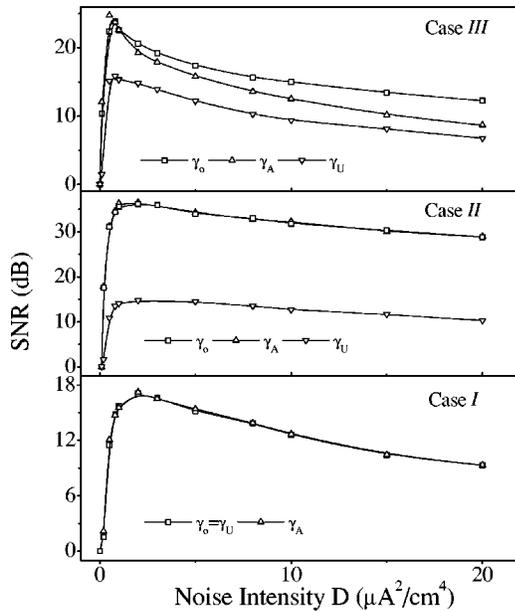


FIG. 8. γ_0 , γ_A , and γ_U vs the noise intensity D for three cases in the presence of a periodic signal with $f_s = 100$ Hz and $A = 0.9$.

fect is somewhat enhanced as N increases. For Case II, due to the independent nature of the noise, the averaging effect apparently improves with N . These results further imply that in the presence of correlated noise it may be unlikely to improve the SNR by pooling more neurons to process information.

When the signal frequency differs, similar phenomena can also be observed. Figure 8 shows the SNR in the case of $f_s = 100$ Hz (with the same stimulus strength). The results are consistent with those in the case of $f_s = 50$ Hz. However, here the corresponding values of the SNR become small owing to the frequency sensitivity. As discussed in Sec. III for Case II, there exists a frequency sensitivity range resulting from the resonance effect. The system is more sensitive to those signals when their frequencies fall into such a range. Clearly, such a frequency range is related to the main frequency of the ongoing activity in the absence of stimulus.

V. CONCLUSION

In this paper we have discussed the effects of input noise on signal processing when they are independent of each

other or spatially correlated among the neurons. The network can exhibit a coherent activity without input signal and such ongoing activity has a large impact on neuronal responses. In the presence of a subthreshold periodic signal, the averaged activity over the neurons can contain precise information about the stimulus in the case of independent noise. Whereas, for the case of correlated noise, the average activity is nearly as noisy as the responses of the individual neurons. Thus, the beneficial effect of pooling is diminished. Physically, the correlation in noise makes the neurons prone to behave synchronously, that is, most neurons may discharge spikes simultaneously within one driving cycle and not fire at all within another. This leads to large fluctuations in the average activity. It also seems unlikely to improve the performance of the average activity by pooling more neurons. These results suggest that the response variability may be related to the correlation in input noise among the neurons. Our simulation results indicate that in the light of the SNR and the correlation between the averaged activity and the signal, signal processing is more efficient in the case of independent noise. But for the case of correlated noise, there might be potential benefits for the neurons to transmit redundant messages, such as coding a rapidly changing dynamic variable [12]. It is stressed that the above conclusions can also be drawn in other neuronal models, such as the HR model [4]. Finally, we make a remark on the noise $\eta_i(t) = \xi_i(t) + \chi(t)$ considered in this paper. As discussed in Sec. II, the first term describes the uncorrelated fluctuations on each neuron, while the second term describes an identical Gaussian colored noise. Thus, the total noise has a spatial correlation among the neurons as expressed in Eq. (7). But this is a somewhat specific form of the spatially correlated noise. If the noise correlation decays spatially over the system according to a specified law, there might appear some new phenomena. This deserves a further study.

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