

Frequency sensitivity in weak signal detection

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The phenomenon of frequency sensitivity in weak signal detection has been studied via numerical simulation in the cases of a single neuron and a neuronal network, respectively. The membrane potential undergoes a damping oscillation to the quiescent state with a frequency of 11–33 Hz under a subthreshold bias. In the presence of a subthreshold sinusoidal signal and noise, the signal-to-noise ratio (SNR) of either the single neuron or the network presents the typical characteristic of stochastic resonance. In particular, there exists a frequency sensitivity range of 15–60 Hz, over which the SNR has a large value, implying that the system is more sensitive to signals with these frequencies in signal detection. Such frequency sensitivity is of functional significance, and results from the resonance between the intrinsic oscillation of the system and the input signal. In addition, two cases where either the values of the bias or the signal strength for neurons may be different are studied, respectively. The results indicate that the effect of frequency sensitivity generally exists in signal encoding. These enable us to interpret the experimental observation. [S1063-651X(99)09003-0]

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I. INTRODUCTION

Recently, stochastic resonance (SR) has attracted considerable attention, since it was shown that noise can play a constructive role in a variety of systems ranging from ring lasers and various solid state devices to sensory nervous systems. SR is a phenomenon wherein the response of a nonlinear system to a weak (subthreshold) input signal is optimized by the presence of a particular level of noise. That is, the output signal-to-noise ratio (SNR) first rises to a peak and then drops as the intensity of noise increases (see Refs. [1,2], and references therein). A number of experiments on neuronal systems have been reported showing such nonlinear phenomena. For example, SR has been observed in the activity of single mechanoreceptive sensory neurons from crayfish [3] and rat skin [4], of single interneurons from cricket abdominal ganglia [5], and of neuronal networks from mammalian brain [6]. The occurrence of SR has been argued to be a mechanism for weak signal detection.

In particular, it was reported in Ref. [5] that there exists a frequency sensitivity range of 5–60 Hz, over which the coherence of the spiking response of the neuron to the input signal is evidently enhanced, improving its encoding of the signal. Significant improvements in the SNR were indeed observed across most of the range of frequencies to which the neuron showed sensitivity. Such frequency sensitivity is of functional importance for information processing. For this interesting experimental observation, a modeling study was made in the case of a single neuron subjected to a subthreshold periodic signal and constant bias [7]. It was suggested that the frequency sensitivity results from the resonance between the intrinsic oscillation of the system and the periodic signal. However, the dynamic behavior relative to the frequency sensitivity has not been clearly clarified, and the effect of noise on signal detection was not considered. Moreover, it is well known that neurons are always coupled together via excitatory or inhibitory synapses. Therefore, it is more reasonable to explore the effect of frequency sensitivity

in the cases of a single neuron and a neuronal network, respectively, within the context of SR.

On the other hand, much study has been concentrated on the subthreshold dynamics of neuronal systems. It was reported that there exist subthreshold oscillations of membrane potential in various nervous systems, such as those observed in stellate cells of entorhinal cortex layer II [8]. It was argued that such subthreshold oscillations are intrinsic in the absence of external stimulus. Moreover, it was experimentally demonstrated that subthreshold intrinsic oscillations play a role in information carrying and, together with noise, can encode both environmental changes and modality-specific information [9]. In particular, it is suggested that SR could enhance the effects of weak intrinsic θ (4–10 Hz) or more widespread γ (30–70 Hz) rhythmic oscillations in the brain (see Ref. [6], and references therein). These further urge us to consider whether the effect of frequency sensitivity is correlated with the intrinsic oscillation of the system.

Motivated by the aforementioned considerations, we start with the Hindmarsh and Rose (HR) neuronal model [10], and construct a network composed of globally coupled HR neurons. Only with a subthreshold bias does the membrane potential undergo a damping oscillation with a frequency of 11–33 Hz to the quiescent state [11]. In the presence of a subthreshold sinusoidal signal and noise, the SNR of either the single neuron or the network presents the typical characteristic of SR. In particular, when the signal frequency is within the range of 15–60 Hz, the SNR has a large value, implying that the neuronal system is more sensitive to these signals in weak signal detection. This is due to the resonance between the intrinsic oscillation of the system and the input signal. Moreover, two interesting cases where either the values of the bias or the signal strength for the neurons may be different are studied, respectively. The results further indicate that the effect of frequency sensitivity generally exists in signal encoding. This paper is organized as follows. In Sec. II a model is described. The results and discussion for the single neuron case are presented in Sec. III, while those for

the neuronal network case are given in Sec. IV. The results for the cases where the value of the bias or the signal strength is distributed on the network are presented in Sec. V. Finally, a conclusion is given in Sec. VI.

II. MODEL

The dynamic equations for the network consisting of HR neurons are presented as follows [12]:

$$\frac{dX_i}{dt} = Y_i - aX_i^3 + bX_i^2 - Z_i + \sum_{j=1, j \neq i}^N \frac{J_{ij}}{N} S_j(t) + I_{0i} + I_{1i} \sin(2\pi f_s t) + \xi_i(t), \quad (1)$$

$$\frac{dY_i}{dt} = c - dX_i^2 - Y_i, \quad (2)$$

$$\frac{dZ_i}{dt} = r[s(X_i - X_0) - Z_i], \quad i = 1, \dots, N. \quad (3)$$

Here all parameters are held constant at $a=1.0$, $b=3.0$, $c=1.0$, $d=5.0$, $s=4.0$, $r=0.006$, and $X_0=-1.6$. Each neuron is characterized by three time-dependent variables: the membrane potential X , the recovery variable Y , and the slow adaptation variable Z . The synaptic input from the j th to i th neurons is modeled as $JS_j(t)$ when the j th neuron is active, i.e., $S_j(t) = \theta(X_j(t) - X^*)$, with X^* a threshold value for membrane potential taken as 0.8 and $\theta(x) = 1$ if $x \geq 0$ and $\theta(x) = 0$ if $x < 0$. The coupling strength J_{ij} is randomly distributed in a range, say $J_{ij} \in [-4, 20]$, with $J_{ij} < 0$ for inhibitory coupling and $J_{ij} > 0$ for excitatory one. The number of neurons in the network is taken as $N=200$.

Since the neurons always receive synaptic inputs from those located outside the network considered and have various fluctuations in membrane, a bias I_0 is considered to model all these effects. The term $I_1 \sin(2\pi f_s t)$ is a subthreshold input signal, i.e., it alone is insufficient to evoke neurons to fire. In view of the complex origins of noise, $\xi_i(t)$ is chosen as the Gaussian white noise and is uncorrelated with any other, i.e., it is a local noise, with

$$\langle \xi_i(t) \rangle = 0, \quad \langle \xi_i(t_1) \xi_j(t_2) \rangle = 2D \delta_{ij} \delta(t_1 - t_2), \quad (4)$$

where $\langle \rangle$ represents the ensemble average and D the noise intensity [13].

The output of the network is defined as

$$I^{\text{out}}(t) = \frac{1}{N} \sum_{i=1}^N \theta(X_i(t) - X^*). \quad (5)$$

Here we consider the average of the firing activities of all neurons as the output of the network, which may encode the input signal. The SNR of the network is defined as $10 \log_{10}(S/B)$ with S and B representing the signal peak and the mean amplitude of the background noise at the input signal frequency in the power spectrum density of $I^{\text{out}}(t)$, respectively [14]. The numerical integration of Eqs. (1)–(3) is done by using a second-order algorithm suggested in Ref.

[15], and the integration step is taken as 0.01. The final result is obtained by taking an average over 50 different realizations.

III. SINGLE NEURON CASE

Let us first discuss the single neuron case. Only with a constant bias I_0 does the membrane potential undergo a subthreshold damping oscillation to the quiescent state or a limit cycle oscillation (suprathreshold), depending on whether the value of I_0 is larger than the threshold $I_c = 1.32$ or not [7]. The damping oscillation due to the excitability inherent in neurons is considered to be intrinsic, and its frequency rises monotonically from 11 to 33 Hz as I_0 increases [11]. Such an intrinsic oscillation has a significant effect on the responses of the neuronal system to periodic signals. The lasting time of the oscillation increases with I_0 , and when $I_0 = I_c$ the neuron fires periodically with a frequency about 33 Hz. For $I_0 > I_c$, the neuron fires periodically or chaotically, as shown in Ref. [16].

In the case of a subthreshold bias I_0 , when subjected to a periodic signal, the neuron oscillates in the subthreshold range of voltage or fires spikes, decided by the amplitude I_1 of the signal. Figure 1(a) shows the threshold amplitude I_{1c} versus the signal frequency f_s , which separates the diagram into two regions, namely, the nonfiring and firing regions. The curves present a concave shape with a minimum around $f_s = 26$ Hz, which coincides with the most sensitive frequency found in Ref. [5]. This is different from the case where I_{1c} increases monotonically with the signal frequency in the nonexcitable double-well system [17]. It is noted that, in the range of $4 < f_s < 100$ Hz, the threshold I_{1c} is even less than $I_c = 1.32$ in the case of $I_0 = 0$. In particular, for both curves there exists a frequency range of 15–60 Hz, where a lower signal strength can evoke the neuron to fire. The existence of such a frequency range is due to a kind of resonance between the aforementioned intrinsic oscillation and the periodic signal. When both frequencies are matchable, the input signal can most effectively transfer energy to the neuron to evoke the firing of spikes. In other words, less stimulus strength is needed for the neuron to fire.

To study the responses of the neuron to periodic signals with different frequencies, the signal amplitude I_1 is assumed to be identical for each frequency. At the same time, all the signals are kept as subthreshold. When subjected to a subthreshold periodic signal, the neuron is only evoked to fire by noise. The output SNR is calculated to quantify this noise-induced effect. Figure 1(b) shows the SNR of a neuron versus noise intensity D , which clearly presents the typical characteristic of SR: first a rise and then a drop. When a very low noise is added to the neuron, say $D = 0.01$, the SNR for the signal with the frequency $f_s = 30$ Hz rises rapidly from zero, because in this case the neuron is easy to be induced to fire by noise. The SNR is nearly zero for both signals, with frequencies $f_s = 15$ and 100 Hz, respectively. In the case of low noise, since the effective stimulus strength is small, the firing of the neuron is often interrupted during several driving cycles, resulting in a low SNR. At the moderate noise level, the firing shows strong coherence with the signal, i.e., the neuron always fires spikes when the signal is around its maxima. Therefore, the SNR rises, and reaches its maximum

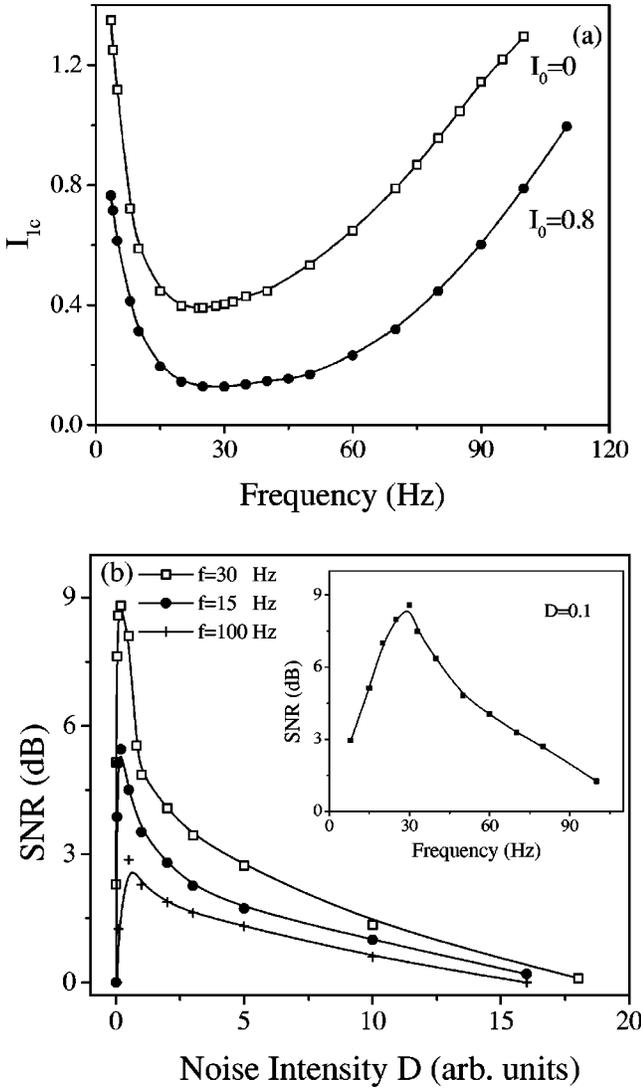


FIG. 1. (a) Threshold amplitude I_{1c} vs signal frequency for $I_0 = 0$ and 0.8 , respectively. (b) SNR of the single neuron vs noise intensity D for $I_0 = 0.8$ and $f_s = 30, 15$, and 100 Hz, respectively. The inset is the SNR vs signal frequency in the case of $D = 0.1$.

at an optimal noise intensity. In the case of high noise, the firing shows a rather random behavior, and the output carrying the component of the input signal is almost buried in noise. Therefore, the SNR drops quickly and even disappears.

Obviously, the SNR for $f_s = 30$ Hz is always larger than that for $f_s = 15$ and 100 Hz, respectively. On the other hand, the difference in the SNR between various frequencies at a low noise level is much larger than that at a high noise level, since in the latter case the noise dominates the firing dynamics of the neuron. The inset of Fig. 1(b) clearly shows that the SNR for the frequency located around 30 Hz has a large value in the case of $D = 0.1$. All these imply that the neuron is more sensitive to the signals with frequencies in the range of 15–60 Hz. Physically, this is due to the resonance between the intrinsic oscillation and the signal, by which the neuron fires spikes around the maxima of the signal and more energy of the noise is transferred to the output signal, leading to a high SNR. Remarkably, a similar frequency sen-

sitivity was reported experimentally [5]. The coherence of the response of the neuron to the input signal is evidently enhanced in the frequency sensitivity range (~ 5 – 60 Hz). This improves the signal-encoding capability of the system. In comparison with those discussed in Ref. [7], we have studied not only the frequency dependence of the threshold amplitude of the input signal, but also the frequency sensitivity of the neuron to weak signals with the SNR measure. These enable us to interpret the experimental result very well.

IV. NEURONAL NETWORK CASE

When single neurons are coupled into a network, the SNR of an individual neuron within the network greatly increases for signals with frequencies in the sensitivity range, as shown in Fig. 2(a). This implies that the coupling does improve the signal-detecting capability of neurons [18], and can be understood as follows. Here all neurons are assumed to have the identical bias and signal strength. Thus, the effective stimulus strength for each neuron is

$$I_i^{\text{eff}}(t) = I_0 + I_1 \sin(2\pi f_s t) + \sum_{j=1, j \neq i}^N \frac{J_{ij}}{N} S_j(t) + \xi_i(t), \quad (6)$$

and the average synaptic input is

$$I_{\text{syn}}(t) = \frac{1}{N^2} \sum_{i=1}^N \sum_{j=1, j \neq i}^N J_{ij} S_j(t). \quad (7)$$

It is found that $I_{\text{syn}}(t)$ presents a periodic feature unless the noise is very large. It is this periodic synaptic input that results in an evident increase in the SNR. For $f_s = 30$ Hz, in the case of very low noise ($D < 0.08$), $I_{\text{syn}}(t)$ presents peaks around the maxima of the signal. But the peaks are often separated by several periods, and the height of them also varies evidently. As a result, there exists a slight increment in the SNR in comparison with that in Fig. 1(b). For the case of low noise ($0.08 \leq D \leq 0.8$), $I_{\text{syn}}(t)$ shows a sharp peak once the signal is at its maxima; that is, $I_{\text{syn}}(t)$ presents a pulselike shape, and varies with the same period as the signal. The height of the peaks in $I_{\text{syn}}(t)$ is far larger than the amplitude of the signal, as shown in Fig. 2(b), where it is of the order 2.9–4.1 for $D = 0.1$. Accordingly, the neurons fire spikes when the signal is around its maxima, i.e., the firings show to be phase locked to the signal. Therefore, the SNR largely increases. As the noise intensity further rises ($0.8 < D < 5$), the peaks in $I_{\text{syn}}(t)$ broaden and shorten, while the range where the value of $I_{\text{syn}}(t)$ is zero between neighboring peaks becomes narrow or even disappears since the neurons fire spikes in bursts. But there still exists an evident periodicity in $I_{\text{syn}}(t)$, resulting in an increase in the SNR. In the case of high noise ($D \geq 5$), the value of $I_{\text{syn}}(t)$ rises with increasing noise, but it contains an evident random component, as shown in Fig. 2(b) for $D = 5$. Thus the SNR increases slightly. In contrast, for $f_s = 100$ Hz, $I_{\text{syn}}(t)$ has a much smaller value at a low noise level, say ~ 0.04 – 0.08 for $D = 0.1$, since the firing of neurons is more frequently interrupted during several driving cycles. As the noise intensity rises, $I_{\text{syn}}(t)$ evidently increases but includes a large random component. These give rise to a small increment in the SNR,

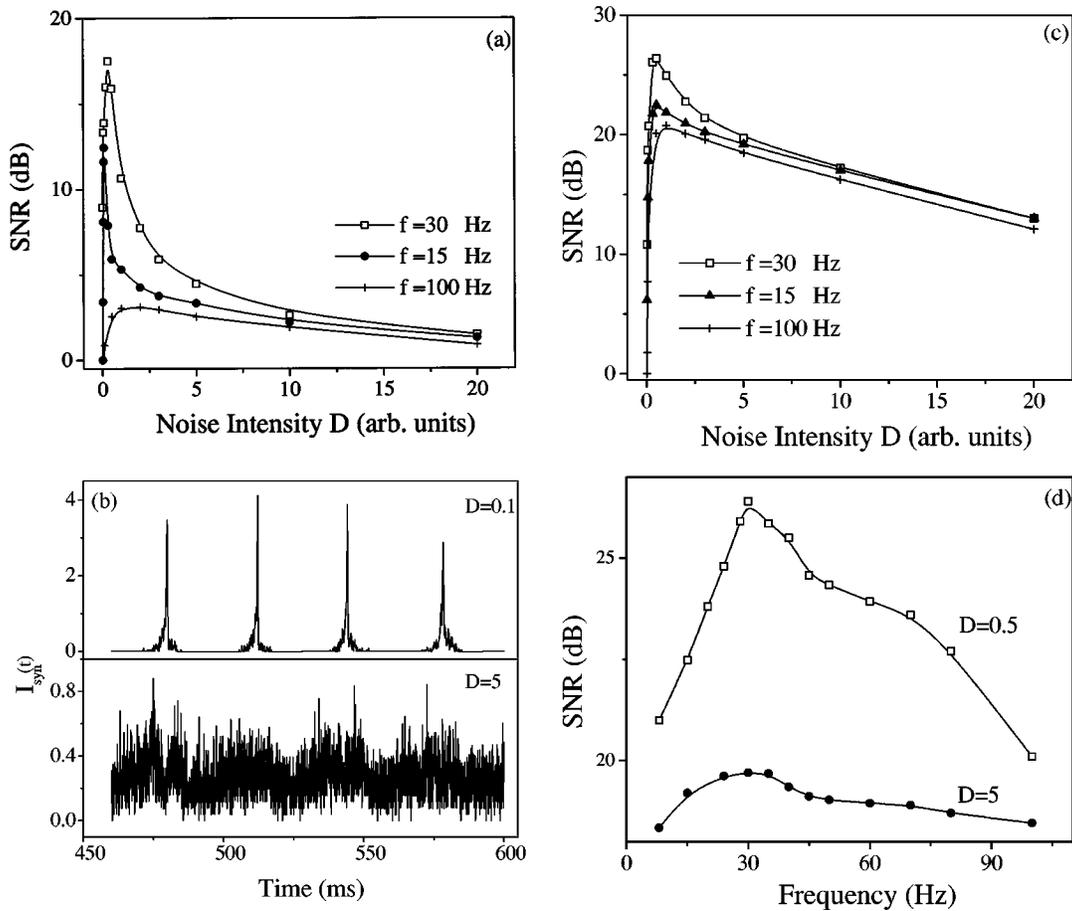


FIG. 2. $I_{0i}=0.8$ and $I_{1i}=0.11$. (a) SNR of the first neuron for $f_s=30$, 15, and 100 Hz, respectively. (b) Average synaptic input $I_{\text{syn}}(t)$ vs time for $f_s=30$ Hz and $D=0.1$ and 5, respectively. (c) SNR of the network for $f_s=30$, 15, and 100 Hz, respectively. (d) The SNR of the network vs signal frequency in the cases of $D=0.5$ and 5, respectively.

compared with Fig. 1(b). Therefore, the difference in the SNR between various frequencies becomes large, and the effect of frequency sensitivity is more notable. It is remarked that the coupling can apparently enhance the frequency sensitivity of neurons.

The effect of frequency sensitivity revealed in the single or individual neurons is also reflected in the activity of the coupled network. Figure 2(c) shows the SNR of the network for the signals with $f_s=30$, 15, and 100 Hz, respectively. Clearly, the SNR for $f_s=30$ Hz is always larger than that for $f_s=15$ and 100 Hz, respectively. As a matter of fact, the dependence of $I^{\text{out}}(t)$ on noise intensity resembles that of $I_{\text{syn}}(t)$. For $f_s=30$ Hz, at a low noise level, $I^{\text{out}}(t)$ presents a sharp peak when the signal is around its maxima, and the peaks are of large amplitude. In the case of high noise, $I^{\text{out}}(t)$ contains a random component though it is still modulated by the periodic signal. Therefore, the SNR first sharply rises and then drops as the noise intensity increases, which presents the typical characteristic of SR. Differently, for $f_s=100$ Hz, $I^{\text{out}}(t)$ is very small at a low noise level, e.g., ~ 0.01 for $D=0.1$. As the noise intensity rises, $I^{\text{out}}(t)$ increases, and contains a periodic component of the signal. Thus the SNR rises and reaches its maximum at an optimal noise level. In the case of high noise, as the neurons fire repetitively and randomly, $I^{\text{out}}(t)$ largely increases but includes a rather random component. Therefore, the SNR first slowly rises and then drops with increasing noise, while the value of optimal noise

intensity slightly rises. It is noted that, according to the definition of $I^{\text{out}}(t)$, the average of the firings of all neurons strengthens the periodic feature of the output of the network, and averages out the random feature of firing of the individual neurons. Therefore, the SNR of the network has a large value and does not drop so fast as that of the individual neurons at a high noise level.

Obviously, such frequency sensitivity depends on the noise intensity. When the noise is large, the sensitivity decreases. Figure 2(d) shows the SNR for different frequencies in the cases of $D=0.5$ and 5, respectively. It is clearly seen that at a low noise level the SNR for frequencies in the range of 15–60 Hz has a large value, due to the cooperation of the intrinsic oscillation with the input signal. This verifies that the neuronal system is more sensitive to signals with these frequencies. As a matter of fact, the frequency corresponding to the maximum of the SNR is about 30 Hz, which is coincident with the intrinsic oscillation frequency for $I_0=0.8$ [11]. Such a large SNR for the signal frequency around 30 Hz is due to the resonance between the input signal and the intrinsic oscillation. Moreover, it is noted that there exists a “shoulder” around $f_s=60$ Hz, which is nearly twice the intrinsic oscillation frequency. This is also due to the resonance between the input signal and the second-order harmonic of the intrinsic oscillation, but its effect is secondary and not evident. Thus there does not appear another peak around 60 Hz. In the case of high noise, however, the differ-

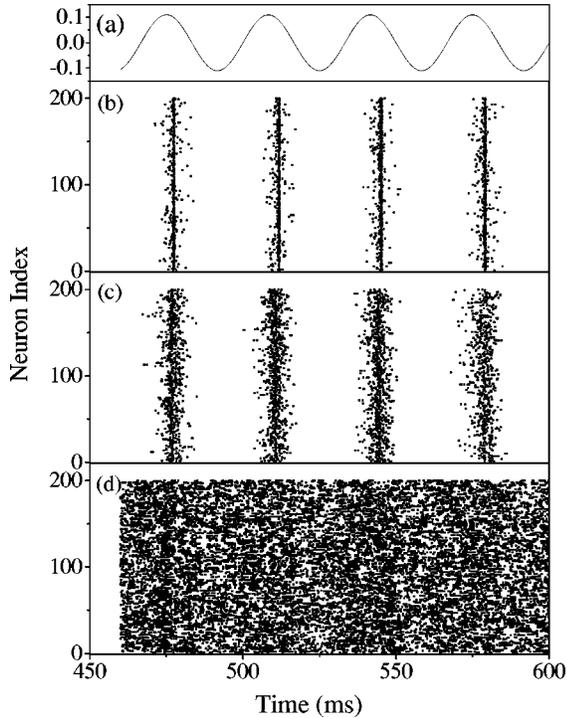


FIG. 3. The spatiotemporal firing pattern is plotted by recording the firing time t_n^i defined by $X_i(t_n^i) > 0.8$ and $X_i(t_n^{i-}) < 0.8$ vs the neuron index for $f_s = 30$ Hz and $D = 0.05$ (b), 0.3 (c), and 5 (d), respectively. (a) shows the input signal. The other parameters are as used in Fig. 2.

ence in the SNR between various frequencies becomes small since the noise dominates the firing dynamics. In other words, the frequency sensitivity decays at a high noise level.

Interestingly, the large value of the SNR of the coupled network is associated with the synchronous firings of neurons. Figure 3 shows the spatiotemporal firing patterns for the case of the signal with $f_s = 30$ Hz. Clearly, the neurons fire synchronously with the same period as the signal at a low noise level [see Figs. 3(b) and 3(c)]. The combination of the intrinsic oscillation and the input signal makes the neurons ready for firing once the low noise is added. The firing maintains a strong coherence with the signal, that is, the neurons fire a single spike or even successively fire spikes in bursts when the signal is around its maxima. Thus the network exhibits a strong spatiotemporal synchronization. Both $I_{\text{syn}}(t)$ and $I^{\text{out}}(t)$ present sharp peaks and vary periodically, resulting in a high SNR. However, in the case of high noise [see Fig. 3(d)], the effective stimulus strength is rather large, so that the neurons fire more frequently, and the firing dynamics presents a random behavior. Therefore, the spatiotemporal synchronization becomes weak or even is destroyed, and $I^{\text{out}}(t)$ contains an evident random component. As a result, the SNR drops quickly. In summary, the network presents a strong spatiotemporal synchronization when the SNR is around its maximum.

Physically, the spatiotemporal synchronization mainly results from the effects of resonance between the periodic signal and those the intrinsic oscillation, and those of nonlinear spatiotemporal summation of post-synaptic potentials. The latter is an intrinsic feature of neurons. The periodic signal makes the neurons fire synchronously, which is strengthened

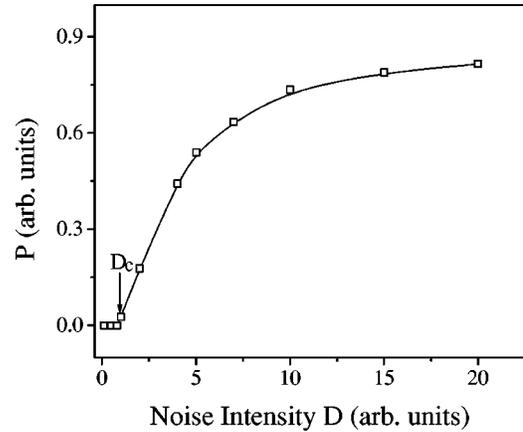


FIG. 4. P vs noise intensity D . P is an average of the ratio of the number of firing events at the minima to that at the maxima of the signal over 100 periods. The signal frequency is taken as $f_s = 30$ Hz, and the number of neurons is $N = 200$.

in the presence of coupling. At a low noise level, owing to the resonance between the intrinsic oscillation and the periodic signal, the firings of neurons show to be phase locked to the input signal, leading to synchronized firings. As a matter of fact, when stimulated by a signal with a low frequency [19], the neurons take less times of spatiotemporal summation to fire, due to long duration of the signal staying around its maxima. The neurons fire nearly every period of the signal, which is beneficial to synchronous firing. However, in the case of a signal with a high frequency, the firings of neurons may be interrupted in several driving cycles because the neurons need more times of spatiotemporal summation to fire. Thus the network presents a weak synchronization. In addition, the coupling strength $J_{ij} \in [-4, 20]$ represents a strong coupling [12], which also contributes to the large value of the SNR and synchronous firings of neurons.

In fact, how the coherence of the firing of neurons with the input signal varies with increasing noise can be more clearly seen as follows. For the case of the signal with $f_s = 30$ Hz, we count a number M of firing events of all the neurons within a certain time interval, say 1 ms. We define P as an average of $M(\text{min})/M(\text{max})$ over 100 periods to characterize the firing coherence with the signal, with $M(\text{min})$ and $M(\text{max})$ corresponding to the number of firing events around the minima and maxima of the signal, respectively. Figure 4 shows P versus noise intensity D . Clearly, P is zero when $D < 1$, which means that there are no firings around the minima of the signal, and the neurons show a strong coherence with the signal. When $1 \leq D < 5$ there appear more firings around the minima of the signal, but the value of P is smaller than 0.5, which indicates that the neuronal firings still show some coherence with the signal. Thus $D = 1$ may be defined as a ‘‘critical’’ noise intensity D_c where the firings are no longer localized to peaks of the signal. However, the value of D_c may be different for various input signals. For $D > 5$ the high noise dominates the firing dynamics, and the coherence of firings with the signal becomes weak with $P > 0.5$. Obviously, the low P is associated with the synchronous firings of the neurons and the large value of the SNR [cf. Figs. 2(c) and 3].

V. DISTRIBUTED BIAS OR SIGNAL STRENGTH

So far, we have discussed the phenomenon of frequency sensitivity in signal detection in both a single neuron and a coupled network. Such frequency sensitivity results from the resonance between the intrinsic oscillation of the system and the input signal. However, it is noted that the frequency sensitivity has no specific demand that all neurons be of an identical bias or signal strength. As a matter of fact, if $I_0 < I_c$, there always exists a resonance effect when the signal frequency is around 30 Hz, as seen in Fig. 1(a). In other words, the effect of frequency sensitivity can be generally interpreted in our model, independent of the specific value of the bias or the signal amplitude for each neuron. To check this argument, we discuss the following two interesting cases: case I, in which the neurons have distributed values of bias; and case II, when the signal strength is Gaussian-like distributed on the network.

Case I. It is well known that in a real neuronal system each neuron may receive different synaptic inputs from the outside of the network considered, and have various fluctuations in membrane, such as the thermal one. Therefore, as a simple consideration for a total result of these effects, we introduce a distribution of the bias I_{0i} ; that is, neurons may have different values of bias. For simplicity, I_{0i} is assumed to be uniformly distributed between 0 and 1, with a maximum $I_{0i}^{\max} < I_c = 1.32$ and a minimum $I_{0i}^{\min} \sim 0$ [20], while the signal strength is assumed to be identical for all neurons. With such a limitation of $I_{0i} \in [0, 1]$, the minimal threshold amplitude is $I_{1c} = 0.08$, related to $f_s = 26$ Hz. The signal amplitude is taken as $I_{1i} = 0.072$, so that all the signals are subthreshold. It is noted that the above consideration may model such a situation where the neurons are subjected to a common weak signal but have different values of bias due to the configuration of the network or to different features of neurons themselves. Clearly, the dynamic behavior of neurons is modulated by the same signal throughout the local network.

Figure 5(a) shows the SNR of the network for signals with frequencies of $f_s = 24, 15,$ and 100 Hz, respectively. Similar characteristics to those in Fig. 2(c) can be seen. However, compared with Fig. 2(c), the difference in the SNR between various frequencies becomes somewhat large, while the magnitude of the SNR apparently drops. This can be understood as follows. For $f_s = 24$ Hz, since the neurons have different bias values, the network presents a weak spatiotemporal synchronization even at a low noise level. Owing to the small effective stimulus strength, the firings of neurons are often interrupted during several driving cycles, resulting in a low SNR. As the noise intensity further rises, $I^{\text{out}}(t)$ increases and presents a periodic feature. Thus the SNR rises and reaches its maximum. In the case of high noise, since the noise dominates the firing dynamics, $I^{\text{out}}(t)$ apparently increases but contains an obvious random component. This is why the value of the SNR becomes small. For $f_s = 100$ Hz, a similar dependence of $I^{\text{out}}(t)$ on noise intensity can be observed. But $I^{\text{out}}(t)$ has a very small value at a low noise level due to the effect of more times of spatiotemporal summation. This results in large differences in the SNR between various frequencies at a low noise level. Figure 5(b) shows the SNR for different frequencies in the cases of $D = 0.5$ and 5 , respectively. Clearly, at a low noise level, the SNR for those

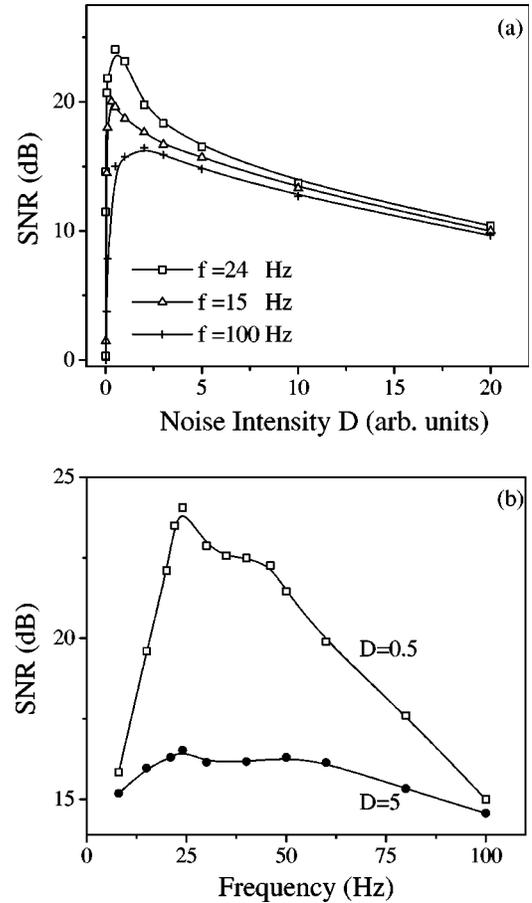


FIG. 5. $I_{0i} \in [0, 1]$ and $I_{1i} = 0.072$. (a) SNR of the network vs D for $f_s = 24, 15,$ and 100 Hz, respectively. (b) SNR vs signal frequency for $D = 0.5$ and 5 , respectively.

in the frequency sensitivity range of 15–60 Hz has a large value. There also exists a “shoulder” around 50 Hz. This further verifies that the frequency sensitivity does exist in signal detection, and imposes slight restrictions on the values of bias for neurons. In the case of high noise, however, the difference in the SNR between various frequencies becomes small as the noise dominates the firing dynamics of the neurons. This means that the effect of frequency sensitivity may be distorted by high noise.

Case II. In real experimental situations the signal strength, i.e., the amplitude I_{1i} of the input signal, exerted on each neuron may be different due to different features of neurons themselves. When a periodic signal is applied to the network, the neurons may “feel” different stimulus strengths; some feel the signal as a suprathreshold stimulus, while others feel it as a subthreshold one. For simplicity, here we assume that all neurons feel the signal as a subthreshold input with strength Gaussian-like distributed on the network, e.g.,

$$I_{1i} = \frac{34}{\sqrt{2\pi\sigma}} e^{-(i-100)^2/2\sigma}, \quad (8)$$

with $\sigma = 1400$. This means that the value of I_{1i} is continually distributed between 0 and 0.36, and is symmetrical about $I_1 = 0.36$ at the 100th neuron. In this case, the maximum I_1^{\max} is smaller than the minimal threshold amplitude $I_{1c} = 0.41$ in

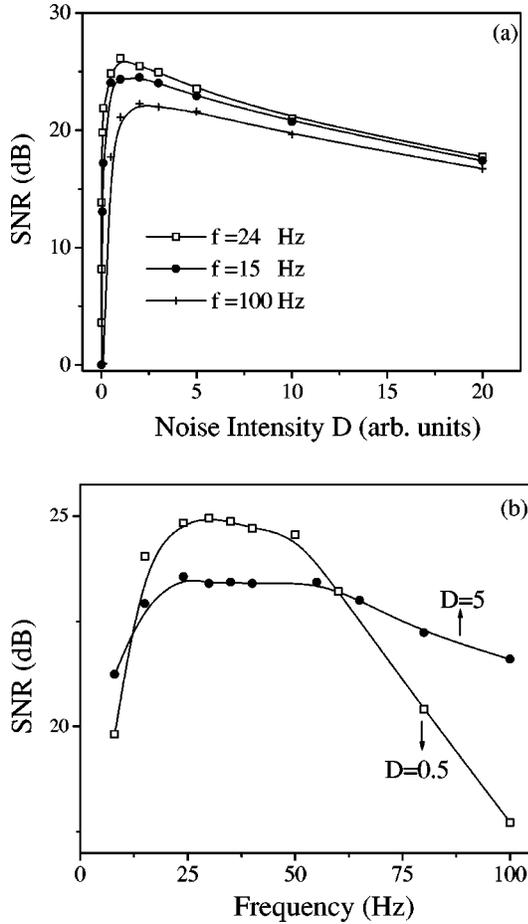


FIG. 6. (a) SNR of the network vs D for $f_s=24$, 15, and 100 Hz, respectively. (b) SNR vs signal frequency for $D=0.5$ and 5, respectively.

the case of $I_{0i}=0$ [see the curve for $I_0=0$ in Fig. 1(a)], and hence all signals with different frequencies are subthreshold. The above consideration also enables us to discuss the relationship between the stimulus strength and the signal-detecting ability of neurons. Indeed, the curve of the SNR of the individual neurons versus the neuron index presents a Gaussian-like shape. This means that the signal detection ability is proportional to the signal strength. This will be reported in detail elsewhere. Figure 6(a) shows the SNR for $f_s=24$, 15, and 100 Hz, respectively. Owing to the relatively small effective stimulus strength (here $I_0=0$), the SNR does not vary as sharply as that in Fig. 2(c) with increasing noise, and the optimal noise intensity shifts to a large value. Obviously, the SNR for frequencies in the range of 15–60 Hz has a large value, as shown in Fig. 6(b) for $D=0.5$. This indicates that the frequency sensitivity only relies on the frequency matching between the input signal and the intrinsic oscillation of the system. In the case of high noise, the difference in the SNR between various frequencies becomes small since the firings of neurons are dominated by noise. That is, the frequency characteristic of the signal is no longer so important for signal detection at a high noise level.

VI. CONCLUSION

In this paper we have discussed the effect of frequency sensitivity in weak signal detection via numerical simulation.

In the case of a subthreshold bias, the membrane potential undergoes a damping oscillation to the quiescent state with a frequency of 11–33 Hz. Such an oscillation is considered as intrinsic, and has a significant effect on the responses of the neuronal system to subthreshold periodic signal plus white noise. The SNR of either a single neuron or a network has been studied, and is found to present the typical characteristic of SR. Particularly, a frequency sensitivity range of 15–60 Hz for weak signal detection is found. For signals with frequencies in such a range, the SNR has a large value, implying that the neuronal system is more sensitive to these signals. Such a frequency sensitivity results from resonance between the intrinsic oscillation and the periodic signal. It is noted that, in the case of the signal with $f_s=30$ Hz, the network presents a strong spatiotemporal synchronization when the SNR is around its maximum. When the noise intensity $D < D_c=1$, the neurons show coherent firings, phase locked to the signal, whereas the coherence of firings with the signal becomes less evident when D is much larger than D_c . Moreover, we have investigated two interesting cases where either the values of the bias or the signal strength for the neurons may be different. The results indicate that the effect of the frequency sensitivity generally exists in the signal detection.

The existence of the frequency sensitivity range is of functional significance for signal encoding. This can enhance the sensitivity of the neuronal system to weak signals with frequencies in such a range and improve its encoding of these signals, which has been experimentally demonstrated. In addition to the report in Ref. [5], it was also found that during the attack of the wasp, air particles oscillate in the same frequency range as we found, and the escape behavior was reliably observed [5,21]. Such escape responses might take advantage of SR and the effect of frequency sensitivity; otherwise it may be difficult to understand the fast escape behavior of the cricket. In short, the effect of frequency sensitivity can effectively improve the signal-detecting ability of the system.

Finally, it is worth noting that the frequency range of 15–60 Hz is reminiscent of the synchronous 40-Hz oscillation, i.e., the fast synchronous rhythm of electrophysiological activities in the γ frequency band, observed in the olfactory system, the cat visual cortex, the awake state of a human being, etc. [12]. Such synchronized oscillations may result from the intrinsic features of neurons and the long-range interactions between them. However, whether the 40-Hz oscillations relate to the intrinsic oscillation of the system remains an interesting question which deserves further study. In conclusion, the intrinsic oscillation underlying the frequency sensitivity is of importance for information processing.

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