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Generation of Spontaneous Synchronized Rhythm and its Role in Information Processing *

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The generation of spontaneous synchronized rhythm and its role are studied by using a globally coupled excitable stochastic neuronal network. When the coupling strength exceeds a critical value, the neurons with a suitable noise in the network exhibit a strong tendency to synchronize and display a spontaneous rhythm. The coherence of the network can be enhanced by a suitable noise and a coupling of the network. The spontaneous rhythm enhances the ability of the network in processing weak periodic signals.

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Recently, spontaneous synchronized rhythms have been observed in experiments in various neural systems.[1] It is suggested that these rhythms may serve as a mechanism for binding spatially distributed features into a coherent object in higher brain functions.[2] In lower level processes, they may be used for information processing of neuronal activity.[3] But the mechanisms underlying the generation of these rhythms are not clear yet. The factors affecting the frequencies of the rhythms are also unknown.

In addition, a phenomenon called the autonomous stochastic resonance (SR) or coherence resonance (CR) has been examined in excitable neurons.[4,5] A common feature of this type of system is the increasing coherence of the motion and resonant-like behaviour of the coherence induced purely by noise without any external signal. Note that, in this case, a noiseless neuron does not exhibit any self-sustained oscillations but a noise of an optimal intensity can enable the neurons to generate a coherent firing around a main frequency.[4,5] The noise-induced firings lead to a peak at a definite frequency in the power spectrum density (PSD). The signal-to-noise ratio (SNR) of the output of the neuron can be maximized by the noise with an optimal intensity (see Fig. 1). Thus, a noise-driven excitable neuron can be viewed as a CR oscillator. Since such a stochastic neuron displays noise-optimized spontaneous oscillations, interesting questions arise. How do these stochastic neurons behave when they are coupled with each other? Can they display a spontaneous synchronized rhythm? What role does the possible generated rhythm play in the information processing of the neuron to external stimuli?

In this letter, we address these questions by a globally coupled stochastic Hodgkin–Huxley (HH) neuronal network which is described by:

$$C_m\frac{\mathrm{d}V_i}{\mathrm{d}t} = -g_{\mathrm{Na}}m_i^3h_i(V_i-V_{\mathrm{Na}})-g_{\mathrm{K}}n_i^4(V_i-V_{\mathrm{K}}) -g_{\mathrm{l}}(V_i-V_{\mathrm{l}})+\xi_i(t)+I_i^{\mathrm{syn}}(t), \quad (1)$$

$$\frac{\mathrm{d}m_i}{\mathrm{d}t} = \frac{m_\infty(V_i)-m_i}{\tau_m(V_i)}, \quad (2)$$

$$(3)$$

$$\frac{\mathrm{d}h_i}{\mathrm{d}t} = \frac{h_\infty(V_i)-h_i}{\tau_h(V_i)}, \quad (4)$$

$$\frac{\mathrm{d}n_i}{\mathrm{d}t} = \frac{n_\infty(V_i)-n_i}{\tau_n(V_i)}, \qquad i=1,\cdots N, \quad (5)$$

where V_i, m_i, h_i and n_i are the membrane potential, the gating variables of Na^+ and K^+ channels, respectively, $g_{\mathrm{Na}}, g_{\mathrm{K}}$ and g_{l} are the maximal values of conductance of the sodium, potassium and leakage currents; and $V_{\mathrm{Na}}, V_{\mathrm{K}}$ and V_{l} are the corresponding reversal potentials. The number of neurons is taken as $N = 100$. The parameter values are:[6,7] $V_{\mathrm{Na}} = 50\,\mathrm{mV}$, $V_{\mathrm{K}} = -77\,\mathrm{mV}$, $V_{\mathrm{l}} = -54.4\,\mathrm{mV}$, $g_{\mathrm{Na}} = 120\,\mathrm{mS/cm^2}$, $g_{\mathrm{K}} = 36\,\mathrm{mS/cm^2}$, $g_{\mathrm{l}} = 0.3\,\mathrm{mS/cm^2}$, and $C_{\mathrm{m}} = 1\,\mu\mathrm{F/cm^2}$. The functions $m_\infty(V)$, $h_\infty(V)$, and $n_\infty(V)$ and the characteristic times (in milliseconds) τ_m, τ_h, τ_n are given by: $x_\infty(V) = a_x/(a_x+b_x)$, $\tau_x = 1/(a_x+b_x)$ with $x = m,\ h,\ n$ and $a_m = 0.1(V+40)/\{1-\exp[(-V-40)/10]\}$, $b_m = 4\exp[(-V-65)/18]$, $a_h = 0.07\exp[(-V-65)/20]$, $b_h = 1/\{1+\exp[(-V-35)/10]\}$, $a_n = 0.01(V+55)/\{1-\exp[(-V-55)/10]\}$, $b_n = 0.125\exp[(-V-65)/80]$.

There are numerous noise sources in nervous systems,[8] such as thermal fluctuations, the variability of membrane parameters, and spontaneous opening or closing of ion channels, which can be modelled as a Gaussian white noise with

$$\langle\xi_i(t)\rangle = 0, \quad \langle\xi_i(t_1)\xi_j(t_2)\rangle = 2D\delta_{ij}\delta(t_1-t_2). \quad (6)$$

Each neuron in the network is subjected to an independent noise but with the same intensity D.

Here all neurons are assumed to be globally coupled with each other, and the coupling is described as

$$I_i^{\mathrm{syn}}(t) = -\sum_{j=1,j\neq i}^{N}\frac{g_{\mathrm{syn}}}{N}\alpha(t-t_j)(V_i-V_{\mathrm{syn}}^{ij}), \quad (7)$$

with $\alpha(t-t_j) = \alpha(t') = (t'/\tau_s)\mathrm{e}^{t'/\tau_s}$.[7] Here, t_j is the firing time of the jth neuron; $\tau_s = 2\,\mathrm{ms}$ is the characteristic time of the synaptic interactions, V_{syn}^{ij} is the synaptic reversal potential taken as $30\,\mathrm{mV}$, corresponding to the excitatory coupling (here, we only study the case of the excitatory couplings and do not consider the inhibitory ones) and g_{syn} is the coupling strength. The coupling model used here is based on

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its physiological meaning and relatively for simplicity in physics.[7] A more complicated (or simple) coupling model may change slightly the dynamics evolution of the HH neuronal network, but the related physical picture will be the same.

The numerical integration of Eqs. (1)–(4) is done by using a second-order algorithm suggested in Ref. 9, and the integration step is taken as 0.03 ms.

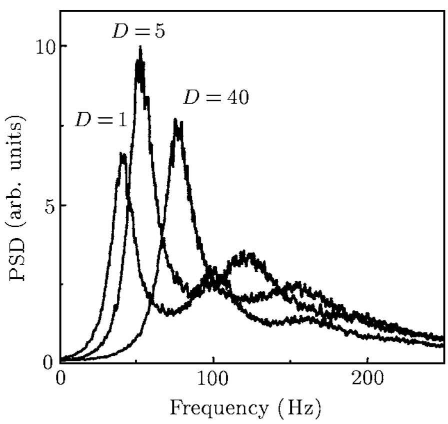

Fig. 1. PSD of the firings of a single neuron for various noise intensities $D = 1$, 5 and 40.

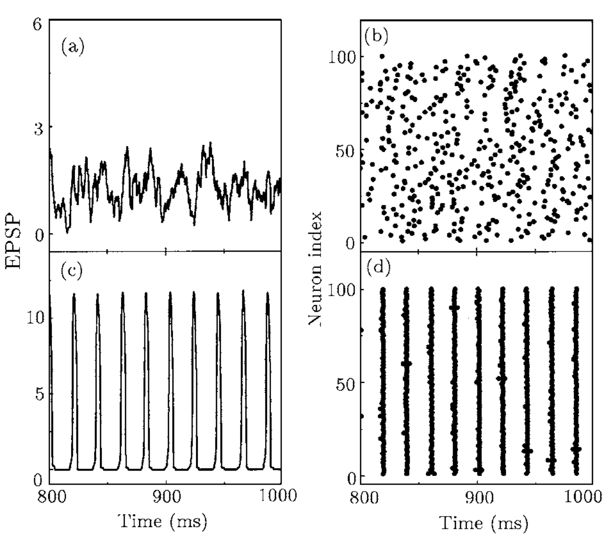

Fig. 2. For $D = 5$, the EPSP of a neuron in the network with $g_{\rm syn} = 0.1$ (a), the corresponding raster plot of firings of the network (b), the EPSP of a neuron in the network with $g_{\rm syn} = 5$ (c) and the corresponding raster plot of firings of the network (d).

To quantify the synchronization of neuronal firings in the network, we introduce a coherence measure based on the normalized cross-correlations of neuronal pairs in the network.[10] The coherence between two neurons i and j is measured by their cross-correlation of spike trains at zero time lag within a time bin of $\Delta t = \tau$. More specifically, suppose that a long time interval T is divided into small bins of τ and that two spike trains are given by $X(l) = 0$ or 1, $Y(l) = 0$ or 1, with $l = 1, 2, \cdots, K$ (here $T/K = \tau$). Thus, a coherence measure for the pair is defined as:

$$k_{ij}(\tau) = \frac{\sum_{l=1}^{K} X(l)Y(l)}{\sqrt{\sum_{l=1}^{K} X(l) \sum_{l=1}^{K} Y(l)}}. \tag{8}$$

The population coherence measure $k(\tau)$ is defined by the average of $k_{ij}(\tau)$ over all pairs of neurons in the network, where τ is taken as 1 ms. We use $k(\tau)$ to quantify the synchronization of coherent firings of the network.

We first examine the role of the coupling strength $g_{\rm syn}$ and the noise on the collective properties of the network. For a noise with $D = 5$, from Fig. 1 we know that the neuron exhibits coherent firings around a main frequency of 50 Hz. When such neurons interact with each other with a weak coupling strength, e.g. $g_{\rm syn} = 0.1\,{\rm mS/cm^2}$, the corresponding excitatory postsynaptic potential (EPSP) is very small and random [see Fig. 2(a)]. The neurons in the network oscillate with a weak correlation with each other and display stochastic firing phases. Thus, the raster recording all the firing events of the network exhibits an asynchronous state [see Fig. 2(b)]. When the coupling strength increases, e.g. $g_{\rm syn} = 5\,{\rm mS/cm^2}$, the excitatory postsynaptic potential (EPSP) becomes large and displays a distinct periodic characteristic [see Fig. 2(c)]. Thus, the firing phases of the neurons are driven in step by the strong coupling. The output of the network shows a fine synchronization and the spatiotemporal order is achieved [see Fig. 2(d)]. The neurons in the network show a strong tendency to cooperate with each other and to display a synchronized rhythm. These results suggest that the coupling among the neurons plays an important role in generating the spatiotemporal synchronization.

Now, we vary the coupling strength of the network from $g_{\rm syn} = 0.1$ to 20 and examine the population coherence $k(\tau)$ of the network varying with the noise intensity. From Fig. 3(a), we note that for $g_{\rm syn} = 0.1$, $k(\tau)$ takes a very small value in a large range of the noise. The synchronization cannot be obtained for such a weak coupling. When the coupling strength exceeds a critical value, i.e. $g_{\rm syn} = 1$, the synchronization still cannot be obtained for a weak noise. However, when the noise intensity increases, the coherence of the spatiotemporal firings of the network increases quickly and is optimized by a region of noise with suitable intensities. When the noise intensity further increases, $k(\tau)$ decreases slowly and finally reaches its saturation in a high noise level due to the strong coupling. The evolution of the population coherence of the network with the noise intensity shows an SR-like behaviour which can be called the CR of the network. This phenomenon suggests that the coherence of the spatiotemporal firings of the network can be enhanced by two factors, i.e., the coupling and the suitable noise level.

Figure 3(b) shows the PSD of the firings of a neuron in the network with $g_{\rm syn} = 5$ for different noise intensities. It is noted that the peak in the PSD is very small when the noise is too weak, i.e., $D \le 1$.

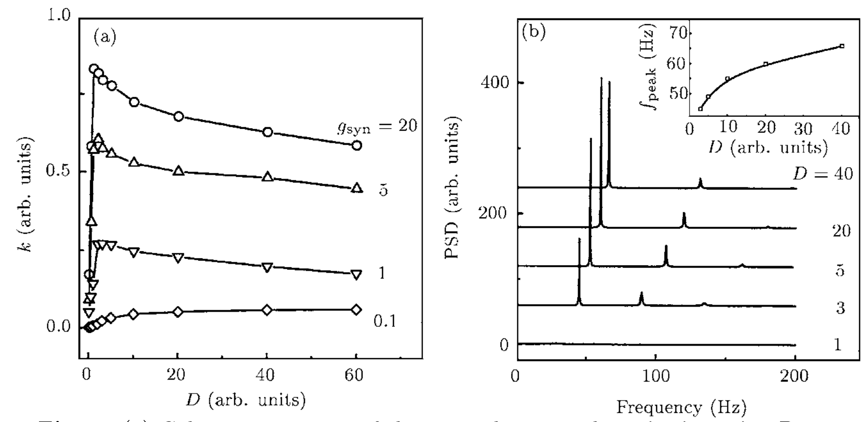

Fig. 3. (a) Coherence measure of the network versus the noise intensity D for four coupling strengths, $g_{syn} = 0.1$, 1, 5, and 20. (b) PSD of the firings of a neuron in the network with $g_{syn} = 5$ for different noise intensities $D = 1$, 3, 5, 20 and 40. Values for each curve except for $D = 1$ have been shifted by a factor of 60 on the vertical axis. Inset: the frequency of the first peak of PSD versus different noise intensities.

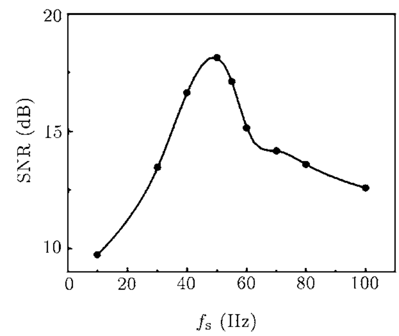

Fig. 4. For $D = 5$, SNR of a neuron in the network with $g_{syn} = 5$ versus input signal frequency f_s.

When the noise intensity increases, the sharp coherent peaks are generated and optimized by a region of the noise with suitable intensities, which is in agreement with the coherence measure of the network [see Fig. 3(a)]. The sharp peak is induced by the network itself and is locked at the frequency of the rhythm. The highest and the most narrow peak related to the most coherence[5] of the network is obtained at an optimal noise level ($D = 5$). All the main peaks of the PSD are in the range of $30 - 70$ Hz which are the frequencies of the synchronized rhythms [see the inset of Fig. 3(a)]. The frequency of the rhythm can also increase with increase of the coupling g_{syn}, and finally saturate for a large g_{syn} (the data is not shown). Both the noise and the coupling, together with the excitability of the neuron, affect the frequency characteristic of the rhythm.

Finally, we study the role of the synchronized rhythms in information processing. Here we input a subthreshold periodic signal $A\cos(2\pi f_s t)$ with $A = 1\,\mu\text{A/cm}^2$ to the sustaining-oscillationed network (all the neurons are subject to an independent noise with intensity $D = 5$) with $g_{syn} = 5$. From Fig. 4 it is worthwhile to note that the SNR of the output of a neuron in the network has a maximum for the signals with frequencies around 50 Hz. This suggests that the weak signals with frequencies around 50 Hz are more sensitive to being detected and transmitted than other signals with high or low frequencies. From Fig. 3, we know that the frequency of the synchronized rhythm of the network for $g_{syn} = 5$ and $D = 5$ is about 50 Hz. Physically, when the frequency of the input signal is close to that of the oscillation of some kinds of oscillators, a resonance will occur. The same cases occur when the periodic signals are input to the sustaining-oscillationed network. It is the resonance between the spontaneous oscillation of the network and the input signal that makes the network absorb the energy of the environment and become more coherent with the signal. Thus, the output of the neuron in the network displays a high SNR. The rhythm of the network seems to provide a time clock for neurons in information processing. The processing ability for external signals of the network around the frequency of the rhythm is significantly enhanced. This phenomenon can help us in understanding the role of various spontaneous rhythms in brain. In addition, the noise plays an important role in enhancing the ability of the neuron in processing weak signals via SR,[11,12] which has been discussed widely but is not the focus of this letter.

In conclusion, when the coupling of the network is strong enough, the spontaneous rhythm is generated and even enhanced by the suitable noise. The CR effect due to the noise and the synaptic coupling play an important role in generating these rhythms. The frequency of the rhythm is determined by the excitability of a single neuron, the synaptic coupling, and the noise. For a signal with a frequency near that of the spontaneous rhythm to the network, the responses of the neurons are significantly enhanced and their ability is improved in information processing.

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