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Phase-disorder-induced double resonance of neuronal activity

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It is well known that resonance can be induced by external noise or diversity. Here we show that resonance can be induced even by a phase disorder in coupled excitable neurons with subthreshold activity. In contrast to the case of identical phase, we find that phase disorder plays an active role in enhancing neuronal activity. We also uncover that the presence of phase disorder can induce a double resonance phenomenon: phase disorder and coupling strength both can enhance neuronal firing activity. A physical theory is formulated to help understand the mechanism behind this double resonance phenomenon.

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In the human brain, there is a large variety of chaotic firings of neuron networks and columns that function as complex oscillators in noisy electrochemical environment [1]. Phase synchronization of firings is closely associated with higher order brain functions such as perceptual binding [2–4]. In such brain processes, synchronization occurs in the γ (approximately between 30–90 Hz) wave across different regions of the brain [4]. In the awaked cat, for example, synchronization occurs between areas of the visual and parietal cortex and between areas of the parietal and motor cortex as a means of integrating various aspects of perceptual properties being observed [3]. This synchrony is particularly strong between areas subserving related functions. Thus, the correlated or synchronized firings in different parts of the brain underlie the information processing associated with cognition and perception. How does phase disorder in input signals affect such coherent neuronal firings?

It is well known that noise plays a surprising role in enhancing the detection and transmission of weak signals via a mechanism commonly known as stochastic resonance (SR) [5–9]. Interestingly, it has been revealed that the electrochemical noises in neural firing process provide internal noise sources to trigger SR in the brain and thus profit the cognition, perception, and behavior [1,9]. Except noise, it is also found that the diversity of neurons or excitable oscillators can induce SR [10]. To advance our understanding of SR in excitable systems further, here we examine the role of phase disorder in coherent activity of neurons.

Considering the diversity of neurons and their different distances to signal source, neurons will have different response abilities to external signals, which may be equivalent to the same strength of signal with different phases. For example, surface-feeding fish can determine the prey angle highly accurate through discriminating the target signal's arriving time or phase difference between the distributed lateral line organs [11]. This is in fact a random phase that benefits signal detection. This idea may be useful in making efficient artificial neural devices [12–14]. In this Rapid Communication, we study how the randomized phases influence firing synchronization of neurons. We find that the SR can be induced even by phase disorder in coupled excitable neurons with subthreshold activity. Furthermore, we find that phase disorder may play an active role in neural firings and can induce a double resonance on both the range of phase disorder and the coupling strength, which is impossible in the case of identical phase. A physical theory is formulated to provide an understanding of the mechanism behind this double resonance phenomenon. These findings may be useful in improving the quality of artificial devices and helpful in understanding higher-level cognitive and perceptual brain functions.

As a paradigmatic model, FitzHugh-Nagumo (FHN) neuron is usually used to describe the dynamics of spiking of neural activities. Here, we use it to investigate the effect of phase disorder. Consider N coupled excitable FHN neurons as follows:

$$\epsilon\dot{x}_i = x_i - \frac{x_i^3}{3} - y_i + \frac{g}{N-1}\sum_{j=1}^{N}(x_j - x_i),$$

$$\dot{y}_i = x_i + b + A\sin\left(\frac{2\pi}{T}t + \varphi_i\right), \quad i,j, = 1, \ldots, N, \qquad (1)$$

where x_i and y_i represent the fast activator and slow inhibitor variables, respectively, g denotes the coupling strength, ϵ is a small parameter, and $A\sin(\frac{2\pi}{T}t+\varphi_i)$ is the external signal received by neuron i. When the amplitude A is not strong enough to stimulate firings, the signal is called subthreshold signal. For a single neuron without external signal, it will be excitable when $b>1$. We here focus on the case of subthreshold signal with randomized initial phase φ_i, which may come from the distributed time delays or nonuniform media in signal transmission channel. Here, we set $N=1000$, $b=1.02$, $\epsilon=0.01$, $A=0.05$, and $T=5$. There is no firing activity in an isolated neuron with these parameters. For simplicity, the initial phases φ_i are chosen randomly from the interval $(-k\pi, k\pi)$.

We study the effect of increasing the range k from 0 to 1. To observe the effect easily, we rearrange the neuron indexes

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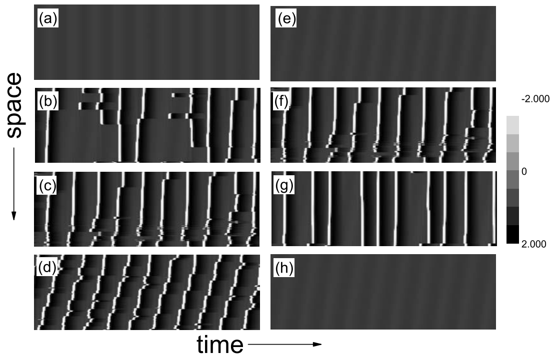

FIG. 1. Spatiotemporal patterns for $N=1000$ and $10T$ time series $x_i(t)$. Left panels with $g=10^{-2}$: (a) $k=0$, (b) $k=0.43$, (c) $k=0.5$, and (d) $k=1$; right panels with $k=0.5$: (e) $g=10^{-2.6}$, (f) $g=10^{-2.0}$, (g) $g=10^{-1.6}$, and (h) $g=10^{-1.0}$. The indices are rearranged based on the ordered phase values.

from 1 to N according to their sorted values of phase φ_i. The results are calculated after discarding $400T$ transient process. Let the coupling strength $g=10^{-2}$. We first consider the case of identical phase with $k=0$. Our numerical simulations show that there are no firings in Eq. (1) [see Fig. 1(a)]. Then we gradually increase k from 0 to 0.43. We surprisingly find that it is possible for part or all neurons to fire or spike coherently [see Fig. 1(b)]. As k is increased to $k=0.5$, the firing rate is enhanced and almost all neurons show sustained spikes coherently [see Fig. 1(c)]. Further increase in k will result in decrease in firing coherence, see Fig. 1(d), which appears as a traveling wave. Therefore, we have observed a phenomenon, i.e., firing synchronization, which is purely induced by disordered phases.

Does the firing pattern induced by phase disorder depend on the coupling strength? Our numerical simulations show that for a fixed k, there is a critical g_c. The firing patterns show up only when $g > g_c$. Very interestingly, we find that the firing patterns disappears when g is too large. Figures 1(e)–1(h) show the results of $k=0.5$ for $g=10^{-2.6}$, $10^{-2.0}$, $10^{-1.6}$, and $10^{-1.0}$, respectively. Therefore, we conclude from Figs. 1(a)–1(h) that there is a double resonance of firing synchronization on both the range of phase disorder and the coupling strength, which is impossible in the case of identical phase.

From Fig. 1(d) we see that the population forms a traveling wave although they are not synchronized. As firing is the basic requirement for cognition and perception, we calculate the firing rate r which is defined as the average number of spikes in a period T of the external signal. Figure 2(a) shows the numerical results for the range of phase disorder where the "squares" and "circles" represent the cases for $g=10^{-2.6}$ and 10^{-2}, respectively. It is easy to see that r becomes greater than 0 at a critical k_c and then increase to a saturate value 1 when k increases further. We have observed the similar situation for the coupling strength, see Fig. 2(b) where the squares and circles represent the cases for $k=0.4$ and 0.5, respectively.

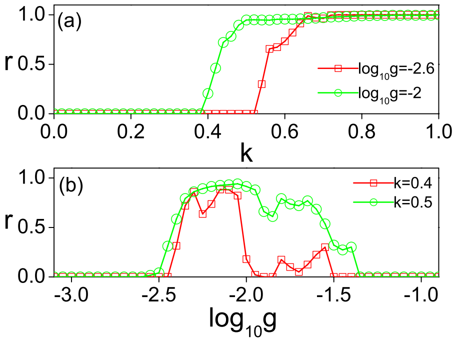

FIG. 2. (Color online) How the phase disorder and coupling strength influence the firing rate r with (a) r versus k and (b) r versus g.

From Fig. 1 we see that there is an optimal k and g for the firing coherence. To measure the degree of coherence, we calculate the signal amplification factor Q which characterizes the response to external signal and is defined at the signal frequency $\omega=\frac{2\pi}{T}$ as follows [8,15,16]:

$$Q_{\sin} = \frac{1}{nT}\int_0^{nT} 2X(t)\sin(\omega t)dt,$$

$$Q_{\cos} = \frac{1}{nT}\int_0^{nT} 2X(t)\cos(\omega t)dt,$$

$$Q = \sqrt{Q_{\sin}^2 + Q_{\cos}^2}, \tag{2}$$

where $X(t)=\frac{1}{N}\Sigma_{i=1}^{N}x_i(t)$. In our simulations, we set $n=50$ and Q is averaged with 20 realizations. Figure 3 shows the results corresponding to Fig. 2. Obviously, there is a finite range for both k and g where Q is bell shaped, which is the signature of SR.

To observe how the double resonance behaves for other fixed g or k, Fig. 4 shows the dependence of Q on both the g and k. From Fig. 4 it is easy to see that the positive Q can only appear when k is greater than a critical range k_c, indicating that a finite range of phase disorder is a necessary condition for coupled neurons with subthreshold signal to have firing synchronization.

Let us turn to the mechanism of firings induced by phase disorder. For the case of fixed coupling g, weak phase disorder for $k < k_c$ will not make a significant difference among the trajectories of neurons and thus the resulted coupling

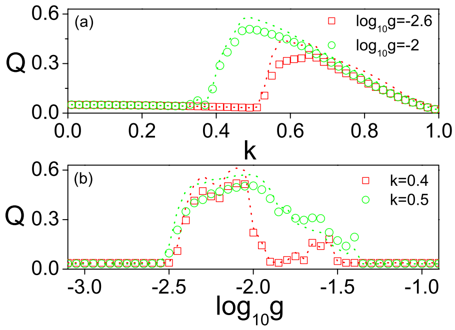

FIG. 3. (Color online) How the phase disorder and coupling strength influence the signal amplification factor Q with (a) Q versus k and (b) Q versus g.

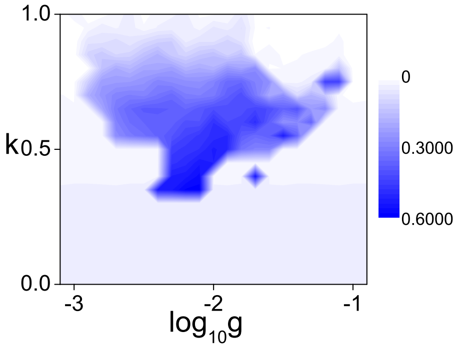

FIG. 4. (Color online) The dependence of Q on both the g and k.

interaction is not strong enough to induce firing in the systems with subthreshold signal. Increasing k to the range $[k_c, k^*)$, where k^* are the values corresponding to the optimal Q, the resulted coupling interaction by the phase disorder will be strong enough to trigger firing and the firing rate will increase with k. On the other hand, the coupling is drawing the neurons together and thus make the firings be synchronized. However, when we further increase k to $k^* < k \leq 1$, the weak coupling strength g is not strong enough to control the firing steps and thus results in a self-organized traveling wave. When $k = k^*$, the coupling g is the appropriate value to balance the firing step and thus make a largest Q. While for the case of fixed coupling k, we can make the similar analysis on the varying of g. The only difference is that when g is too larger, the coupling will suppress the firings induced by phase disorder.

Now we present a physical theory through a simplified model to explain the mechanism of firings induced by phase disorder. Letting $X(t) = \frac{1}{N}\sum_{i=1}^{N} x_i(t)$ and $Y(t) = \frac{1}{N}\sum_{i=1}^{N} y_i(t)$ be the means of $x_i(t)$ and $y_i(t)$, we can rewrite Eq. (1) as

$$\dot{X} = \frac{1}{\epsilon}\left(X(1-M) - \frac{X^3}{3} - Y\right),$$

$$\dot{Y} = X + b + \frac{A}{N}\sum_{i=1}^{N} \sin\left(\frac{2\pi}{T}t + \varphi_i\right), \tag{3}$$

where $M = \frac{1}{N}\sum_{i=1}^{N}(x_i - X)^2$. Assuming the uniformly distributed φ_i is symmetrical and N is very large, we have $\sum_{i=1}^{N} \sin(\frac{2\pi}{T}t + \varphi_i) \approx 2\sin(\frac{2\pi}{T}t)\int_1^{N/2}\cos(\frac{2k\pi}{N}z)dz \approx N\sin(\frac{2\pi}{T}t)\frac{\sin(k\pi)}{k\pi}$. Putting it into Eq. (3), we obtain

$$\dot{X} = \frac{1}{\epsilon}\left(X(1-M) - \frac{X^3}{3} - Y\right),$$

$$\dot{Y} = X + b + A\sin\left(\frac{2\pi}{T}t\right)\frac{\sin(k\pi)}{k\pi}. \tag{4}$$

Equation (4) can be treated as a single neuron under the influences of an external signal $A\sin(\frac{2\pi}{T}t)\frac{\sin(k\pi)}{k\pi}$ and a perturbation M. Since Y changes slowly, we may assume $Y \approx \text{const}$ and then the dynamics of X can be considered as independent on Y. In this situation, the influence from M to X becomes extremely important. Considering that M is determined by g and k through x_i, we would like to study how g and k influence the value of M. The left panels of Fig. 5 shows the influence of phase disorder for $g = 10^{-2}$ where Figs. 5(a)–5(d) denote the cases of $k = 0$, 0.43, 0.5, and 1, respectively. It is easy to see that $M \approx 0$ for $k = 0$ and then gradually becomes oscillations with the increase in k until an approximate periodic oscillation at $k = 1$. For the case of Fig. 5(c) with $k = 0.5$, we may treat M approximately as a periodic signal $1 + \sin(\frac{2\pi}{T}t)$. The right panels of Fig. 5 shows the influence of coupling strength for $k = 0.5$ where Figs. 5(e)–5(h) denote the cases of $g = 10^{-2.6}$, 10^{-2}, $g = 10^{-1.6}$, and 10^{-1}, respectively. It is easy to see that M also looks like the signal $1 + \sin(\frac{2\pi}{T}t)$ for $g = 10^{-2}$ in Fig. 5(f). The reason for M to have the same period T with the external signal can be understood as follows. The firings do not occur at the precisely same time [see Fig. 1(c) or Fig. 1(f)], which results in a nonzero M. After firing, the neurons return to the resting state and wait for the next firing. The resting state corresponds to the stable fixed point of single neuron. During the interval of resting state, the neuron's behavior are almost the same, resulting a zero M and thus the same T with the signal. When M is large, the excitability threshold of Eq. (4) is lowered and hence the neuron becomes excitable. Therefore, M induces and enhances the resonance.

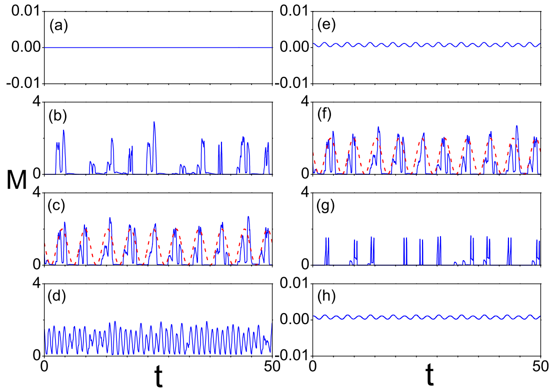

FIG. 5. (Color online) Evolution of M as function of k and g. Left panels with $g = 10^{-2}$: (a) $k = 0$, (b) $k = 0.43$, (c) $k = 0.5$, and (d) $k = 1$; right panels with $k = 0.5$: (e) $g = 10^{-2.6}$, (f) $g = 10^{-2}$, (g) $g = 10^{-1.6}$, and (h) $g = 10^{-1}$. The dashed lines are the signal $1 + \sin(\frac{2\pi}{T}t)$.

To show the connection between the approximate periodic M and the optimal k and g in detail, we simplify M as a period signal $A'[1 + \sin(\frac{2\pi}{T'}t)]$, where A' is the average of half values of the local highest amplitudes of M and T' is the average time intervals between two successive peaks. Take $k = 0.5$ as an example. According to Figs. 5(e)–5(h), we plot the corresponding numerical values of T' and A' versus g for $k = 0.5$ in Figs. 6(a) and 6(b), respectively. From Fig. 6(a) it is easy to see that T' has apparently larger values in the range $10^{-2.5} < g < 10^{-1.3}$ than other ranges. The similar situation occurs for A' in Fig. 6(b). To check the correctness of approximately treating M as periodic perturbation, we substitute $k = 0.5$ and $M = A'[1 + \sin(\frac{2\pi}{T'}t)]$ into Eq. (4), the corresponding Q' is obtained in Fig. 6(c). From Fig. 6(c) we see that Q' shows larger values in the moderate range of g only. Comparing Fig. 6(c) with Fig. 4, we see that they are approxi-

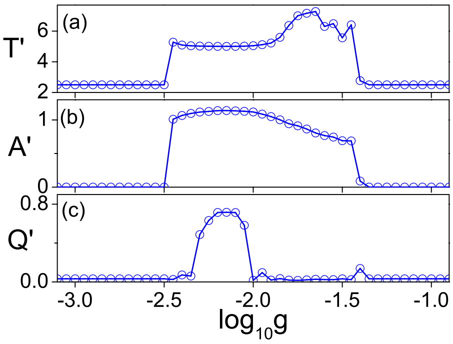

FIG. 6. (Color online) (a) The period T' of M versus g; (b) the period A' of M versus g; (c) Q' versus g. The range of phase disorder is fixed at $k=0.5$.

mately consistent. Furthermore, we find that if we substitute the exact M obtained from Eq. (1) into Eq. (4), we will get the same results of Q as in Fig. 3. The dashed lines in Fig. 3 shows the results from Eq. (4) by the recorded data of M. Obviously, the symbols and the dashed lines in Fig. 3 have the same trends, indicating that the Eq. (4) is in charge of the mechanism of the double resonance from Eq. (1).

Finally, we briefly discuss the influence of network size N and the nonidentity of neurons. We find that the observed double resonance phenomenon remains for different number N and is robust to the nonidentity of neurons, indicating its universality in excitable systems.

In conclusion, based on the interesting problem that how random phases influence the signal detection and transmission, we have studied the effects of phase disorder on the collective behavior of globally coupled excitable neurons with subthreshold activity. We have uncovered a double resonance phenomenon that the signal amplification factor Q shows resonance on both the phase disorder and the coupling strength. The resonance on coupling strength may show up only when the range of phase disorder k is greater than the critical value k_c. A physical theory is provided to explain the mechanism of the double resonance. This phenomenon may occur in the case where a weak signal's arriving time to each receptor is not always the same, thus the neuron tissue may benefit from this randomness to enhance signal detection and further transmission.

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