Phase-noise-induced resonance in a single neuronal system

Xiaoming Liang,[1] Liang Zhao,[1] and Zonghua Liu[2]

[1]*Institute of Mathematics and Computer Science, University of São Paulo, São Carlos 13560-970, Brazil*
[2]*Institute of Theoretical Physics and Department of Physics, East China Normal University, Shanghai 200062, China*

Phase-disorder-induced resonance has been recently uncovered in an ensemble of coupled excitable neurons with weak external signal, where each neuron takes a constant initial signal phase [Phys. Rev. E **82**, 010902(R) (2010)]. However, it is unclear how the initial phase disorder influences the behavior of a single or isolated neuron, which constitutes the ensemble. In order to answer this question, we here consider the case of a single neuron with phase noise originated from the time-varying initial signal phase, in contrast to the constant initial phase in each neuron studied in the above referenced paper. Interestingly, we find that the phase noise can induce resonance even in the single neuronal system with subthreshold signal. Moreover, we reveal that, with the presence of phase noise, the neuron also shows another resonance behavior by varying the period of the external signal. An analysis is conducted to uncover the mechanisms behind these resonance phenomena.

PACS number(s): 87.19.lc, 05.45.Xt

I. INTRODUCTION

The sensory organs of biological systems from insects to mammals have evolved to accurately detect and locate the external stimuli, even if these are very weak ones. For example, it was experimentally demonstrated that the paddlefish is very sensitive to weak electric fields evoked by its prey in a muddy river with the aid of electroreceptor cells on its rostrum [1]. A subsequent experiment reported that the fly Ormia ochracea can localize a salient sound source with a precision up to $2°$ azimuth [2]. How can they achieve such an impressive ability? Perhaps the first step toward answering this question is to understand how neurons extract a faint but relevant signal from a noisy environment.

Neurons are inherently information processing devices. This feature demands them to have specialized mechanisms for reliably detecting extremely weak signals at complex situations. Stochastic resonance (SR) is one of such mechanisms, commonly known by the surprising role of noise in enhancing the detection and the transmission of weak signals. SR has been first discovered for explaining why the earth ice ages occurred periodically [3]. After that, this mechanism has been widely employed in explaining the phenomenon of signal detection in biological systems [1,3–7]. In Ref. [5], Douglass *et al.* reported that the crayfish mechanoreceptor has a better performance at detecting distant fin movements of predatory fish when the water is turbulent rather than still. In Ref. [6], Simonotto *et al.* showed that humans are more efficient to recognize a faint image on a screen with the help of added noise. Except noise, feedback is another mechanism found to play a significant role in stochastic resonance in neurons or bistable oscillators [8–10]. In contrast to regular periodic signals, Collins *et al.* generalized the theory of stochastic resonance to aperiodic stochastic resonance, given that real-world external signals are often irregular [11,12]. Recently, Liang *et al.* uncovered that phase-disorder-induced resonance may serve as a simple but efficient method for an ensemble of coupled excitable neurons to catch weak signals [13]. In that work, the received signals of neurons have different constant initial phases satisfying a given distribution. It is the difference of the initial phases

among neurons which results in the resonance. However, the mechanism of phase disorder is unclear yet for a single neuronal system. Since an individual neuron is a basic signal processing unit, its performance gives an important cue for understanding the whole system. Thus an interesting question is what happens if a single neuron has a time-varying initial phase rather than a constant one.

Actually, in real situations, the initial phase of received signals may change with time. For instance, the variation of the distance to the signal source makes the neuron sensors receive external signal with continuous phase shift. To pinpoint prey in a dark environment, the barn owl adjusts the direction of its head toward the sound source for obtaining optimal interaural time difference between both ears. During the adjustment, the arriving times and intensities of sound between the ears change accordingly [14,15]. In addition, a periodic wave traveling through a fluctuating medium or interface also may generate phase variation [16]. In addition, some sensory organs are very sensitive to phase difference of the received stimulus [2,17–19]. For example, the weakly electric fish Eigenmannia has a sensory capability of discriminating subtle time disparities on the order of 10^{-8}–10^{-5} s [17,18], by which it can keep changing its signal phase in order to avoid jamming among signals coming from other nearby fishes. Eigenmannia is not the only one to have such an ability; surface-feeding fish also can determine the prey's angle with excellent accuracy by discriminating the target signal's arriving time or phase difference between the distributed lateral line organs [19]. Summing up all these facts, it is necessary for us to know how the variation of the initial phase influences the neuronal performance in signal detection.

In this paper, we examine the effect of phase noise on the dynamics of a single excitable neuronal system, where the initial phase is time-varying by noise. We find that even a small phase noise can assist the neuron to efficiently detect subthreshold external signals. Moreover, we show the existence of an optimal value on both the phase noise and the signal period, where the detection can be significantly improved, resulting in a double-resonance-like behavior. Finally, we analyze the underlying mechanisms behind these phenomena. As reported

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by a recent research that noise can act as a controller in signal transmission in a multithread semiconductor neuron [20], we hope that our findings are useful not only for understanding the signal processing of biology systems but also for making artificial devices.

II. MODEL AND SIMULATIONS

As a paradigmatic model, the FitzHugh-Nagumo (FHN) model is usually used to describe the firing activities of sensory neurons. Here, we use it to investigate the effect of phase noise, considering the following system:

$$\epsilon \dot{x} = x - \frac{x^3}{3} - y,$$
$$\dot{y} = x + b + A \sin\left[\left(\frac{2\pi}{T}t + \varphi(t)\right)\right], \quad (1)$$

where x is a fast variable, y is a slow variable, ϵ is a small parameter allowing one to separate the fast and slow dynamics, and $A \sin[\frac{2\pi}{T}t + \varphi(t)]$ is the external signal received by the neuron. When the amplitude A is not strong enough to stimulate spikes, the signal is called subthreshold. For a single neuron without external signal, the system is excitable if $b > 1$; otherwise, the system generates a stable periodic sequence of spikes. As real signals are often irregular, we here pay attention to the case of subthreshold signal with phase noise, i.e., the initial signal phase $\varphi(t)$ of the signal phase $\frac{2\pi}{T}t + \varphi(t)$ is not constant but noiselike. For simplicity, $\varphi(t)$ is set to be varied as a Wiener process. The other parameters are set as $b = 1.02$, $\epsilon = 0.01$, $A = 0.05$. References [21,22] show that the threshold for firing depends on the signal frequency. To ensure that the external signal is subthreshold, we let T be in the range $[3,15]$ where there is no firing for Eq. (1) with $\varphi(t) = 0$.

In numerical simulations, Eq. (1) is discretized as follows [23,24]:

$$x(t + \Delta t) = x(t) + \frac{1}{\epsilon}\left[x(t) - \frac{x(t)^3}{3} - y\right]\Delta t,$$
$$y(t + \Delta t) = y(t) + [x(t) + b + A \sin[z(t)]]\Delta t, \quad (2)$$
$$z(t + \Delta t) = z(t) + \frac{2\pi}{T}\Delta t + \sqrt{2D\Delta t}\zeta,$$

where ζ is a random number with standard Gaussian distribution and $\Delta t = 0.001$ is the step size. The last term in the third line of Eq. (2) represents a phase noise, where the parameter D governs its intensity. In the numerical simulations of this paper, Eq. (2) is integrated by Euler's method with the initial condition $(x(0), y(0), z(0)) = (-1.02, -0.67, 0)$.

Let the signal period $T = 5$. If the initial phase is constant, i.e., $D = 0$, Eq. (1) does not have spikes because the subthreshold signal is incapable of inducing firing. Surprisingly, we find that it is possible for the neuron to generate spikes when D increases to $10^{-3.5}$; see Fig. 1(a). This means that the phase noise can improve neuronal response to a weak signal. As D is increased to 10^{-2}, we find that the firing rate is enhanced and the intervals between two successive spikes are more regular and close to the period of the external signal; see Fig. 1(b). Further increasing of D to 1 results in the increase of the firing rate but decrease of the firing regularity; see Fig. 1(c). When
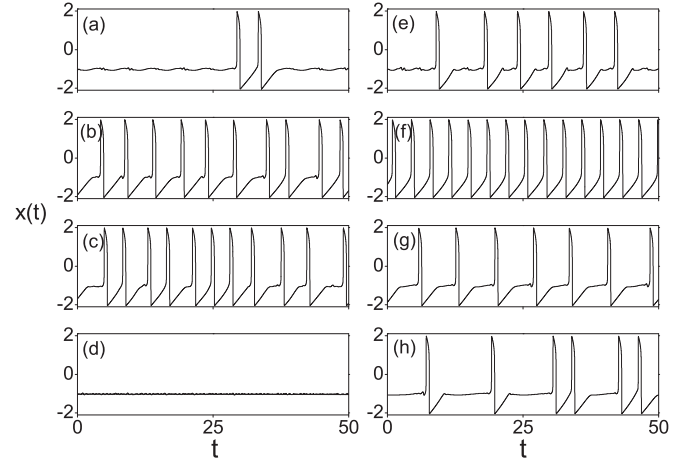

FIG. 1. Time series of the FHN model for $b = 1.02$ and $A = 0.05$. Left panels with $T = 5$: (a) $D = 10^{-3.5}$, (b) $D = 10^{-2}$, (c) $D = 1$, and (d) $D = 100$. Right panels with $D = 10^{-2}$: (e) $T = 3$, (f) $T = 3.5$, (g) $T = 7$, (h) $T = 12$.

D is increased to relatively large values, Fig. 1(d) shows that the spikes vanish. Therefore we observe here an interesting phenomenon that the firing pattern is purely induced by phase noise in a single neuron and it is enhanced when the intensity of phase noise is at the intermediate level. Next, we study how the signal period T influences the behavior of neural firing in the presence of phase noise. Interestingly, we note a similar resonant behavior on T shown by Figs. 1(e)–1(h). From these figures, we see that the spikes are more regular at the intermediate values of T, which is quite different from the cases of small or large values of T. In addition, the spike intervals for $T = 3.5$ and $T = 7$ are very close to their respective external signal periods.

To characterize the firing rate shown by Fig. 1, we introduce an indicator f, which is defined as the average number of spikes within each signal period T:

$$f = \lim_{n \to \infty} \frac{N}{n}, \quad (3)$$

where n is the number of periods and N is the total number of spikes within nT intervals. $f = 0$ means there are no spikes, while $f \approx 1$ indicates that the neuron generates one spike in each period T. In the simulations throughout the paper, $n = 50$ is used and f is averaged over 20 realizations. For $T = 5$, Fig. 2(a) shows that the firing rate f quickly approaches 1 until $D < 10^{-2}$, it slowly increases until $D = 10^{0.6}$, and it decreases to 0 as D is further increased, forming a finite range of firing. Figure 2(b) shows that f always grows with T except at the intermediate values, where f seems independent of T and remains at 1, confirming the observations shown by Figs. 1(f) and 1(g). The plateaus of $f \approx 1$ in Fig. 2(b) is a typical feature of phase locking, i.e., phase-noise-induced firing rhythm coincides with the driving period [21,25–27]. To systematically investigate the phase locking behavior, Fig. 2(c) depicts the effective locking region $(|\Delta f| < 0.01)$ of $f \approx 1$. We see that the $f \approx 1$ region continuously extends as T is increased, but it shrinks considerably at large D.

As mentioned above, the neuron exhibits different responses to weak external signals with phase noise. A common
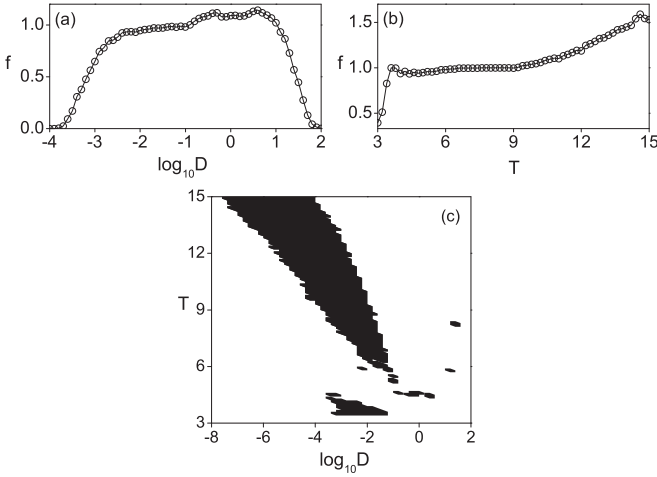
FIG. 2. The firing rate per period f of the FHN model. (a) f versus D for $T = 5$. (b) f versus T for $D = 10^{-2}$. (c) Phase locking regions of $f \approx 1$ for different pairs of D and T.

measure to characterize such responses is to quantify the output at the input frequency. Thus we define the signal amplification Q at the signal frequency $\omega = \frac{2\pi}{T}$ as follows [13,28–30]:

$$Q = \left| \frac{2}{nT} \int_0^{nT} x(t) e^{i\omega t} dt \right|. \tag{4}$$

Here, $n = 50$ and Q is calculated over 20 realizations. The numerical results of Q on D and T are plotted in Figs. 3(a) and 3(b), respectively. We see that both figures show the bell shape, which is the signature of SR. Moreover, the optimal D and T corresponding to the maximal values of Q are $D = 10^{-2}$ for $T = 5$ and $T = 3.5$ for $D = 10^{-2}$, respectively. These quantities are supported by the regular firing activities shown by Figs. 1(b) and 1(f). To see how the resonance behavior depends on the phase noise D and the period T, we plot Q in Fig. 3(c) by changing both D and T. Clearly, the plateau of high values of Q appears at the intermediate intensities of D. Moreover, we see that Q starts to increase when D is
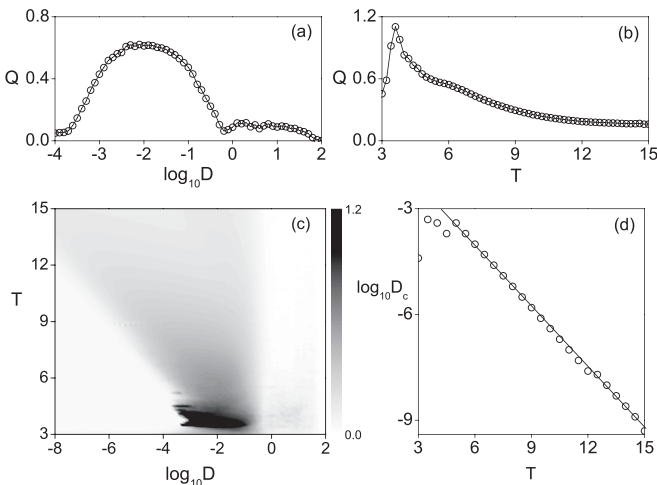

FIG. 3. (a) Signal amplification Q versus D for $T = 5$. (b) Signal amplification Q versus T for $D = 10^{-2}$. (c) Signal amplification Q versus both D and T. (d) Critical D_c versus T. The slope of fitting line is -0.57.

beyond a critical value D_c for each T, indicating the onset of successful signal detection. Besides this, we find that D_c appears to decrease as a function of T. Let $Q > 0.1$ as the onset of successful detection; Fig. 3(d) shows the relationship between T and D_c, which approximately obeys $D_c \sim e^{-\mu T}$ with $\mu = 0.57$. This function means that the longer the external period T is, the less the intensity D is demanded for signal detection.

III. ANALYSIS

We now analyze the mechanism of neuron firing patterns induced by phase noise. We plot the phase portrait of the FHN model in Fig. 4, where the dotted lines $x = -b$ and $y = x - \frac{x^3}{3}$ denote the nullclines. The intersection of the two nullclines is the resting state. Without phase noise, the forced neuron oscillates around the resting state along a limit cycle orbit, see the inset of Fig. 4, where the two "points" L and R denote the left and right boundaries of the orbit. When the external signal increases from $-A$ to A, x remains negative and decreases from $-b + A$ to $-b - A$. Thus the trajectory from R and L represents continuous hyperpolarization. Instead, with the decrease of external signal from A to $-A$. the trajectory from L and R corresponds to depolarization since x increases. Due to the slow depolarization by the external signal, the system (1) can remain silent even when $b + A \sin(\frac{2\pi}{T}t) < 1$, i.e., the firing threshold is increased by the slow depolarization [31,32]. Here the mechanism of increased firing threshold by external signal is only valid for small value of the period T. For relatively large value of T, such as $T \to \infty$, the external signal is so slow that the neuron does not remain silent when $b + A \sin(\frac{2\pi}{T}t) < 1$ even without phase noise. From the inset of Fig. 4, we also see that the hyperpolarization and the depolarization are approximately separated into upper and lower parts by the nullcline $y = x - \frac{x^3}{3}$. For small intensity of phase noise,
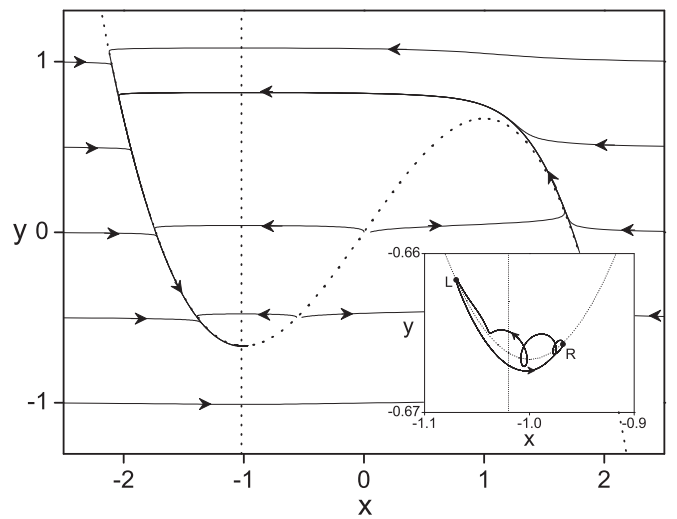

FIG. 4. Phase portrait of the FHN model at $\epsilon = 0.01$, $b = 1.02$. Dotted lines correspond to the nullclines of the FHN model and solid lines with arrows correspond to deterministic trajectories. Inset: Trajectory of system (1) at $T = 5$ and $D = 0$ in the vicinity of resting state, where the arrows represent trajectory direction and dots L and R denote the left and right boundaries of trajectory.

the system cannot generate spikes because the variance of the initial phase is not sufficient to disturb the orbit. For slightly stronger, but still small intensity of phase noise, there exists a low probability to suddenly change the wave of the external signal. During the depolarization, such change of the external signal may force the system into a new orbit. As a result, the system state will be deviated far from the original orbit and thus is unstable. Then, the trajectory goes to the right branch of the nullcline $y = x - \frac{x^3}{3}$, which induces a spike. On the contrary, the system is more robust to perturbation during the hyperpolarization since the left branch of the nullcline $y = x - \frac{x^3}{3}$ is attractive. So the trajectory perturbed by phase noise will go back to the original orbit without firing. Since the phase noise is still small now, it is insufficient to maintain the regular firing pattern. However, for large intensity of phase noise, it is easier for the phase noise to disturb the trajectory. Therefore the firing rate is sharply increased. When the noise intensity is sufficiently large, the external signal is dominated by the phase noise. Thus it turns out to be a bounded noise, but it is not a signal anymore. Consequently, the trajectory oscillates around the resting state and no spikes are generated. Summing up, when the intensity D is at its optimal value, the neuron can fire more regularly at the forcing rhythm, yielding the best detection performance in this regime. In the case of fixed phase noise D, the resonancelike behavior is due to the frequency matching between the intrinsic period T' of the neuron and the period of the external signal T. The intrinsic period T' is the duration of the excursion time after firing [21,26,27,33]. When the external period T matches the intrinsic period T', the response of the neuron can be significantly enhanced; otherwise, the response is relatively small. This situation is shown by Fig. 2(b). In this case, the intrinsic period is $T' \approx 3.5$; we see that the largest amplification occurs when T closes to T'. Therefore we can draw a conclusion that phase noise can significantly change the firing pattern of the neuron.

In order to quantitatively explain the above arguments, we consider a simple external signal $A \sin(\frac{2\pi}{T} t + \varphi')$ and feed it to a single FHN model. We let the initial signal phase φ' vary as

$$\varphi' = \begin{cases} 0, & t < t_1, \\ k\pi, & t \geqslant t_1, \end{cases} \quad (5)$$

where k and t_1 denotes the strength and the onset of the initial phase variation, respectively. When $k = 0$, the external signal is perfectly regular. In the following, we examine the effect of $k \neq 0$ on the dynamics of neuron system.

Let $T = 5$ and $k = \pm 0.02$. We first consider the case of $t_1 = 2.5$. This is the depolarization process, since the signal $A \sin(\frac{2\pi}{T} t + \varphi')$ decreases for $1.25 < t < 3.75$ and thus results in the increase of x. We find that the trajectory goes to the limit cycle orbit from the initial condition when $k = 0$; see the black line in Fig. 5(a). However, when k is changed to $k = \pm 0.02$ at $t_1 = 2.5$, such small change of external signal makes the trajectory deviate from the original orbit during the depolarization process. When the depolarization process is finished, the orbit becomes unstable and goes to the right branch of the nullcline $y = x - \frac{x^3}{3}$, i.e., the neuron generates a spike; see the red dashed and blue dotted lines in Fig. 5(a). In order to investigate the effect of the initial phase variation
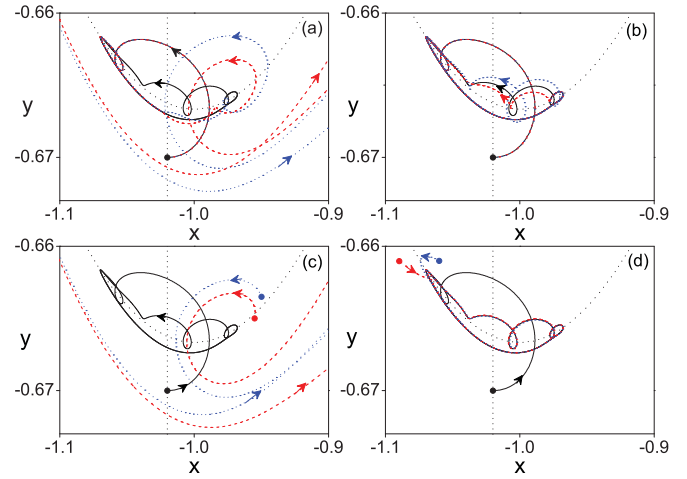

FIG. 5. (Color online) (a) Trajectories of the FHN model with signal (5), $k = \pm 0.02$ and $t_1 = 2.5$. (b) Trajectories of the FHN model with signal (5), $k = \pm 0.02$ and $t_1 = 4$. In both panels, the red dashed and the blue dotted lines represent the results of k and $-k$, respectively. (c) Trajectories of FHN model with signal $A \sin(\frac{2\pi}{T} t - \frac{\pi}{2})$ (red dashed and blue dotted lines), and (d) trajectories of FHN model with signal $A \sin(\frac{2\pi}{T} t + \frac{\pi}{2})$ (red dashed and blue dotted lines). In all panels, black lines denote the trajectory without phase noise. Arrows represent the trajectory direction. Black dotted lines correspond to the nullclines of the FHN model. Parameter $T = 5$ is used.

during hyperpolarization, we set $t_1 = 4$. Figure 5(b) shows the result, where the perturbed trajectory quickly returns to the original orbit. Thus we conclude that the instability of the deviated orbit during the maximum depolarization plays a key role to cause spikes. To confirm it, we check the system stability at the region of maximum depolarization and maximum hyperpolarization, respectively. Specifically, we use the deviated states [see the red and blue "dots" in Figs. 5(c) and 5(d)] as initial conditions to integrate the FHN model with external signal $A \sin(\frac{2\pi}{T} t - \frac{\pi}{2})$ and $A \sin(\frac{2\pi}{T} t + \frac{\pi}{2})$, respectively. Here, the starting value $A \sin(\frac{2\pi}{T} t - \frac{\pi}{2})$ corresponds to the maximum depolarization, while $A \sin(\frac{2\pi}{T} t + \frac{\pi}{2})$ represents the case of maximum hyperpolarization. It can be seen from Fig. 5(c) that the trajectories display a similar behavior during the maximum depolarization as shown in Fig. 5(a). Unlike Fig. 5(c), the trajectories in Fig. 5(d) quickly go to the left branch of the nullcline $y = x - \frac{x^3}{3}$ and then are confined to the limit cycle orbit during the maximum hyperpolarization. In this way, Figs. 5(c) and 5(d) again confirm our analysis. We have also changed k and t_1 to other values and we have observed a similar phenomenon. Note that our finding is similar to the phenomenon of postinhibitory rebound (PIR), where the neuron fires after being released from hyperpolarization [34,35]. The mechanism of PIR is that, due to the hyperpolarization, the resting state of the neuron is shifted. When the neuron is suddenly released from the hyperpolarization, the trajectory is far from the resting state and is unstable. Thus it makes a long excursion to go back to the resting state, i.e., the neuron generates a transient spike. The main difference is that, in our case, the firing is caused by phase noise as shown above.

Finally, we explain the relationship between D_c and T. For a large T, the external signal varies so slowly that a small intensity of phase noise may significantly change the signal wave, in contrast to the case of small T. Thus it is easier for a small phase noise to disturb the trajectory of the neuron at large T. Then, we perceive that the threshold of noise intensity D_c decays with period T and the decay rate reduces as T increases, obeying the relationship $D_c \sim e^{-\mu T}$.

IV. CONCLUSIONS

In conclusion, we have investigated the effects of phase noise in relation to the firing pattern of a single excitable neuron with subthreshold signal, where the phase noise mimics the time-varying initial phase of the received signal. The signal amplification factor Q shows bell-shaped behavior by varying both the phase noise and the signal period, indicating that we have uncovered a double resonance phenomenon. The former resonance implies that biological systems may exploit the power of randomness to enhance signal detection,

while the latter demonstrates that the detection is frequency selective. Finally, we explain the mechanism of phase noise in signal amplification. Here the mechanism is different from Ref. [13]. In that case, the initial phases are not time-varying and their influences on the firing pattern of the neuron ensemble are realized through the coupling strengths in a network of interactive neurons. Both findings indicate that the initial phase of external signal plays a key factor to induce resonance no matter whether the system is a single neuron or an ensemble. Since noise is inevitable in real systems, our findings are useful to study the capability of signal detection by neural sensors. This topic deserves further experimental and theoretical investigation.

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