

Noise-induced synchronization and coherence resonance of a Hodgkin–Huxley model of thermally sensitive neurons

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We study nontrivial effects of noise on synchronization and coherence of a chaotic Hodgkin–Huxley model of thermally sensitive neurons. We demonstrate that identical neurons which are not coupled but subjected to a common fluctuating input (Gaussian noise) can achieve complete synchronization when the noise amplitude is larger than a threshold. For nonidentical neurons, noise can induce phase synchronization. Noise enhances synchronization of weakly coupled neurons. We also find that noise enhances the coherence of the spike trains. A saddle point embedded in the chaotic attractor is responsible for these nontrivial noise-induced effects. Relevance of our results to biological information processing is discussed. © 2003 American Institute of Physics.

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Nontrivial effects of noise in nonlinear dynamical systems have been a subject of great interest and importance, in the context of stochastic resonance,¹ coherence resonance,² and noise-induced synchronization.³ In particular, synchronization of chaotic dynamical systems by a common random forcing is a topic of relevance to neuroscience. Experiments have demonstrated a remarkable reliability of repetitive spike sequences in neocortical neurons in response to repeated fluctuating stimuli, which is a feature not observed in response to constant input currents.⁴ This reliability is of importance for information encoding by spike timing of neurons. The underlying mechanism, however, has not been addressed clearly. In this contribution, we study synchronization behavior of a chaotic Hodgkin–Huxley model of thermally sensitive neurons⁵ subjected to a common noise, and investigate the mechanism of noise-induced synchronization. We find that the existence of a saddle point S in the phase space plays an important role. Noise induces synchronization when the contraction close to the stable manifold of S becomes dominant over the expansion close to the unstable manifold of S . We also investigate non-identical neurons in terms of phase synchronization of the spike sequences. In an ensemble of weakly coupled neurons, a common random forcing can enhance phase synchronization among the elements. As a consequence of this enhanced synchronization, the ensemble establishes a higher degree of sensitivity in the collective response to fluctuating stimuli. On the other hand, in the presence of noise, the trajectory is prevented from staying close to the saddle point for long time. This can generate much larger spiking rates and reduce considerably the fluctuation of the interspike intervals. We demonstrate that noise can optimize the coherence of the spike trains. This mechanism of noise-induced synchronization and coherence resonance is general in systems displaying spiking behavior due to a saddle point.

I. INTRODUCTION

The subject of this contribution is at the borderline of two basic families of phenomena in nonlinear systems nowadays attracting large interest: noise-induced effects and synchronization. Constructive effects of noise in nonlinear systems have been investigated extensively in the context of stochastic resonance¹ and coherence resonance.² By stochastic resonance, noise can optimize a system's response to an external signal and induces stochastic phase synchronization to the external forcing.³ With coherence resonance, pure noise without an external signal can generate the most coherent motion in the system, as has been mainly observed in excitable systems.²

The study of coupled oscillators is one of the fundamental problems in nonlinear dynamics and has applications in various fields.⁶ Mutual synchronization is of great interest and importance among the collective dynamics of coupled oscillators. The notion of synchronization has been extended to include a variety of phenomena in the context of interacting chaotic oscillators, such as complete synchronization,⁷ generalized synchronization,⁸ phase synchronization,⁹ and lag synchronization.¹⁰

Noise influences synchronization in different ways. In complete synchronization of coupled chaotic systems, noise may induce intermittent loss of synchronization due to a local instability of the synchronization manifold.¹¹ In phase synchronization of coupled oscillators, noise can generate phase slips in phase-locked periodic oscillators¹² as well as in chaotic ones.¹³

On the other hand, identical systems which are not coupled but subjected to a common noise may achieve complete synchronization at a large enough noise intensity, as has been demonstrated both in periodic^{14,15} and chaotic systems.^{16,17} For complete synchronization to occur, it is necessary that the largest Lyapunov exponent becomes negative in the presence of noise.^{16,17} The circumstance that different systems are not or only weakly coupled but subjected to a common random forcing is of great relevance, especially in neuroscience. Different neurons commonly connected to an-

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other group of neurons receive a common input signal which often approaches a Gaussian distribution as a result of integration of many independent synaptic currents. It is important to emphasize experimental observations of a remarkable reliability of spike timing of animal neocortical neurons.⁴ In these experiments, rat neocortical neurons are stimulated by input currents. When the input is a constant current, a neuron generates independent spike trains in repeated experiments with the same input. This is evidence that the constant input when viewed as a control parameter has moved the neuron dynamics from a fixed point into a chaotic spiking regime. In contrast, when a Gaussian white noise is added to the constant current, the neuron generates repetitive spike trains in repeated experiments with the same fluctuating stimulus. Repeatable firing means that a common synaptic current induces complete synchronization in two identical neurons with different initial conditions. This behavior is of great importance for signal encoding and transmission in the information processing of neurons: (i) single neurons may faithfully encode temporal information in the timing of successive spikes, (ii) a group of neurons can respond collectively to a common synaptic current due to synchronization.

The mechanism underlying such a remarkable noise-induced synchronization of chaotic neurons, however, has not been clearly explained. In Ref. 15, synchronization of randomly driven nonlinear oscillators has been studied in terms of phase synchronization of the oscillators to the phase of the external random forcing. This is useful for analyzing synchronization of periodic oscillators subjected to a slowly fluctuating forcing. Unfortunately, typical noise sources that arise in many situations are not of this case. Furthermore, the approach in Ref. 15 cannot explain complete synchronization of two chaotic oscillators subjected to a common fluctuating input. For example, chaotic Rössler oscillators can achieve phase synchronization to a random forcing,¹⁸ but complete synchronization of two identical chaotic Rössler oscillators with a common random forcing has never observed.¹⁹ In fact, whether noise can induce synchronization of chaotic systems has been subjected to a strong controversy. In some systems, noise with a nonzero mean value can induce synchronization but unbiased noise cannot,²⁰ while in some other systems, unbiased noise can also achieve synchronization.¹⁷ So far, the mechanism of noise-induced synchronization is not completely understood. In particular, in what type of systems noise can induce synchronization is still an open problem.

In this contribution, we present a mechanism of noise-induced synchronization which occurs in systems displaying spiking behavior, such as neurons. An important characteristic of many biological,²¹ chemical,²² and physical oscillators²³ displaying spiking behavior is the existence of a saddle point S in the phase space. In these systems, the orbit comes back to a neighborhood of S and slows down after each or a burst of a few quick spikes away from S . The dynamics is characterized by rather regular orbits in the phase space and widely fluctuating time intervals T_I between successive returns to S . In neuroscience, the significance of interspike interval T_I in biological information processing has been discussed.⁴ It is important to note that this type of

systems has intrinsically a highly nonuniform dynamics and the sensitivity to small perturbations is high only in the vicinity of S . Hence, the basic geometrical structure of the orbits is preserved, while T_I may be changed significantly, so that information of the input may be encoded by the timing of the spike train. In particular, a noise input may reduce the fluctuation of T_I and enhance the coherence of spike sequences.

There is another feature that makes the system behavior nontrivial in the presence of noise input. Accompanying the saddle point S , there exists a contraction region close to the stable manifold of S , where nearby orbits converge temporally. There also exists an expansion region close to the unstable manifold of S . The contraction region is essential for noise-induced synchronization. It is possible that noise alters the dynamics and makes the contraction dominant, so that systems with different initial conditions converge to an identical response in the presence of a common random forcing.

We demonstrate these nontrivial effects of noise input in a chaotic Hodgkin–Huxley (HH) model of thermally sensitive neurons possessing such a saddle point.⁵ Rather weak noise can already induce synchronization, while stronger noise can optimize the coherence of the spike train patterns.

II. THE MODEL

A HH model of thermally sensitive neurons has been proposed by Braun *et al.*⁵ which mimics various types of spike train patterns observed in electroreceptors from dogfish and catfish, and from facial cold receptors and hypothalamic neurons of the rat.^{5,24} The model equations read

$$\begin{aligned} C_M \frac{dV}{dt} &= -I_l - I_d - I_r - I_{sd} - I_{sr} + D\xi(t), \\ \frac{da_r}{dt} &= \frac{\varphi(T)(a_{r\infty} - a_r)}{\tau_r}, \\ \frac{da_{sd}}{dt} &= \frac{\varphi(T)(a_{sd\infty} - a_{sd})}{\tau_{sd}}, \\ \frac{da_{sr}}{dt} &= \frac{\varphi(T)(-\eta I_{sd} - \theta a_{sr})}{\tau_{sr}}, \end{aligned} \quad (1)$$

with

$$I_d = \rho(T)g_d a_{d\infty}(V - V_d),$$

and

$$I_k = \rho(T)g_k a_k(V - V_k), \quad (k=r, sd, sr),$$

where

$$a_{k\infty} = [1 + \exp(-s_k(V - V_{0k}))]^{-1}, \quad (k=d, r, sd, sr)$$

and

$$\rho(T) = A_1^{(T-T_0)/10}, \quad \varphi(T) = A_2^{(T-T_0)/10}.$$

Here V is the membrane potential, and I_l is the leakage current $I_l = g_l(V - V_l)$; I_d and I_r are fast Hodgkin–Huxley currents representing Na and K channels. a_k ($k=r, sd, sr$) are activation variables, and $\rho(T)$ and $\varphi(T)$ are temperature-dependent scaling factors. With this model, the classical

Hodgkin–Huxley (HH) model,²¹ on the one hand, has been simplified, but on the other hand, has been extended by two additional slow currents I_{sd} and I_{sr} according to the experimental findings of spike-independent oscillations.²⁵

In numerical simulations, we employ the same set of parameter values as in Ref. 24, i.e., $g_{sd}=0.25$ mS/cm², $g_{sr}=0.4$ mS/cm², $g_d=1.5$ mS/cm², $g_r=2.0$ mS/cm², $g_l=0.1$ mS/cm², $\tau_{sd}=10$ ms, $\tau_{sr}=20$ ms, $\tau_r=2.0$ ms, $s_{sd}=0.09$ mV⁻¹, $s_d=0.25$ mV⁻¹, $s_{sr}=0.25$ mV⁻¹, $V_{0sd}=-40$ mV, $V_{0d}=-25$ mV, $V_{0r}=-25$ mV, $V_{sd}=V_d=50$ mV, $V_{sr}=V_r=-90$ mV, $V_l=60$ mV, $\eta=0.012$, $\theta=0.17$. These parameter values yield a good agreement of the model with experimentally observed temperature dependence of spike train patterns. The spike trains are chaotic in a broad range of temperatures (e.g., $7 < T < 13$). A more detailed description of the model and a comparison with the experimentally observed temperature dependence of spike train patterns can be found in Refs. 5 and 24. In our study, we consider Gaussian noise $\xi(t)$ with zero mean value and δ correlation in time. The noisy equations are integrated using a Heun algorithm²⁶ with a time step $\Delta t=0.05$ ms which is rather small compared to the duration (~ 100 ms) of a single spike.

In the chaotic spiking regime, the system possesses an unstable fixed point which has both stable and unstable directions. Thus it is a saddle point S . A trajectory starting close to the stable directions will approach the neighborhood of S and leave it along the unstable directions. This saddle point S is embedded in the chaotic attractor, i.e., typical chaotic trajectory may have very close recurrence to S after a burst of spikes. The eigenvalues corresponding to stable directions, are real ($\lambda_3 < 0, \lambda_4 < 0$) and the eigenvalues corresponding to unstable directions are complex ($\lambda_{1,2} = \mu \pm i\nu$), and $-\lambda_{3,4} > \mu$,²⁴ and the chaotic dynamics results from this Shilnikov condition²⁷ are a typical mechanism of chaotic spiking in neuron models.²⁸ Close to the stable manifold, a large contraction region exists in the phase space where the largest local Lyapunov exponent is negative and nearby trajectories converge, while close to the unstable manifold, the largest local Lyapunov exponent is positive and nearby trajectories diverge. Since the eigenvalues satisfy $-\lambda > \mu$, the contraction rate is stronger than the expansion rate. It has been shown that this system exhibits a homoclinic bifurcation, where the interspike interval becomes very long, when the control parameter temperature T is varied.²⁴

To manifest the change of local stability close to the saddle point during the evolution of the neuron, we consider the largest local Lyapunov exponent Λ_τ ,

$$\Lambda_\tau(t) = \frac{1}{\tau} \ln \left| \frac{\delta x(t)}{\delta x(t-\tau)} \right|, \quad (2)$$

where $|\delta x(t)|$ is a small distance between two trajectories in the phase space at time t and τ is a finite time. Λ_τ measures the average expansion or contraction rate during the finite interval τ . In numerical simulations, Λ_τ is calculated using a standard method²⁹ which integrates the variational (linearized) equation of the neuron model Eq. (1) and computes the largest exponent of the matrix solution of the linearized equation within every interval τ . Here we chose $\tau=50$ ms,

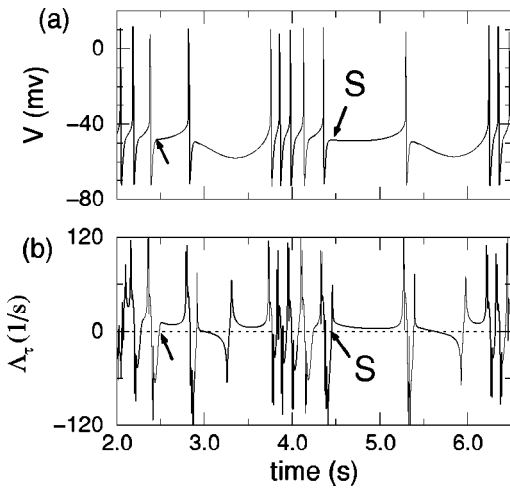


FIG. 1. Spike train (a) and local Lyapunov exponent (b) of the chaotic neuron at $T=10$.

which is about half of the duration of a single spike, but is much smaller than the average interspike interval $T \sim 400$ ms. With this τ value, quick and large changes of local stability along the orbits during the spike have been smoothed out considerably and we can see clearly the changes of the stability close to the saddle point where the orbits slow down.

A typical chaotic spike sequence of the neuron at $T=10$ (without noise input) is shown in Fig. 1, along with the largest local Lyapunov exponent Λ_τ . The neuron undergoes bursts of spikes between successive returns to the neighborhood of S (indicated by arrows in Fig. 1 close to $t=2.5$ and $t=4.5$). After a few (3–5) successive spikes away from S , the orbit approaches S , and is guided by the stable manifold as seen by negative Λ_τ ; then it departs from S following the guidance of the unstable manifold for a long time, as manifested by small positive Λ_τ . A single spike (e.g., close to $t=3$ and $t=5.5$ in Fig. 1) follows this recurrence to S . Such a single spike is well separated from the next burst of spikes, because the orbit cycles S and slows down around S . For each spike, Λ_τ is positive during the activation phase while it is negative during the relaxation phase. Such a spike train pattern repeats, but the number of spikes within a burst can be different, and the interval T_I between the bursts and the single spikes fluctuates strongly, depending on the closeness of the recurrence to the saddle point S . In the absence of noise, the spike sequence is chaotic so that the largest global Lyapunov exponent, which equals the time average of the largest local Lyapunov exponent Λ_τ , is positive, i.e., $\lambda = \langle \Lambda_\tau \rangle > 0$.

Although the detailed spike train patterns may be different in other systems with a similar saddle point in the phase space, the fluctuation of interspike intervals resulting from the recurrence to S and the stability properties (coexistence of the contraction and expansion regions) are generic. For these reasons, the response behavior to noise input reported in this neuron model should be universal in this type of system.

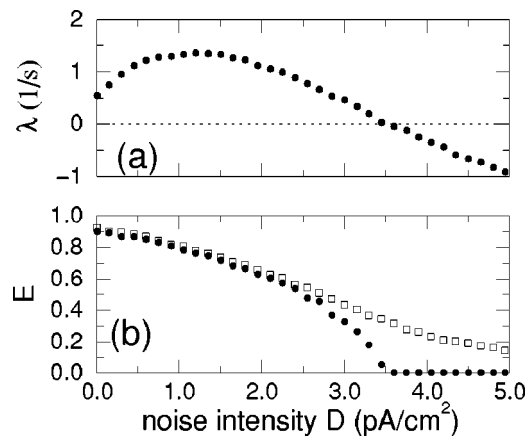


FIG. 2. (a) The largest Lyapunov exponent λ and (b) the relative synchronization error E (closed circles for two identical neurons and squares for two nonidentical neurons with a 5% difference of the leakage parameter g_l) vs the noise intensity D .

III. NOISE-INDUCED COMPLETE SYNCHRONIZATION OF IDENTICAL NEURONS

In this section, we study complete synchronization of two identical chaotic neurons (V_1 and V_2 , with independent initial conditions) which are linked only by a common Gaussian noise input $\xi(t)$. We calculate the largest transverse Lyapunov exponent λ as a function of the noise intensity D . In parallel, we compute the average relative synchronization error $E = \langle |V_1 - V_2| \rangle / \sigma_V$ between both neurons. Here σ_V^2 is the variance of $V(t)$ over time, which increases with D because a larger input generates a more frequent spiking. It is seen in Fig. 2(a) that λ undergoes a transition from positive to negative values around the noise intensity $D_c \approx 3.5$ pA/cm². Beyond this critical point, two identical neurons with the same input converge to an identical spike sequence after a short transient (Fig. 3), and the synchronization error E vanishes [Fig. 2(b), closed circles]. In the synchronized regime, a single neuron (without parameter drifts) will have perfect reliability in response to a repeated fluctuating stimulus.

Note that in this system, the dynamics is sensitive to the noisy input close to the saddle point, while the spikes are not affected much. This property is of importance for biological information processing using spike trains which are well-defined even in the presence of a fluctuating input. In other

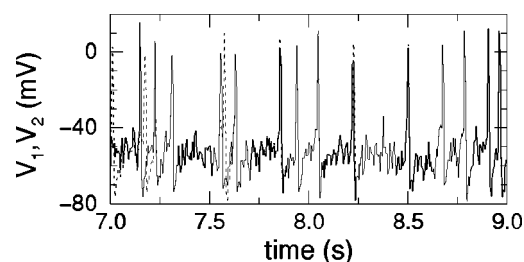


FIG. 3. Synchronization of the spike trains of two identical neurons at $D = 4$. The spike sequences started from different initial conditions converge to an identical one after a short transient.

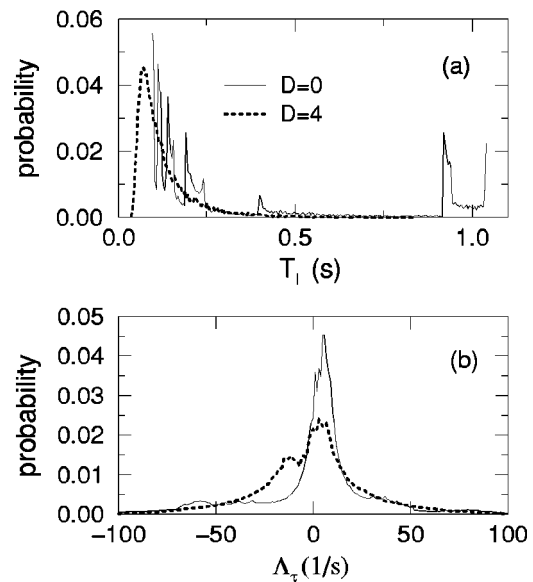


FIG. 4. (a) Distribution of the interspike interval T_I at $D=0$ (solid line) and $D=4$ (dotted line); (b) distribution of the largest local Lyapunov exponent at $D=0$ (solid line) and $D=4$ (dotted line).

systems, the geometry of the dynamics may be distorted significantly by noise when synchronization is achieved at large enough intensities.¹⁷

The synchronization behavior in this system (1) is determined by the competition between contraction and expansion in the phase space. Since the negative eigenvalues have larger amplitudes than the positive ones, the contraction rate is larger than the expansion rate around S . In the presence of a suitable level of noise, the orbits can still approach S and experience contraction, while they cannot follow the guidance of the weakly unstable manifold for a long time. There are two consequences of this result: (i) those long intervals in the noise-free case resulting from following the unstable directions and spiraling around S have been reduced considerably, as seen in Fig. 4(a) showing the distributions of the interspike intervals T_I at $D=0$ and $D=4$; and (ii) the expansion degree is reduced correspondingly compared to the noise-free case. In Fig. 4(b) we have plotted the corresponding distributions of the largest local Lyapunov exponent Λ_τ ($\tau = 50$ ms). At $D=0$, there is a high peak at small positive Λ_τ resulting from a long residence time close to the unstable manifold. The peak becomes much lower at $D=4$, and on average the contraction becomes dominant over the expansion. As a result, the largest Lyapunov exponent $\lambda = \langle \Lambda_\tau \rangle$ becomes negative and synchronization is achieved.

One should have noticed from Fig. 4(b) that even in the synchronization regime, the expansion regions still exist in the phase space, and the orbits still have access to these regions (e.g., during the activation phase of each spike). Small distances between orbits grow temporally in these regions. As a result, synchronization is lost intermittently in the presence of additional perturbations due to parameter mismatches or discrepancies between the noisy driving forces. This situation naturally occurs in repeated experiments with the same neuron and driving signal. Due to this nonidentity, synchronization cannot be perfect. As demonstrated in Fig.

2(b) (squares), the relative synchronization error E between two nonidentical neurons with a 5% difference in the leakage parameter g_l remains rather large even for D well beyond the synchronization threshold. Nonidentity is typical in biological systems. In this context, in Sec. IV we study phase synchronization of nonidentical neurons subjected to a common fluctuating input.

IV. PHASE SYNCHRONIZATION OF NONIDENTICAL NEURONS

Synchronization of nonidentical oscillators has been recently intensively studied in terms of phase synchronization.^{9,10,30} It has been found for coupled chaotic systems that phase synchronization sets in at a much weaker coupling strength compared to that for almost complete synchronization.

In nonidentical neurons, the spike sequences cannot be fully identical. However, since the neurons are sensitive to perturbation when the trajectories are close to the saddle point, the common input may dominate the dynamics and generate similar spike train patterns in a period of time in spite of the nonidentity. To study this similarity in terms of phase synchronization, we define a phase variable for the spike train as³¹

$$\phi(t) = 2\pi k + 2\pi \frac{t - \tau_k}{\tau_{k+1} - \tau_k}, \quad \tau_k \leq t < \tau_{k+1}, \quad (3)$$

where τ_k is the time when the k th spike occurs, as detected in numerical simulations when the membrane potential V exceeds a threshold of -20 mV. In this definition, the spike train is considered as a point process and each spike generation is associated with a 2π phase increase. Phases between two successive spikes are obtained by a linear interpolation. A phase defined in this way is a piecewise-linear function of time, and is closely related to the most important characteristic, i.e., spike timing of the spike trains. Since the spikes are well defined even in the presence of quite large noise input, the phases of the spike trains can be computed without much ambiguity. However, in a noisy system, phase locking cannot be perfect, but rather many phase synchronization epochs may occur where phases are locked temporally, and then interrupted by rapid 2π phase slips. Phase synchronization can be detected by phase locking plateaus in the plot of phase difference $\Delta\phi(t) = \phi_2(t) - \phi_1(t)$ between two neurons. Another approach to detect phase synchronization among phase slips is to examine the distribution of the cyclic phase difference $\Delta_c\phi = \Delta\phi \bmod 2\pi$.³¹ A peak in the distribution exhibits a preferred phase difference¹² between the spike sequences of the two neurons.

In numerical simulations, we introduce a mismatch into the leakage parameter g_l and keep the other parameters identical. We first consider two neurons, with $g_l^1 = 0.1$ for V_1 and $g_l^2 = 1.05g_l^1$ for V_2 . With this parameter heterogeneity, the first neuron has a larger average spiking rate in the absence of a noisy input. The phases are not synchronized, as seen from quick, random-like slips in the plot of the phase difference $\Delta\phi$ [Fig. 5(a), $D=0$ (solid line)] and from the uniform distribution of the cyclic phase difference $\Delta_c\phi$ [Fig. 5(b)]. In

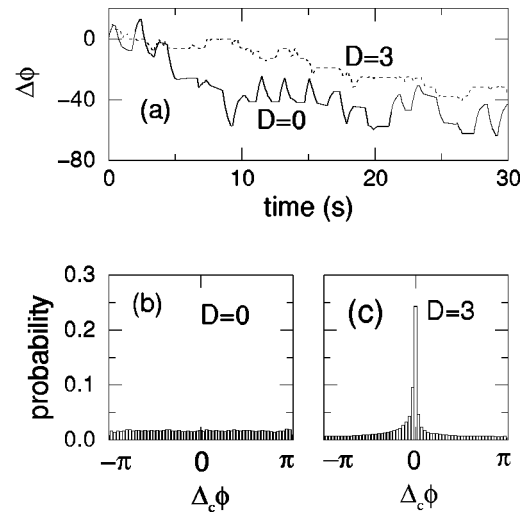


FIG. 5. Phase dynamics between two nonidentical neurons. (a) Phase differences at $D=0$ (solid line) and $D=3$ (dotted line); corresponding distribution of cyclic phase difference at $D=0$ (b) and $D=3$ (c).

the presence of a common noise input with $D=3$, many phase locking plateaus are observed and the distribution of the cyclic phase difference exhibits a sharp peak around $\Delta_c\phi = 0$, indicating that there are many spikes having rather reliable spike timing even though the systems are nonidentical and the input is not strong enough to exceed the threshold of complete synchronization. These results illustrate that a fluctuating input induces phase synchronization between nonidentical neurons.

The sharpness of the distribution of the cyclic phase difference reflects the degree of phase synchronization, which can be quantified by the entropy of the distribution,³¹ i.e., $H = -\sum_{i=1}^M p_i \ln p_i$, where M is the number of bins. Normalizing H into $[0,1]$ by the maximal entropy $H_m = \ln M$ of the uniform distribution, we obtain the phase synchronization index

$$\rho_{ps} = (H_m - H) / H_m. \quad (4)$$

The degree of phase synchronization is higher with larger ρ_{ps} . In Fig. 6, we calculate ρ_{ps} along with the relative difference between the average spiking rates ω_1 and ω_2 of the two neurons, i.e.,

$$\Delta\omega = 2 \frac{|\omega_1 - \omega_2|}{\omega_1 + \omega_2}. \quad (5)$$

It is seen that $\Delta\omega$ decreases and ρ_{ps} becomes appreciably nonzero and increases continuously when D is larger than $D_{ps} \approx 2$. Before D_{ps} , the spike timing of the two neurons keeps effectively independent. After D_{ps} , more and more spikes are evoked with a small variability in the spiking times (a higher peak around $\Delta_c\phi = 0$ in the distribution of the cyclic phase difference).

Note that in repeated experiments, the input signal cannot be fully identical due to unavoidable intrinsic or environmental noises. To take this discrepancy into account, we have also considered the case that the noise inputs between the two neurons are correlated with $C < 1$, where C is the correlation coefficient. While $\Delta\omega$ does not exhibit a clear depen-

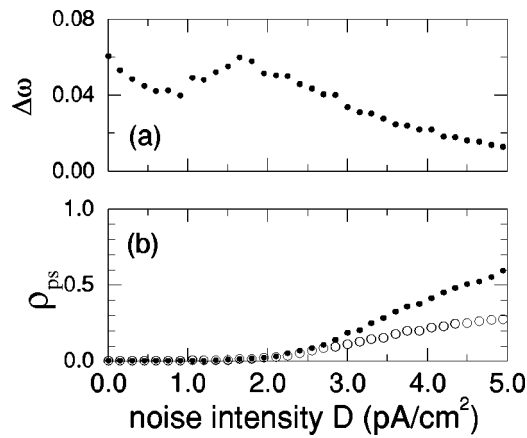


FIG. 6. (a) Relative frequency difference $\Delta\omega$ between the two nonidentical neurons with an identical input. (b) Phase synchronization index ρ_{ps} for identical noise input (closed circles) and nonidentical noise inputs (open circles) with a correlation $C=0.98$.

dence on C when it is close to 1 (results not shown), a small discrepancy increases the variability in spiking times and reduces the degree of phase synchronization considerably [Fig. 6(b)] for a correlation $C=0.98$. Phase synchronization still occurs for D beyond D_{ps} , but ρ_{ps} decreases with decreasing correlation C until it vanishes when the driving signals become independent. These results demonstrate that the reliability of spike timing of the neurons in repeated response is robust to some extent with respect to changes in the system parameters and unavoidable perturbations (e.g., changes of amplitude D and correlation C) to the input signals, which is meaningful for biological information processing.

In the following, we study the collective behavior of an ensemble of nonidentical neurons subjected to a common noise input,

$$C_M \frac{dV_i}{dt} = -I_l - I_d - I_r - I_{sd} - I_{sr} + D\xi(t), \quad (6)$$

which corresponds to the situation where a number of neurons receive a fluctuating stimulus simultaneously. To take heterogeneity into account, the leakage parameters g_i^l of the i th neuron is assumed to be a random variable uniformly distributed in the range $0.1 \times [1 - \delta, 1 + \delta]$ with $\delta=0.05$. We first consider an ensemble of $N=200$ neurons and compute the frequency disorder σ_ω defined similar to Δ_ω , namely

$$\sigma_\omega = \frac{\langle [\omega_i - \langle \omega_i \rangle]^2 \rangle^{1/2}}{\langle \omega_i \rangle}, \quad (7)$$

where $\langle \rangle$ denotes the ensemble average. σ_ω as a function of noise intensity D is plotted in Fig. 8(a), showing a noise-enhanced phase synchronization behavior similar to that of two neurons in Fig. 6(a).

Now we divide the ensemble into two subensembles with different numbers of neurons $N_1=90$ and $N_2=110$. The leakage parameters are independent in these two ensembles. We focus on the mean field $U_k = 1/N_k \sum_{i=1}^{N_k} V_i^k$ ($k=1,2$) of the two ensembles. In the absence of the noisy input, U_1 and U_2 fluctuate independently around a constant value [Fig. 7(a)]. However, in the presence of a strong enough common noise

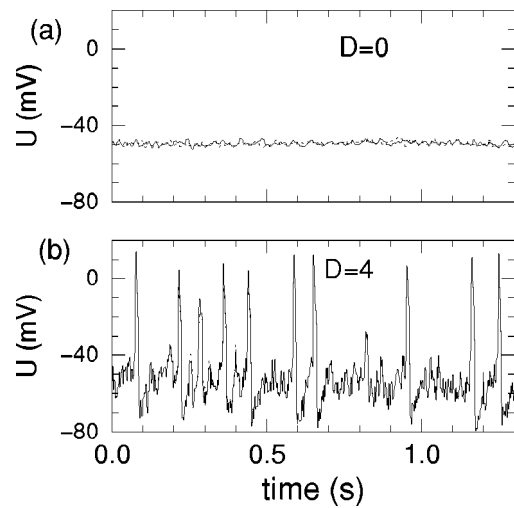


FIG. 7. Mean field U of ensembles of nonidentical neurons. (a) Without input $D=0$, U_1 (solid line) and U_2 (dotted line) have small and independent fluctuations around a constant value; and (b) with a common noise input $D=4$, U_1 and U_2 exhibit almost identical spike sequences (the dotted line is not easily seen now).

input, both U_1 and U_2 exhibit many spikes and become almost identical [Fig. 7(b)] as a result of noise-induced synchronization. To quantify these changes, we calculate the fluctuation amplitude σ_{U_k} (standard deviation) of U_k , and the relative difference between U_1 and U_2 as $E_{ens} = \langle |U_1 - U_2| \rangle / \sqrt{\sigma_{U_1} \sigma_{U_2}}$. σ_{U_1} and σ_{U_2} are almost the same for large enough N_1 and N_2 . The results of σ_U and E_{ens} are shown in Figs. 8(b) and 8(c), respectively. σ_U increases when larger input generates more spikes in the collective motion by phase synchronization. The difference between the meanfield of the two nonidentical ensembles decreases

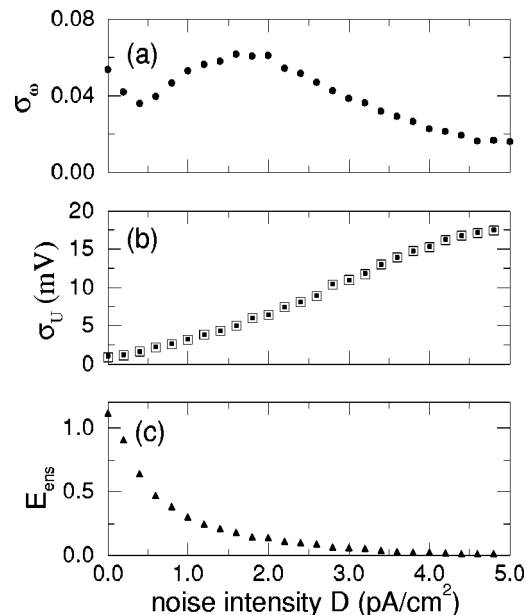


FIG. 8. (a) Frequency disorder σ_ω of an ensemble of $N=200$ nonidentical neurons. (b) Amplitude σ_U of the mean field U of two independent ensembles with $N_1=90$ (closed squares) and $N_2=110$ (open squares); and (c) relative synchronization error E_{ens} between U_1 and U_2 of the two ensembles.

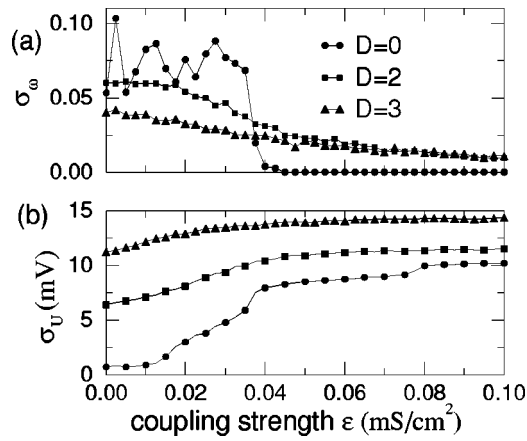


FIG. 9. Frequency disorder σ_ω (a) and amplitude σ_U (b) of an ensemble of $N=200$ globally coupled nonidentical neurons subjected to a common noise input.

quickly and vanishes effectively when $D>3$. Compared to the much larger synchronization error E around $D=3$ between two identical neurons or nonidentical ones [Fig. 2(b)], it is clear that the collective response of an ensemble of neurons has a higher degree of reliability to repeated fluctuating stimulus. In particular, the reliability is robust to parameter drifts and the number of neurons in the ensemble. Since nonidentity is typical in neural systems, this enhanced reliability by collective response may be of relevance to biological information processing.

V. NOISE-ENHANCED PHASE SYNCHRONIZATION IN WEAKLY COUPLED NEURONS

Neurons are often coupled and receive fluctuating stimuli simultaneously. In this section we study the interplay between coupling and common noise input. We consider an ensemble of weakly globally coupled nonidentical neurons,

$$C_M \frac{dV_i}{dt} = -I_l - I_d - I_r - I_{sd} - I_{sr} - \epsilon(V_i - U) + D\xi(t), \quad (8)$$

where U is the mean field of the ensemble and ϵ is the coupling strength. This coupling scheme considered for the sake of simplicity in many theoretical investigations of coupled oscillators, however, may not be fully relevant to biological reality where transmission time of the spikes should be taken into account. The ensemble has distributed leakage parameters g_l^i as in Eq. (6). To characterize phase synchronization of the neurons, we compute the frequency disorder σ_ω and the amplitude σ_U of the collective motion U . The results as a functions of the coupling strength ϵ are shown in Fig. 9 for various noise input intensity D . In the absence of noise $D=0$, there is a transition to perfect phase synchronization among the neurons at a relative weak coupling $\epsilon_{ps} \approx 0.043$ mS/cm². Beyond this critical point, the mean field U exhibits spike train patterns similar to those of a single neuron. In weak coupling regimes, e.g., $\epsilon=0.02$, U does not exhibit spikes but slow and weak oscillations [Fig. 10(a)] resulting from the slow currents I_{sd} and I_{sr} in the model [Eq. (1)]. With a noisy input, the transition is smeared

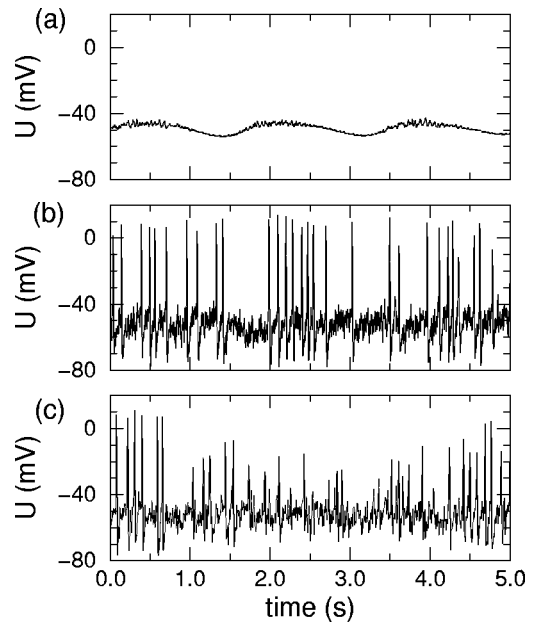


FIG. 10. Mean field U of an ensemble of $N=200$ nonidentical neurons. (a) $\epsilon=0.02$, $D=0$; (b) $\epsilon=0.02$, $D=3$; and (c) $\epsilon=0$ and $D=3$.

and phase synchronization is not perfect even for rather strong coupling strength. However, in the weak coupling region, phase synchronization among the neurons is enhanced significantly by a noisy input, quantified by a much smaller frequency disorder σ_ω and a much larger amplitude σ_U . σ_ω decreases and σ_U increases with increasing coupling strength ϵ . The collective response of the ensemble to a noise input of $D=3$ is shown in Fig. 10(b) for $\epsilon=0.02$. Compared to that in the ensemble of uncoupled neurons [$\epsilon=0$, Fig. 10(c)], it is clear that weak coupling enhances the sensitivity of the collective response to a fluctuating stimulus, although in the absence of a noisy input, both ensembles exhibit no pronounced macroscopic collective behavior.

Combined with the results for the uncoupled neurons in Sec. III, a collective response of weakly coupled (or effectively uncoupled) neurons may be meaningful in biological information processing: without an input, the ensemble does not show a macroscopic mean field, while in the presence of a strong enough fluctuating input, it generates a collective response. The reliability of the collective response is robust to heterogeneity which is generic in biological systems.

VI. NOISE-ENHANCED COHERENCE OF SPIKE TRAINS

We have observed that in the presence of a noise input, the spiking behavior is preserved in the neuron, however, the property of the interspike interval T_I has been altered significantly. Earlier, we have investigated synchronization of neurons due to modified stabilities as a result of the changes in the spike train patterns. In this section, we will concentrate on the coherence of the spike train of a single neuron.

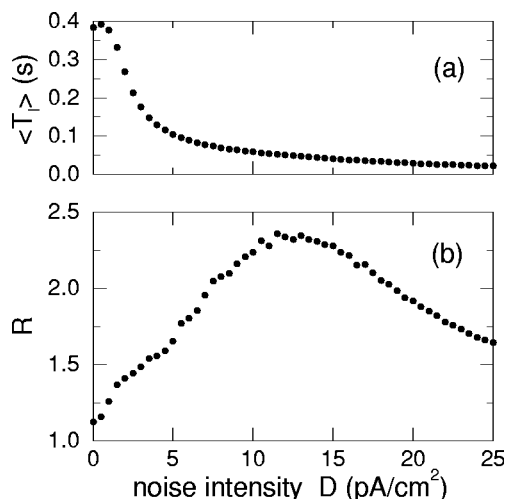


FIG. 11. Average interspike interval $\langle T_I \rangle$ (a) and coherence factor R (b) as functions of noise intensity D .

For each noise intensity D we collect a large number of interspike intervals T_I and compute the average value $\langle T_I \rangle$ and the variance $\text{var}(T_I)$. We employ a measure of coherence proposed in Ref. 2, namely,

$$R = \frac{\langle T_I \rangle}{\sqrt{\text{var}(T_I)}}. \quad (9)$$

R measures the sharpness of the distribution of T_I . As seen in Fig. 4(a), in the absence of noise T_I has a broad distribution which will result in $R \approx 1$, while for $D=4$ the distribution becomes unimodal, and R gets larger than 1. The results of $\langle T_I \rangle$ and R are shown in Fig. 11 as functions of the noise intensity D , which is now extended to much larger values than the threshold of synchronization. Synchronization is found persistent even at very large noise intensity. The average interspike interval $\langle T_I \rangle$ decreases with D . However, R increases, reaches a maximal value around $D=12$, and decreases at larger D . This behavior is very similar to coherence resonance observed in excitable systems,² but with a different mechanism. In excitable systems,² noise induces spiking by kicking the system over an energy barrier. Coherence resonance is a result of the competition between two effects of noise, namely (i) at small intensity it alters mainly the stochastic activation time from the potential well; and (ii) at large intensity, it also affects significantly the dynamics during the spiking, and induce strong fluctuation in the refractory time. In the present system, the spike sequence is generated by chaotic recurrence to the saddle S . Small noise mainly changes the time that the system takes to leave the neighborhood of S , and large noise also perturbs the system strongly during the spiking. The competition between these two effects results in coherence resonance. This mechanism is also different from noise-induced coherent jumping among coexisting attractors.³² Figure 12 illustrates spike train patterns at weak ($D=1$), intermediate ($D=10$), and strong ($D=25$) noise intensities, where the interspike intervals are the most regular for $D=10$.

The coherence of the collective motion U of an ensemble of neurons (uncoupled or coupled) displays similar

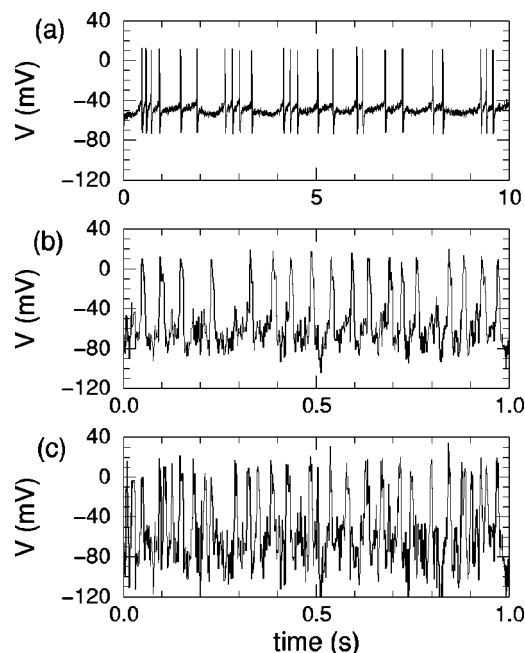


FIG. 12. Spike train patterns of the neuron subjected to different levels of noise input. (a) $D=0$; (b) $D=10$; and (c) $D=25$. Note a different time scale in (a).

features. A difference is that in a weak coupling regime, rather weak input cannot generate spikes in U .

VII. CONCLUSION

In this paper we have studied nontrivial effects of noise on synchronization and coherence of chaotic neurons. Strong enough common noise input induces complete synchronization of two identical neurons due to the existence of contraction regions accompanying a saddle point S in the phase space. The noise input modifies significantly the motion close to S , which reduces the residence time in the neighborhood of S . In the absence of noise, this time is mainly determined by a slow motion along the weak unstable directions of S . As a result of this noise-induced modification, the competition between contraction and expansion is altered, so that synchronization occurs when the contraction becomes dominant.

We have also demonstrated that noise is able to induce phase synchronization in an ensemble of nonidentical neurons, because the systems have high sensitivity to perturbations close to the saddle point where the common noise input may dominate the dynamics over the nonidentity, even at an intensity weaker than that for complete synchronization. The collective response of an ensemble has a higher degree of reliability to a repeated fluctuating stimulus compared to that of a single neuron. Weak coupling in the ensemble enhances the sensitivity of the collective response to the stimulus.

The same mechanism leading to synchronization results in enhanced coherence of the spike train. There exists an optimal input amplitude where the interspike intervals become the most regular. This mechanism of coherence resonance is different from that in excitable systems.

The mechanism presented here for a realistic HH neuron model should interpret the experimental observation of reliability of spike timing of neurons and shed new light on understanding biological information processing. The behavior, however, is not special for this neuron model. It is general for systems possessing a saddle point embedded in a chaotic attractor in the phase space. In fact, we have observed noise-induced synchronization and coherence resonance of a homoclinic chaos laser, both numerically and experimentally.³³

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