Synchronization and quorum sensing in an ensemble of indirectly coupled chaotic oscillators

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The fact that the elements in some realistic systems are influenced by each other *indirectly* through a common environment has stimulated a new surge of studies on the collective behavior of coupled oscillators. Most of the previous studies, however, consider only the case of coupled periodic oscillators, and it remains unknown whether and to what extent the findings can be applied to the case of coupled chaotic oscillators. Here, using the population density and coupling strength as the tuning parameters, we explore the synchronization and quorum sensing behaviors in *an ensemble of chaotic oscillators* coupled through a common medium, in which some interesting phenomena are observed, including the appearance of the phase synchronization in the process of progressive synchronization, the various periodic oscillations close to the quorum sensing transition, and the crossover of the critical population density at the transition. These phenomena, which have not been reported for indirectly coupled periodic oscillators, reveal a corner of the rich dynamics inherent in indirectly coupled chaotic oscillators, and are believed to have important implications to the performance and functionality of some realistic systems.

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I. INTRODUCTION

Many complex systems in nature can be described as an ensemble of coupled oscillators, and the collective behavior of such systems has been a subject of continuous interest in nonlinear science [1–4]. In neural and biological systems, a typical collective behavior observed is the coherent motion of the oscillators, e.g., the synchronization, which has been widely regarded as having important implications to the function and performance of the systems [5,6]. To study the synchronization behaviors, a simple yet efficient approach is to consider an ensemble of directly coupled regular oscillators, and investigate how the system is transited from the nonsynchronous to the synchronous states as a function of certain system parameters [4]. For instance, in the classical Kuramoto model where an ensemble of phase oscillators with distributed frequencies is directly coupled in a global fashion, it has been found that as the coupling strength exceeds some critical value, the phase of the oscillators will be gradually aligned to the same dynamical state [7–10]. This scenario of progressive synchronization transition, however, is drastically changed when the oscillators are coupled indirectly—another important approach in studying the synchronization of coupled systems [11–22]. For instance, in systems such as bacteria [12] and yeast cells [13], the elements are not influenced by each other in a direct fashion, but rather through the common environment indirectly. In such kinds of systems, a common finding is that, as the population density of the element exceeds some threshold value, the system will be *suddenly* switched from the quiescent state to the state of synchronized oscillation for all the elements, i.e., the quorum sensing phenomenon [12]. Although of different coupling fashion, the two approaches do share some common features in the synchronization transitions [14], and are often compared with each other in exploring the synchronization dynamics [13]. In particular, by a chemical experiment of indirectly coupled regular oscillators, it has been shown that both synchronization scenarios, i.e., progressive synchronization and quorum sensing, can be observed in the same dynamical system [15].

In previous studies of indirectly coupled systems, the oscillator dynamics is mostly taken as periodic and the chaotic case is much less considered. (In Refs. [23,24], the authors have investigated the indirectly coupled chaotic oscillators from the viewpoint of synchronization control). As chaos is ubiquitously observed in realistic systems, it is natural to check whether the previous findings established on periodic oscillators [13–15] stand still for chaotic oscillators. Previous works on directly coupled chaotic oscillators have shown that their collective dynamic is much more complicated and offers even richer phenomena [25–28]. For instance, depending on the coupling strength and coupling function, the directly coupled chaotic oscillators could present various synchronous forms, including the complete synchronization [26], the phase synchronization [27], and the generalized synchronization [28], etc. In comparison to directly coupled chaotic oscillators, the collective behavior of indirectly coupled chaotic oscillators is largely unknown. It is thus intriguing to see whether the rich synchronization phenomena observed in directly coupled chaotic systems can be found in indirectly coupled systems as well, and, if yes, what are the roles that these synchronization forms play in the transition of the system collective behaviors. (For the transition of the collective behaviors in directly coupled chaotic oscillators, please refer to Ref. [25], and references therein.)

In addition to the theoretical interest, the study of indirectly coupled chaotic oscillators may also have implications for the functioning and operating mechanisms for some realistic systems, e.g., the emergence of the robust rhythms in biological organisms [29]. For rhythms generators such as the central pattern generator, or the cardiac pacemaker and the circadian clock, the systems are composed of thousands of clock cells

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which normally possess the irregular dynamics. An interesting phenomenon observed in experiments is that, coupled through the common medium, the system could output a robust and regular collective behavior. By studying the indirectly coupled chaotic oscillators, we also wish to gain some insight into the functioning of this kind of system.

Interested by the above questions, in the present work we conduct a systematic analysis on the collective behavior of an ensemble of chaotic oscillators coupled through a common medium, with special attention being paid to the phenomena arisen by the chaotic feature of the oscillators. Our study shows that, while sharing the similar scenarios of synchronization transitions as the periodic oscillators, the chaotic oscillators do possess some unique features and present some new phenomena. Specifically, in the process of progressive synchronization we find that the oscillators reach the state of phase synchronization, i.e., the phases of the oscillators are well constrained while their amplitudes remain uncorrelated [27]. In addition, in the quorum sensing transition, we find that the trajectories of the oscillators become highly regular, despite the chaotic nature of the oscillators. More interestingly, we find that at the quorum sensing transition, the critical population density that characterizes the transition is not monotonically increased with the coupling strength, which is very different from the situation of coupled periodic oscillators. Our findings reveal the rich and unique dynamics arisen by chaotic oscillators, which are necessary and important complements to the current knowledge on the collective behaviors in indirectly coupled systems.

The rest of the paper is organized as follows. In Sec. II, we will give our model of indirectly coupled chaotic oscillators. In Sec. III, using the population density as the parameter, we will investigate systematically the transitions of the system collective behavior, including the progressive synchronization and the quorum sensing. In Sec. IV, we will give a global picture on the transitions, with special attention being paid to the crossover of the transition boundary for quorum sensing. Moreover, by a simplified model, we will also give a physical explanation to this phenomenon. Finally, in Sec. V we will give our discussions and conclusion.

II. THE MODEL

We consider an ensemble of chaotic oscillators diffusively coupled to a homogeneous common medium, with the time evolution of the system as described by the following set of ordinary differential equations [13]:

$$\frac{d\mathbf{z}_i}{dt} = \mathbf{F}(\mathbf{z}_i,\mathbf{p}_i) + \mathbf{K}(\mathbf{Z}-\mathbf{z}_i), \qquad i = 1,2,\ldots,N, \tag{1}$$

$$\frac{d\mathbf{Z}}{dt} = \frac{\rho}{N}\sum_{i=1}^{N}\mathbf{K}(\mathbf{z}_i-\mathbf{Z}) - \mathbf{J}\mathbf{Z}. \tag{2}$$

Here, the vector $\mathbf{z}_i$ denotes the state of the ith oscillator in the system, with $i = 1,2,\ldots,N$, and N is the system size. The vector $\mathbf{Z}$ represents the state of the common medium. In cellular systems, $\mathbf{z}_i$ and $\mathbf{Z}$ represent the chemical *concentrations* in the intracellular and extracellular compartments, respectively [13]. For each of the N oscillators, as shown in Eq. (1), its evolution is governed by two terms. The term $\mathbf{F}(\mathbf{z}_i,\mathbf{p}_i)$ governs the intrinsic dynamics of the oscillator, with $\mathbf{p}_i$ the bifurcation parameter. To have chaotic oscillators, we choose $\mathbf{p}_i$ from the chaotic regime. The other term in Eq. (1), $\mathbf{K}(\mathbf{Z}-\mathbf{z}_i)$, accounts for the diffusion signals that the oscillator receives from the medium, where $\mathbf{K}$ is the diagonal matrix that defines the strength of the couplings. Similarly, the evolution of the medium is also determined by two terms. The term $\bar{\mathbf{Z}} = (\rho/N)\sum_{i=1}^{N}\mathbf{K}(\mathbf{z}_i-\mathbf{Z})$ in Eq. (2) represents the speed of the signals sent out from the oscillators and that are accumulated in the medium solution. The other term, $-\mathbf{JZ}$, accounts for the inflow and outflow of the medium, with $\mathbf{J}$ the diagonal matrix characterizing the losses of the medium signals.

A key parameter in Eq. (2) is ρ, which characterizes the population density of the oscillators in the system. For cellular systems, we have $\rho = V_{\text{cyt}}/V_x$, with V_{cyt} and V_x the total cytosolic and the extracellular volumes, respectively [13,14]. Let $\bar{v}$ be the averaged cytosolic volume for the individual cells, then we have $\rho = N\bar{v}/V_x = n\bar{v}$, with $n = N/V_x$ the real density of the cells. Since $\bar{v}$ is a constant for the chosen type of oscillators, following the traditions in quorum sensing studies [13,14], here we simply use ρ as the oscillator population density. By this definition of ρ, it is straightforward to see that the exchange of the signals between the oscillators and the medium is balanced, as $\bar{\mathbf{Z}}V_x = -\bar{v}\sum_{i=1}^{N}\mathbf{K}(\mathbf{Z}-\mathbf{z}_i)$.

The above model captures the essence of many chemical and biological systems, where the system elements influence, and in turn are influenced by the environment medium through the diffusions, e.g., the coupling between the catalytic microparticles and the surrounding catalyst-free reaction solution [15], or the coupling between the *Escherichia coli* cells and the environmental autoinducer molecule [19]. It should be noted that the present model assumes a homogeneous distribution of the medium, i.e., the common medium, and also assumes an instant coupling between the oscillators and the medium, i.e., no time delay. These assumptions are reasonable for chemical and biological systems, as a homogeneous medium could be realized by either stirring the solution (in chemical systems) or the fast diffusion of the small molecules (in biological systems).

To solidify the study, in the following we will adopt the chaotic Rössler oscillator as the intrinsic dynamics of the elements, using one variable to describe the state of the environmental medium. Specifically, the set of equations we are going to investigate are

$$\begin{aligned}\dot{x}_i &= -\omega_i y_i - z_i + k(e-x_i),\\ \dot{y}_i &= \omega_i x_i + a y_i, \quad \dot{z}_i = 0.4 + (x_i - 8.5)z_i,\end{aligned} \tag{3}$$

and

$$\dot{e} = \frac{\rho}{N}\sum_{i=1}^{N}k(x_i-e) - Je. \tag{4}$$

In Eqs. (3), the parameter ω_i represents the intrinsic frequency of the ith oscillator, which, in general, should be different from each other. Here, for the sake of simplicity, we set ω to be identical, $\omega_i = \omega = 1$ (the nonidentical case will be briefly discussed later). With $a = 0.15$, the dynamics of the isolated oscillator is chaotic, with the largest Lyapunov exponent ~ 1.2. Our main task in the present work is to study how the collective behavior of the indirectly coupled chaotic oscillators will vary with the parameters ρ (the population density) and k (the coupling strength).

III. THE TWO TYPES OF TRANSITIONS

We start by investigating the transition of the system dynamics at some selected coupling strength. Specifically, by a weak coupling, we will check the transition scenario from the nonsynchronous to synchronous states as a function of the population density ρ, whereas by a strong coupling, we will explore the transition scenario from the quiescent to oscillatory states. For the former, special attention will be paid to the synchronization form appearing in the transition process, whereas for the latter, we will focus on the emergence of the synchronous periodic motions. Throughout the paper, we will fix the size of the system at $N = 1 \times 10^3$, except when specifically mentioned, and set the relaxation parameter as $J = 0.1$. Equations (3) and (4) are integrated by the fourth-order Runge-Kutta method, with the time step $\Delta t = 1 \times 10^{-3}$. Random initial conditions are used for the oscillators, and a transient period of $t = 1 \times 10^3$ is discarded when analyzing the properties of the system collective behaviors.

A. Progressive synchronization at weak couplings

We first check the transition of the system dynamics as a function of ρ under a *weak* coupling strength, $k = 2 \times 10^{-2}$. To have a quick look at the picture of the transition, we plot in Fig. 1 the evolution of the system dynamics for two selected population densities. With a small population density, $\rho = 0.5$, it is shown in Fig. 1(a) that the trajectories of the (five) oscillators, which are randomly chosen from the system, are widely separated from each other, indicating the absence of synchronization among the oscillators. The widely separated trajectories, however, are significantly constrained when the population density is large. For instance, by $\rho = 3.8$, we plot in Fig. 1(b) the trajectories for the same group of oscillators.

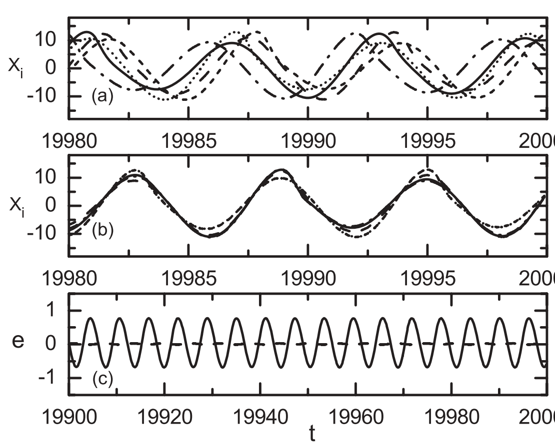

FIG. 1. By a weak coupling strength $k = 2 \times 10^{-2}$, the time evolution of five oscillators that are randomly chosen from the system under a lower population density $\rho = 0.5$ (a) and a larger population density $\rho = 3.8$ (b). (c) The time evolution of the common medium e, under the population densities $\rho = 0.5$ (dashed line) and $\rho = 3.8$ (solid line).

It is found that the phases of oscillators are well locked to each other, while their amplitudes remain uncorrelated. These are the typical features for phase synchronization [27] that have previously been observed in the directly coupled chaotic Rössler system [30].

Accompanied with the phase constraint of the oscillators, the behavior of the environmental medium is also significantly changed. As depicted in Fig. 1(c), when the phases of the oscillators are not synchronized, e.g., $\rho = 0.5$, the value of e remains around 0 throughout the evolution (dashed line), whereas when phase synchronization is reached, e.g., $\rho = 3.8$, the medium is found to be oscillating with a pronounced amplitude (solid line). Moreover, for the latter case it is found that despite the chaotic feature of the oscillators, the motion of the medium is highly regular. The regular motion of the medium could be understood by the mean-field behavior of the oscillators. In Ref. [30] the authors have studied the collective behavior of a large ensemble of globally and *directly* coupled nonidentical chaotic oscillators, and found that when the oscillators are synchronized in phase, the mean field of the oscillators will present a highly regular motion. As shown in Fig. 1(b), under the parameter $\rho = 3.8$ the phases of the oscillator are well locked, which, according to Ref. [30], will generate a highly regular mean field. As one observes from the right-hand side of Eq. (4) that the other term related to the common medium e is linear, the oscillation of the medium thus is governed by the regular mean-field motion.

How is the state of phase synchronization reached, and what is the role it plays in the transition of the system dynamics? To address these questions, we go on to investigate the transition of the system dynamics as a function of the density parameter. Following the tradition of quorum-sensing studies, we measure the degree of phase synchronization of the oscillators by the following order parameter [15,31]:

$$R = \left\langle \left| N^{-1} \sum_{j=1}^{N} \exp[i\theta_j(t)] - \left\langle N^{-1} \sum_{j=1}^{N} \exp[i\theta_j(t)] \right\rangle \right| \right\rangle, \quad (5)$$

with $\langle \cdots \rangle$ representing the time average over a period of $t = 2 \times 10^3$. It is straightforward to see that if the oscillators are out of phase from each other, we have $R = 0$, e.g., the case shown in Fig. 1(a), whereas if the oscillators are of perfect phase synchronization, we have $R = 1$, e.g., the case shown in Fig. 1(b). (Following the tradition, we also set $R = 0$ if the oscillators are quenched from oscillation, which we will meet later in the transition under strong couplings.)

By the same coupling strength as used in Fig. 1, we plot in Fig. 2(a) the variation of the order parameter R, as a function of the population density in the range of $\rho \in [0,5]$. It is observed that as ρ increases, the value of R is *progressively* increased from 0 to 1. In particular, at $\rho = \rho_p \approx 3.0$ we have $R \approx 1$, indicating a strong constraint of the phases of the oscillators. This fashion of progressive transition is very similar to the scenario of directly coupled phase oscillators [4]. Progressive transition is also observed in the dynamics of the medium. In Fig. 2(b), we plot the variation of the time-averaged oscillation amplitude of the medium $\langle A_e \rangle$, as a function of ρ. It is seen that just like the phase order parameters, the value of $\langle A_e \rangle$ is also progressively increased.

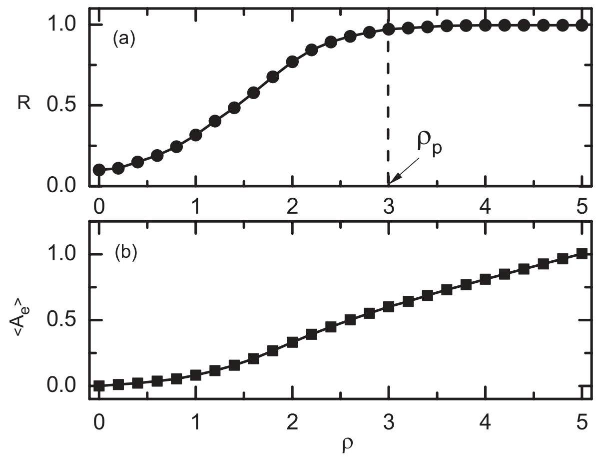

FIG. 2. By $k = 2 \times 10^{-2}$, the variation of (a) the phase order parameter R and (b) the averaged amplitude of the medium oscillation $\langle A_e \rangle$, as a function of the population density ρ. For $\rho > \rho_p \approx 3.0$, we have $R \approx 1$, indicating a strong constraint of the phases of the oscillators, i.e., reaching the state of phase synchronization.

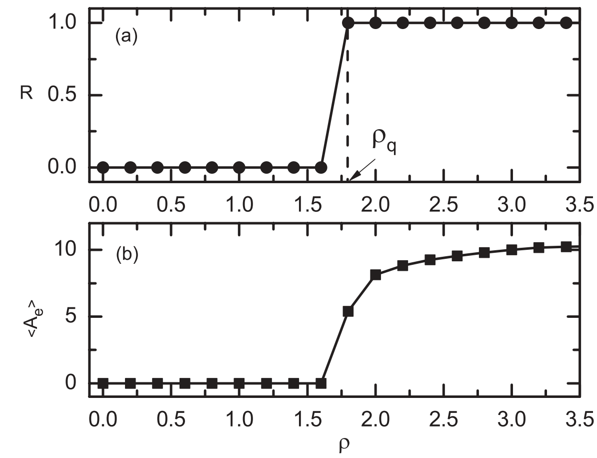

FIG. 4. By $k = 1.0$, the variation of (a) the phase order parameter R, and (b) the averaged amplitude of the medium oscillation $\langle A_e \rangle$, as a function of the population density. For the quiescent state, we have $R = 0$. Quorum sensing occurs at about $\rho_q \approx 1.8$, where R is switched from 0 to 1 and $\langle A_e \rangle$ is starting to increase from 0.

B. Dynamical quorum sensing at strong couplings

We next investigate the transition of the system dynamics as a function of ρ under a *strong* coupling strength, $k = 1.0$. When ρ is very small, from Eq. (4) we know that due to the large relaxation term $-Je$, the medium will be finally ceasing from the oscillation, i.e., reaching the steady state $e = 0$. In this case, the coupling term in Eq. (3) becomes $-kx_i$, which will suppress the oscillation of the oscillators. Once k is larger than some critical value k_c, the oscillators will be stopped from oscillation and, as a consequence, the system will be ceased to the quiescent state $\mathbf{x}_s$. In Fig. 3(a), by a small population density ($\rho = 0.2$), we plot the time evolution for some typical oscillators in the system, in which the ceasing of the oscillators to the quiescent state is evident.

The quiescent state, however, becomes unstable when the population density is large enough. In Figs. 3(b) and 3(c), we plot the time evolution for the same set of oscillators as plotted in Fig. 3(a) under the parameters $\rho = 2.0$ and $\rho = 6.5$, respectively. It is seen that under these densities, the oscillators are oscillatory and synchronized.

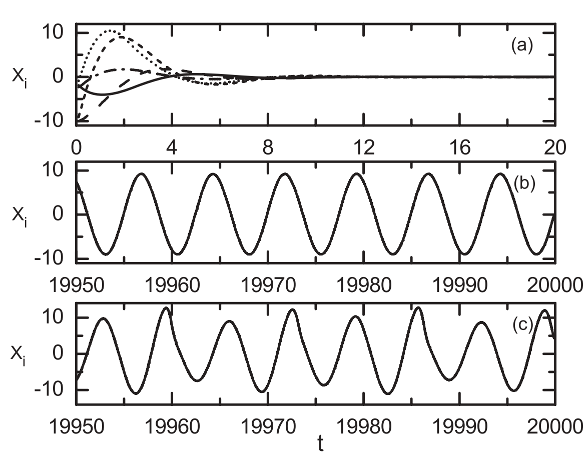

FIG. 3. By a strong coupling strength $k = 1.0$, the time evolution of five oscillators chosen randomly from the system, with the population density as (a) $\rho = 0.2$, (b) $\rho = 2.0$, and (c) $\rho = 6.5$. In (a), the oscillators finally cease from oscillation, and reaching the quiescent state. In (b), the oscillators are synchronized to a periodic-1 trajectory. In (c), the oscillators are synchronized to a chaotic trajectory.

To obtain the details about the transition from the quiescent to the synchronous oscillatory states, we again monitor the variations of the phase order parameter R, and the averaged medium amplitude $\langle A_e \rangle$, as a function of ρ in the regime of strong couplings. The numerical results are plotted in Fig. 4, where the coupling strength is taken as $k = 1.0$. In Fig. 4(a), it is seen that as ρ exceeds the critical density $\rho_q \approx 1.8$, R suddenly jumps from 0 to 1, indicating the switch from the quiescent to the oscillatory and synchronous states at this point. Accompanied with the oscillation of the oscillators, the value of $\langle A_e \rangle$ is also increased from 0 at ρ_q, reflecting the onset of oscillation for the medium at this critical density. Moreover, as ρ increases from ρ_q, the value of $\langle A_e \rangle$ is gradually increased, indicating that the oscillation is enhanced by increasing ρ. This phenomenon, observed in Fig. 4, is much like the quorum sensing phenomenon observed in the bacteria system, where each population of elements undergoes a sudden change in their behaviors, i.e., showing a supercritical increase of the concentration of a signaling molecule in the extracellular solution [12]. For this reason, we call the transition shown in Fig. 4 the quorum sensing transition. This observed sudden transition shares the same features with the oscillator death (OD) transition [32,33], which is just expressed in a different context.

An interesting phenomenon in the above quorum sensing is that, at the boundary of the transition, the synchronous motion of the oscillators is highly regular, despite their chaotic nature. For instance, by $\rho = 2$, the oscillators are observed to oscillate with the period-1 motion [Fig. 3(b)]. The periodicity of the synchronous motion, however, is subjected to the change of the population density. For instance, increasing ρ to 6.5, in Fig. 3(c) it is seen that the synchronous motion becomes chaotic, which resumes the chaotic nature of the individual oscillator. To check out the variation of the synchronous

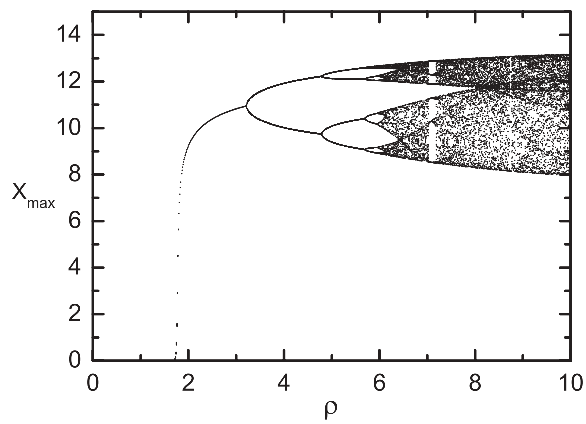

FIG. 5. For the simple case of $N = 2$ indirectly coupled chaotic Rössler oscillators, and by the coupling strength $k = 1$, the variation of the synchronous motion as a function of ρ. The method of Poincaré surface of section has been employed in plotting this bifurcation diagram, where $x_{\max}$ is the local maxima of the variable x_1 of the synchronous motion.

motion, by employing the simple case of $N = 2$ oscillators, in Fig. 5 we plot the bifurcation diagram of the synchronous oscillation as a function of ρ. (Here we wish to note that in experimental realizations the variation of ρ could be accomplished by effectively changing either the averaged cell volume $\bar{v}$, or the total extracellular volume V_x.) Very interestingly, it is found that the oscillation undergoes a standard period-2 bifurcation. The above results (in Figs. 4 and 5) thus suggest that besides inducing the quorum sensing, the population density also plays a role in adjusting the motion of the synchronous oscillation.

The finding that the synchronous motion varies with ρ might have implications for the functioning of some realistic systems, e.g., the robust rhythm appearing in biological systems. Taking the circadian clock residing at the suprachiasmatic nuclei in mammalian brains as an example [34], in this system, due to the intrinsic nonlinear dynamics, the behavior of the individual neuron is normally irregular or chaotic. However, when a population of such neurons is coupled together, they could generate very robust and regular collective behaviors [29]. Since one way of coupling the neurons is the diffusion of certain chemical elements with the environmental medium, this system thus might be regarded as an ensemble of indirectly coupled irregular oscillators. If this is the case, then the numerical results shown in Fig. 5 indicate that for the system to output a regular synchronous motion of a specific period, the number of neurons should be restricted to within a certain range. For instance, in our model of coupled Rössler oscillators, if the period-2 oscillation is desired, from Fig. 5 we know that the value of ρ should be chosen within the range (3.20,4.82).

IV. THE GLOBAL PICTURE

From the mathematical point of view, the value of ρ simply reflects the coupling strength that the medium is influenced by the oscillators, which is similar to the role of k in Eq. (3). It is therefore expected that by varying k, the collective behavior of the system will be undergoing similar transitions as for varying ρ. A question naturally arises: How are these two parameters related, and how do they jointly determine the system dynamics? In particular, in the transition to the quorum sensing, how is ρ_q dependent on k? To answer this question, it is necessary to have a global analysis on the transitions of the system dynamics, i.e., analyzing the transitions in the two-dimensional space spanned by ρ and k. As shown in the previous section, the scenario of the transition is strongly dependent on the value of k. More specifically, when k is smaller than some critical value k_c, the system is oscillatory and, with the increase of ρ, experiences progressive transition, whereas if k is larger than k_c, the system is quiescent and, with the increase of ρ, undergoes the quorum sensing transition. For the model investigated here, numerically we find $k_c \approx 0.15$. Regarding this clear difference, in analyzing the transitions in the two-dimensional parameter space, we will treat the two regimes $k < k_c$ and $k > k_c$ separately.

In the regime of $k < k_c$, i.e., the progressive transition, the system is oscillatory and the role of the coupling is mainly for constraining the motion of the oscillators to that of the media. This is similar to the function of the population density, which is also used to improve the correlation between the media and the oscillators. For this reason, it is straightforward to predict that with the increase of the coupling strength k, the critical population density ρ_p, characterizing the phase synchronization in the progressive transition will be *monotonically* decreased. This prediction is verified by numerical simulations, as shown in Fig. 6, where the order parameter R is plotted as functions of ρ and k in a wide range of the parameter space. In Fig. 6, it is shown clearly that in the regime of $k < k_c$, as k approaches k_c, the boundary of the transition is gradually shifted up, indicating the decreased ρ_p at larger k. It should be noted that there exists another critical coupling

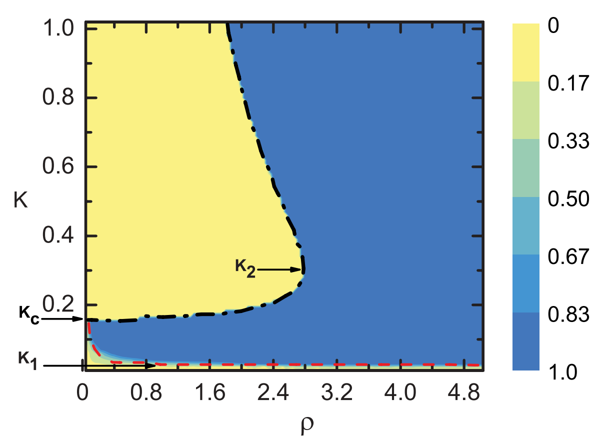

FIG. 6. (Color online) For $N = 100$, the order parameter R, as functions of the coupling constant k and the population density ρ. The boundaries of the progressive and quorum sensing transitions are denoted by, respectively, the dashed and dash-dotted curves. For $k < k_1 \approx 1 \times 10^{-2}$, the system cannot be synchronized whatever the population density takes. For $k_1 < k < k_c \approx 0.15$, with the increase of k, the critical population density characterizing the progressive transition ρ_p is monotonically decreased. For $k > k_c$, the critical population density characterizing the quorum sensing transition ρ_q, is first increased and then decreased, with the maximum density $\rho_q^{\max}$ locating at $k_2 \approx 0.3$.

strength, $k_1 \approx 1 \times 10^{-2}$, below which the system cannot be synchronized whatever the population density takes. The existence of k_1 is understandable, as it stands for the minimum coupling strength required by the medium to constrain the oscillators. From the viewpoint of chaos synchronization, this can also be understood as the critical coupling strength that the oscillators are used to synchronize with the medium in a generalized fashion, i.e., the generalized synchronization [35].

We next investigate the dependence of the critical density ρ_q on the coupling strength in the regime of $k > k_c$, i.e., the boundary of the quorum sensing transition. In previous studies of coupled regular oscillators, a general observation about the quorum sensing transition is that as the value of k increases, the necessary population density for saving the system from the quiescent state will also be increased; that is, the value of ρ_q is monotonically increased with k [15]. This relationship, however, is drastically changed in the system of coupled chaotic oscillators. As can be found in Fig. 6, as k increases from k_c, the value of ρ_q is first increased and then *decreased*, with the maximum density $\rho_q^{\max} \approx 2.75$ locating at about $k_2 \approx 0.3$. The decreased ρ_q in the region of $k > k_2$ seems to suggest that despite the increased damping, the deeply quenched system (with larger k) is easier to save from the quiescent state, which is quite contrary to the results obtained in coupled regular oscillators [15]. In what follows, we again adopt the simple model of $N = 2$ indirectly coupled chaotic oscillators, and explore the underlying mechanism for the nonmonotonic relationship between ρ_q and k in the quorum sensing transition.

Assume that under a strong coupling both oscillators are ceased to the steady state $\mathbf{x}_s = (x_s, y_s, z_s)$, e.g., $\dot{\mathbf{x}}_s = 0$ for Eqs. (3) and (4), then the critical population density for quorum sensing ρ_q is identified as the point where the steady state becomes unstable. To test the stability of the steady state, we add a small perturbation $\delta\mathbf{x} = (\delta x, \delta y, \delta z)$ onto it, and check the evolution of this perturbation. In its linearized form, the perturbation will be evolved according to the equation $\delta\dot{\mathbf{x}} = A\delta\mathbf{x}$, with

$$A = \begin{pmatrix} -k & -1 & -1 & 0 & 0 & 0 & k \\ 1 & 0.15 & 0 & 0 & 0 & 0 & 0 \\ z_s & 0 & x_s - 8.5 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -k & -1 & -1 & k \\ 0 & 0 & 0 & 1 & 0.15 & 0 & 0 \\ 0 & 0 & 0 & z_s & 0 & x_s - 8.5 & 0 \\ k\rho/2 & 0 & 0 & k\rho/2 & 0 & 0 & -k\rho - J \end{pmatrix} \quad (6)$$

the Jacobi matrix evaluated on $\mathbf{x}_s$. Let λ_1 be the largest eigenvalue of the matrix A, then whether the steady state $\mathbf{x}_s$ is stable is determined by the sign of $\mathrm{Re}(\lambda_1)$: If $\mathrm{Re}(\lambda_1) < 0$, the quiescent state is stable, otherwise it is unstable. Thus, for the given coupling strength k, the critical population density ρ_q can be obtained by requiring $\mathrm{Re}(\lambda_1) = 0$. Numerically, we find that the steady state of the chaotic Rössler oscillator is $(x_s, z_s) \approx (7 \times 10^{-3}, 4.7 \times 10^{-2})$. Inserting this into the requirement of $\mathrm{Re}(\lambda_1) = 0$, we then are able to obtain the equation for ρ_q and k. This equation contains high-order polynomials, and is difficult to solve analytically. By numerical simulation, we plot the variation of ρ_q as a function k in Fig. 7.

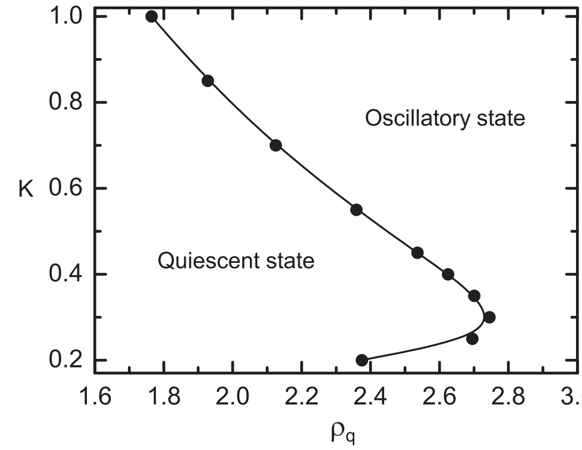

FIG. 7. For the simplified model of $N = 2$ chaotic Rössler oscillators, the variation of the critical population density characterizing the quorum sensing transition ρ_q, as a function of the coupling strength k. The maximum critical density $\rho_q^{\max} \approx 2.75$ locates at about $k \approx 0.3$. The solid curve represents a fitting of the numerical data (symbols) for better visualization.

It is seen that at about $k_2 \approx 0.3$, the maximum critical density $\rho_q^{\max} \approx 2.75$ does exist.

The existence of $\rho_q^{\max}$ at k_2 can be heuristically explained, as follows. For the medium to be oscillatory, a necessary condition is that during the system evolution, the driving signal $\rho k \sum_i (x_i - e)/N$ is able to overcome the damping force $-Je$ [see Eq. (4)]. That is, the time average of the driving signal $F = \rho k F' = \rho k \sum_i \langle x_i - e \rangle / N$ should be larger than some threshold value F_c (which is determined jointly by the relaxation parameter J and the medium dynamics). At the transition boundary, numerically we find that $F' = \alpha + \beta k^{-\gamma}$, with the fitted parameters $\alpha \approx 2.8 \times 10^{-4}$, $\beta \approx 10^{-4}$, and $\gamma \approx 1.45$ (Fig. 8). Inserting this into the function of F and requiring $F = F_c$, after some algebra, we obtain the following

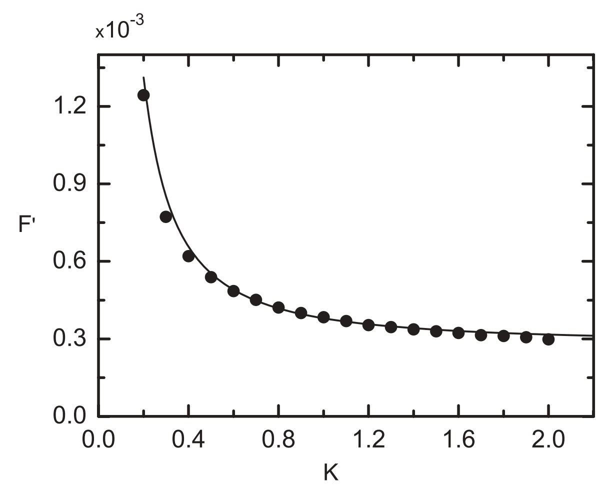

FIG. 8. For $N = 2$ oscillators, the variation of the critical driving signal, $F' \equiv \sum_i \langle x_i - e \rangle / N$, as a function of the coupling strength k. The symbols are the numerical results calculated at the boundary of quorum sensing transition, which are fitted to the function $F_c = \alpha + \beta k^{-\gamma}$ (the solid curve), with $\alpha = 2.8 \times 10^{-4}$, $\beta = 10^{-4}$, and $\gamma = 1.45$.

relation between ρ_q and k:

$$\rho_q = F_c/[k(\alpha + \beta k^{-\gamma})]. \tag{7}$$

By requiring $\partial \rho_q/\partial k = 0$, we finally have

$$k_2 = [\beta(\gamma - 1)/\alpha]^{1/\gamma} \approx 0.28, \tag{8}$$

which is very close to the numerical result in Figs. 6 and 7. The physical meaning of k_2 is the following: When $k < k_2$, as k increases, the value of F' is quickly decreased (roughly with a power-law scaling), which makes kF' become smaller. Since $\rho_q = F_c/(kF')$, the critical density thus increases with k. However, when $k > k_2$, as k increases, the value of F' is only slightly decreased (see Fig. 8). In this case, to keep $\rho_q kF' = F_c$, we need to decrease the value of ρ_q. As a balance of the two trends, there appears the maximum critical density $\rho_q^{\max}$.

V. DISCUSSION AND CONCLUSION

The present work is a necessary and nontrivial extension to the previous studies of indirectly coupled systems. Prior to our work, most of the studies on indirectly coupled systems had been concentrated on the periodic oscillators, and it is poorly known whether the findings obtained can be extended to the chaotic oscillators. The current study, while confirming the general scenarios of synchronization transition observed in the periodic systems, also discloses some unique properties belonging exclusively to the chaotic systems, such as the appearance of phase synchronization, the emergence of the periodic collective behaviors, and the crossover of the critical population density in the quorum sensing transition. Considering the ubiquitous existence of chaos in nature, these findings thus will extend our knowledge on the collective behaviors of indirectly coupled systems, as well as giving indications to the performance and functioning of some realistic complex systems, e.g., the generation of robust rhythm in indirectly coupled irregular oscillators.

It is worth noting that the above findings are general and can be observed in other chaotic systems as well. For instance, we have checked the synchronization transitions of the nonidentical system, in which the intrinsic frequency ω_i of the Rössler oscillators is randomly chosen from the range [0.99,1.01]. In this case, the two types of synchronization scenarios are still clearly observed. Comparing to the identical case, the main difference is that in the nonidentical case the critical coupling strength that characterizes the phase synchronization, i.e., the value of k_1, is increased. In addition to the Rössler oscillator, we have also tested the model of the chaotic Hindmarsh-Rose oscillator, which has been widely used in literature for modeling the spiking-bursting behavior of the membrane potential of the neuron. Again, we find the two types of scenarios for synchronization transition. It should be pointed out that due to the complicated dynamics, at the current stage we are not able to give a rigorous analysis on the bifurcation diagrams for the indirectly coupled Rössler oscillators (see Fig. 5). Also, due to a lack of a relationship between the medium state and oscillator variables, we cannot predict exactly the values of k_2 and $\rho_q^{\max}$ (as the values F_c and F' cannot be analyzed). It is our hope that these questions can be addressed by further studies, e.g., an investigation on the constraint between the oscillators and the medium.

Our findings might be first testified by chemical and biological experiments. For chemical systems, it is well known that chaotic behaviors can be observed in chemical reactions, e.g., the Belousov-Zhabotinsky (BZ) reaction [36,37]. Meanwhile, the chemical elements generated at different areas of the system can be well diffused into the medium environment. This makes it possible to design a similar experiment like the one used in Ref. [15], with the periodic chemical particles now replaced by the localized chaotic BZ oscillations. For biological systems, it has been shown that under certain conditions the glycolytic oscillation of the yeast could be chaotic [38]. It will be interesting to check whether a population of chaotic glycolytic oscillators coupled via a common medium could present the periodic collective behaviors. Meanwhile, it will also be interesting to see, by chaotic oscillators, whether the system could present the progressive synchronization transition—the scenario that has not been reported for the periodic biological oscillators in previous studies.

In summary, by employing chaotic oscillators, we have revisited the transition of the collective behaviors in indirectly coupled systems, in which some interesting phenomena different from traditional studies have been observed, including the emergence of phase synchronization in the progressive transition, the generation of synchronous periodic oscillation nearby the quorum sensing transition, and the crossover of the critical population density under strong couplings. Our findings highlight the unique and rich dynamics in indirectly coupled chaotic oscillators, which are necessary and important complements to the current knowledge.

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[1] A. T. Winfree, *The Geometry of Biological Time* (Springer, New York, 2001).

[2] A. S. Pikovsky, M. Rosenblum, and J. Kurths, *Synchronization: A Universal Concept in Nonlinear Sciences* (Cambridge University Press, Cambridge, UK, 2001).

[3] S. Strogatz, *Sync: The Emerging Science of Spontaneous Order* (Hyperion, New York, 2003).

[4] Y. Kuramoto, *Chemical Oscillations, Waves and Turbulence* (Springer, Berlin, 1984).

[5] A. Goldbeter, *Biochemical Oscillation and Cellular Rhythms: The Molecular Bases of Periodic and Chaotic Behavior* (Cambridge University, Cambridge, 1996).

[6] L. Glass and M. C. Mackey, *From Clocks to Chaos: The Rhythms of Life* (Princeton University, Princeton, NJ, 1988).

[7] I. Z. Kiss, Y. Zhai, and J. L. Hudson, Science **296**, 1676 (2002).

[8] J. Buck, Q. Rev. Biol. **63**, 265 (1988).

[9] T. J. Walker, Science **166**, 891 (1969).

[10] Z. Néda, E. Ravasz, Y. Brechet, T. Vicsek, and A. L. Barabási, Nature (London) **403**, 849 (2000).

[11] J. Aldridge and E. K. Pye, Nature (London) **259**, 670 (1976).

[12] A. Camilli and B. L. Bassler, Science **311**, 1113 (2006).

[13] S. De Monte, F. d'Ovidio, S. Danø, and P. G. Sørensen, Proc. Natl. Acad. Sci. USA **104**, 18377 (2007).

[14] J. Garcia-Ojalvo, M. B. Elowitz, and S. H. Strogatz, Proc. Natl. Acad. Sci. USA **101**, 10955 (2004).

[15] A. F. Taylor, M. R. Tinsley, F. Wang, Z. Huang, and K. Showalter, Science **323**, 614 (2009).

[16] R. Toth R, A. F. Taylor, and M. R. Tinsley, J. Phys. Chem. B **110**, 10170 (2006).

[17] J. Zamora-Munt, C. Masoller, J. Garcia-Ojalvo, and R. Roy, Phys. Rev. Lett. **105**, 264101 (2010).

[18] T. Gregor, K. Fujimoto, N. Masaki, and S. Sawai, Science **328**, 1021 (2010).

[19] T. Danino, O. Mondragón-Palomino, L. Tsimring, and J. Hasty, Nature (London) **463**, 326 (2010).

[20] V. Resmi, G. Ambika, and R. E. Amritkar, Phys. Rev. E **81**, 046216 (2010).

[21] G. Russo and Jean Jacques E. Slotine, Phys. Rev. E **82**, 041919 (2010).

[22] W. Y. Chiang, Y. X. Li, and P. Y. Lai, Phys. Rev. E **84**, 041921 (2011).

[23] V. N. Belykh, G. V. Osipov, N. Kuckländer, B. Blasius, and J. Kurths, Physica D **200**, 81 (2005).

[24] N. Tukhlina, M. Rosenblum, A. Pikovsky, and J. Kurths, Phys. Rev. E **75**, 011918 (2007).

[25] S. Boccaletti, J. Kurths, G. Osipov, D. L. Valladares, and C. S. Zhou, Phys. Rep. **366**, 1 (2002); K. Kaneko, J. Phys. A **24**, 2107 (1991); H. Sakaguchi, Phys. Rev. E **61**, 7212 (2000).

[26] H. Fujisaka and T. Yamada, Prog. Theor. Phys. **69**, 32 (1983); V. S. Afraimovich, N. N. Verichev, and M. I. Rabinovich, Radiophys. Quantum Electron. **29**, 795 (1986); L. M. Pecora and T. L. Carroll, Phys. Rev. Lett. **64**, 821 (1990).

[27] M. G. Rosenblum, A. S. Pikovsky, and J. Kurths, Phys. Rev. Lett. **76**, 1804 (1996).

[28] N. F. Rulkov, M. M. Sushchik, L. S. Tsimring, and H. D. I. Abarbanel, Phys. Rev. E **51**, 980 (1995).

[29] The central pattern generator is a typical example of such a system; see, for example, R. M. Harris-Warrick *et al.*, in *Dynamics Biological Networks: The Stomatogastric Nervous System*, edited by R. M. Harris-Warrick *et al.*, (MIT Press, Cambridge, MA, 1992).

[30] A. S. Pikovsky, M. G. Rosenblum, and J. Kurths, Europhys. Lett. **34**, 165 (1996).

[31] S. Shinomoto and Y. Kuramoto, Prog. Theor. Phys. **75**, 1105 (1986).

[32] K. Bar-Eli, Physica D **14**, 242 (1985).

[33] R. E. Mirollo and S. H. Strogatz, J. Stat. Phys. **60**, 245 (1990); D. G. Aronson, G. B. Ermentrout, and N. Kopell, Physica D **41**, 403 (1990); G. B. Ermentrout, *ibid.* **41**, 219 (1990); F. M. Atay, Phys. Rev. Lett. **91**, 094101 (2003).

[34] S. M. Reppert and D. R. Weaver, Cell **89**, 487 (1997).

[35] Z. Zheng, X. Wang, and M. C. Cross, Phys. Rev. E **65**, 056211 (2002).

[36] R. A. Schmitz, K. R. Graziani, and J. L. Hudson, J. Chem. Phys. **67**, 3040 (1977).

[37] F. Rossi *et al.*, Chem. Phys. Lett. **480**, 322 (2009).

[38] K. Nielsen, P. G. Sørensen, and F. Hynne, J. Theor. Biol. **186**, 303 (1997).