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Authors	Hiroshi Kori, Yoji Kawamura, Hiroya Nakao, Kensuke Arai, Yoshiki Kuramoto
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Collective-phase description of coupled oscillators with general network structure

Hiroshi Kori,^{1,2,*} Yoji Kawamura,³ Hiroya Nakao,⁴ Kensuke Arai,⁵ and Yoshiki Kuramoto^{6,7}

¹*Division of Advanced Sciences, Ochadai Academic Production, Ochanomizu University, Tokyo 112-8610, Japan*

²*PRESTO, Japan Science and Technology Agency, Kawaguchi 332-0012, Japan*

³*Institute for Research on Earth Evolution, Japan Agency for Marine-Earth Science and Technology, Yokohama 236-0001, Japan*

⁴*Department of Physics, Graduate School of Sciences, Kyoto University, Kyoto 606-8502, Japan*

⁵*Brain Science Institute, RIKEN, Wako 351-0198, Japan*

⁶*Research Institute for Mathematical Sciences, Kyoto University, Kyoto 606-8502, Japan*

⁷*Institute for Integrated Cell-Material Sciences, Kyoto University, Kyoto 606-8501, Japan*

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We develop a collective-phase description for a population of nonidentical limit-cycle oscillators with any network structure undergoing fully phase-locked collective oscillations. The whole network dynamics can be described by a single collective-phase variable. We derive a general formula for the collective-phase sensitivity, which quantifies the phase response of the whole network to weak external perturbations applied to the constituent oscillators. Moreover, we consider weakly interacting multiple networks and develop an effective phase coupling description for them. Several examples are given to illustrate our theory.

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I. INTRODUCTION

An assembly of coupled limit-cycle oscillators often behaves like a single large oscillator. This general scenario occurs in a wide variety of rhythmic phenomena in living organisms, ranging from circadian oscillations, cardiac rhythms to pathological phenomena such as epilepsy and Parkinsonian disease [1–5]. Recent experiments using electrochemical oscillators simulate such naturally arising populations of oscillators in an idealized form [6].

Many previous studies have been devoted to answering how and under what conditions oscillators mutually synchronize. In comparison, little attention has been paid to investigating the dynamical response of an oscillator network to external stimuli. There are open fundamental problems related to this issue. For example, which oscillator should be perturbed to give the largest phase shift to a network? How are the phase sensitivity [19] of each oscillator and that of a whole network (i.e., a large oscillator) related? Such inquiries would shed light on mechanisms underlying biological functions (including the link between the cell-level [7] and the system-level [8] phase response curves of circadian rhythms), external control, and internetwork synchronization of oscillator networks [9].

In the present paper, we develop a collective-phase description for a population of nonidentical limit-cycle oscillators undergoing fully phase-locked collective oscillations. By reducing the whole network dynamics to a single collective-phase variable, we clarify how weak microscopic forcing (i.e., forcing given to constituent oscillators) results in the macroscopic phase response. A general formula for the collective-phase sensitivity is derived, which links the phase sensitivity functions of individual oscillators and that of a whole network. Similar issues have been studied very recently [10,11] for populations of identical oscillators under

independent noise [10] or nonidentical oscillators without noise [11], but both of these results apply only to the simplest global-coupling case. We consider a similar case as in Ref. [11] of noiseless, nonidentical oscillators. However, a distinct advantage of our present approach from those previous studies is that we can systematically treat any system size, any connectivity, any heterogeneity in the coupling, and nonuniform external forcing. Moreover, the theory is extended to describe the dynamics of multiple interacting networks by reinterpreting the external stimuli applied to a given network as the coupling forces originating from the other networks, which enables us to predict the synchronization behavior among multiple interacting networks.

II. FORMULATION

A. Basic model

Consider a network of N coupled limit-cycle oscillators under external forcing. As is well known [2], if the heterogeneity of oscillators, the coupling between oscillators, and external forcing are weak, the system is describable by the phase equation (for details, see the Appendix)

$$\dot{\phi}_i = \omega_i + \sum_{j=1}^N \Gamma_{ij}(\phi_i - \phi_j) + \epsilon Z(\phi_i) \xi_i(t). \quad (1)$$

Here ϕ_i is the phase of the i th oscillator ($i=1, \dots, N$), ω_i its natural frequency, and Γ_{ij} is the coupling force from the j th oscillator to the i th oscillator. The parameter ϵ is the characteristic intensity of the external forcing. The terms $\xi_i(t)$ and $Z(\phi_i)$ respectively represent the time-dependent external force and the phase sensitivity of the oscillator i in the direction of the forcing (see the Appendix).

More generally, we can consider vector forcing $\xi_i(t)$ to the limit-cycle oscillator. The corresponding forcing term in Eq. (1) will then be a scalar product $Z(\phi_i) \cdot \xi_i(t)$, where $Z(\phi_i)$ is the phase sensitivity vector of the oscillator i . Although our theory may be formulated similarly for such a general forc-

*Corresponding author. kori.hiroshi@ocha.ac.jp

ing term, we have assumed a simpler form as in Eq. (1) to avoid unnecessary complication.

B. Collective-phase description

Our aim is to establish the collective-phase description for Eq. (1), i.e., to derive the dynamical equation for a suitably defined macroscopic variable that describes the response to external forcing. This is generally formulated under two basic assumptions. (i) In the absence of external forcing a stable periodic solution corresponding to a fully phase-locked state exists, and thus, the oscillator network behaves as a single large limit-cycle oscillator. (ii) The external force is even weaker than the coupling force, i.e., $\epsilon \ll 1$, so that the synchronized state is almost unaltered under external forcing. Under these assumptions, the phase reduction method applicable to a weakly perturbed oscillator [2] can be applied once again to the oscillator network by treating the unperturbed system, Eq. (1) with $\epsilon=0$, as a single limit-cycle oscillator.

For convenience, we begin by rewriting Eq. (1) in terms of the N -dimensional state vector $\mathbf{X}=(\phi_1, \phi_2, \dots, \phi_N)^T$ as

$$\dot{\mathbf{X}} = \mathbf{F}(\mathbf{X}) + \epsilon \mathbf{p}(\mathbf{X}, t), \quad (2)$$

where $F_i(\mathbf{X}) = \omega_i + \sum_{j=1}^N \Gamma_{ij}(\phi_i - \phi_j)$ and $p_i(\mathbf{X}, t) = Z(\phi_i) \xi_i(t)$.

We first consider the unperturbed system ($\epsilon=0$):

$$\dot{\mathbf{X}} = \mathbf{F}(\mathbf{X}). \quad (3)$$

A fully phase-locked solution $\mathbf{X}_0(t)$ represents the state in which all the oscillators have an identical, constant frequency Ω . Thus, $\mathbf{X}_0(t)$ is found as a solution of $F_i(\mathbf{X}_0) = \Omega$ for all i . This solution is denoted by

$$\mathbf{X}_0(t) = (\Omega t + \phi_1^0, \Omega t + \phi_2^0, \dots, \Omega t + \phi_N^0)^T, \quad (4)$$

where ϕ_i^0 is constant and represents the phase distribution of the fully phase-locked state. Note that Eq. (4) can be regarded as an N -dimensional limit-cycle solution.

We now define the *collective phase* $\Theta(\mathbf{X})$ as a scalar field of $\mathbf{X}$ such that $\dot{\Theta} = \Omega$ identically holds in the unperturbed system ($\epsilon=0$). Note the identity

$$\dot{\Theta} = \frac{d\Theta}{d\mathbf{X}} \cdot \frac{d\mathbf{X}}{dt}. \quad (5)$$

This identity and Eq. (3) implies

$$\frac{d\Theta}{d\mathbf{X}} \cdot \mathbf{F}(\mathbf{X}) = \Omega. \quad (6)$$

For later convenience, we express the limit-cycle solution, Eq. (4), as a function of Θ :

$$\mathbf{X}(\Theta) = (\Theta + \phi_1^0, \Theta + \phi_2^0, \dots, \Theta + \phi_N^0)^T, \quad (7)$$

where we have set $\Theta(t=0)=0$ as the initial value of Θ , which can be set arbitrarily.

The dynamical equation of Θ for the perturbed system ($\epsilon \neq 0$) may be derived by substituting Eq. (2) into the identity, Eq. (5). We then obtain

$$\dot{\Theta} = \Omega + \epsilon \frac{d\Theta}{d\mathbf{X}} \cdot \mathbf{p}(\mathbf{X}, t). \quad (8)$$

To proceed further, notice that the second term in Eq. (8) may be evaluated at $\mathbf{X}=\mathbf{X}(\Theta)$ to the lowest order in ϵ . For convenience, we introduce the row vector $\mathbf{w}=(w_1, w_2, \dots, w_N)=(d\Theta/d\mathbf{X})^T$. Then, Eq. (8) reduces to $\dot{\Theta} = \Omega + \epsilon \mathbf{w} \mathbf{p}(\mathbf{X}, t)$, or

$$\dot{\Theta} = \Omega + \epsilon \sum_{i=1}^N w_i Z(\Theta + \phi_i^0) \xi_i(t). \quad (9)$$

This equation, which is free of the microscopic variables ϕ_i , describes the response of the collective phase of the synchronized network. The effect of the forcing to the i th oscillator on the collective phase is weighted by w_i . We thus call $\mathbf{w}$ the *weight vector* henceforth. A larger overall phase response arises when an oscillator with larger w_i is forced [20].

In what follows, we often consider uniform forcing, i.e., $\xi_i(t)=\xi(t)$ for all i . In such a case, Eq. (9) is further reduced to

$$\dot{\Theta} = \Omega + \epsilon \zeta(\Theta) \xi(t), \quad (10)$$

where $\zeta(\Theta)$ is the *collective-phase sensitivity* defined for uniform forcing [10],

$$\zeta(\Theta) = \sum_{i=1}^N w_i Z(\Theta + \phi_i^0). \quad (11)$$

Generally speaking, the shape of $\zeta(\Theta)$ deviates from that of $Z(\phi)$ more significantly as the phases of the fully phase-locked state becomes more widely distributed.

Finally, we emphasize that the collective phase Θ corresponds to various macroscopic phases that may be observed in experiments. For example, the phase $\Psi(t)$ of the order parameter defined by $Re^{i\Psi} \equiv N^{-1} \sum_{j=1}^N e^{i\phi_j}$ (where R and Ψ are real) approximately agrees with the collective phase $\Theta(t)$ with some constant offset because $\phi_j(t) \approx \Theta(t) + \phi_j^0$. Similarly, other macroscopic phases may be employed to measure the collective-phase response.

C. Weight vector

It is known that the phase gradient $d\Theta/d\mathbf{X}$ at the limit-cycle orbit is actually the left zero eigenvector of the linearized system [2]. In our particular system it is easy to show that the weight vector $\mathbf{w}$ is the left zero eigenvector of the Jacobian of $\mathbf{F}(\mathbf{X}_0)$. Note that a similar proof is given in Refs. [12,13] for Malkin's theorem.

The linearized equation for Eq. (3) around the limit-cycle solution is given by

$$\dot{\mathbf{x}} = \mathbf{L} \mathbf{x}, \quad (12)$$

where $\mathbf{x} \equiv \mathbf{X} - \mathbf{X}_0$ is a small perturbation and $\mathbf{L}$ is the Jacobian, elements of which are given by $L_{ij} = \partial F_i(\mathbf{X}_0) / \partial X_j$, or

$$L_{ij} = \delta_{ij} \sum_{k \neq i}^N \Gamma'_{ik}(\phi_i^0 - \phi_k^0) - (1 - \delta_{ij}) \Gamma'_{ij}(\phi_i^0 - \phi_j^0). \quad (13)$$

Due to the symmetry of $F(X)$ with respect to a global phase shift, the Jacobian L is a constant matrix, one eigenvalue of which equals zero with the corresponding right eigenvector given by $U = (1, 1, \dots, 1)^T$, i.e., $LU = 0$. Because of the assumption of the stability of the fully locked state, the real parts of the other eigenvalues are all negative.

Now we prove that the weight vector is the left zero eigenvector of the Jacobian L ,

$$wL = 0, \quad (14)$$

satisfying the normalization condition

$$\sum_{i=1}^N w_i = 1. \quad (15)$$

Consider two trajectories $X_0(t)$ and $X(t)$, each obeying the unperturbed dynamical equation, Eq. (3). Let the trajectories $X_0(t)$ and $X(t)$ start from a point on the limit cycle and an arbitrary nearby point, respectively. We denote the difference by $x(t) = X(t) - X_0(t)$. All equations below are valid to the lowest order in $\|x\|$. The difference $\Delta\Theta = \Theta(X) - \Theta(X_0)$ in the collective phase between the two trajectories is given by

$$\Delta\Theta = \frac{\partial\Theta}{\partial\chi} \cdot x = wx. \quad (16)$$

In the unperturbed system, $\dot{\Theta}(X) = \dot{\Theta}(X_0) = \Omega$ holds so that $\Delta\Theta$ is time independent. We thus obtain

$$0 = \Delta\dot{\Theta} = w\dot{x} = wLx, \quad (17)$$

where we have used Eq. (12). This equation holds for any small x . We may thus conclude that w is the left zero eigenvector of L , i.e., Eq. (14). The normalization condition for w is required by Eq. (6): for $X = \chi$, Eq. (6) implies $\sum_{i=1}^N w_i \Omega = \Omega$, or Eq. (15). In Sec. III, we provide convenient methods to calculate the weight vector w for a given L and some examples of w .

D. Multiple interacting networks

Next, we formulate the collective-phase description for multiple interacting networks of phase oscillators. We are concerned with the case in which external forcing is absent, while $\epsilon\xi_i(t)$ in the last term in Eq. (1) is interpreted as the coupling force coming from oscillators of other networks. For clarity, we first consider a simple system in which two identical networks composed of N oscillators, called group A and group B, are uniformly coupled (the extension to a more general case is given later). The dynamical equations for such a system are given by

$$\dot{\phi}_i^A = \omega_i + \sum_{j=1}^N \Gamma_{ij}(\phi_i^A - \phi_j^A) + \epsilon Z(\phi_i^A) \xi(\{\phi_k^B\}),$$

$$\dot{\phi}_i^B = \omega_i + \sum_{j=1}^N \Gamma_{ij}(\phi_i^B - \phi_j^B) + \epsilon Z(\phi_i^B) \xi(\{\phi_k^A\}), \quad (18)$$

where ϕ_i^X is the phase of the i th oscillator in group X ($X = A, B$), and $\xi(\{\phi_k^X\})$ denotes a function of $\phi_1^X, \phi_2^X, \dots, \phi_N^X$, which represents the uniform coupling force coming from group X. Denoting the collective phases of the respective groups by Θ_A and Θ_B , we obtain the resulting phase equation in the form

$$\dot{\Theta}_A = \Omega + \epsilon \zeta(\Theta_A) \xi(\Theta_B),$$

$$\dot{\Theta}_B = \Omega + \epsilon \zeta(\Theta_B) \xi(\Theta_A), \quad (19)$$

where $\xi(\Theta_X) \equiv \xi(\{\Theta_X + \phi_k^0\})$. To the lowest order in ϵ , we may time average the coupling terms in Eq. (19) over the common period $2\pi/\Omega$ (or, we may adopt a near-identity transformation, as done in the Appendix, to get the same result). We perform the averaging as

$$\gamma(\Theta_A - \Theta_B) = \frac{1}{2\pi} \int_0^{2\pi} \zeta(\lambda + \Theta_A) \xi(\lambda + \Theta_B) d\lambda, \quad (20)$$

where γ rather than Γ has been used to indicate that this coupling function acts between the groups. In this way, we succeeded in deriving the collective-phase equation in the simple form

$$\dot{\Theta}_A = \Omega + \epsilon \gamma(\Theta_A - \Theta_B),$$

$$\dot{\Theta}_B = \Omega + \epsilon \gamma(\Theta_B - \Theta_A). \quad (21)$$

It is straightforward to extend this description to a system of M multiple networks. We allow that the networks are non-identical and the coupling force is nonuniform (i.e., i dependent). The dynamical equation for group X ($X = 1, \dots, M$) is given by

$$\dot{\phi}_i^X = \omega_i^X + \sum_{j=1}^{N_X} \Gamma_{ij}^X(\phi_i^X - \phi_j^X) + \epsilon Z(\phi_i^X) \sum_{Y=1}^M \xi_i^{XY}(\{\phi_k^Y\}), \quad (22)$$

where N_X is the number of oscillators in group X, Γ_{ij}^X is the intragroup coupling inside group X, and ξ_i^{XY} is the intergroup coupling from oscillators in group Y to the i th oscillator in group X. The corresponding collective-phase equation is given by

$$\dot{\Theta}_X = \Omega_X + \epsilon \sum_{Y=1}^M \gamma_{XY}(\Theta_X - \Theta_Y), \quad (23)$$

$$\gamma_{XY}(\Theta_X - \Theta_Y) = \frac{1}{2\pi} \int_0^{2\pi} \sum_{i=1}^{N_X} w_i^X Z(\Theta_X + \phi_i^{X0} + \lambda) \times \xi_i^{XY}(\Theta_Y + \lambda) d\lambda, \quad (24)$$

where Ω_X , ϕ_i^{X0} , and w_i^X are, respectively, the collective frequency, the locking phase, and the weight vector defined for group X.

III. CALCULATION OF THE WEIGHT VECTOR

We have found in Sec. II B that a key quantity linking microscopic and macroscopic dynamics is the weight vector $\mathbf{w}$, and shown in Sec. II C that it is the left zero eigenvector of the Jacobian L . In this section, we provide both analytic and numerical methods to calculate the weight vector for a given L . Also, several examples of the weight vector are given.

A. Algebraic method

An algebraic expression for the left zero eigenvector of the Laplacian matrix is known [14]. This expression holds for any matrix L satisfying $\sum_{j=1}^N L_{ij}=0$ as shown below. We define the (i, j) cofactor of L as

$$D(i, j) \equiv (-1)^{i+j} \det L(i, j), \quad (25)$$

where the matrix $L(i, j)$ is L with the i th row and j th column removed. We also define the matrix $L(i)$ as L with the i th row removed and express it as a series of column vectors, $L(i) = [L_{i1}, L_{i2}, \dots, L_{iN}]$. Then, using the relation $\sum_{j=1}^N L_{ij}=0$, or $L_{i1} + L_{i2} + \dots + L_{iN}=0$, we obtain

$$\begin{aligned} \det L(i, 1) &= \det [L_{i2}, L_{i3}, \dots, L_{iN}] = \det [L_{i2} + L_{i3} + \dots + L_{iN}, L_{i3}, \dots, L_{iN}] \\ &= \det [-L_{i1}, L_{i3}, \dots, L_{iN}] = -\det L(i, 2). \end{aligned} \quad (26)$$

Similarly, one may show $(-1) \det L(i, 1) = (-1)^j \det L(i, j)$. Combining this fact and definition (25), we find that $D(i, j)$ is j independent, or

$$D(i, 1) = D(i, 2) = \dots = D(i, N). \quad (27)$$

Now we define the row vector $\mathbf{m} = (m_1, \dots, m_N)$ where

$$m_i = D(i, i) = \det L(i, i). \quad (28)$$

Then, $\mathbf{m}$ is the left zero eigenvector of L because

$$\begin{aligned} \sum_{i=1}^N m_i L_{ij} &= m_1 L_{1j} + \dots + m_N L_{Nj} \\ &= L_{1j} D(1, j) + \dots + L_{Nj} D(N, j) \\ &= \det L = 0, \end{aligned} \quad (29)$$

where we have used the cofactor expansion and the fact that one eigenvalue of L is zero. Finally, combined with the normalization condition, we find an algebraic expression of the weight vector given by

$$w_i = \frac{m_i}{\sum_{j=1}^N m_j}, \quad m_i = \det L(i, i). \quad (30)$$

Note that in Eq. (28) it is also possible to define m_i by $D(i, j)$ with any j . We chose $m_i = D(i, i)$ because it has the simplest form [see Eq. (25)].

B. Numerical method

Although the algebraic expression is useful for the analytic calculation, this is not suitable for numerical calculation

FIG. 1. Examples of the weight vector in identical oscillators. Using Eq. (30), we find (a) $w_1:w_2=1:\kappa$ and (b) $w_1:w_2:w_3:w_4=2:4:3:1$.

because of its large numerical cost. Instead, the following dynamical equation is useful:

$$\dot{u}_j(t) = \sum_{i=1}^N u_i L_{ij}. \quad (31)$$

By the assumption of the stability of the fully phase-locked solution, the real parts of all the eigenvalues of L are negative except for a zero eigenvalue. Thus, starting from a general initial condition, the vector $\mathbf{u} = (u_1, u_2, \dots, u_N)$ asymptotically converges to the left zero eigenvector of L . Thus, taking into account the normalization condition, the weight vector is obtained as

$$w_i = \frac{u_i}{\sum_{j=1}^N u_j}. \quad (32)$$

Note that when the network is undirected and the coupling function $\Gamma_{ij}(\phi)$ is an odd function for all i and j , L is symmetric and w_i is trivially $1/N$ for all i . This is the case even for networks with strongly heterogeneous connectivity including scale-free networks [15]. Except for such a special case, L is usually asymmetric and $\mathbf{w}$ is heterogeneous.

C. Example I: networks of identical oscillators

We consider a network of identical oscillators with homogeneous coupling, whose evolution is given by

$$\dot{\phi}_i = \omega + \sum_{j=1}^N A_{ij} \Gamma(\phi_i - \phi_j), \quad (33)$$

where A is the adjacency matrix describing the connectivity, which is generally asymmetric and weighted. We further assume that $\Gamma(0)=0$ and $\Gamma'(0)<0$, which is often the case in diffusively coupled oscillator networks [2]. In such a network, the phase synchronized solution, $\phi_i = \phi_j$ for all i and j , always exists and we assume its stability. By going into a rotating frame and rescaling t , we put $\omega=0$ and $\Gamma'(0)=-1$ without loss of generality. Then, Eq. (13) reduces to a network Laplacian generalized for asymmetric and weighted networks given by

$$L_{ij} = \begin{cases} A_{ij} & \text{for } j \neq i, \\ -\sum_{j \neq i} A_{ij} & \text{for } j = i. \end{cases} \quad (34)$$

We illustrate the weight vector using two small networks shown in Fig. 1. In both cases, the weight vector can be easily calculated via the algebraic expression, Eq. (30). Fig-

ure 1(a) is a weighted network. The corresponding Laplacian is

$$L = \begin{pmatrix} -\kappa & \kappa \\ 1 & -1 \end{pmatrix}. \quad (35)$$

The weight vector is $\mathbf{w} = (1, \kappa)/(1 + \kappa)$, being a simple reflection of the connection weights. Figure 1(b) is a directed unweighted network. The corresponding Laplacian is

$$L = \begin{pmatrix} -2 & 0 & 1 & 1 \\ 1 & -1 & 0 & 0 \\ 0 & 1 & -1 & 0 \\ 0 & 1 & 1 & -2 \end{pmatrix}, \quad (36)$$

and we find $\mathbf{w} = (2, 4, 3, 1)/10$. Here, it is worth noticing that $w_2 > w_3$; i.e., oscillator 2 is more influential than oscillator 3, although they have locally the same topological properties: one inward and two outward connections. In general, the weight vector depends on the global topology.

D. Example II: globally coupled nonidentical oscillators

We next consider globally coupled nonidentical oscillators

$$\dot{\phi}_i = \omega_i + \frac{K}{N} \sum_{j=1}^N \sin(\phi_j - \phi_i + \alpha), \quad (37)$$

where $K > 0$ is the coupling strength and α is a parameter of the coupling function. For simplicity, we assume the attracting coupling, $-\pi/2 < \alpha < \pi/2$, implying that the oscillators tend to synchronize in phase when the oscillators are identical, i.e., $\omega_i = \omega$. Such a coupling function appears in various coupled oscillator systems [2, 6, 16]. Below we consider two cases, (i) $N=2$ and (ii) $N=100$.

(i) $N=2$. We put $\omega_1=1$ and $\omega_2=0$ without loss of generality. The phase-locked solution is given by

$$\Delta\phi^0 \equiv \phi_1^0 - \phi_2^0 = \arcsin\left(\frac{1}{K \cos \alpha}\right), \quad (38)$$

and $\Omega = (K/2)[\sin(\Delta\phi^0 + \alpha) + \sin \alpha]$. The stable solution exists in the region $0 < \Delta\phi^0 < \pi/2$. Because $m_1 = L_{2,2} = \Gamma'(-\Delta\phi^0) = -(K/2)\cos(\Delta\phi^0 + \alpha)$ and $m_2 = L_{1,1} = \Gamma'(\Delta\phi^0) = -(K/2)\cos(\Delta\phi^0 - \alpha)$, we obtain

$$w_1 = \frac{1 - \tan \Delta\phi^0 \tan \alpha}{2}, \quad w_2 = 1 - w_1. \quad (39)$$

Thus, for $\alpha < 0$ ($\alpha > 0$), the faster oscillator has a larger (smaller) weight, as displayed in Fig. 1(a). Interestingly, either of the weights can take a negative value, which actually occurs when $|\tan \Delta\phi^0 \tan \alpha| > 1$. In such a situation, when a perturbation is given to an oscillator having negative weight, the perturbation instantaneously advances the phase of the oscillator but eventually results in the delay of the phases of both oscillators.

(ii) $N=100$. Natural frequency ω_i is chosen randomly from the uniform distribution $(-0.5, 0.5)$ and the oscillators are sorted according to the natural frequencies. A particular

FIG. 2. (Color online) Examples of the weight vector in globally coupled nonidentical oscillators. (a) The weights w_i for $N=2$, i.e., Eq. (39), as a function of α with fixed $K=2$. There is no phase-locked solution in the region of α where the weights are absent. (b) The natural frequencies ω_i , (c) the relative phases $\phi_i^0 - \phi_{50}^0$ in a fully phase-locked state, and (d) the weights multiplied by the system size, Nw_i , for $N=100$, $K=1.5$, and $\alpha=0, \pm 0.7$.

realization is presented in Fig. 2(b). We fix $K=1.5$ and consider three values of $\alpha=0, \pm 0.7$, for which all the oscillators fully phase lock, with the phase distributions shown in Fig. 2(c). Given a phase-locked solution, $\mathbf{w}$ can be numerically calculated by Eqs. (31) and (32). The result is displayed in Fig. 2(d). Although the phase distributions for different α are similar, the corresponding weight vectors differ considerably. For large $|\alpha|$, the weight vector is highly heterogeneous. For instance, there is about a 20-fold difference in the weights between the fastest and the slowest oscillators for $\alpha=-0.7$. Similar to the case of $N=2$, faster oscillators have larger (smaller) weights for $\alpha < 0$ ($\alpha > 0$). For $\alpha=0$, the weight vector is homogeneous because the Jacobian L is symmetric.

IV. TWO COUPLED GROUPS OF LIMIT-CYCLE OSCILLATORS

As a demonstration of our theory, we illustrate that the collective-phase sensitivity of a group of coupled limit-cycle oscillators varies with intragroup coupling strength. We then consider two groups of coupled oscillators with an additional intergroup coupling of fixed strength and show that a non-trivial qualitative change in the synchronization behavior *between* the groups occurs when the collective-phase sensitivity changes as a result of modifications to the intragroup coupling strength.

As schematically illustrated in Fig. 3(a), we consider a pair of identical groups A and B, each of which consists of two coupled limit-cycle oscillators. We use the Hindmarsh-Rose model as the limit-cycle oscillator, a model originally proposed as a neural model. The system reads

$$\dot{x}_i = 3x_i^2 - x_i^3 + y_i - \mu_i + \sum_{j=1}^4 D_{ij}x_j,$$

FIG. 3. (Color online) Results for a network of limit-cycle oscillators. (a) Network structure under consideration. (b) Wave form $x(\phi)$ and phase sensitivity $Z(\phi)$ of an individual oscillator. (c) Antisymmetric part of the coupling function, $\Gamma_a(\Delta\phi)$. (d) Phase difference $\Delta\phi^0$ between oscillators in each group. (e) Collective-phase sensitivity $\zeta(\Theta)$ defined for uniform forcing. For $K=0.007, 0.002, 0.0015$, (w_1, w_2) is respectively about $(1.35, -0.35)$, $(2.87, -1.87)$, and $(2.89, -1.89)$. (f) Antisymmetric part of the collective coupling function, $\gamma_a(\Delta\Theta)$. (g) Phase difference $\Delta\Theta$ between the groups.

$$\dot{y}_i = 1 - 5x_i^2 - y_i. \quad (40)$$

Here, the coupling matrix D is given as $D_{12,21,34,43}=K$, $D_{11,22,33,44}=-K$, $D_{13,23,31,41}=\epsilon$ with K and ϵ being the coupling intensities for intragroups and intergroups, respectively. We assume $1 \gg K \gg \epsilon = 1.0 \times 10^{-5}$. We set $\mu_1 = \mu_3 = -3.000$ and $\mu_2 = \mu_4 = -3.001$, corresponding to $\omega_{1,3} \approx 1.80476$, $\omega_{2,4} \approx 1.80443$, and thus $\Delta\omega \approx 3.3 \times 10^{-4}$. The wave form $x(\phi)$ and the phase sensitivity $Z(\phi)$ of an isolated oscillator obtained numerically are shown in Fig. 3(b).

The corresponding phase model is given by

$$\begin{aligned} \dot{\phi}_{1,2} &= \omega_{1,2} + K\Gamma(\phi_{1,2} - \phi_{2,1}) + \epsilon Z(\phi_{1,2})x(\phi_3), \\ \dot{\phi}_{3,4} &= \omega_{3,4} + K\Gamma(\phi_{3,4} - \phi_{4,3}) + \epsilon Z(\phi_{3,4})x(\phi_1). \end{aligned} \quad (41)$$

Here, the notation is slightly different from Eq. (18): $\phi_{1,2}^A$ and $\phi_{1,2}^B$ are denoted by $\phi_{1,2}$ and $\phi_{3,4}$, respectively. The coupling function Γ is calculated as

$$\Gamma(\phi_1 - \phi_2) = \frac{1}{2\pi} \int_0^{2\pi} d\psi Z(\phi_1 + \psi) \{x(\phi_2 + \psi) - x(\phi_1 + \psi)\}. \quad (42)$$

For convenience, we display $\Gamma_a(\Delta\phi) \equiv \Gamma(\Delta\phi) - \Gamma(-\Delta\phi)$ in Fig. 3(c). The phase difference $\Delta\phi^0$ between the oscillators 1 and 2 of a synchronized state is found as a stable solution of $\dot{\phi}_1 = \dot{\phi}_2$ (where $\epsilon=0$ is assumed), and thus, a solution of $\Gamma_a(\Delta\phi^0) = \Delta\omega/K$. The predicted phase difference is plotted in Fig. 3(d) as a curve. It agrees well with numerical data obtained through direct numerical integration of Eq. (40). Using $Z(\phi)$, $\Delta\phi^0$, $\Gamma(\Delta\phi)$, and its derivative $\Gamma'(\Delta\phi)$ obtained numerically, we can calculate w_1 , w_2 , and $\zeta(\Theta)$. The results are shown in Fig. 3(e) and its caption. For large K (compared

to $\Delta\omega$), $\zeta(\Theta)$ is indistinguishable from $Z(\phi)$. As K decreases, $\Delta\phi^0$ becomes larger and w_1 and w_2 (having different signs in this case) become more heterogeneous resulting in considerable variation in $\zeta(\Theta)$.

Given $\zeta(\Theta)$, the synchronization behavior between groups is now predicted. The collective coupling function $\gamma(\Delta\Theta)$ is calculated from Eq. (20) where $\xi(\phi) = x(\phi)$ in the system under consideration. For convenience, we display the antisymmetric part of $\gamma(\Delta\Theta)$ in Fig. 3(f). Putting $\dot{\Theta}_A = \dot{\Theta}_B$, we find the stable phase-locked state, $\Delta\Theta \equiv \Theta_A - \Theta_B$. The predicted $\Delta\Theta$ is exhibited by the curve in Fig. 3(g), implying that the in-phase solution becomes unstable at around $K = 0.006$ (via a pitch-fork bifurcation) and the out-of-phase solution appears below. The phase difference $\Delta\Theta$ (or approximately, $\phi_1 - \phi_3$) obtained from direct numerical integration of Eq. (40) is plotted in Fig. 3(g), which convinces us of the precision of the phase description.

V. CONCLUSIONS

In summary, we have formulated the collective-phase description for a population of limit-cycle oscillators with any network structure. This theory describes how the collective state of the whole network responds to external inputs to its constituent oscillators. Moreover, the theory has been extended to describe the synchronization behavior among multiple interacting networks. We have demonstrated (i) that in a network of two coupled limit-cycle oscillators the collective-phase sensitivity varies with the coupling intensity and (ii) that in two such networks with additional intergroup coupling the synchronization behavior between the networks undergoes a qualitative change that may be interpreted by the variation in the collective-phase sensitivity.

A key quantity linking individual and collective dynamics is the weight vector, which is the left-zero eigenvector of the Jacobian matrix. The weight of an oscillator describes how much influence the oscillator has on the collective behavior. We have provided convenient methods, both analytical and numerical, to calculate the weight vector for a given oscillator network. For networks composed of identical oscillators, the Jacobian matrix is identical to the Laplacian matrix defined for directed, weighted networks. Thus, our study would also be of interest to those working on complex networks [15].

We remark on the limitations of our approach. We have employed the phase model, Eq. (1), as our starting point. To a good approximation, the phase model describes the dynamics of coupled limit-cycle oscillators when the coupling is weak. In Eq. (1), we have considered even weaker external forcing. Based on this assumption, we were able to formulate the collective-phase description. Similarly, in the collective-phase description of multiple interacting networks, the coupling between the networks must be sufficiently weaker than the coupling inside each network. When one applies our approach to real oscillator systems, these assumptions should be taken into account.

Nevertheless, our theory is very general. It can deal with nonidentical oscillators, any system size, any connectivity, any heterogeneity in the coupling, and nonuniform forcing. Thus, a broad applicability would be expected.

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APPENDIX: DERIVATION OF EQ. (1)

Here we derive our basic model, Eq. (1), from limit-cycle oscillators with weak heterogeneity, weak coupling, and weak external forcing. The aim of this presentation is to derive the phase model in which the coupling term is a function of the phase differences between pairs of oscillators. To this end, we usually employ a time averaging method (presented below). However, if we naively average the dynamical equation in our case (where the external forcing as well as the coupling between oscillators is present), the resulting equation does not have the form of Eq. (1). To derive Eq. (1), it is more appropriate to use a *formal* averaging method [2,13,17], which is done via a near-identity transformation of the phase variable. For the clarity of the presentation, we consider two coupled oscillators, as the smallest conceivable system suffices to explain the essence of the derivation. The extension to a large population is straightforward.

We consider two coupled limit-cycle oscillators subject to external forcing, whose dynamical equations are given by

$$\begin{aligned}\dot{\mathbf{W}}_1 &= \mathbf{F}(\mathbf{W}_1) + \delta \mathbf{F}_1(\mathbf{W}_1) + \delta \mathbf{G}_{12}(\mathbf{W}_1, \mathbf{W}_2) + \delta \boldsymbol{\xi}_1(t), \\ \dot{\mathbf{W}}_2 &= \mathbf{F}(\mathbf{W}_2) + \delta \mathbf{F}_2(\mathbf{W}_2) + \delta \mathbf{G}_{21}(\mathbf{W}_2, \mathbf{W}_1) + \delta \boldsymbol{\xi}_2(t),\end{aligned}\quad (\text{A1})$$

where $\mathbf{W}_i$ is the state variable of the i th oscillator ($i=1,2$), $\mathbf{F}(\mathbf{W}) + \delta \mathbf{F}_i(\mathbf{W})$ describes intrinsic self-sustained oscillation with homogeneous part $\mathbf{F}(\mathbf{W})$ and inhomogeneous part $\mathbf{F}_i(\mathbf{W})$, $\mathbf{G}_{ij}$ describes interaction force from the j th to the i th oscillators, and $\boldsymbol{\xi}_i$ is external forcing (generally i dependent). We have introduced a small parameter δ to represent that the inhomogeneity of the intrinsic dynamics, the interaction force, and the external forcing are small.

The limit-cycle solution for Eq. (A1) with $\delta=0$, i.e., $\dot{\mathbf{W}} = \mathbf{F}(\mathbf{W})$, is denoted by $\mathbf{W}^0(t)$. Its intrinsic frequency is denoted by $\omega_0 = 2\pi/T$ where T is the period of the oscillation of the limit-cycle solution. The phase $\varphi_i(\mathbf{W}_i)$ of an oscillator is defined as a scalar field of $\mathbf{W}_i$ such that $\dot{\varphi}_i = \omega_0$ identically holds for $\delta=0$. Then, because of the identity $\dot{\varphi}_i = (\partial \varphi_i / \partial \mathbf{W}_i) \cdot (d\mathbf{W}_i / dt)$, we obtain

$$\begin{aligned}\dot{\varphi}_1 &= \omega_0 + \delta \frac{\partial \varphi_1}{\partial \mathbf{W}_1} \cdot [\mathbf{F}_1(\mathbf{W}_1) + \mathbf{G}_{12}(\mathbf{W}_1, \mathbf{W}_2) + \boldsymbol{\xi}_1(t)], \\ \dot{\varphi}_2 &= \omega_0 + \delta \frac{\partial \varphi_2}{\partial \mathbf{W}_2} \cdot [\mathbf{F}_2(\mathbf{W}_2) + \mathbf{G}_{21}(\mathbf{W}_2, \mathbf{W}_1) + \boldsymbol{\xi}_2(t)].\end{aligned}\quad (\text{A2})$$

To the lowest order in δ , $(\partial \varphi_i / \partial \mathbf{W}_i)$ in Eq. (A2) can be evaluated on the limit-cycle solution $\mathbf{W}^0$. Thus, defining $(\partial \varphi / \partial \mathbf{W}^0) = \mathbf{Z}(\varphi)$, we get

$$\begin{aligned}\dot{\varphi}_1 &= \omega_0 + \delta [f_1(\varphi_1) + g_{12}(\varphi_1, \varphi_2) + \mathbf{Z}(\varphi_1) \cdot \boldsymbol{\xi}_1(t)], \\ \dot{\varphi}_2 &= \omega_0 + \delta [f_2(\varphi_2) + g_{21}(\varphi_2, \varphi_1) + \mathbf{Z}(\varphi_2) \cdot \boldsymbol{\xi}_2(t)],\end{aligned}\quad (\text{A3})$$

where

$$\begin{aligned}\omega_0 &= \mathbf{Z}(\varphi_1) \cdot \mathbf{F}(\varphi_1) = \mathbf{Z}(\varphi_2) \cdot \mathbf{F}(\varphi_2), \\ f_1(\varphi_1) &= \mathbf{Z}(\varphi_1) \cdot \mathbf{F}_1(\varphi_1), \\ f_2(\varphi_2) &= \mathbf{Z}(\varphi_2) \cdot \mathbf{F}_2(\varphi_2), \\ g_{12}(\varphi_1, \varphi_2) &= \mathbf{Z}(\varphi_1) \cdot \mathbf{G}_{12}(\varphi_1, \varphi_2), \\ g_{21}(\varphi_2, \varphi_1) &= \mathbf{Z}(\varphi_2) \cdot \mathbf{G}_{21}(\varphi_2, \varphi_1).\end{aligned}$$

To reduce Eq. (A3) to an even more tractable form, we employ a near-identity transformation [2,17]: we introduce the new phase variables ϕ_1 and ϕ_2 as

$$\begin{aligned}\varphi_1 &= \phi_1 + \delta a_1(\phi_1, \phi_2), \\ \varphi_2 &= \phi_2 + \delta a_2(\phi_2, \phi_1),\end{aligned}\quad (\text{A4})$$

where a_i is a 2π -periodic function and satisfies $a_i(0, \phi) = 0$ for any ϕ . Then, as shown below, by choosing appropriate a_i , Eq. (A3) results in the following equation to the lowest order in δ :

$$\begin{aligned}\dot{\phi}_1 &= \omega_0 + \delta [\omega_1 + \Gamma_{12}(\phi_1 - \phi_2) + \mathbf{Z}(\phi_1) \cdot \boldsymbol{\xi}_1(t)], \\ \dot{\phi}_2 &= \omega_0 + \delta [\omega_2 + \Gamma_{21}(\phi_2 - \phi_1) + \mathbf{Z}(\phi_2) \cdot \boldsymbol{\xi}_2(t)],\end{aligned}\quad (\text{A5})$$

where ω_i and Γ_{ij} are obtained as the averaged quantities,

$$\omega_i = \frac{1}{2\pi} \int_0^{2\pi} f_i(\lambda) d\lambda, \quad (\text{A6})$$

$$\Gamma_{ij}(\psi_i - \psi_j) = \frac{1}{2\pi} \int_0^{2\pi} g_{ij}(\lambda, \lambda - \psi_i + \psi_j) d\lambda. \quad (\text{A7})$$

To find a_i , we take a time derivative of Eq. (A4),

$$\begin{pmatrix} \dot{\phi}_1 \\ \dot{\phi}_2 \end{pmatrix} = (I + \delta B) \begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix}, \quad (\text{A8})$$

where I is the identity matrix and the elements of matrix B are given by $B_{ij} = \partial a_i / \partial \phi_j$. We then obtain

$$\begin{pmatrix} \dot{\phi}_1 \\ \dot{\phi}_2 \end{pmatrix} = (I + \delta B)^{-1} \begin{pmatrix} \dot{\phi}_1 \\ \dot{\phi}_2 \end{pmatrix} = (I - \delta B) \begin{pmatrix} \dot{\phi}_1 \\ \dot{\phi}_2 \end{pmatrix} + O(\delta^2) = \begin{pmatrix} \omega_0 \\ \omega_0 \end{pmatrix} + \delta \begin{pmatrix} f_1(\phi_1) + g_{12}(\phi_1, \phi_2) + \mathbf{Z}(\phi_1) \cdot \boldsymbol{\xi}_1(t) - \omega_0(B_{11} + B_{12}) \\ f_2(\phi_2) + g_{21}(\phi_2, \phi_1) + \mathbf{Z}(\phi_2) \cdot \boldsymbol{\xi}_2(t) - \omega_0(B_{21} + B_{22}) \end{pmatrix} + O(\delta^2), \quad (\text{A9})$$

where we have redefined f_i , g_{ij} , and $\mathbf{Z}_i$ as the functions of ϕ_1 and ϕ_2 instead of φ_1 and φ_2 , as the error involved with this replacement is of $O(\delta^2)$. Comparing Eqs. (A5) and (A9), and using the transformations $B_{11} + B_{12} = \partial_\theta a_1(\theta + \psi_1, \theta + \psi_2)$ and $B_{21} + B_{22} = \partial_\theta a_2(\theta + \psi_2, \theta + \psi_1)$ with $\theta = \omega_0 t$, we obtain

$$\begin{aligned} \partial_\theta a_1(\theta + \psi_1, \theta + \psi_2) &= \omega_0^{-1} [f_1(\theta + \psi_1) + g_{12}(\theta + \psi_1, \theta + \psi_2) \\ &\quad - \omega_1 - \Gamma_{12}(\psi_1 - \psi_2)], \\ \partial_\theta a_2(\theta + \psi_2, \theta + \psi_1) &= \omega_0^{-1} [f_2(\theta + \psi_2) + g_{21}(\theta + \psi_2, \theta + \psi_1) \\ &\quad - \omega_2 - \Gamma_{21}(\psi_2 - \psi_1)]. \end{aligned} \quad (\text{A10})$$

Because a_i is a 2π -periodic function, the integration of Eq. (A10) over one period results in Eqs. (A6) and (A7). The function a_i is then obtained as

$$\begin{aligned} a_1(\theta + \psi_1, \theta + \psi_2) &= \omega_0^{-1} \int_0^{\theta + \psi_1} [f_1(\lambda) + g_{12}(\lambda, \lambda - \psi_1 + \psi_2) \\ &\quad - \omega_1 - \Gamma_{12}(\psi_1 - \psi_2)] d\lambda, \end{aligned}$$

$$\begin{aligned} a_2(\theta + \psi_2, \theta + \psi_1) &= \omega_0^{-1} \int_0^{\theta + \psi_2} [f_2(\lambda) + g_{21}(\lambda, \lambda - \psi_2 + \psi_1) \\ &\quad - \omega_2 - \Gamma_{21}(\psi_2 - \psi_1)] d\lambda. \end{aligned} \quad (\text{A11})$$

Thus, Eq. (A5) is indeed a lowest order approximation to Eq. (A1).

There are a few differences between Eqs. (1) and (A5). To get exactly the same form as Eq. (1), we need the following manipulation. Without loss of generality, we may put $\omega_0 = 0$ and $\delta = 1$ and add ϵ to the forcing term $\boldsymbol{\xi}_i$. Moreover, by assuming that the direction of the forcing $\boldsymbol{\xi}_i$ is time independent, i.e., $\boldsymbol{\sigma}(t) \equiv \boldsymbol{\xi}_i(t) / \|\boldsymbol{\xi}_i(t)\|$ is a time-independent unit vector, we may rewrite $\mathbf{Z}(\phi_i) \cdot \boldsymbol{\xi}_i(t) = Z(\phi_i) \boldsymbol{\xi}_i(t)$ where $Z(\phi) \equiv \mathbf{Z}(\phi) \cdot \boldsymbol{\sigma}$ and $\boldsymbol{\xi}_i(t) \equiv \|\boldsymbol{\xi}_i(t)\|$. Here, $Z(\phi)$ is interpreted as the phase sensitivity function defined for the direction of the forcing. In many systems, the forcing vector $\boldsymbol{\xi}_i(t)$ has only one nonvanishing component, so that this assumption is often reasonable.

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- [1] A. T. Winfree, *The Geometry of Biological Time* (Springer, New York, 1980).
 - [2] Y. Kuramoto, *Chemical Oscillations, Waves, and Turbulence* (Springer, New York, 1984).
 - [3] P. A. Tass, *Phase Resetting in Medicine and Biology: Stochastic Modeling and Data Analysis* (Springer, Berlin, 1999).
 - [4] A. Pikovsky, M. Rosenblum, and J. Kurths, *Synchronization: A Universal Concept of Nonlinear Sciences* (Cambridge University Press, Cambridge, 2001).
 - [5] S. M. Reppert and D. R. Weaver, *Nature* (London) **418**, 935 (2002).
 - [6] I. Z. Kiss, Y. M. Zhai, and J. L. Hudson, *Science* **296**, 1676 (2002); I. Z. Kiss, C. G. Rusin, H. Kori, and J. L. Hudson, *ibid.* **316**, 1886 (2007); H. Kori, C. G. Rusin, I. Z. Kiss, and J. L. Hudson, *Chaos* **18**, 026111 (2008).
 - [7] H. Ukai, T. Kobayashi, M. Nagano, K. Masumoto, M. Sujino, T. Kondo, K. Yagita, Y. Shigeyoshi, and H. Ueda, *Nat. Cell Biol.* **9**, 1327 (2007).
 - [8] C. H. Johnson, *Chronobiol. Int.* **16**, 711 (1999).
 - [9] K. Okuda and Y. Kuramoto, *Prog. Theor. Phys.* **86**, 1159 (1991); E. Montbrio, J. Kurths, and B. Blasius, *Phys. Rev. E* **70**, 056125 (2004); I. Z. Kiss, M. Quigg, S.-H. C. Chun, H. Kori, and J. L. Hudson, *Biophys. J.* **94**, 1121 (2008); J. H. Sheeba, A. Stefanovska, and P. V. E. McClintock, *ibid.* **95**, 2722 (2008); E. Ott and T. M. Antonsen, *Chaos* **18**, 037113 (2008); E. Barreto, B. Hunt, E. Ott, and P. So, *Phys. Rev. E* **77**, 036107 (2008).
 - [10] Y. Kawamura, H. Nakao, K. Arai, H. Kori, and Y. Kuramoto, *Phys. Rev. Lett.* **101**, 024101 (2008).
 - [11] T.-W. Ko and G. B. Ermentrout, *Phys. Rev. E* **79**, 016211 (2009).
 - [12] E. Brown, J. Moehlis, and P. Holmes, *Neural Comput.* **16**, 673

- (2004).
- [13] E. M. Izhikevich, *Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting* (MIT Press, Cambridge, 2007).
 - [14] N. Biggs, Bull. Lond. Math. Soc. **29**, 641 (1997).
 - [15] R. Albert and A. L. Barabási, Rev. Mod. Phys. **74**, 47 (2002).
 - [16] H. Sakaguchi, S. Shinomoto, and Y. Kuramoto, Prog. Theor. Phys. **79**, 1069 (1988).
 - [17] F. C. Hoppensteadt and E. M. Izhikevich, *Weakly Connected Neural Networks* (Springer-Verlag, New York, 1997).
 - [18] A. T. Winfree, J. Theor. Biol. **16**, 15 (1967).
 - [19] The phase sensitivity is a function of the phase of an oscillator describing the phase shifts (relative to the unperturbed evolution) normalized by the intensity of weak pulsative perturbation given to the oscillator [1,2,18]. It is also often called the infinitesimal phase response curve [13].
 - [20] Note that, in the case of quenched disorder, i.e., if p_i in Eq. (2) is constant, a similar equation to Eq. (9) has also been derived by R. Toenjes and B. Blasius, Phys. Rev. E **80**, 026202 (2009) to derive the first-order correction of the synchronized frequency, $\dot{\Theta} = \Omega + \epsilon \sum_{i=1}^N w_i p_i$.