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Phase description of stable limit-cycle solutions in reaction-diffusion systems

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Abstract

Phase reduction theory for stable limit-cycle solutions of one-dimensional reaction-diffusion systems is developed. By locally approximating the isochrons of the limit-cycle orbit, we derive the phase sensitivity function, which is a key quantity in the phase description of limit cycles. As an example, synchronization of traveling pulses in a pair of mutually interacting reaction-diffusion systems is analyzed. It is shown that the traveling pulses can exhibit multi-modal phase locking.

Keywords: reaction-diffusion systems; limit cycles; phase reduction; synchronization

1. Introduction

Spontaneous rhythms naturally arise in nonlinear dissipative systems. Interactions of rhythms can organize complex collective dynamics, which may play important functional roles. The phase reduction method is a powerful technique for analyzing interacting groups of regular rhythmic elements typically modeled as coupled limit-cycle oscillators. It is well established for low-dimensional limit-cycle oscillators [1-4]. Non-trivial collective dynamics of coupled oscillator systems have been revealed with this method, including the macroscopic synchronization transition as a prominent example.

The purpose of this work is to extend the applicability of the phase reduction method to stable limit-cycle oscillations in reaction-diffusion systems with infinite-dimensional phase space. The isochron of

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the system, which assigns a scalar phase value to a given spatial pattern in the basin of the limit-cycle orbit, can locally be approximated near the unperturbed limit-cycle orbit. The phase sensitivity function of the limit-cycle solution, which quantifies linear response of the phase to weak spatial perturbations, is then derived from the approximated isochrons. Based on this formulation, we analyze a pair of interacting traveling pulses in coupled reaction-diffusion systems and reveal their synchronization property. In particular, we show that the traveling pulses can exhibit multi-modal phase locking phenomena due to their complex oscillatory spatial profiles.

2. Phase reduction

2.1. Phase reduction method for low-dimensional limit-cycle oscillators

Here we briefly summarize the phase reduction theory for stable limit-cycle solutions of low-dimensional ordinary differential equations (ODEs) [1-4]. Let us assume that a dynamical system described by $\dot{\boldsymbol{X}}(t) = \boldsymbol{F}(\boldsymbol{X})$ has a stable limit-cycle solution $\boldsymbol{X_0}(t+T) = \boldsymbol{X_0}(t)$, where $\boldsymbol{X}(t)$ is a real vector representing the state variable at time t and T is the period of the limit-cycle oscillation. Along this limit cycle $\boldsymbol{X_0}(t)$, we can define a scalar phase variable ϕ $(0 \le \phi < T)$ which increases at a constant rate 1 as $\dot{\phi}(t) = 1$ with time. This phase can then be extended to the neighbourhood of $\boldsymbol{X_0}(t)$ by assigning the same phase value to the set of points in the phase space which eventually converge to the same orbit. This gives a function from a state $\boldsymbol{X}$ near the limit cycle $\boldsymbol{X}_0(t)$ to a scalar phase $\phi(\boldsymbol{X})$, which is called the isochron. The isochron $\phi(\boldsymbol{X})$ satisfies $\dot{\phi} = \dot{\phi}\big(\boldsymbol{X}(t)\big) = \nabla_{\boldsymbol{X}}\phi \cdot \dot{\boldsymbol{X}}(t) = \nabla_{\boldsymbol{X}}\phi \cdot \boldsymbol{F}(\boldsymbol{X}) = 1$, so that the time and phase are equivalent, and the location on the limit cycle can be specified using the phase ϕ as $\boldsymbol{X_0}(\phi)$. Now, if this oscillator is weakly perturbed as $\dot{\boldsymbol{X}}(t) = \boldsymbol{F}(\boldsymbol{X}) + \varepsilon\boldsymbol{p}(t)$, where $\boldsymbol{p}(t)$ represents perturbations, the corresponding phase equation at the lowest order is given by $\dot{\phi}(t) \cong 1 + \varepsilon\boldsymbol{Z}(\phi)\cdot\boldsymbol{p}(t)$, where the *phase sensitivity function* $\boldsymbol{Z}(\phi) = \nabla_{\boldsymbol{X}=\boldsymbol{X}_0(\phi)}\phi(\boldsymbol{X})$, gradient of the isochron estimated on the limit cycle at $\boldsymbol{X_0}(\phi)$, is introduced. Thus, the dynamics of a weakly perturbed limit-cycle oscillator can be described by a simple scalar phase equation, which drastically reduces the dimensions of the model. This is quite useful in studying the dynamics of interacting oscillators.

The phase sensitivity function $\boldsymbol{Z}(\phi)$ encapsulates essential dynamical properties of the weakly perturbed oscillator and plays a central role in the phase reduction theory. It is given by a periodic solution of an adjoint equation [4] to the linearized equation of the system near the limit-cycle solution (referred to as Malkin's theorem by Hoppensteadt and Izhikevich in [3]). It can also be measured experimentally by weakly perturbing an oscillator and measuring its phase responses.

2.2. Extension to reaction-diffusion systems

The purpose of this study is to extend the phase reduction method for low-dimensional ODEs to stable periodic solutions of reaction-diffusion (RD) systems. For simplicity, we consider a RD system on a one-dimensional ring of length L with periodic boundary conditions described by

$$\frac{\partial}{\partial t}\boldsymbol{X}(x,t) = \boldsymbol{F}(\boldsymbol{X}) + \mathbf{D}\frac{\partial^2}{\partial x^2}\boldsymbol{X}, \tag{1}$$

where $\boldsymbol{X}(x,t)$ represents the field variables, $0 \le x < L$ is the location on the ring, and $\mathbf{D}$ is a diffusion matrix. We assume that Eq. (1) has a stable periodic solution $\boldsymbol{X}_0(x,t+T) = \boldsymbol{X}_0(x,t)$ with period T. As an example of such periodic solutions, we will consider stable traveling pulses in the FitzHugh-Nagumo model of neuronal spike transmission on a ring, which can be considered limit-cycle solutions in infinite-dimensional phase space of Eq. (1). Other periodic solutions such as nonlinear standing waves or localized breathing modes can also be analyzed in the same way.

As in the case of low-dimensional ODEs, we can introduce a scalar phase variable ϕ $(0 \le \phi < T)$ along the limit-cycle solution $\boldsymbol{X}_0(x,t)$ which increases at a constant rate 1 as $\dot{\phi}(t) = 1$ with time, and use this ϕ to represent the location on the limit cycle. To extend the phase reduction method for limit-cycle solutions of the RD equation, we need further to define the *isochron functional* $\phi\{\boldsymbol{X}(x,t)\}$, which assigns a scalar phase value $0 \le \phi < T$ to a given spatial profile $\boldsymbol{X}(x,t)$ of the system which eventually converges to the limit-cycle solution $\boldsymbol{X}_0(x,t)$. This is generally difficult, however, for spatial patterns near the limit-cycle solution, $\boldsymbol{X}(x) \cong \boldsymbol{X}_0(x;\phi_0)$, a linear approximation to $\phi\{\boldsymbol{X}(x)\}$ can be given as

$$\phi\{\boldsymbol{X}(x)\} \cong \phi_0 + [\boldsymbol{Q}(x,\phi_0), \boldsymbol{X}(x) - \boldsymbol{X}_0(x;\phi_0)]\,, \tag{2}$$

where the bracket represents the inner product,

$$[\boldsymbol{A}(x), \boldsymbol{B}(x)] = \int_0^L \boldsymbol{A}(x) \cdot \boldsymbol{B}(x) dx, \tag{3}$$

and the function $\boldsymbol{Q}(x, \phi = t)$ is a time-periodic solution to the following adjoint equation:

$$\frac{\partial}{\partial t}\boldsymbol{Q}(x,t) = -\hat{\mathrm{L}}^{\dagger}(x,t)\boldsymbol{Q}(x,t) \tag{4}$$

with the initial condition $\boldsymbol{Q}(x,0) = \boldsymbol{u}^{\dagger}(x,0)$. Here, $\hat{\mathrm{L}}^{\dagger}(x,t)$ is an adjoint operator to the linearlized operator $\hat{\mathrm{L}}(x,t)$ of the RD equation (1) near the limit-cycle solution $\boldsymbol{X}_0(x,t)$ with respect to the inner product (3), and $\boldsymbol{u}^{\dagger}(x,0)$ is a zero eigenvector of $\hat{\mathrm{L}}^{\dagger}(x,0)$. The function $\boldsymbol{Q}(x,\phi)$ is the *phase sensitivity function* of the limit-cycle solution $\boldsymbol{X}_0(x,t)$ of the RD equation (1).

Similarly to the case of low-dimensional ODEs, once we now the function $\boldsymbol{Q}(x,\phi)$, we can simplify the RD equation (1) to a single scalar phase equation. Suppose that a RD system possessing a limit-cycle solution $\boldsymbol{X}_0(x,t)$ is weakly perturbed as

$$\frac{\partial}{\partial t}\boldsymbol{X}(x,t) = \boldsymbol{F}(\boldsymbol{X}) + \mathbf{D}\frac{\partial^2}{\partial x^2}\boldsymbol{X} + \varepsilon\boldsymbol{h}(x,t), \tag{5}$$

where $\boldsymbol{h}(x,t)$ represents spatio-temporal perturbations. We assume that the limit-cycle solution persists and can still be approximated as $\boldsymbol{X}(x,t) \cong \boldsymbol{X}_0(x;\phi(t))$, namely, only its phase is affected by the perturbation. The phase dynamics of the perturbed solution can then given at the lowest order as

$$\dot{\phi}(t) = 1 + \varepsilon[\boldsymbol{Q}(x,\phi(t)), \boldsymbol{h}(x,t)]. \tag{6}$$

Thus, the weakly perturbed RD equation (5), which is originally infinite-dimensional, can approximately be reduced to a single scalar phase equation (6) near the unperturbed limit-cycle solution $\boldsymbol{X}_0(x,t)$.

We here presented the above results without derivations; details will be reported elsewhere [5,6]. However, we would stress the similarity of Eq. (4) to the conventional adjoint equation for the phase sensitivity function $\boldsymbol{Z}(\phi)$ of ODEs [3,4]. Similar results for a nonlinear Fokker-Planck equation describing phase distributions of coupled oscillators have also been obtained in [7-10], which gives the collective phase sensitivity of a group of phase oscillators undergoing macroscopic oscillations.

3. Phase sensitivity functions of traveling pulses

Let us illustrate the above result using an example of the FitzHugh-Nagumo (FHN) model of neuronal spike transmission [11]. The FHN model is a two-variable activator-inhibitor system,

$$\boldsymbol{X}(x,t) = (u(x,t), v(x,t))^T, \quad \boldsymbol{F}(\boldsymbol{X}) = (u(1-\alpha)(1-u) - v, \tau(u-\gamma v))^T, \quad \mathbf{D} = \mathrm{diag}(\kappa, 0), \tag{7}$$

where u represents the activator which spontaneously increases, v represents the inhibitor which suppresses the activator, and $\alpha, \gamma, \tau, \kappa$ are parameters. It is assumed that only the activator diffuses while the inhibitor does not diffuse at all. In Fig.1, two typical limit-cycle solutions (traveling pulses) $\boldsymbol{X_0}(x,\phi)$ of the FHN model are shown as well as their phase sensitivity functions $\boldsymbol{Q}(x,\phi)$ obtained by numerically solving the adjoint equation (4). Only the components corresponding to the activator variable at $\phi = 0$ are plotted. Figure 1(a) shows a normal solution with a simple tail, and Fig. 1(b) shows a "wavy" solution with an oscillatory tail (see the caption for detailed parameter values), each of which moving to the right with a constant velocity and without changing the spatial profile.

From Fig. 1(a), we see that the phase sensitivity function $\boldsymbol{Q}(x,\phi)$ of the normal traveling pulse takes large positive values immediately in front of the pulse, then takes negative values slightly more ahead of this region, and vanishes elsewhere. This shape of the phase sensitivity function can be understood as follows. When the activator is raised by the external perturbation at the pulse front, the traveling pulse can proceed more quickly, resulting in the advance in its phase (note that the phase of the pulse is simply its location on the ring). However, if the activator is raised slightly more ahead of the pulse front, the increase in the activator then induces inhibitor growth, which eventually suppresses the progress of the pulse front and leads to the delay in its phase. In other regions, the movement of the pulse is not affected by external perturbations (as long as the perturbations are weak). Figure 1(b) shows a traveling pulse with a wavy tail. Correspondingly, the phase sensitivity function $\boldsymbol{Q}(x,\phi)$ has a complex shape, which oscillates in front of the pulse. Thus, the phase of the pulse can advance or retard depending on the timing and location of the perturbation applied to the activator. This leads to an interesting multi-modal phase locking behavior between two traveling pulses as we illustrate in the next section.

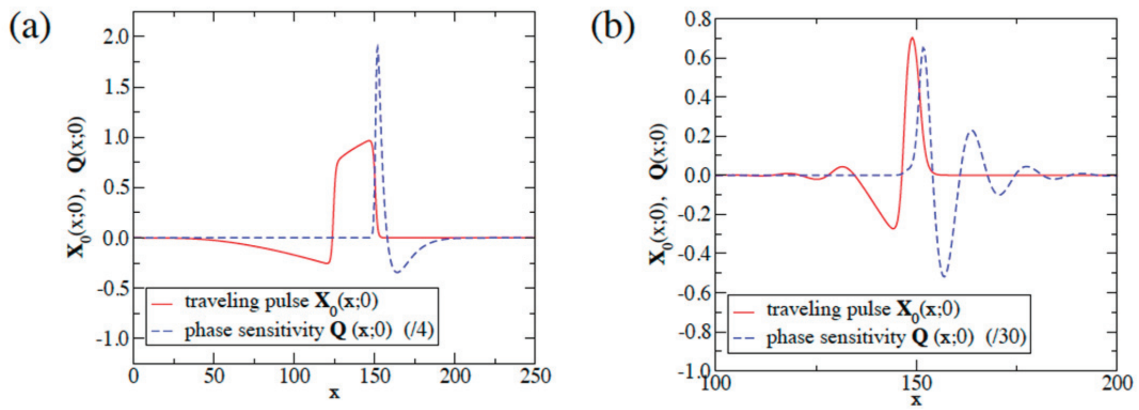

Fig. 1. Stable traveling pulses $\boldsymbol{X}_0(x, \phi = 0)$ and phase sensitivity function $\boldsymbol{Q}_0(x, \phi = 0)$ of the FitzHugh-Nagumo model (activator components). (a) Normal pulse at $\alpha = 0.1, \tau = 0.002, \gamma = 2.5, \kappa = 0.25$; (b) Wavy pulse at $\alpha = 0, \tau = 0.0185, \gamma = 1.0, \kappa = 0.25$

4. Synchronization between traveling pulses in coupled reaction-diffusion systems

As an application of the theory, we consider synchronization between traveling pulses of two coupled RD systems [11]. Suppose two coupled layers of identical RD systems described by

$$\frac{\partial}{\partial t}\boldsymbol{X}^A(x,t) = \boldsymbol{F}(\boldsymbol{X}^A) + \mathbf{D}\frac{\partial^2}{\partial x^2}\boldsymbol{X}^A + \varepsilon\{\boldsymbol{X}^B(x,t) - \boldsymbol{X}^A(x,t)\},$$
$$\frac{\partial}{\partial t}\boldsymbol{X}^B(x,t) = \boldsymbol{F}(\boldsymbol{X}^B) + \mathbf{D}\frac{\partial^2}{\partial x^2}\boldsymbol{X}^B + \varepsilon\{\boldsymbol{X}^A(x,t) - \boldsymbol{X}^B(x,t)\}, \tag{8}$$

where $\boldsymbol{X}^A(x,t)$ and $\boldsymbol{X}^B(x,t)$ represent the RD systems in layers A and B, respectively, and the two layers are diffusively coupled with each other through a small coupling constant ε. We assume that each of the RD systems has a stable traveling-pulse solution $\boldsymbol{X}_0(x,\phi^{A,B}(t))$ when the mutual coupling is absent ($\varepsilon = 0$), where $\phi^A(t)$ and $\phi^B(t)$ represent the phases (locations) of the unperturbed stable traveling pulses in layers A and B, respectively, and that these traveling-pulse solutions persist even if weak coupling is introduced between the layers ($\varepsilon > 0$)

Using the phase sensitivity function $\boldsymbol{Q}(x,\phi)$ obtained in the previous section, we can reduce the coupled RD systems described by Eq. (8) to a pair of coupled phase equations,

$$\dot{\phi}^A(t) \cong 1 + \varepsilon[\boldsymbol{Q}(x,\phi^A), \boldsymbol{X}_0(x,\phi^B) - \boldsymbol{X}_0(x,\phi^A)],$$
$$\dot{\phi}^B(t) \cong 1 + \varepsilon[\boldsymbol{Q}(x,\phi^B), \boldsymbol{X}_0(x,\phi^A) - \boldsymbol{X}_0(x,\phi^B)], \tag{9}$$

by plugging the mutual coupling $\boldsymbol{X}_0(x,\phi^B) - \boldsymbol{X}_0(x,\phi^A)$ or $\boldsymbol{X}_0(x,\phi^A) - \boldsymbol{X}_0(x,\phi^B)$ as the perturbation $\boldsymbol{h}(x,t)$ in Eq. (6). Moreover, we can adopt the averaging procedure [1-3] to Eq. (9) because ε is assumed to be small, which yields the following coupled phase equations:

$$\dot{\phi}^A(t) \cong 1 + \varepsilon\Gamma(\phi^B - \phi^A), \quad \dot{\phi}^B(t) \cong 1 + \varepsilon\Gamma(\phi^A - \phi^B), \tag{10}$$

where the phase coupling function Γ is given by

$$\Gamma(\phi^B - \phi^A) = \frac{1}{T}\int_0^T ds\,[\boldsymbol{Q}(x,s), \boldsymbol{X}_0(x,\phi^B - \phi^A + s) - \boldsymbol{X}_0(x,s)]\,, \tag{11}$$

and similarly for $\Gamma(\phi^A - \phi^B)$. From Eq. (10), the phase difference $\theta = \phi^A - \phi^B$ obeys

$$\dot{\theta}(t) \cong -\varepsilon\Gamma_a(\theta), \tag{12}$$

where $\Gamma_a(\theta) = \Gamma(\theta) - \Gamma(-\theta)$ is the antisymmetric part of the phase coupling function Γ. Therefore, the phase difference $\theta = \phi^A - \phi^B$ between the traveling pulses in systems A and B can take stationary values at the stable fixed points of Eq. (12) satisfying $\Gamma_a(\theta^*) = 0$ and $\mathrm{d}\Gamma_a(\theta^*)/d\theta > 0$. In particular, the in-phase locked state $\phi^A = \phi^B$ of the two traveling pulses is stable if $\mathrm{d}\Gamma_a(0)/d\theta > 0$.

In Fig. 2, results of the phase reduction for the wavy traveling pulse of the FHN equation, shown in Fig. 1(b), are summarized. Figure 2(a) shows the asymmetric part of the phase coupling function, Γ_a. Reflecting the wavy shape of the traveling pulse and the corresponding phase sensitivity function, Γ_a has also a wavy shape with many zero crossings satisfying $\Gamma_a(\theta^*) = 0$ and $\mathrm{d}\Gamma_a(\theta^*)/d\theta > 0$. Therefore, the two traveling pulses can synchronize at various phase differences, which we call multi-modal phase locking [12]. Figure 2(b) plots the asymptotic stationary phase differences between the pulses obtained by direct numerical simulations of Eq. (8) as a function of the initial phase differences and compares them with the prediction of the phase-reduced equation (10) or (12) with Γ_a plotted in Fig. 2(a), showing reasonably good agreement. Figures 2(c) and 2(d) show typical states of the system sufficiently after initial transient, in which snapshots of the activator components of the two RD layers are plotted. We can observe that the two pulses are phase locked with the phase differences shown in Fig. 2(b). It is interesting that the completely in-phase synchronized state with $\phi^A = \phi^B$ has a very small basin of attraction, while other phase-locking states have wider basins of attraction. Similar multi-modal phase locking is also observed in coupled delay-induced oscillators, which are also infinite-dimensional [12].

5. Summary

We briefly explained the framework of phase reduction approach to limit-cycle solutions in infinite-dimensional reaction-diffusion systems using the traveling pulse on a one-dimensional ring as an example, and showed that the reduced phase equations can nicely predict the synchronization property of two coupled layers of reaction-diffusion systems exhibiting traveling pulses. Interacting traveling pulses have been analyzed within the interface dynamics approach in the past. An advantage of our approach to the conventional method is that it can be applicable to systems without spatial translational symmetry. For example, we can also analyze synchronization of coupled breathing modes, target patterns, and spirals in coupled reaction-diffusion systems as well. Essentially the same framework can also be generalized to synchronization between coupled fluid convections [13]. Further details will be reported in [6] and [13].

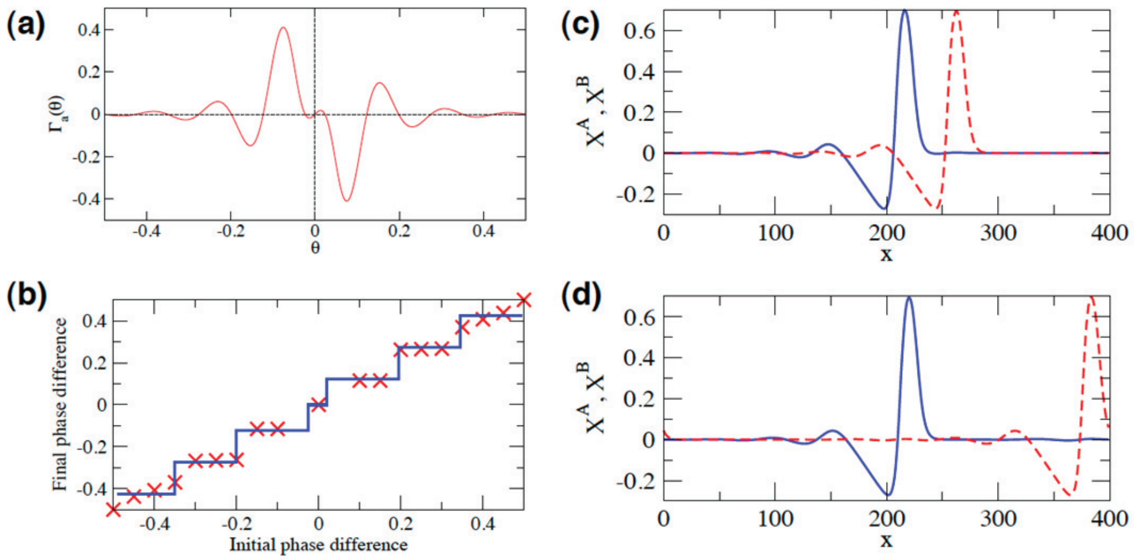

Fig. 2. Phase locking between two coupled reaction-diffusion layers of the FitzHugh-Nagumo model exhibiting traveling pulses. The parameters of each layer are the same as in Fig. 1(b) (wavy pulse). The coupling strength between the layers is $\varepsilon = 0.01$. (a) Antisymmetric part of the phase coupling function Γ_a; (b) Asymptotic phase differences obtained by direct numerical simulations of the original model compared with the prediction of the phase reduction method; (c), (d) Stable phase-locked traveling pulses (activator components) sufficiently after initial transient, started from varied initial phase differences.

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