Synchronization Analysis of Resonate-and-Fire Neuron Models with Delayed Resets

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***Abstract*—We analyzed the synchronization properties of coupled resonate-and-fire neuron models with delayed resets. The conventional phase reduction method cannot be applied to the system as it shows periodicity only under time-delayed feedback and cannot be treated as a dynamical system. Therefore, we generalized the conventional phase reduction method to include dynamics with delay-induced periodicity. Then we applied the theory to the system and utilized the reduced phase dynamics for analyzing the synchronization properties.**

I. Introduction

The phase reduction is a powerful method for simplifying a dynamical system with a periodic solution to a one-dimensional phase equation [1], [2], [3], [4], [5]. The reduction enables us to predict various synchronization properties such as mutual entrainments of coupled oscillators [6], [7], [8], [9], [10], [11], entrainment to external forces [12], and patterns of chemical oscillations [13], [14].

This conventional phase reduction is widely applicable to many problems because it is formalized for general dynamical systems of finite dimensions [4], [15], [16]. However, many systems such as neural systems [17], [18] and CMOS circuits [19], [20] can have intrinsic time-delays in their differential equations [21], [22], [23]. In this case, the system cannot be described as a dynamical system and beyond the scope of the conventional phase reduction.

It is still possible to perform phase reduction for a system with a delay for some specific cases. For example, a delay can be incorporated into phase equations when it appears only in the couplings between oscillators [18]. However, in general, a system may require a time-delayed feedback to form a periodic solution. This delay-induced oscillation cannot be treated within the conventional phase reduction framework. Therefore, we need to generalize a conventional phase reduction method to predict the synchronization properties of delay-induced oscillators.

In this paper, we generalize the conventional phase reduction method to include delay-induced oscillators. Then we apply the general reduction method to coupled resonate-and-fire neuron models with delayed resets to demonstrate that the reduced, low dimensional phase dynamics is useful for predicting the synchronization properties up to small perturbations.

II. Theory

Here we derive phase reduction formula for general delay-induced oscillators in an intuitive manner (e.g. we use Dirac's delta function). Note that the derivation needs a rigorous proof by mathematicians although we have engineering applications in mind.

Our goal is to perform the phase reduction for a system of ordinary differential equations with the following form,

$$\frac{d\boldsymbol{x}(t)}{dt} = \boldsymbol{f}(\boldsymbol{x}(t), \boldsymbol{x}(t-\tau)), \qquad \boldsymbol{x} \in \mathbb{R}^n \tag{1}$$

which has a stable periodic solution, $\boldsymbol{x}(t) = \boldsymbol{p}(t)$, satisfying

$$\boldsymbol{p}(t) = \boldsymbol{p}(t+T) \tag{2}$$

for all t with a constant $T > 0$. Note that if the righthand side of Eq. 1 does not depend on the time-delayed variable, $\boldsymbol{x}(t-\tau)$, the system becomes a dynamical system and the phase reduction can be performed in a conventional way [1].

A. Conventional Phase Reduction for Dyanamical Systems

We begin with a brief review of the conventional phase reduction of a dynamical system with a limit cycle [1].

Consider a system of ordinary differential equations,

$$\frac{d\boldsymbol{x}(t)}{dt} = \boldsymbol{f}(\boldsymbol{x}(t)), \qquad \boldsymbol{x} \in \mathbb{R}^n \tag{3}$$

which has a stable periodic solution, $\boldsymbol{x}(t) = \boldsymbol{p}(t)$, satisfying

$$\boldsymbol{p}(t) = \boldsymbol{p}(t+T), \tag{4}$$

for all t with a constant $T > 0$. Then, a phase $\phi(\boldsymbol{x})$ can be defined in the vicinity of the limit cycle as

$$\begin{aligned}\frac{d\phi(\boldsymbol{x}(t))}{dt} &= \left.\frac{d\phi(\boldsymbol{x})}{d\boldsymbol{x}}\right|_{\boldsymbol{x}=\boldsymbol{x}(t)} \cdot \frac{d\boldsymbol{x}(t)}{dt} \\ &= \left.\frac{d\phi(\boldsymbol{x})}{d\boldsymbol{x}}\right|_{\boldsymbol{x}=\boldsymbol{x}(t)} \cdot \boldsymbol{f}(\boldsymbol{x}(t)) \\ &= \frac{1}{T}.\end{aligned} \tag{5}$$

In the presence of a perturbation, $\epsilon \boldsymbol{g}(\boldsymbol{x}, t)$, the system can be described as

$$\frac{d\boldsymbol{x}(t)}{dt} = \boldsymbol{f}(\boldsymbol{x}(t)) + \epsilon \boldsymbol{g}(\boldsymbol{x}(t), t). \tag{6}$$

The phase dynamics up to the first order of ϵ becomes

$$\begin{aligned}\frac{d\phi(\boldsymbol{x}(t))}{dt} &= \frac{d\phi(\boldsymbol{x})}{d\boldsymbol{x}}\Big|_{\boldsymbol{x}=\boldsymbol{x}(t)} \cdot \frac{d\boldsymbol{x}}{dt} \\ &= \frac{d\phi(\boldsymbol{x})}{d\boldsymbol{x}}\Big|_{\boldsymbol{x}=\boldsymbol{x}(t)} \cdot \Big(\boldsymbol{f}(\boldsymbol{x}(t)) + \epsilon \boldsymbol{g}(\boldsymbol{x}(t), t)\Big) \\ &\approx \frac{1}{T} + \epsilon \frac{d\phi(\boldsymbol{x})}{d\boldsymbol{x}}\Big|_{\boldsymbol{x}=\boldsymbol{x}(t)} \cdot \boldsymbol{g}(\boldsymbol{x}(t), t) \qquad (7)\end{aligned}$$

where we used Eq. 5. If the perturbation ϵ is small enough, the solution can be written as

$$\boldsymbol{x}(t) = \boldsymbol{p}(\phi(t)T) + O(\epsilon), \qquad (8)$$

and righthand side of Eq. 20 can be evaluated on the limit cycle, $\boldsymbol{p}(\phi)$, up to the first order of ϵ, leading to the phase equation

$$\frac{d\phi}{dt} = \frac{1}{T} + \epsilon \boldsymbol{Z}(\phi(t)) \cdot \boldsymbol{g}(\phi(t), t). \qquad (9)$$

where we defined

$$\boldsymbol{Z}(\phi) := \frac{d\phi(\boldsymbol{x})}{d\boldsymbol{x}}\Big|_{\boldsymbol{x}=\boldsymbol{p}(\phi)}. \qquad (10)$$

This phase equation can be used to predict synchronization properties under any perturbation $\boldsymbol{g}$ [1], [3], once the phase response curve, $\boldsymbol{Z}(\phi)$, is theoretically computed [9] or experimentally measured [24]. In many cases, the perturbation has only one degree of freedom, that is, $\boldsymbol{g} = (g, 0, 0, \dots, 0)$, which simplifies the equation further. This happens naturally, for example, when electric current injection to a neuron directly affects only its voltage [25].

B. Phase Reduction of Deley-Induced Oscillators

Eq. 1 is not a dynamical systems, because it has $\boldsymbol{x}(t-\tau)$ in the righthand side. To make it a dynamical system, we need to include $\boldsymbol{x}(t-\tau)$ in the state variables and write down a differential equation for its time evolution [21], [22], [23]. We can consider more general state variables (or a state function),

$$\boldsymbol{x}_t(\cdot) = \{\boldsymbol{x}(t-\tau) : \tau \in [0, T]\}. \qquad (11)$$

That is,

$$\boldsymbol{x}_t(\tau) = \boldsymbol{x}(t-\tau). \qquad (12)$$

We could intuitively understand the function space as a discretized vector,

$$\boldsymbol{x}_t(\cdot) = \Big(\boldsymbol{x}(t), \boldsymbol{x}(t-dt), \boldsymbol{x}(t-2dt), \dots, \boldsymbol{x}(t-T)\Big). \qquad (13)$$

where $dt = \frac{T}{N}$ for some large integer N. Then you can realize that the following derivation is quite similar to the conventional phase reduction for finite dimensional dynamical systems in the previous section.

Let us consider a general delay-induced oscillator,

$$\frac{d\boldsymbol{x}(t)}{dt} = \boldsymbol{f}(\boldsymbol{x}_t(\cdot)), \quad \boldsymbol{x} \in \mathbb{R}^n \qquad (14)$$

which has a stable periodic solution, $\boldsymbol{x}(t) = \boldsymbol{p}(t)$, satisfying

$$\boldsymbol{p}(t) = \boldsymbol{p}(t+T) \qquad (15)$$

for all t with a constant $T > 0$. Notice that $\boldsymbol{x}_t(\cdot)$ is also periodic:

$$\boldsymbol{x}_t(\cdot) = \boldsymbol{x}_{t+T}(\cdot). \qquad (16)$$

From this equation, we can get differential equations for the time-evolution of the state variables, $\boldsymbol{x}(\cdot)$,

$$\frac{\partial \boldsymbol{x}_t(\tau)}{\partial t} = \begin{cases} \boldsymbol{f}(\boldsymbol{x}_t(\cdot)) & (\tau = 0), \\ -\frac{\partial \boldsymbol{x}_t(\tau)}{\partial \tau} & (\tau > 0). \end{cases} \qquad (17)$$

The second equation for $\tau > 0$ was derived so that the field $\boldsymbol{x}_t(\cdot)$ has a propagating wave solution. Although the solution of the ordinary differential equation is easily available, we dared to write down the partial differential equation in order to derive the phase dynamics later (Eq. 18). Therefore we do not care about the existence and uniqueness of the solutions in this paper [21].

This equation is closed and, therefore, can be regarded as a dynamical system in a high-dimensional function space. Here we assume that a phase on the functional space (Banach space), $\phi(\boldsymbol{x}(\cdot))$, can be defined in the vicinity of the limit cycle. We can use the same definition of phase as in [1] in the functional space. That is, roughly speaking, the states that asymptotically converge to each other should have the same phase. (The distance of two states or functions is conventionally measured by the supremum (∞-)norm [21].) From this definition, you can assign a phase at each state and the continuity of the phase looks obvious. Therefore, it seems quite reasonable to assume the existence and differentiability of the phase.

The phase should satisfy

$$\frac{d\phi(\boldsymbol{x}_t(\cdot))}{dt} = \int_0^T \frac{\delta\phi(\boldsymbol{x}(\cdot))}{\delta \boldsymbol{x}(\tau)}\Big|_{\boldsymbol{x}(\cdot)=\boldsymbol{x}_t(\cdot)} \cdot \frac{\partial \boldsymbol{x}_t(\tau)}{\partial t} d\tau = \frac{1}{T}, \qquad (18)$$

where $\frac{\delta\phi(\boldsymbol{x}(\cdot))}{\delta \boldsymbol{x}(\tau)}$ is a functional derivative (Frechet derivative), which is an analogue of the gradient of a function in the vector calculus [26]. The Frechet derivative is unique if it exists and is a linear functional. That is why an integral appears in the equation. In the context of variation, the energy or cost function typically takes the form of an integral of a function, an explicit form of the Frechet derivative can be written down as the Euler-Lagrange equation. However, here we consider a more general case where the functional is not necessarily the integral form and the derivative cannot be obtained analytically. Still, we know the differentiability of a map on the Banach space guarantees linearity, uniqueness, continuity, chain rule, mean value theorem, Gateau derivatives (partial derivatives), bilinearity of the second derivative, Taylor expansion and so on. Because a functional space is a special instance of the Banach space, all these properties and tools can be inherited from the real analysis. In the above equation, for example, we used the chain rule of derivatives.

In the presence of a perturbation, $\epsilon \boldsymbol{g}(\boldsymbol{x}(\cdot), t)$, the system can be described as

$$\frac{\partial \boldsymbol{x}_t(\tau)}{\partial t} = \begin{cases} \boldsymbol{f}(\boldsymbol{x}_t(\cdot)) + \epsilon \boldsymbol{g}(\boldsymbol{x}_t(\cdot), t) & (\tau = 0), \\ -\frac{\partial \boldsymbol{x}_t(\tau)}{\partial \tau} & (\tau > 0). \end{cases} \qquad (19)$$

Note that the perturbation appears only in the first component (when $\tau = 0$). The phase dynamics up to the first order of ϵ becomes

$$\begin{aligned}
&\frac{d\phi(\boldsymbol{x}_t(\cdot))}{dt} \\
&= \int_0^T \frac{\delta\phi(\boldsymbol{x}(\cdot))}{\delta\boldsymbol{x}(\tau)}\Big|_{\boldsymbol{x}(\cdot)=\boldsymbol{x}_t(\cdot)} \cdot \frac{\partial\boldsymbol{x}_t(\tau)}{\partial t} d\tau \\
&\approx \frac{1}{T} + \epsilon \int_0^T \frac{\delta\phi(\boldsymbol{x}(\cdot))}{\delta\boldsymbol{x}(\tau)}\Big|_{\boldsymbol{x}(\cdot)=\boldsymbol{x}_t(\cdot)} \cdot \frac{\partial \frac{\partial \boldsymbol{x}_t(\tau)}{\partial t}}{\partial \frac{\partial \boldsymbol{x}_t(\tau')}{\partial t}}\Big|_{\tau'=0} \frac{\partial \frac{\partial \boldsymbol{x}_t(0)}{\partial t}}{\partial \boldsymbol{f}} \cdot \boldsymbol{g} d\tau \\
&= \frac{1}{T} + \epsilon \int_{0-0}^{T-0} \frac{\delta\phi(\boldsymbol{x}(\cdot))}{\delta\boldsymbol{x}(\tau)}\Big|_{\boldsymbol{x}(\cdot)=\boldsymbol{x}_t(\cdot)} \cdot \delta(\tau-\tau')\Big|_{\tau'=0} 1\boldsymbol{g} d\tau \\
&= \frac{1}{T} + \epsilon \frac{\delta\phi(\boldsymbol{x}(\cdot))}{\delta\boldsymbol{x}(\tau)}\Big|_{\boldsymbol{x}(\cdot)=\boldsymbol{x}_t(\cdot),\tau=0} \cdot \boldsymbol{g}(\boldsymbol{x}_t(\cdot), t)
\end{aligned} \tag{20}$$

where we assumed the periodicity of $\boldsymbol{x}_t(\tau)$ and shifted the domain of the integral for the Dirac delta function. The reason is that if the perturbation ϵ is small enough, the solution can be written as

$$\boldsymbol{x}_t(\tau) = \boldsymbol{x}(t-\tau) = \boldsymbol{p}(\phi(t)T-\tau) + O(\epsilon) \quad (\tau \in [0,T]), \tag{21}$$

and righthand side of Eq. 20 can be evaluated on the limit cycle, $\boldsymbol{p}(\phi)$, up to the first order of ϵ, leading to the phase equation

$$\frac{d\phi(t)}{dt} = \frac{1}{T} + \epsilon \boldsymbol{Z}(\phi(t)) \cdot \boldsymbol{g}(\phi(t), t) + O(\epsilon^2). \tag{22}$$

where we defined

$$\boldsymbol{Z}(\phi) := \frac{\delta\phi(\boldsymbol{x}(\cdot))}{\delta\boldsymbol{x}(\tau)}\Big|_{\boldsymbol{x}(\cdot)=\boldsymbol{p}(\phi T),\tau=0}. \tag{23}$$

This phase equation can be used to predict synchronization properties under any perturbations $\boldsymbol{g}$ [1], [3], once the phase response curve $\boldsymbol{Z}(\phi)$ is theoretically computed [9] or experimentally measured [24]. Notice that because the perturbation appears only in the first component, $\boldsymbol{x}(t)$, the dimension of the phase response curve is the same as the dimension of $\boldsymbol{x}$. This reduces the original problem to a low dimensional problem. In many cases, the perturbation has only one degree of freedom, that is, $\boldsymbol{g} = (g, 0, 0, \ldots, 0)$, which simplifies the equation further. This happens naturally, for example, when electric current injection to a neuron directly affects only its voltage [25].

This result looks quite reasonable intuitively, because, only linear response should matter under the presence of a robust limit cycle. If you can measure the phase response curve experimentally, this intuition might suffice. However, when a mathematical model is explicitly given, our derivation can lead to an explicit form the phase response curve by taking the function space of a state variable into account.

III. Application to Coupled Resonate-and-Fire Model with Delayed resets

We applied the theory to coupled neuron models. As a benchmark model, we incorporated delayed feedback [17] into a resonate-and-fire neuron model which is multidimensional, but still analytically tractable [27]. Here delayed reset is necessary for single neurons to fire repetitively. Thus, the feedback of the past states of the neuron is essential for oscillations. Note that we prefer to consider multidimensional models because one-dimensional models such as integrate-and-fire models are essentially equivalent to phase dynamics from the beginning.

A. Resonate-and-Fire Model

The resonate-and-fire model [27], [25], [9] is defined by

$$\begin{cases} \frac{dx}{dt} = -bx - \omega y + I \\ \frac{dy}{dt} = \omega x - by, \end{cases} \tag{24}$$

where x and y are internal state variables of the neuron. If y exceeds the threshold ($y = 1$), the internal state is reset to $(0, -1)$ after the time-delay τ. We can set $b = 1$ by scaling t without loss of generality. In what follows, we use $b = 1$ and $\omega = 10$ for which the property of single neuron dynamics has been investigated in detail [27] (but only for $\tau = 0$). The constant external current input (I) is large enough for neurons to fire periodically.

B. Phase Response Curve

A phase response curve shows the shift of firing times in response to an infinitesimal input current $I + \delta I(t_1)$ at time t_1. Here we consider $\frac{\partial\phi}{\partial x}$ because current inputs enter in the x direction. The phase response curve can be obtained as follows.

The orbit of the resonate-and-fire model can be obtained analytically as a function of time owing to its piecewise linearity [9]. We consider the following orbit. First, a neuron is reset. Next, it evolves for time t_1 and receives the infinitesimal pulse input with amplitude δI. Then, it evolve for $t_2+\delta t_2$ and arrives at the threshold. The orbit satisfies $y(t_1, \delta I, t_2 + \delta t_2) = 1$, where t_2 denotes the firing time without the perturbation. Taking the lowest order term of δI and δt_2, the phase response curve becomes [9]

$$\begin{aligned}
Z &= -\frac{1}{T}\frac{dt_2}{dI} \\
&= \frac{1}{T}\frac{\exp(t_1)\sin(\omega t_2)}{\cos(\omega(t_1+t_2)) + I_0 \sin(\omega(t_1+t_2)) + \omega \sin(\omega(t_1+t_2))},
\end{aligned}$$

where $\frac{1}{T} = \frac{1}{t_1+t_2+\tau}$ is multiplied so that the phase ranges from 0 to 1 where T denotes the period. I_0 is a total stationary current input which can be obtained as a function of $T - \tau$ from the self-consistency equation:

$$I_0 = \frac{(1+\omega^2)e^{-(T-\tau)}\cos\omega(T-\tau) + (1+\omega^2)}{\omega - e^{-(T-\tau)}\sin\omega(T-\tau) - \omega e^{-(T-\tau)}\cos\omega(T-\tau)} \tag{25}$$

Using $T = t_1 + t_2 + \tau$ and $\phi = \frac{t_1}{T}$, the phase response curve can be rewritten as

$$Z(\phi) = \frac{1}{T}\frac{e^{T\phi}\sin(\omega(T-\tau-T\phi))}{\cos(\omega(T-\tau)) + I_0\sin(\omega(T-\tau)) + \omega\sin(\omega(T-\tau))}, \tag{26}$$

for $\phi < \frac{T-\tau}{T}$ and 0 for $\phi > \frac{T-\tau}{T}$. Notice that the phase ϕ advances in proportion to the time when there is no perturbation.

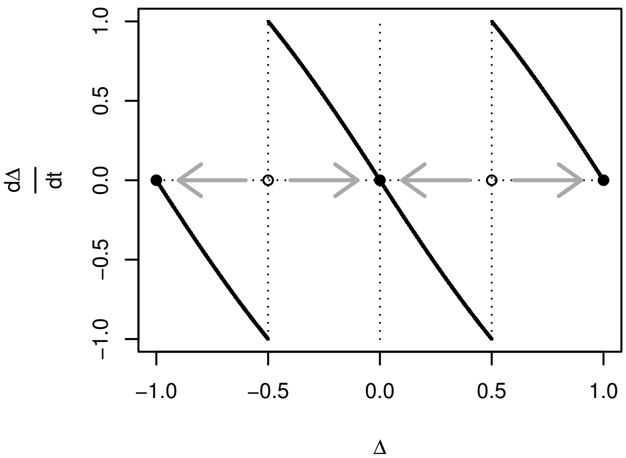

Fig. 1. Dynamics of $\Delta = \phi_1 - \phi_2$ in Eq. 29. $\omega = 10, T = 0.1$.

C. Synchronization Property

When the two identical oscillators (neurons) are connected in the following way,

$$\frac{d\phi_1}{dt} = 1 + \epsilon Z(\phi_1) \sum_i \delta(t - t_2^{(i)})$$
$$\frac{d\phi_2}{dt} = 1 + \epsilon Z(\phi_2) \sum_i \delta(t - t_1^{(i)}) \tag{27}$$

where t_j^i denotes the i-th firing time of the j-the neuron. That is, the interaction is immediate (there is no delay). For simplicity, we use $\tau = \frac{T}{2}$ for the reset delay where T denotes the period. Then,

$$Z(\phi) = \frac{1}{T} \frac{e^{T\phi} \sin(\omega T(1/2 - \phi))}{\cos(\omega(T/2)) + I_0 \sin(\omega(T/2)) + \omega \sin(\omega(T/2))}, \tag{28}$$

Then the dynamics of $\Delta = \phi_1 - \phi_2$ after averaging a period [1] is obtained as

$$\frac{d\Delta}{dt} = \begin{cases} -\epsilon Z(\frac{1}{2} - \Delta) & (\Delta < \frac{1}{2}), \\ \epsilon Z(\Delta - \frac{1}{2}) & (\Delta > \frac{1}{2}). \end{cases} . \tag{29}$$

Because $\omega T < 2\pi$ [25], $Z(\phi) > 0$ for $\phi < \frac{1}{2}$. Then this predicts that the in-phase locked synchronized state ($\Delta = 0$) is the globally stable fixed point whereas the anti-phase locked state $\Delta = \frac{1}{2}$ is an unstable fixed point for the positive coupling coefficient $\epsilon > 0$ (opposite for $\epsilon < 0$). The summary of the dynamics is shown in Figure 1.

IV. Conclusion

We derived the phase reduction of general delay induced oscillators in a manner where functional space was treated heuristically. The merit of the reduction is that the reduced dynamics can be described only by a single phase variable up to small perturbations. We utilized the theory and successfully analyzed the synchronization properties of coupled resonate-and-fire models with delayed resets.

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