

Stochastic Phase Reduction for Noisy Limit-cycle Oscillators

Shigefumi Hata and Hiroya Nakao

Department of Physics, Kyoto University, Kyoto 606-8502, Japan, hata@ton.scphys.kyoto-u.ac.jp

The phase reduction [1] is a standard technique for limit-cycle oscillators, which approximately describes the dynamics of an oscillator using only its phase. With this technique, various synchronization phenomena can be analyzed in mathematically tractable ways. However, when we apply the phase reduction to experimental data, a problem may arise. Rhythmic elements in nature are often very noisy and their phase response to external stimuli may not be unique but fluctuating. In such cases, the conventional deterministic phase reduction method can not describe the dynamics of the oscillator. To overcome this problem, we try to establish a quantitative stochastic phase reduction method for noisy limit-cycle oscillators. We demonstrate that our method can quantitatively predict synchronized phase distributions of impulse-driven oscillators.

Stochastic Phase Reduction

We propose a stochastic phase reduction method, in which we incorporate stochasticity of the phase response as white-Gaussian noise term to the phase model. We characterize the stochastic noise term by its mean M and variance D , and evaluate them from experimentally measured phase responses. The method has the following steps: (I) introduction of the phase, and (II) measurement of the phase response.

(I) Introduction of the phase

First, we introduce the phase to the noisy limit-cycle oscillator. In the deterministic case, we can define the phase $\theta \in [0, 1)$ on each point of the limit-cycle such that $\theta(t)$ increases with a constant frequency rate. However, in the presence of the noise, the frequency rate fluctuates and varies from trial to trial. Thus we define the oscillator phase as the trial average,

$$\theta(t) = \left\langle \frac{t - T_k}{T_{k+1} - T_k} \right\rangle, \quad (T_k \leq t < T_{k+1}), \quad (1)$$

where T_k is the k th crossing time of the oscillator over the phase origin.

(II) Measurement of the phase response

As in the deterministic case, we measure the phase response as the phase difference between a pair of unperturbed and stimulated oscillators. It is noteworthy that the phase response depends on the measurement duration as well as on the stimulated phase in the noisy situation, because the phase difference diffuses over time even without external stimuli. Thus, the mean M and the variance D depend on the stimulated phase θ and the measurement duration Δt .

We evaluate the mean phase response $M(\theta, \Delta t)$ and the variance $D(\theta, \Delta t)$ as follows: (i) We prepare two identical oscillators, apply an impulsive stimulus to one of them at phase θ , and then evolve them freely. (ii) When the stimulated oscillator has rotated the limit-cycle orbit N times and comes to the phase θ , we apply an impulse again. (iii) The step(ii) is repeated until the oscillator receives k impulses at the given phase θ . (iv) When the perturbed oscillator comes to the phase θ after having received the k th impulse and then finished rotating the limit-cycle orbit N times, we measure the phase response, namely, the phase difference between the two oscillators. We denote the measured phase response in this single trial as $A_k(\theta, N)$. (v) Repeating the above trial many times, we determine $M(\theta, \Delta t)$ and $D(\theta, \Delta t)$ with $\Delta t = NT$ as

$$M_k(\theta, NT) = \frac{1}{k} \text{mean}(A_k(\theta, N)), \quad M(\theta, NT) = \lim_{k \rightarrow \infty} M_k(\theta, NT), \quad (2)$$

$$D_k(\theta, NT) = \frac{1}{k} \text{var}(A_k(\theta, N)), \quad D(\theta, NT) = \lim_{k \rightarrow \infty} D_k(\theta, NT) - D_0(N), \quad (3)$$

where $\text{mean}(\cdot)$ and $\text{var}(\cdot)$ denote sample mean and variance, respectively, T is the mean period of the oscillator, and $D_0(N)$ is the variance of the unperturbed oscillator during N periods of oscillations.

From Eqs. (2) and (3), we can calculate M and D for $\Delta t = NT$ ($N = \{1, 2, 3, \dots\}$). For other values of t , we assume the dependence of $D(\theta, \Delta t)$ on Δt as $D(\theta, \Delta t) = \alpha(\theta)\Delta t + \beta(\theta)$ and determine $\alpha(\theta)$ and $\beta(\theta)$ by linear regression of $D(\theta, NT)$ ($N = \{1, 2, 3, \dots\}$).

Example

Now we demonstrate that the phase model derived by the the above stochastic phase reduction method is capable of reproducing synchronization behavior of the Hodgkin-Huxley (HH) oscillators [4] subjected to white-Gaussian (WG) or Ornstein-Uhlenbeck (OU) channel noise. The parameters of the HH model is fixed at the standard values as used in [3]. The dependence of the channel noise on the membrane potential is as given in [5]. We consider phase locking [2, 6] and noise-induced synchronization [3, 6] between a pair of non-interacting identical oscillators, which are caused by periodic and Poisson impulses, respectively. In each case, we calculate stationary distributions of the phase difference $\theta^A - \theta^B$ between the pair of oscillators.

We assume that successive impulses kick the oscillators at time $\{t_1, t_2, \dots\}$, and that each impulse perturbs the membrane potential with a constant amplitude a . We denote the phase of the oscillator just before the n th impulse by θ_n . For an impulsively driven oscillator, the phase dynamics is described by a random phase map [3]. Similarly, the phase dynamics in the present case is given by

$$\theta_{n+1} = \theta_n + M(\theta_n, \tau_n) + \omega\tau_n + \eta_n, \quad (4)$$

where ω is the frequency of the oscillator, $\tau_n = t_{n+1} - t_n$ is the n th inter-impulse interval whose distribution is given by $W(\tau_n)$, and η_n is the noise which obeys the zero-mean Gaussian distribution with variance $D(\theta_n, \tau_n) = a(\theta_n)\tau_n + b(\theta_n)$, namely, $R(\eta_n; \theta_n, \tau_n) = \mathcal{N}[\eta_n; 0, D(\theta_n, \tau_n)^{1/2}]$. Here, $W(\tau_n) = \delta(\tau_n - \langle\tau\rangle)$ for periodic impulses leading to phase-locking, and $W(\tau_n) = \exp[-\tau_n/\langle\tau\rangle]/\langle\tau\rangle$ for Poisson random impulses that induce noise-induced synchronization.

Figure 1 illustrates the stationary distributions of the phase differences obtained by direct numerical simulations of the noisy HH oscillators and the reduced phase equations obtained by the stochastic phase reduction method described above. We can see that our method can quantitatively predict the synchronization behavior of the original noisy HH oscillators for various parameter sets.

Summary

We proposed a stochastic phase reduction method for noisy limit-cycle oscillators. By replacing the fluctuations of the phase response with a noise term, we constructed a stochastic phase model. We applied our method to the phase locking and the noise-induced synchronization of the Hodgkin-Huxley oscillators with channel noise, and confirmed that our method can predict the stationary distributions of the phase differences of the original oscillator model quantitatively. With our method, we will be able to analyze various rhythmic systems in nature as noisy oscillators within the stochastic phase description.

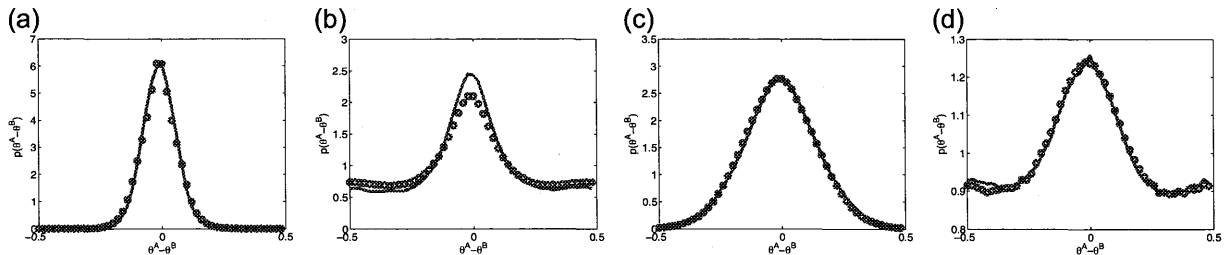


Figure 1: Stationary distributions of the phase differences. In each figure, the solid curve plots the result of the original noisy HH oscillators, and the circles show the result of reduced phase model. The mean inter-impulse interval is fixed at $\langle\tau\rangle = 1$. Amplitude of the impulses are fixed at $a = 1.0$. In the case of the OU channel noise, we fix the correlation time of the noise at half the period of the HH oscillator, $T/2 = 5.75$. (a) WG channel noise, phase-locking. (b) WG channel noise, noise-induced synchronization. (c) OU channel noise, phase-locking. (d) OU channel noise, noise-induced synchronization.

References

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