Period variability of coupled noisy oscillators

Fumito Mori1,* and Hiroshi Kori1,2

1Department of Information Sciences, Ochanomizu University, Tokyo, Japan
2PRESTO, Japan Science and Technology Agency, Kawaguchi, Japan

(Received 24 March 2012; revised manuscript received 25 September 2012; published 15 March 2013)

Period variability, quantified by the standard deviation (SD) of the cycle-to-cycle period, is investigated for noisy phase oscillators. We define the checkpoint phase as the beginning or end point of one oscillation cycle and derive an expression for the SD as a function of this phase. We find that the SD is dependent on the checkpoint phase only when oscillators are coupled. The applicability of our theory is verified using a realistic model. Our work clarifies the relationship between period variability and synchronization from which valuable information regarding coupling can be inferred.

DOI: 10.1103/PhysRevE.87.030901

PACS number(s): 05.45.Xt, 05.40.Ca, 87.18.Yt

Oscillators functioning as clocks, such as crystal oscillators [1], spin torque oscillators [2–5], and circadian and heart pacemakers [6–8], play an important role in various systems. Although these clocks are subjected to various types of noise, including thermal, quantum, and molecular noise, they are required to perform temporally precise oscillations; i.e., oscillations with only a small variability in the period (known as “period jitter” in electronic engineering [9]).

In many cases, it is sufficient for the clock to strike precisely at a specific time in each oscillation cycle, and thus a perfectly regular oscillation wave form is not needed. For cardiac pacemakers only the moment of stimulation is relevant. Experimental data regarding circadian activity in mice [10] indicate that the variability in the period between each activity onset is smaller than that between each offset. Similar results have also been obtained in explant circadian pacemaker tissue (the suprachiasmatic nucleus (SCN)) [10]. These observations suggest that the onset is more important than the offset in a circadian clock, which may be designed in such a way that the crucial moment is expressed with high precision.

Remember that the definition of an oscillation period requires a fixed beginning or end point for each oscillation cycle, hereafter referred to as the checkpoint (Fig. 1). Although the average period does not depend on the particular choice of checkpoint, the period variability may be sensitive to the checkpoint. In order to clarify whether the checkpoint dependence in circadian activity is an artifact due to a technical problem in determining the onset and offset times or an essential property of the circadian clock, we need to investigate under what conditions the period variability is dependent on the checkpoint; this has received scant attention to date.

Another important aspect of the period variability is its relationship to synchronization. A clock is commonly synchronized to its master clock such as in the case of the SCN in response to the daily variation of sunlight, and in peripheral clocks in response to the SCN. In addition, most biological clocks, including the SCN, cardiac pacemakers, and pacemakers in weakly electrical fish, are composed of a population of synchronized oscillators [6,7,11]. It is known, both experimentally and theoretically, that period variability

\[ \frac{d\theta}{dt} = \omega + Z(\theta)\sqrt{D}\xi(t), \]

where \( \theta \) and \( \omega \) are the phase and natural frequency, respectively. The \( 2\pi \)-periodic function \( Z(\theta) \) is a phase sensitivity function, which quantifies the phase response of the oscillator to noise, and \( \xi(t) \) denotes independent and identically distributed (i.i.d.) noise; each random variable \( \xi(t) \) for all \( t \) obeys the same probability distribution and all are mutually independent. The positive constant \( D \) denotes the noise strength. Note that our proof below holds even if we permit \( \omega \) and the probability distribution of \( \xi \) to be \( 2\pi \)-periodic functions of \( \theta \): \( \omega(\theta) \) and \( \xi(t, \theta) \).

The \( k \)th oscillation time of an oscillator \( t_{\theta=k}^{\text{cp}} \) is defined as the time at which \( \theta \) passes through \( 2\pi k + \theta_{\text{cp}} \) (0 \( \leq \theta_{\text{cp}} < 2\pi \))
for the first time [Fig. 1(b)]. We define $\theta_{cp}$ as the checkpoint phase. The $k$th oscillation period $\Delta t^k_{cp}$ is defined as $\Delta t^k_{cp} = t^k_{cp} - t^{k-1}_{cp}$, and the SD is defined as

$$\sigma(\theta_{cp}) = \sqrt{E[(\Delta t^k_{cp} - \tau)^2]}, \quad (2)$$

where $E[\cdots]$ represents the statistical average over $k$, and $\tau$ is the average period given by $\tau = E[\Delta t^k_{cp}]$. Note that $E[\cdots]$ denotes both the statistical average taken over $k$ and the ensemble average in the present paper, which are identical in the steady state. The system given by Eq. (1) is always in the steady state.

To prove that the SD is independent of $\theta_{cp}$, we introduce two checkpoint phases denoted by $\alpha$ and $\beta$ [Fig. 1(b)]. Since the processes $\alpha \to \beta$ and $\beta \to \alpha$ for any $k$ are independent, we arrive at $\sigma(\alpha) = \sigma(\beta)$ for any arbitrary checkpoint phases $\alpha$ and $\beta$. A detailed proof is given in the Supplemental Material [19].

Next, we consider a pair of coupled phase oscillators subjected to noise. When limit cycle oscillators are weakly coupled to each other and subjected to weak noise, the dynamics can be described by [17,18]

$$\dot{x} = \omega + \kappa J(x_1, x_2) + Z\xi_1(t), \quad \dot{y} = \omega + \kappa J(y_1, y_2) + Z\xi_2(t), \quad (3)$$

where $\dot{x}$ and $\dot{y}$ are the phase of the oscillator $i$ and the coupling strength, respectively. The i.i.d. noise $\xi_i(t)$ satisfies $E[\xi_i(t)\xi_j(t')] = \delta_{ij}\delta(t-t')$. The $2\pi$-periodic function $J(x, y)$ describes the interaction between oscillators, which leads to synchronization. We assume that, in the absence of noise ($D = 0$), the oscillators are synchronized in phase, i.e., $\theta_{1,2}(t) \to \phi(t)$ ($t \to \infty$), where $\phi(t)$ is a solution of

$$\dot{\phi}(t) = \omega + \kappa J(\phi, \phi). \quad (4)$$

The necessary condition for the stability of in-phase synchronization for $D = 0$ is provided below [see Eq. (11)]. We also assume that $\omega + \kappa J(\phi, \phi) > 0$ for any $\phi$ for the coupled system to be oscillatory.

Our particular interest is in the relationship between the SD [Eq. (2)] and the synchronization of two oscillators. We thus introduce the following order parameter that measures the phase distance from the in-phase state:

$$d(\theta_{cp}) = \sqrt{E[\|\theta_1 - \theta_2\|^2]_{\theta_1 = \theta_{cp}}}, \quad (5)$$

where $E[x(t)]_{\theta_1 = \theta_{cp}}$ represents the average of $x_i$ over $k$ [where $x_i$ is the value of $x(t)$ taken when $\theta_1$ passes through $2\pi k + \theta_{cp}$ for the first time], and $\|\theta_1 - \theta_2\|$ is the phase difference defined on the ring $[-\pi, \pi]$. The phase distance $d(\theta_{cp})$ is zero when the oscillators are completely synchronized in phase, and increases with the phase difference.

As we demonstrate below, the relationship between $\sigma(\theta_{cp})$ and $d(\theta_{cp})$ is qualitatively different for the two cases where $J(\phi, \phi)$ is (A) independent of $\phi$ and (B) dependent on $\phi$. Cases (A) and (B) imply that $\phi$ given in Eq. (4) is independent of $\phi$ and dependent on $\phi$, respectively. Phase reduction theory indicates that it is appropriate to assume the form $J(x, y) = z(x)G(x, y)$, where $z(x)$ is the phase sensitivity function for the interaction $G(x, y)$ [17,18]. It is known that diffusive coupling between chemical oscillators and gap-junction coupling between cells yields $J(x, y) = z(x)h(x - h(y))$, where $h$ represents a chemical concentration [20,21] or membrane potential, which corresponds to case (A). Case (A) also allows the form $J(x, y) = z(x)h(y)$, which has been employed in many models such as the Kuramoto model [18]; however, we do not employ this form in the demonstration, since the term $j(x - y)$ is derived as a result of averaging the interaction $z(x)G(x, y)$ over one oscillation period [18], and, by this approximation, the information about the $\theta_{cp}$ dependence is lost. Many other types of coupling, such as $J(x, y) = z(x)h(y)$ employed below, correspond to case (B) [22].

As an example of case (A), we consider $z(\theta) = \sin \theta$ for $0 \leq \theta < \pi$, $z(\theta) = 0$ for $\pi \leq \theta < 2\pi$, and $h(\theta) = \cos \theta$, and the following as an example of case (B): $z(\theta) = -\sin \theta$ and $h(\theta) = 1 + \cos \theta$ [22]. We set $\theta(\theta) = 1$, $\omega = 2\pi$, $\sqrt{D} = 0.03 \times 2\pi$, and $\theta_1(0) = \theta_2(0) = 0$, and assume $\xi_1,\xi_2$ to be white Gaussian noise. We integrate Eq. (3) using the Euler scheme with a time step of $5 \times 10^{-4}$ for $t = 0$–1000 and discard the $t = 0$–100 data as transient.

Using these examples, numerically obtained $\sigma$ values for $\theta_1$ are plotted as a function of $\theta_{cp}$ in Figs. 2(a) and 2(b). The results indicate clearly the existence of $\theta_{cp}$ dependence in both cases, which was absent in the single phase oscillator system. This dependence becomes stronger for larger $\kappa$ values. In contrast, for $\kappa \ll \omega$, the dependence vanishes because $J(x, y)$ is well approximated by $j(x - y)$ [18], and thus, the system effectively has rotational symmetry. The $\theta_{cp}$ value at which $\sigma(\theta_{cp})$ assumes its minimum represents the most precise timing.

The $\theta_{cp}$ dependence of $d(\theta_{cp})$ for the two cases is shown in Figs. 2(c) and 2(d). A comparison with $\sigma(\theta_{cp})$ shows that the checkpoint phase maxima and minima of each $\kappa$ value coincide in the case of (A). Thus, the most precise timing is obtained when the oscillators are synchronized. By contrast, the $\theta_{cp}$ dependence is considerably different in the case of (B). Therefore, we expect that nontrivial factors, apart from synchronization, influence the SD. We also examined several other functions, $z(\theta)$, $h(\theta)$, and $G(x, y)$, and found a similar relationship between $\sigma(\theta_{cp})$ and $d(\theta_{cp})$ (data not shown).

We now derive an expression for the SD. The derivation consists of two steps: (i) calculation of the phase diffusion $\eta(\theta_{cp})$ [defined by Eq. (7)] with a linear approximation, and (ii) transformation from $\eta(\theta_{cp})$ to $\sigma(\theta_{cp})$. Here, we employ the solution $\phi(t)$ of Eq. (4) with $\phi(0) = 0$ and the time $t_{cp}$
The correlation $E[X(t)^2]$, $E[Y(t)^2]$, and $E[X(t)Y(t)]$ are given in the Supplemental Material [19]. Since Eq. (6) can be rewritten as $P(|\Delta_1 - \Delta_2|; t) \equiv P(|\Delta_1 - \Delta_2|; t + \tau)$, then $E[X(t)^2] = E[Y(t + \tau)^2]$ holds approximately, leading to

$$E[Y(0)^2] = 2D \frac{\exp[2|x|]}{1 - \exp[2|x|]} \int_0^\tau Z(\phi(t'))^2 \times \exp[-2\kappa F_y(\phi(t'))] d\tau'. \quad (12)$$

In addition, because $d(\theta_{cp})^2 = E[(\Delta_1(\theta_{cp}) - \Delta_2(\theta_{cp}))^2] = E[Y(\theta_{cp})^2]$, we obtain

$$d(\theta_{cp})^2 = 2E[f_y(\phi(t))] \left[ E[Y(0)^2] + 2D \int_0^{\theta_{cp}} Z(\phi)^2 \times \exp[-2\kappa F_y(\phi)] \frac{ds}{d\phi(s)} d\phi \right]. \quad (13)$$

which is generally $\theta_{cp}$ dependent even if $Z(\phi)$ is constant.

Using these correlations and Eq. (10), we obtain the following expression for the phase diffusion [19]:

$$\eta(\theta_{cp})^2 = E[(\Delta_1(\theta_{cp} + \tau) - \Delta_1(\theta_{cp}))^2]$$

$$= C_1 \dot{\phi}(\theta_{cp})^2 + C_2 d(\theta_{cp})^2, \quad (14)$$

where the $C_{1,2}$ are independent of $\theta_{cp}$ and are given by $C_1 = \frac{D}{2} f_0 Z(\theta_{cp})^2 d\theta$ and $C_2 = (1 - \exp(\kappa\epsilon)) / 2$. The $C_1$ term is an effective diffusion constant for the center of the two oscillators, which is half that of an uncoupled oscillator, and the $C_2$ term is associated with the stability of the synchronization.

To transform $\eta(\theta_{cp})$ to $\sigma(\theta_{cp})$, we note that when the noise intensity is low, most of the trajectories of $\theta_1(t)$ are very close to the unperturbed trajectory $\phi(t)$ (see the Supplemental Material [19]). In such a case, the following relation approximately holds true:

$$\frac{\eta(\theta_{cp})}{\sigma(\theta_{cp})} = \dot{\phi}(\theta_{cp}). \quad (15)$$

The same approximation (but for constant $\phi$) was employed in Ref. [16] and verified numerically.

From Eqs. (14) and (15), we finally arrive at

$$\sigma(\theta_{cp}) = \sqrt{C_1 + C_2 / \dot{\phi}(\theta_{cp})^2}. \quad (16)$$
The analytical results given by Eqs. (16) and (13) are in excellent agreement with the numerical results (Fig. 2). Although we have only discussed paired identical phase oscillators, our theory can easily be extended to other cases, e.g., $N$ globally coupled (all-to-all) identical oscillators or a periodically driven noisy oscillator.

Equation (16) shows that the periodicity of the SD $\sigma(\theta_{cp})$ is based on the synchronization $d(\theta_{cp})$ and phase velocity $\phi(\theta_{cp})$. For case (A), since $\phi(\theta_{cp})$ is constant, there is one-to-one correspondence between $\sigma(\theta_{cp})$ and $d(\theta_{cp})$; i.e., the most precise timing, referred to as $\theta_{cp,\text{min}}$, is the timing at which the best synchronization is achieved. This was observed in Figs. 2(a) and 2(c), where $\theta_{cp,\text{min}} = \pi/2 + O(\kappa^{-1})$ can be obtained from $dd(\theta_{cp})/d\theta_{cp} = 0$. For case (B), however, the SD also depends on $\phi(\theta_{cp})$; this is in contrast to that observed for the single phase oscillator system in which the phase velocity of $\dot{\theta}$ does not contribute to the checkpoint dependence of the SD. Figures 2(b) and 2(d) showed that $\sigma(\theta_{cp})$ and $d(\theta_{cp})$ are considerably different, which indicates the strong effect of $\phi$ in this particular example. Indeed, $\sigma(\theta_{cp})$ assumes its minimum around a maximum $\phi(\theta_{cp})$ ($\theta_{cp,\text{min}} \approx 5\pi/3$).

To investigate whether Eq. (16) holds for a more realistic model, we employ the FitzHugh-Nagumo model given by

$$V_1 = V_1(V_1 - a)(1 - V_1) - W_1 + \xi_i(t) + K_V(V_2 - V_1),$$

$$W_1 = \epsilon(V_1 - bW_1) + K_W(W_2 - W_1),$$

(17)

in which the second oscillator is described in a similar way. We fixed $a = -0.1$, $b = 0.5$, and $\epsilon = 0.01$. This system shows limit-cycle oscillations with a period of $\tau \approx 126$ when noise and coupling are absent. The white Gaussian noise $\xi_i(t)$ has an intensity of 0.01. The interaction is diffusive, i.e., case (A), and we consider the following two types: $V$ coupling ($K_V = 0.01$, $K_W = 0$) and $W$ coupling ($K_V = 0$, $K_W = 0.01$). The phase $\theta$ was defined properly (see the Supplemental Material [19]), and $\sigma(\theta_{cp})$ and $d(\theta_{cp})$ were obtained numerically. Figure 3 shows that the $\theta_{cp}$ dependence of the SD is different in the two cases, suggesting a significant effect from the coupling. We estimated the $C_1$ and $C_2$ values using Eq. (16) and the least-squares method under the condition that both cases have the same $C_1$ value, resulting in $C_1 = 5.4$, $C_2^{(V)} = 0.20$, and $C_2^{(W)} = 0.48$. In Fig. 3, we can see that the SD is described well by Eq. (16) using the fitted $C_1$ and $C_2$ values. This demonstrates that the theory is valid for this biological model.

In many cases, only the SD measured at a functionally relevant checkpoint characterizes the performance of a clock. When designing a precise clock, we only have to reduce $\sigma(\theta_{cp})$ for any functionally relevant $\theta_{cp}$ to zero. Equation (16) implies that $\sigma(\theta_{cp})$ at a given $\theta_{cp}$ decreases with decreasing $d(\theta_{cp})$ and increasing $\phi(\theta_{cp})$. Therefore, attractive coupling between oscillators should be activated around the functionally relevant timing point. In addition, in case (B), the phase velocity should be increased through coupling.

Our theory enables us to infer the coupling timing or form by measuring $\sigma(\theta_{cp})$ at several checkpoints. Although this is, in principle, possible with $d(\theta_{cp})$, using $\sigma(\theta_{cp})$ has the added advantages that $\sigma(\theta_{cp})$ can be measured from a single time series and that $d(\theta_{cp})$ is sensitive to the definition of phase. From the observations of circadian periods in mice [10] referred to in the introduction of the present paper, it is possible that the SCN sends signals to the peripheral clocks around the onset of a subjective day. An experimental observation of the checkpoint dependence in other biological clocks would be a new source of coupling information.

We thank Hiroshi Ito for valuable discussions. This work was supported by JSPS KAKENHI Grant No. 23-11148.