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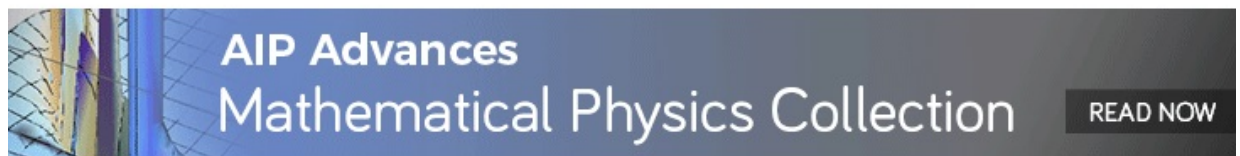
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Vladimir Klinshov,^{1,a)} Leonhard Lücken,^{2,b)} and Petro Feketa^{3,c)}

AFFILIATIONS

¹Institute of Applied Physics of the Russian Academy of Sciences, 46 Ul'yanov Street, 603950 Nizhny Novgorod, Russia

²Institute for Chemistry and Biology of the Marine Environment, University of Oldenburg, 26111 Oldenburg, Germany

³Chair of Automatic Control, Kiel University, Kaiserstraße 2, 24143 Kiel, Germany

^{a)}Author to whom correspondence should be addressed: vladimir.klinshov@ipfran.ru

^{b)}Electronic mail: leonhard.luecken@uni-oldenburg.de

^{c)}Electronic mail: pf@tf.uni-kiel.de

ABSTRACT

In this note, we discuss the usage of the Dirac δ function in models of phase oscillators with pulsatile inputs. Many authors use a product of the delta function and the phase response curve in the right-hand side of an ordinary differential equation to describe the discontinuous phase dynamics in such systems. We point out that this notation has to be treated with care as it is ambiguous. We argue that the presumably most canonical interpretation does not lead to the intended behavior in many cases.

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In many real-life systems, interactions are mediated by short pulses resulting in abrupt changes of the system state. A popular tool for modeling such pulses is Dirac δ functions that represent pulses of zero length but finite energy. When such a function appears in the right-hand side of a differential equation, the solution becomes discontinuous. This note discusses a proper way to calculate the size of this discontinuity, i.e., the magnitude of the system state jump.

Pulse-coupled phase oscillators are a popular framework used for modeling of various systems, among which biological oscillators, such as pacemaker cells, the circadian rhythm, or pulsating fireflies, are prototypical examples. In this framework, each oscillator is described by its phase $\varphi(t)$, a variable that can be introduced for an arbitrary dynamical system with a stable limit cycle.^{1–3} The phase is defined in the attraction basin of the limit cycle as a circular variable $\varphi \in S^1 \simeq \mathbb{R} \bmod 1$. In the autonomous system, the phase grows uniformly so that $d\varphi/dt = \omega = 1/T$, where T is the period of the limit cycle. The effect of an incoming pulse is modeled as the instantaneous phase change leading to a discontinuous evolution of $\varphi(t)$. The amount of the phase shift is determined as a function of the phase *before* the pulse arrival: for the pulse arriving at the moment t_p ,

$$\varphi_p^+ = \varphi_p^- + Z(\varphi_p^-), \quad (1)$$

where $\varphi_p^\pm := \varphi(t_p \pm 0) = \lim_{\varepsilon \searrow 0} \varphi(t_p \pm \varepsilon)$. The function Z is called the phase response curve (PRC).^{4–6} It is a scalar, continuous function that can be calculated numerically or even measured experimentally for any real-life oscillator and any pulse with a finite duration τ . To do so, one should place the system's state on the limit cycle with a certain phase φ , apply a pulse, and measure the phase φ^* just after the pulse end. Then, the PRC

$$Z(\varphi) := \varphi^* - \varphi - \omega\tau$$

and the repetition of the procedure for all points of the limit cycle would result in obtaining the complete function profile. For short pulses, a good approximation is to ignore the dynamics during the pulse and to assume that the phase changes instantly according to (1). Then, the once obtained PRC allows predicting the phase dynamics of the oscillator subject to stimulation in the form of pulse trains if only the pulses are not too strong or frequent.

There exist generalizing approaches, which include amplitude perturbations or higher order terms to extend the region of validity of the phase reduction.^{7–9} In any case, the interplay between the timescales for the amplitude relaxation, the oscillation frequencies, and the pulse duration can limit the suitability of a reduced representation of a specific system.^{10,11} Furthermore, we do not consider these issues and treat the phase reduction as exactly reproducing the dynamics of the original system.

Many authors (including the ones of this note) have defined models for oscillators interacting via phase response curves with the help of Dirac δ functions in the right-hand side of the equations for the phase dynamics.^{12–19} In this formulation, delta functions are multiplied by the phase response curve leading to the equations of the form

$$\frac{d\varphi}{dt} = \omega + Z(\varphi) \sum_p \delta(t - t_p). \tag{2}$$

Here, ω is the native frequency of the oscillator, and t_p are the moments when it receives pulses. The interpretation of (2) is the following: the phase grows uniformly with $d\varphi/dt = \omega$ except for the moments t_p of the pulses' arrival, and at these moments, the phase instantly changes according to (1). However, as we explain below, the presumably most canonical interpretation of the delta function suggests a different behavior for (2). Therefore, we consider it worthwhile to raise this subject to attention.

First, let us recall the basic properties of the Dirac δ -function. From the physical perspective, it represents a signal having a negligibly short duration but a finite integral. In this sense, it can be defined as the limit of a sequence of suitable (e.g., continuous) functions δ_n that have unit integral $\int_{\mathbb{R}} \delta_n(t) dt = 1$ and fulfill for any $\varepsilon > 0$ that

$$\lim_{n \rightarrow \infty} \int_{-\varepsilon}^{\varepsilon} \delta_n(t) dt = 1.$$

Such a sequence $\{\delta_n\}_{n \in \mathbb{N}}$ is called a Dirac sequence. Despite all δ_n being functions, their limit

$$\delta(t) := \lim_{n \rightarrow \infty} \delta_n(t) \tag{3}$$

is not a regular \mathbb{R} -valued function. For instance, choosing any sequence of even, unimodal δ_n , would imply

$$\delta(t) = \begin{cases} \infty & \text{for } t = 0, \\ 0, & \text{otherwise.} \end{cases}$$

To give it a mathematical definition, δ is usually introduced as a distribution.²⁰ As such, the distribution D_δ associated with δ is defined by its action as a linear functional on a set of test functions \mathcal{C} (e.g., smooth, real-valued functions with compact support in \mathbb{R}), which is the mapping $D_\delta(f) := f(0) \in \mathbb{R}$ for $f \in \mathcal{C}$. Distributions are also called “generalized functions” because for each regular (e.g., integrable) function $\psi : \mathbb{R} \rightarrow \mathbb{R}$, there exists a canonical association of a distribution $D_\psi : \mathcal{C} \rightarrow \mathbb{R}$, defined as

$$D_\psi(f) := \int_{-\infty}^{\infty} \psi(t) f(t) dt. \tag{4}$$

In order to ensure that (4) defines a continuous functional on \mathcal{C} , different choices for the spaces of test functions and regular functions are possible. In any case, a sequence of distributions D_n is said to converge toward a limit D_0 if for all $f \in \mathcal{C}$: $\lim_{n \rightarrow \infty} D_n(f) = D_0(f)$, and this gives a rigorous meaning to convergence $\delta_n \rightarrow \delta$

by requiring

$$\begin{aligned} \lim_{n \rightarrow \infty} D_{\delta_n}(f) &= \lim_{n \rightarrow \infty} \int_{-\infty}^{\infty} \delta_n(t) f(t) dt \\ &= D_\delta(f) = f(0) \text{ for all } f \in \mathcal{C}. \end{aligned}$$

The main difficulty for the interpretation of (2) is that the solution $\varphi(t)$, and, therefore, the time course of the PRC $Z(\varphi(t))$ as well, is discontinuous at the point t_p , where $\delta(t - t_p)$ is affecting it. In that case, the notion of δ as a limit of a general Dirac sequence $\{\delta_n\}$ mediated by a space of discontinuous test functions is ambiguous. To see that, consider a piecewise continuous function f with discontinuity at $t = 0$. Depending on the choice of the sequence, it is possible to obtain

$$\lim_{n \rightarrow \infty} \int_{-\infty}^{\infty} \delta_n(t) f(t) dt = cf(t - 0) + (1 - c)f(t + 0) \tag{5}$$

for any value of $c \in [0, 1]$. In general, the limit does not exist at all. Apparently, the ambiguity might be resolved by restricting the notion of a Dirac sequence to a specific proportion. In the case of (2), this resolution would amount to defining φ_p^+ as a solution of

$$\varphi_p^+ + (c - 1)Z(\varphi_p^+) = \varphi_p^- + cZ(\varphi_p^-). \tag{6}$$

For example, using δ_n with $\delta_n(t) = 0$ for $t \geq 0$ would lead to $c = 1$, presumably indicating the behavior (1). Alternatively, opting to restrict δ_n to even functions would give $c = 1/2$, as noted by Griffith and Walborn.²¹ Obviously, the particular choice of c influences the resulting magnitude of the discontinuous phase jump. In the following, we suggest to employ another possible interpretation of Eq. (2), which is based on an unambiguous interpretation of the δ function and leads to a discontinuity different from (6) for any value of c .

While studying the discontinuity in the next paragraphs, let us assume that Z is a continuous function and $Z(\varphi_p^-) \neq 0$ [note that the case $Z(\varphi_p^-) = 0$ is less interesting as $\varphi(t)$ would simply be continuous at $t = t_p$]. Then, $Z(\varphi)$ does not change its sign inside some interval $I = (\alpha, \beta)$, with $\varphi_p^- \in I$. For φ from this interval, we consider a transformation

$$\psi := F(\varphi) = \int_{\xi}^{\varphi} \frac{dx}{Z(x)}, \tag{7}$$

where F is an invertible, differentiable function on I and $\xi \in I$ is arbitrarily chosen. Note that one can extend the interval of definition I as long as $Z(\varphi) \neq 0$ inside I ; cf. Figure 1. If there exists a point φ with $Z(\varphi) = 0$, the boundaries of the maximal interval must fulfill $Z(\alpha) = Z(\beta) = 0$ and

$$\lim_{\varphi \rightarrow \alpha, \beta} F(\varphi) \in \{\pm\infty\}. \tag{8}$$

If we assume that the discontinuity does not convey φ out of I , i.e., $\varphi_p^+ \in I$, we can use (2) and apply the chain rule for the differentiation

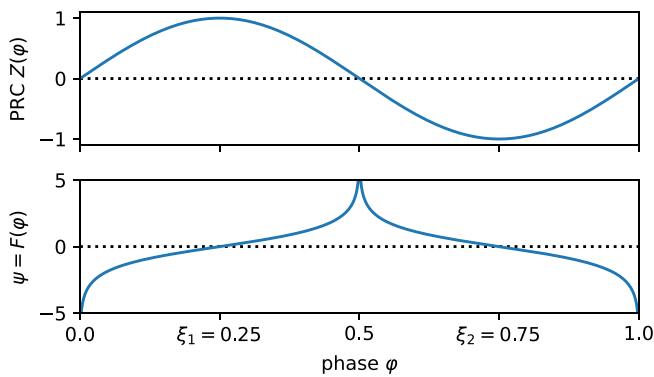


FIG. 1. Exemplary partition $\bigcup_j I_j = [0, 1] \setminus \{\varphi : Z(\varphi) = 0\}$ and graphs of Z and F_j for $Z(\varphi) = \sin(2\pi\varphi)$ and reference points $\xi_1 = 0.25 \in I_1 = (0, 0.5)$ and $\xi_2 = 0.75 \in I_2 = (0.5, 1)$.

of $\psi(t) = F(\varphi(t))$ to obtain

$$\frac{d\psi}{dt} = \frac{1}{Z(F^{-1}(\psi))} + \sum_p \delta(t - t_p), \tag{9}$$

where F^{-1} is the inverse of F defined on its range $F(I)$. Integration of (9) over a sufficiently short time interval $[t_p - \tau; t_p + \tau]$ gives

$$\begin{aligned} &\psi(t_p + \tau) - \psi(t_p - \tau) \\ &= \int_{t_p - \tau}^{t_p + \tau} \left(\frac{1}{Z(F^{-1}(\psi(t)))} + \delta(t - t_p) \right) dt, \end{aligned} \tag{10}$$

where the interpretation of δ is unambiguous since it is not multiplied by a discontinuous function. For the other integrand, we have

$$\begin{aligned} &\int_{t_p - \tau}^{t_p + \tau} \frac{dt}{Z(F^{-1}(\psi(t)))} \\ &= \int_{t_p - \tau}^{t_p} \frac{dt}{Z(F^{-1}(\psi(t)))} + \int_{t_p}^{t_p + \tau} \frac{dt}{Z(F^{-1}(\psi(t)))} \\ &= \frac{\tau}{Z(\varphi_p^-) + \mathcal{O}(\tau)} + \frac{\tau}{Z(\varphi_p^+) + \mathcal{O}(\tau)} \rightarrow 0 \text{ for } \tau \searrow 0. \end{aligned}$$

Thus, in the limit of $\tau \searrow 0$, (10) yields

$$1 = \psi(t_p + 0) - \psi(t_p - 0) = F(\varphi_p^+) - F(\varphi_p^-). \tag{11}$$

Finally, the phase φ_p^+ after the pulse arrival can be evaluated as

$$\varphi_p^+ = F^{-1}\left(F(\varphi_p^-) + 1\right), \tag{12}$$

where the resulting value of φ_p^+ is independent of the specific choice for ξ in (7).

In general, the phase value given by (12) differs from that given by (1) or any other fixed choice of $c \in [0, 1]$ in (6). Interestingly, there exists a different interpretation of Eq. (2), which leads to the

same notion for a solution.^{22,23} Let us calculate a sequence of solutions φ_n of (2), where δ has been substituted by elements of a Dirac series $\{\delta_n\}$,

$$\frac{d\varphi_n}{dt} = \omega + Z(\varphi_n) \sum_p \delta_n(t - t_p). \tag{13}$$

Then, the solution $\varphi(t)$ of (2) can be defined as a limit of the solutions of (13) for $n \rightarrow \infty$. This definition is physically motivated since the delta function is an approximation for pulses with a short but finite duration. Therefore, it is natural to expect that the behavior of Eq. (2) with the delta pulses will be similar to the behavior of Eq. (13) with short enough but finite pulses. The solution $\varphi_*(t) := \lim_{n \rightarrow \infty} \varphi_n(t)$ coincides with the solution $\varphi(t)$ obtained by (12). Indeed, defining $\psi_n := F(\varphi_n)$ gives

$$\begin{aligned} &\psi(t_p + 0) \\ &= \lim_{\tau \searrow 0} \lim_{n \rightarrow \infty} \psi_n(t_p + \tau) \\ &= \lim_{\tau \searrow 0} \lim_{n \rightarrow \infty} \left(\psi_n(t_p - \tau) \right. \\ &\quad \left. + \int_{t_p - \tau}^{t_p + \tau} \left(\frac{1}{Z(F^{-1}(\psi_n(t)))} + \delta_n(t - t_p) \right) dt \right) \\ &= \lim_{\tau \searrow 0} \left(\psi(t_p - \tau) + \lim_{n \rightarrow \infty} \underbrace{\int_{t_p - \tau}^{t_p + \tau} \frac{dt}{Z(F^{-1}(\psi_n(t)))}}_{\rightarrow 0, \text{ as } \tau \rightarrow 0} \right. \\ &\quad \left. + \lim_{n \rightarrow \infty} \int_{t_p - \tau}^{t_p + \tau} \delta_n(t - t_p) dt \right) \\ &= \psi(t_p - 0) + 1, \end{aligned} \tag{14}$$

which leads to the phase jump (12). Note that the derivation of the solution φ_* does not rely on the assumption that $\varphi_p^+ \in I$ but implies this property.

As noted above, the maximal range of definition for (7) is always a maximal interval I such that $Z(\varphi) \neq 0$ for all $\varphi \in I$. If Z has no zeros at all, F is a bijection over \mathbb{R} , resp. $[0, 1]$ and its image is $F([0, 1])$. Otherwise, the bounds of the interval $I = (\alpha, \beta)$ fulfill $Z(\alpha) = Z(\beta) = 0$. Effectively, this partitions the whole range of possible phases $\varphi \in [0, 1]$ into disjoint intervals I_j and points where $Z = 0$; see Fig. 1. That is,

$$\bigcup_j I_j = [0, 1] \setminus \{\varphi : Z(\varphi) = 0\}.$$

If we denote for each I_j the corresponding transformation (7) by $\psi = F_j(\varphi)$, we may define

$$\tilde{Z}(\varphi) := \begin{cases} 0 & \text{for } Z(\varphi) = 0, \\ F_j^{-1}(F_j(\varphi) + 1) - \varphi & \text{for } \varphi \in I_j. \end{cases} \tag{15}$$

Then, (15) describes the discontinuous phase reset obtained in the limit of a Dirac sequence approximation of (2).

The functions Z and \tilde{Z} are in general different and can be equal or close only in some particular cases, for example:

(i) If the PRC is flat, i.e., it does not depend on the phase: $Z(\varphi) = Z_0 = \text{const}$, then $F(\varphi) = \varphi/Z_0$ and $\tilde{Z}(\varphi) = Z_0$ as well. In this case, the interpretation issue is absent because the delta function is not multiplied by a discontinuous function. For the same reason, the interpretation is unambiguous for the models that are based not on phase oscillators but on integrate-and-fire neurons^{24,25} or quadratic integrate-and-fire neurons^{26,27} (note that for theta-neurons,^{28–30} the ambiguity exists, although they can be transformed to quadratic integrate-and-fire neurons).

(ii) If the PRC is small, i.e., $Z(\varphi) \ll 1$, then $F(\varphi) \gg 1$, and F^{-1} can be expanded into the Taylor series

$$F^{-1}(F(\varphi) + 1) = F^{-1}(F(\varphi)) + (F^{-1})'(F(\varphi)) + \dots \approx \varphi + \frac{1}{F'(\varphi)} = \varphi + Z(\varphi) \tag{16}$$

from where $\tilde{Z}(\varphi) \approx Z(\varphi)$. Thus, the ambiguity problem vanishes for phase oscillators with weak coupling.¹⁹

Except for these two cases, the functions Z and \tilde{Z} are different. To illustrate this difference, we plot these two functions for the PRC

$$Z(\varphi) = \kappa \sin^q(\pi \varphi), \tag{17}$$

where $\kappa = 0.1$ is the coupling strength and q is a parameter controlling the PRC steepness.¹⁶ Note that the maximal value of the phase is set equal to 1, not 2π . The functions $Z(\varphi)$ and $\tilde{Z}(\varphi)$ are plotted in Fig. 2 (top row). One sees that these functions are indeed different, and the difference is more pronounced for larger steepness q . Note also that although Eq. (1) might give non-monotone dependence of φ_p^+ vs φ_p^- for large q , the dependence given by (12)

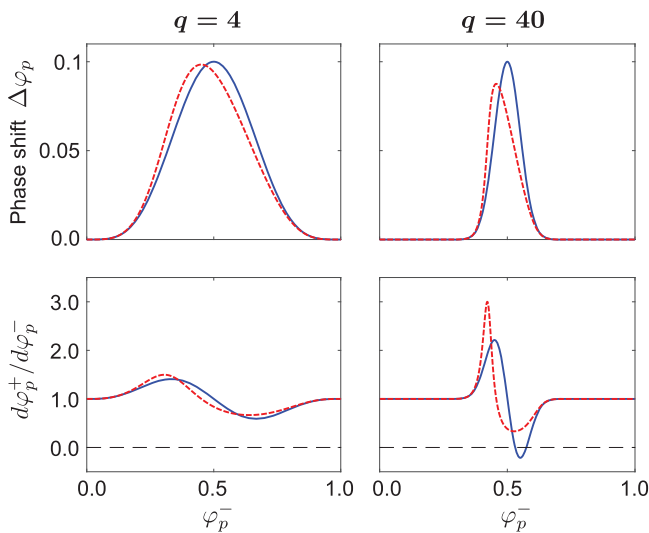


FIG. 2. Top row: the phase shift $\Delta\varphi_p = \varphi_p^+ - \varphi_p^-$ after the pulse arrival vs the phase φ_p^- before the pulse arrival given by the original PRC $Z(\varphi)$ as in (17) (blue solid line) and by the modified PRC $\tilde{Z}(\varphi)$ calculated on its base according to (15) (red dashed line). Bottom row: the slope $d\varphi_p^+/d\varphi_p^-$. The steepness parameter equals $q = 4$ for the left column and $q = 40$ for the right column.

is always strictly monotone. In order to demonstrate that, the slope $d\varphi_p^+/d\varphi_p^- = 1 + Z'(\varphi_p^-)$ is plotted in Fig. 2 (bottom row), which can be negative for $Z(\varphi)$ but is strictly positive for $\tilde{Z}(\varphi)$.

The difference between the two PRCs becomes even more critical when one considers not a perturbation by a single pulse but the dynamics of coupled pulse oscillators. Consider the simplest system with pulse coupling, a single oscillator with pulse delayed feedback studied in Refs. 15 and 16. The oscillator emits pulses when its phase reaches unity (the phase is considered modulo 1). These pulses are sent to the delay line and arrive back to the oscillator after the delay τ . When the pulse is received, the oscillator’s phase changes according to (1).

We simulated the system twice with the same delay and the same initial conditions but with the different PRCs (for the details of numerical implementation, see Refs. 31 and 32). For the first simulation, we used the PRC (17) with $q = 30$, and for the second simulation, we used the modified PRC calculated on its base. The results of both simulations are shown in Fig. 3. As can be seen from the phase dynamics (top panel), the two solutions diverge even if they start from the same initial conditions. Moreover, the magnitudes of the phase shifts (bottom panel) reveal the qualitative difference between the solutions. For the original PRC, the phase shifts are not equal but form a sequence of period 5, which is a manifestation of the so-called jittering.^{15,16} In contrast, the modified PRC shows no jittering, and the phase shifts converge to a constant value.

To conclude, we have shown that Eq. (2) in general does not show the phase jumps corresponding to the PRC $Z(\varphi)$ and, therefore, should not be used for phase oscillators. In order to unambiguously define the system where the phase jumps correspond to

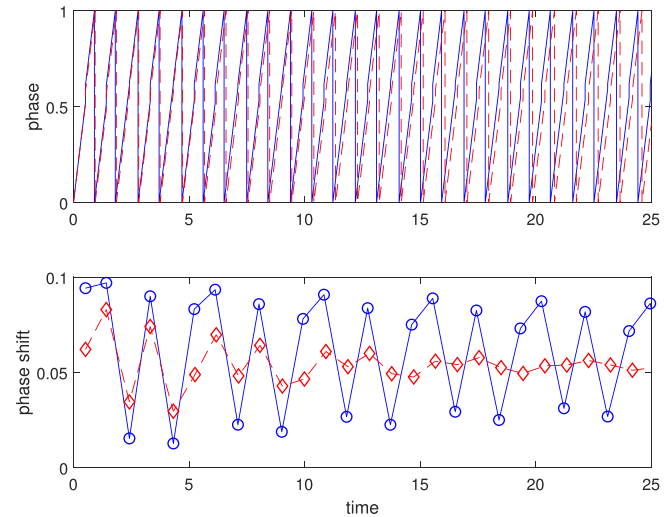


FIG. 3. Top panel: the temporal evolution of the oscillator phase for the original PRC $Z(\varphi)$ (blue solid line) and for the modified PRC $\tilde{Z}(\varphi)$ (red dashed line). Bottom panel: the magnitudes of the phase shifts $\Delta\varphi_p = \varphi_p^+ - \varphi_p^-$ for the original PRC $Z(\varphi)$ (blue solid line with circles) and for the modified PRC $\tilde{Z}(\varphi)$ (red dashed line with diamonds). The steepness parameter equals $q = 30$, and the delay $\tau = 4.32$.

the PRC $Z(\varphi)$, one should rather use the notation

$$\frac{d\varphi}{dt} = \omega + Z(\varphi_-) \sum_p \delta(t - t_p) \quad (18)$$

or

$$\frac{d\varphi(t)}{dt} = \omega + Z(\varphi(t_p - 0)) \sum_p \delta(t - t_p), \quad (19)$$

indicating directly that the value $\varphi_- \equiv \varphi(t_p - 0)$ should be used to calculate the magnitude of the jump at t_p . Similar notations were used, for example, in a popular model of synaptic plasticity.³³ Note, however, that (18) and (19) are not ordinary differential equations (ODEs) but rather shortcuts for the impulsive differential equations (IDEs),^{34,35}

$$\frac{d\varphi}{dt} = \omega, \quad t \neq t_p, \quad (20)$$

$$\varphi(t) = \varphi(t_-) + Z(\varphi(t_-)), \quad t = t_p. \quad (21)$$

The benefit of using the formulation in the form of an IDE is double. First, one can directly choose the PRC $Z(\varphi)$ governing the phase jumps and does not need to calculate the modified PRC $\tilde{Z}(\varphi)$. Second, in the IDE formulation, the phase resetting is free of any limitations, for example, one can select it such that the new phase is a non-monotonic function of the old phase,

$$\varphi_2 + Z(\varphi_2) < \varphi_1 + Z(\varphi_1) \text{ for } \varphi_2 > \varphi_1. \quad (22)$$

In particular, this possibility of the phase “reordering” is crucial for the multi-jitter instability.^{15,16} Obviously, the phase reordering is impossible for the ODEs (13) corresponding to a Dirac sequence $\{\delta_n\}$ and likewise for (2) with the Dirac delta function if interpreted as a limit of ODEs.

For curiosity, we remark that it is possible to define a solution to (1) as a limit of solutions to a sequence of delay differential equations (DDEs), though. Since $\varphi(t_-) = \lim_{\tau \searrow 0} \varphi(t - \tau)$, we can define $\varphi_{n,\tau}(t)$ as a solution to

$$\dot{\varphi}_{n,\tau} = \omega + Z(\varphi_{n,\tau}(t - \tau)) \sum_p \delta_n(t - t_p), \quad (23)$$

with a Dirac sequence $\{\delta_n\}$ and obtain a solution to (1) as $\varphi(t) := \lim_{\tau \searrow 0} \lim_{n \rightarrow \infty} \varphi_{n,\tau}(t)$.

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DATA AVAILABILITY

The data that support the findings of this study are available within the article.

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