Jittering waves in rings of pulse oscillators

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(Received 1 June 2016; published 6 July 2016)

Rings of oscillators with delayed pulse coupling are studied analytically, numerically, and experimentally. The basic regimes observed in such rings are rotating waves with constant interspike intervals and phase lags between the neighbors. We show that these rotating waves may destabilize leading to the so-called jittering waves. For these regimes, the interspike intervals are no more equal but form a periodic sequence in time. Analytic criterion for the emergence of jittering waves is derived and confirmed by the numerical and experimental data. The obtained results contribute to the hypothesis that the multijitter instability is universal in systems with pulse coupling.

DOI: 10.1103/PhysRevE.94.012206

I. INTRODUCTION

Interaction by pulses is typical for dynamical networks of various nature, including neuronal populations, cardiac tissues, and many others [1–3]. Pulses are signals characterized by temporal duration much smaller than the oscillation period. This property allows to consider pulse emission and arrival as discrete instantaneous events. A popular model utilizing this idea is pulse-coupled oscillators. In this model, the effect of a pulse depends on the dynamical state of the oscillator at the time of the pulse arrival. Under weak coupling, the oscillators are usually described by their phases, and the influence of a pulse is determined by the so-called phase resetting curve (PRC) [4].

The PRC tabulates the effect of an incoming pulse depending on the phase at which it arrives. For an oscillatory system, the PRC can be computed numerically or measured experimentally [5–10]. Thus, pulse-coupled phase oscillators can be considered either as stand-alone models, or as approximations of more complex systems. The main advantage of such models is their simplicity for numerical implementation and theoretical analysis [6,11–15]. A number of important results on collective behavior of networks have been obtained within the framework of pulse-coupled oscillators. In particular, the synchronous [16] and asynchronous [17] regimes have been studied, as well as cluster states [18–20] and splay states [21].

In realistic networks, pulses propagate with finite speed leading to nonzero coupling time delays. The influence of delays has been proven significant in many cases and may result in new dynamical phenomena, such as multistability [22–25], oscillations death [26], strong and weak chaos [27], and other complicated regimes [28–32].

Recently we have reported a surprising dynamical phenomenon in spiking oscillators subject to delayed feedback [33,34]. In such systems, if the PRC is steep enough, regular spiking may destabilize and give birth to the so-called "jittering" regimes with nonequal interspike intervals (ISIs). The number of different coexisting jittering regimes grows exponentially with the delay, which makes the system highly multistable. The corresponding transition was called "a multijitter bifurcation." Moreover, it is shown that in a system of two oscillators with pulse delayed coupling [35], the in-phase and antiphase regimes may destabilize through multijitter bifurcations. These findings indicate that the jittering instability is common for systems with pulse interactions, and it is important to understand its role in networks of pulse-coupled oscillators. The current study provides a step in this direction.

The paper investigates unidirectional rings of phase oscillators with pulse delayed coupling. A feed-forward ring is one of the fundamental network motif and often appears in nature [36–40]. We start with an analytical study of rotating waves and demonstrate that they may destabilize through the multijitter bifurcation. Subsequent numerical and experimental study shows that jittering waves with distinct ISIs are born at the bifurcation points. The period of these regimes is proportional to the delay, and their number grows exponentially. The most interesting distinctive feature is that in rings the jittering regimes appear at much shorter delays than in a single oscillator with delayed feedback.

II. THE MODEL

The basic model of our study is a ring of N oscillators with pulse delayed coupling as depicted in Fig. 1(a). Its dynamics is governed by the equations

$$\frac{d\varphi_j}{dt} = \omega_j + Z(\varphi_j)\sum_{t_s^{j-1}} \delta\big(t - t_s^{j-1} - \tau_j\big). \qquad (1)$$

Here $j = 1,\dots,N$ is the oscillator number, and each oscillator is described by its phase $\varphi_j \in \mathbb{S}^1$. Without coupling, the phase grows uniformly with $d\varphi_j/dt = \omega_j$. When the phase reaches unity, it resets to zero and the oscillator emits a spike. The instants when this happens are denoted by t_s^j, $s \in \mathbb{Z}$. Each jth oscillator receives input from its previous neighbor, the $(j-1)$-st oscillator (the first one receives input from the last one, so we identify 0 and N). This means that each spike produced by the $(j-1)$-st oscillator at t_s^{j-1} results in a pulse arriving to the jth one after the delay τ_j. When the oscillator receives a pulse, its phase instantly changes to the new value: $\varphi_j \mapsto \varphi_j + Z(\varphi_j)$, where the function $Z(\varphi)$ is the phase resetting curve (PRC) [4].

In the analytical part of our paper, we consider identical oscillators with $\omega_j = 1$. However, in the numerical part we

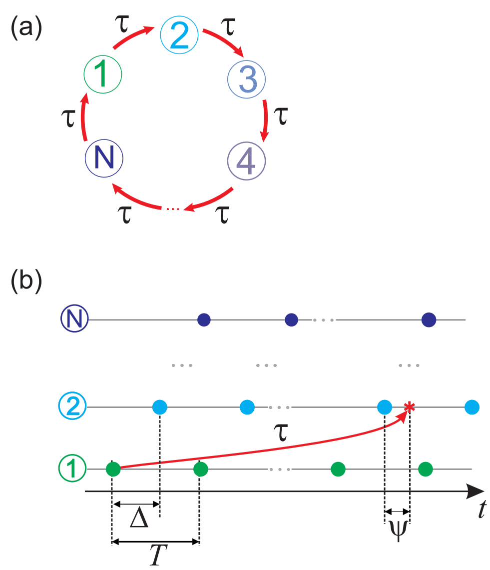

FIG. 1. (a) A feed-forward ring of N oscillators with pulse delayed coupling. (b) Dynamics of the ring demonstrating a rotating wave with a period T and lag Δ. Symbols denote the time instants when the oscillators produce spikes. A spike emitted at a certain moment of time by an oscillator arrives to the next oscillator after the delay τ.

study the influence of frequency mismatch. They are also inevitable in the experimental study. We also set all delays equal to $\tau_j = \tau$, which can be easily generalized to an arbitrary delay distribution [41].

III. ROTATING WAVES AND THEIR STABILITY

The basic dynamical regimes observed in rings of unidirectionally coupled oscillators are rotating waves [42–44]. Such waves are characterized by the same dynamical profile of all oscillators that is shifted by a constant time lag between the neighbors, i.e., $\varphi_j(t) = \varphi_{j-1}(t+\Delta)$. Suppose that system (1) demonstrates such a regime with the period T and the lag Δ, as depicted in Fig. 1(b). Then each oscillator receives one pulse per period at phase $\psi = (\tau - \Delta) \mod T$, which allows to determine the period as $T = 1 - Z(\psi)$, which is the time between the consecutive spikes of one oscillator. The total time lag over the whole ring must be a multiple of the period, i.e., $\Delta = RT/N$, where $R = 0,\dots,N-1$ is the wave number which characterizes the type of the rotation wave. Taking this into account, the equations for the rotating waves can be written as

$$T = 1 - Z(\psi),\ \Delta = RT/N,\ \tau = PT + \Delta + \psi. \quad (2)$$

Here $\psi \in [0,1]$ is the phase at which oscillators receive input The wave number $R = 0$ corresponds to a complete synchronization, $R = 1$ to the splay state, etc. P is the integer number controlling the value of the delay or, more exactly, the number of full periods in the delay τ.

Equation (2) can be understood as follows: for any given PRC function $Z(\cdot)$, wave number R, and the number of oscillators N, the three equations (2) provide the three parameters of the rotating wave: period T, phase of the spike arrival ψ, and the lag Δ. An integer value of P can be considered as an additional parameter tuned in such a way that (2) admits a solution. Alternatively, (2) can be considered as a countable set of equations for all integer values of P. Any solution $0 \leqslant \psi \leqslant 1, T > 0, 0 \leqslant \Delta < T$ of any such equation corresponds to a rotating wave. From (2) we can obtain the following explicit parametric representation of the period and lag of the rotating waves as a function of the delay:

$$\begin{aligned} T(\psi) &= 1 - Z(\psi), \\ \tau(\psi) &= \left(P + \frac{R}{N}\right)T(\psi) + \psi, \\ \Delta(\psi) &= RT(\psi)/N, \end{aligned} \quad (3)$$

where ψ plays the role of a free parameter.

Further we study the local stability of the rotating waves. For this we consider a perturbed solution with spiking times $t_s^j = sT + j\Delta + \delta_s^j$, where $\delta_s^j \ll T$ are deviations from the periodic regime. Then the interspike interval $T_s^j = t_{s+1}^j - t_s^j$ can be determined as $T_s^j = 1 - Z(\psi_s^j)$, where ψ_s^j is the phase at which the pulse arrives. It is influenced by the timing of a spike emitted by the $(j-1)$-st oscillator P periods earlier: $\psi_s^j = t_{s-P}^{j-1} + \tau - t_s^j = \psi + \delta_{s-P}^{j-1} - \delta_s^j$. Thus, we obtain an equation, which determines the dynamics of the perturbation:

$$\delta_{s+1}^j = \delta_s^j + 1 - T - Z\big(\psi + \delta_{s-P}^{j-1} - \delta_s^j\big). \quad (4)$$

Note that the deviations in the period $(s+1)$ depend on the deviations in the previous period s as well as on the deviations P periods ago. Thus, the map has dimension $N(P+1)$, which agrees with the results from Ref. [45]. For small deviations, (4) can be linearized,

$$\delta_{s+1}^j = (1+\alpha)\delta_s^j - \alpha\delta_{s-P}^{j-1}, \quad (5)$$

where $\alpha = Z'(\psi)$. System (5) is a linear discrete map, the stability of which determines the local stability of the rotating wave. Let k be the wave number of the perturbation (not to be confused with R) $\delta_s^j \sim \exp(ikj)$, then the stability of this kth mode can be found from the ansatz $\delta_s^j = \lambda(k)^s \exp(ikj)$, where λ is the multiplier of the rotating wave corresponding to the spatial perturbation mode $\exp(ikj)$. In particular, the bifurcation condition is given by $\lambda(k) = \exp(i\omega)$, where ω is the frequency. We obtain the characteristic equation

$$\lambda^{P+1}(k) - (1+\alpha)\lambda^P(k) + \alpha e^{-ik} = 0. \quad (6)$$

Note that the periodic boundary conditions on the ring allow only a limited set of wave numbers $k = 2\pi n/N$, where $n = 0,\dots,N-1$.

Let us consider first homogeneous perturbations $k = 0$. Then Eq. (6) possesses the trivial multiplier $\lambda(0) = 1$ corresponding to the phase shift (Goldstone mode). Further, dividing Eq. (6) by $\lambda - 1$ we obtain the equation

$$\lambda^P(0) - \alpha \sum_{j=0}^{P-1} \lambda^j(0) = 0, \quad (7)$$

which possesses the critical root $\lambda(0) = 1$ for $\alpha = 1/P$ and $P+1$ critical roots $\lambda_m(0) = \exp[i2\pi m/(P+1)]$, $m = 0,\dots,P$ for $\alpha = -1$ [33,34]. In fact, Eq. (7) for the homogeneous perturbations is the same as the characteristic equation for one oscillator with delayed feedback [33,34]. Hence, we have the same conclusions for the stability of the homogeneous mode as for just one oscillator: the mode is stable for $\alpha \in (-1,1/P)$, there is a saddle node bifurcation at $\alpha = 1/P$, and the multijitter bifurcation $\alpha = -1$, when all multipliers $\lambda(0)$ become unstable at once.

Now let us consider all other spatial modes $k \neq 0$. The critical case corresponds to $\lambda(k) = e^{i\omega(k)}$, and we obtain

$$e^{i\omega(k)(P+1)} - (1+\alpha)e^{i\omega(k)P} + \alpha e^{-ik} = 0. \tag{8}$$

This equation has no solutions with $k \neq 0$ for $\alpha \notin \{0, -1\}$. Indeed, it can be written in a general form

$$e^{i\varphi_1} + \alpha e^{i\varphi_3} = (1+\alpha)e^{i\varphi_1},$$

and it is straightforward to see (e.g., a geometric considerations in the complex plane) that for $\alpha \notin \{0, -1\}$ it can be fulfilled only if $\varphi_1 = \varphi_2 = \varphi_3$ modulo 2π. Hence, we obtain

$$(P+1)\omega(k) = P\omega(k) = -k \mod 2\pi,$$

which implies $k = \omega = 0$. Thus, for $\alpha \notin \{0, -1\}$ the only critical multiplier $\lambda(0) = 1$ exists.

Other critical multipliers may emerge only in the two cases: $\alpha = 0$ or $\alpha = -1$. For $\alpha = 0$, Eq. (6) implies $\lambda(k) = 1$ for any k. For $\alpha = -1$, (8) implies $\omega(k) = (-k + 2\pi m)/(P+1)$, where $m = 0,\ldots,P$.

Let us summarize the results for the characteristic equation (6). Its spectrum has the form $\Lambda \cup \{1\}$, where $\lambda(0) = 1$ is the trivial multiplier corresponding to the neutral stability along the phase shift. Stability of the limit cycle is defined by the set Λ, which includes critical multipliers only in the following cases:

(i) $\alpha = 1/P$: one critical multiplier $\lambda(0) = 1$ for $k = 0$.

(ii) $\alpha = 0$: $(N-1)$ critical multipliers $\lambda(k) = 1$ for $k = 2\pi n/N, n = 1,\ldots,N-1$.

(iii) $\alpha = -1$: $N(P+1) - 1$ critical multipliers $\lambda_m(k) = \exp[-ik + i2\pi m/(P+1)]$, where $m = 0,\ldots,P$ for $k \neq 0$ and $m = 1,\ldots,P$ for $k = 0$.

Thus, the rotating wave may change its stability only at the parameter values $\alpha \in \{-1,0,1/P\}$. It is easy to check that it is stable in the parameter interval $-1 < \alpha < 0$ and loses its stability on the boundaries of this interval. At $\alpha = 0$, the emergence of $N-1$ critical multipliers $\lambda(k) = 1$ indicates the occurrence of pitchfork bifurcations for each spatial mode $k \neq 0$, where $N-1$ nonsymmetric spiking regimes are born simultaneously. In this paper, do not focus of these regimes.

A more remarkable scenario is observed at $\alpha = -1$ where *all* multipliers become critical at once. The rotating wave loses its stability, and the so-called jittering waves or regimes with distinct interspike intervals emerge. Because of the coexistence of a big number of these solutions, the corresponding scenario is called a "multijitter bifurcation"; see also Refs. [33,34]. A more detailed study of this bifurcation and the jittering waves is carried out in the following sections.

IV. NUMERICAL STUDY OF THE JITTERING WAVES

As shown in the previous section, the stability criterion for the rotating waves relies on the steepness of the PRC. The multijitter bifurcation occurs when the slope of the PRC is less than minus one. For our numerical illustrations, we chose the PRC in the form [20]

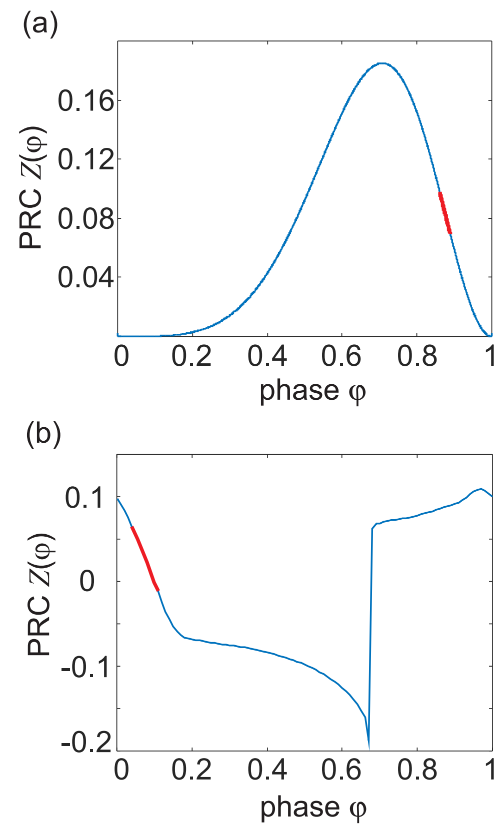

FIG. 2. (a) The PRC (9) for $\kappa = 0.185$. (b) The PRC of the electronic oscillator used in the experiments. In both panels the intervals with the slope < -1 are marked by red line.

$$Z(\varphi) = \frac{\kappa}{2}[1 - \cos(2\pi\varphi^2)]. \tag{9}$$

Here κ is the coupling strength and controls both the magnitude and slope of the PRC. We used $\kappa = 0.185$ for which the PRC is shown in Fig. 2(a). For this value, two points φ exist with $Z'(\varphi) = -1$, and an interval with $Z'(\varphi) < 1$ is between them [red line in Fig. 2(a)].

We varied the delay and simulated system (1) directly for $N = 6$ starting from 20 different initial conditions for each value of τ. For each trial, the initial phases of the oscillators at $t = 0$ were chosen randomly with a uniform distribution, and it was assumed that no spikes were produced by any of the oscillators for $t < 0$. The obtained numerical results are depicted in Fig. 3(a) by dots. The color of each dot corresponds to the wave number of the established regime (see the legend). Gray dots correspond to asymmetric regimes. The branches obtained theoretically according to (3) are plotted by thin dashed lines. The points of the stability loss are marked by circles (for $\alpha = 0$) and stars (for $\alpha = -1$). One can see that the numerically obtained dots coincide with the stable parts of the theoretical branches. There are also several branches of asymmetric regimes, but, most importantly, the jittering wave regimes are observed, which emerge from the multijitter bifurcations (stars).

Jittering waves are characterized by distinct interspike intervals, and they emerge from the rotating wave at the

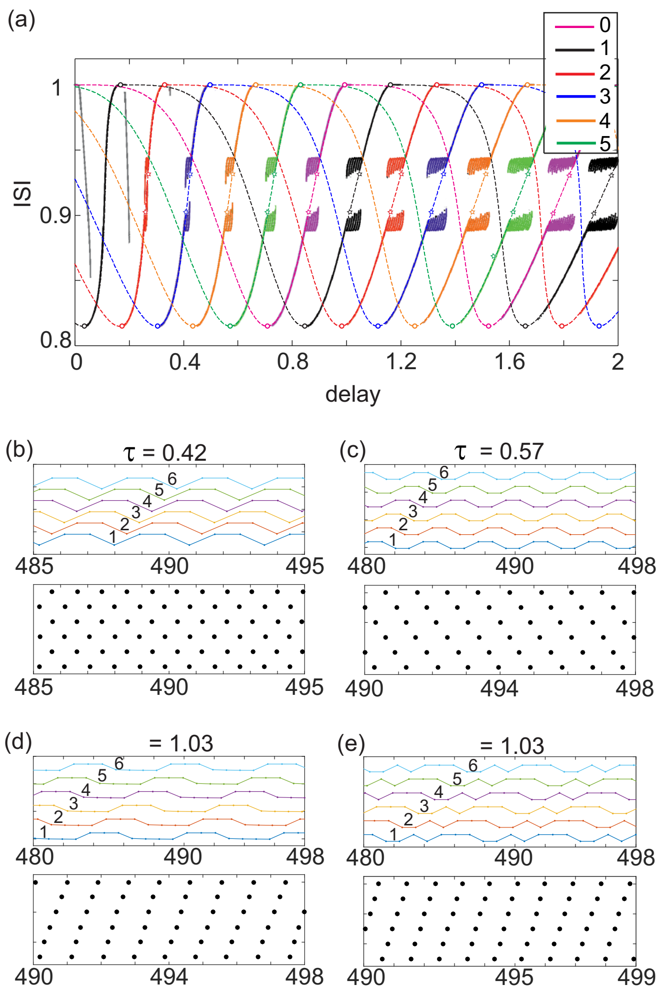

FIG. 3. Periodic rotating waves and jittering wave regimes in a ring of $N = 6$ oscillators. (a) The bifurcation diagram, the observed interspike intervals versus the delay. Different colors correspond to the different wave numbers; see the legend. Thin dashed and thick lines correspond to unstable and stable rotating waves, respectively. Both are given by Eq. (3), and thick lines are checked numerically. Circles denote pitchfork bifurcations, stars the multijitter bifurcations. Jittering regimes are characterized by several distinct ISIs for the same value of delay. (b–e) Examples of jittering regimes. In the top of each panel the ISI demonstrated by each oscillator is plotted versus time. The plots are shifted along the vertical axis for the convenience. In the bottom of each panel, the time instants of the spikes emission are depicted by dots. Note that the firing patterns are close to the rotating waves, and the deviations are visible only after a careful examination or a zoom.

multijitter bifurcation; see Figs. 3(b)–3(e). Each such solution is close to the rotating wave from which it is born. However, the intervals between the consecutive spikes of each oscillator are not constant anymore but constitute a periodic sequence of two distinct ISIs. We use this property to encode the jittering regimes by binary sequences, where 0 corresponds to the shorter, and 1 to the longer interval. For example, a regime when oscillators produce two long and then one short ISIs periodically is encoded as 110; see Fig. 3(b). The other regimes shown are 1100 (c), 1110000 (d), and 1110010 (e). Note that in Fig. 3 the plots of the ISIs for different oscillators are shifted along the vertical axis.

All the jittering regimes that emerge at the same bifurcation point are characterized by the same period of the binary sequences. This period is longer for larger delays. We found that the period of the emergent jittering solutions equals

$$\Pi = R + (P + 1)N. \tag{10}$$

Moreover, we discovered that for each periodic binary sequence the parameter interval can be found where the corresponding jittering regime is observed. The regimes consisting of the same number of zeros and ones exist in the same parameter intervals and possess absolutely the same values of the ISIs. This implies that such the regimes are plotted by the same set of points in the bifurcation diagram. An example of such regimes can be seen in Figs. 3(d) and 3(e).

V. EXPERIMENTAL STUDY

We have also experimentally studied jittering waves in a pair of electronic FitzHugh-Nagumo oscillators with mutual pulse delay coupling [9]. This system is the simplest example of a "ring" consisting of just two oscillators. Two basic regimes exist in the system: the in-phase and the antiphase ones. Below we show that each of these regimes may give birth to jittering regimes.

The circuitry of the electronic system used in the experiment is the same as in Ref. [9]. In the absence of coupling each oscillator spikes periodically with period 2.95 ms. The parameters of the oscillators are set as in Ref. [34]. The coupling is organized as follows: When the output voltage of one oscillator exceeds the threshold value, a spike is produced and sent to the delay line. The delay lines are realized on FPGA Xilinx Virtex-5 LX50 as shift registers consisting of 2000 elements with time of the shift 10 μs. When the spike passes the delay line, a pulse of amplitude 5 V and duration 42 μs is sent to the target oscillator. The phase resetting curve corresponding to such a pulse is depicted in Fig. 2(b). It exhibits an interval with the slope less than -1, indicated by red.

The system can demonstrate only two different rotation waves, with $R = 0$ and 1. We call the first regime in-phase, the second antiphase. During the experiment, we gradually selected different values of the feedback delay time τ and recorded the observed dynamical regimes. The results are depicted in the experimental bifurcation diagram in Fig. 4(a). Here for each delay τ the observed ISIs are plotted analogously to the presentation in Fig. 3(a). The experimental data points are plotted by gray, and the color of solid lines marks the type of the regime: black for in-phase, red for antiphase. The corresponding theoretical curves are plotted by thin dashed lines. One may see that both in-phase and antiphase regimes may destabilize, giving rise to the jittering regimes. The examples of the in-phase and antiphase jittering regimes are given in Figs. 4(b)–4(c). Figure 4(b) depicts the antiphase jittering regime 1101000 observed at $\tau = 7.3$ ms, and Fig. 4(c) the in-phase regime 111100 observed at $\tau = 6.18$ ms.

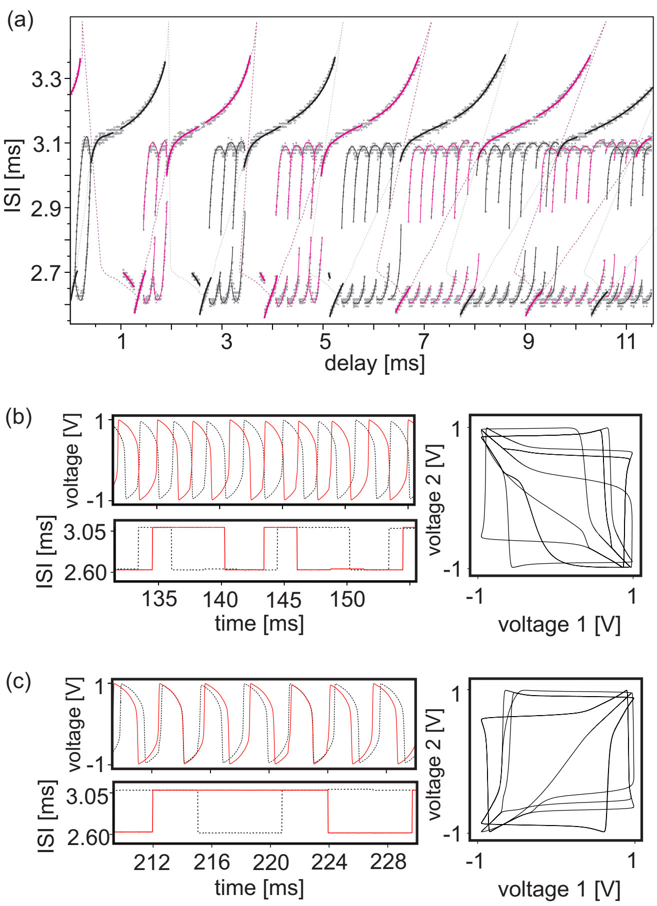

FIG. 4. Experimental study of a ring of two electronic oscillators with pulse delayed coupling. (a) Experimental bifurcation diagram. Gray dots represent data points, approximated by thick lines, black for in-phase regimes, and red for antiphase. Thin dashed lines plot theoretical branches. (b–c) Examples of jittering regimes. In each panel, on the top the output voltages of both oscillators are plotted versus time. On the bottom, the interspike intervals are plotted. On the right are the Lissajous figures.

VI. DISCUSSION AND CONCLUSIONS

We have studied the dynamics of rings of pulse oscillators with delayed coupling. In such systems, the base dynamical regimes are rotating waves. We have shown that each rotating wave may destabilize in the multijitter bifurcation. This bifurcation was previously introduced for a single delayed oscillator in Refs. [33,34]. In such a scenario, all the multipliers of the corresponding limit cycle become critical simultaneously. When the rotating wave destabilizes, it gives rise to the so-called jittering wave regimes with distinct ISIs. In the jittering regime, each oscillator produces a periodic sequence of long and short ISIs. These sequences are the same for all oscillators although shifted in phase.

Many common features are shared by the multijitter bifurcations observed in a single oscillator with delayed feedback and in a ring of oscillators considered here. In both cases, the regular regime destabilizes and the irregular, jittering regimes are born. In the case of one oscillator the regular regime is the periodic spiking; in the case of the ring of oscillators it is the rotating wave. First, the condition for the bifurcation is exactly the same for the both systems. Namely, the slope of the PRC at the phase at which the oscillator is simulated must be equal to -1. In generic situations, if the PRC is smooth, the points with slope -1 appear in pairs. In this case, the regular regime is unstable in the interval between the two of these points.

Second, the properties of the emergent jittering regimes are quite similar. These regimes are bipartite, i.e., the ISIs constituting them have one of two distinct values. As a result, the corresponding bifurcation diagram has a typical form with multiple two-branch loops [Fig. 3(a)]. Bipartite regimes can be encoded by binary sequences, which we did in the case of both one oscillator and the ring. In both cases the period of the observed sequences is proportional to the delay. The most surprising feature also observed in both cases is the following: for an arbitrary binary sequence of a given period, the parameter interval does exist where the corresponding jittering regime is present and stable. The regimes with the same number of long and short ISIs are stable in the same parameter interval. This feature leads to high multistability of the system, which develops exponentially as the delay grows.

In spite of similarity between the two systems, multijitter bifurcation in rings has an important distinction from that in one oscillator with feedback. For one oscillator, the value of the delay must be large compared to the oscillator's natural period. Specifically, the multijitter bifurcation giving birth to jittering regimes of period Π takes place at the delay

$$\tau_\Pi = (\Pi - 1)[1 - Z(\psi^*)] + \psi^*,$$

where ψ^* is the phase with $Z'(\psi^*) = -1$. Since the PRC $Z(\varphi)$ is typically small, the period of jittering regimes is roughly the delay divided over the natural period. Thus, to obtain jittering regimes with long periods one needs delays several times larger than the natural period.

For rings the situation is different. As follows from (2), multijitter bifurcations take place at delays $\tau = (P + R/N)[1 - Z(\psi^*)] + \psi^*$. According to (10), this implies that jittering regimes with period Π emerge at the delay

$$\tau_\Pi = (\Pi/N - 1)[1 - Z(\psi^*)] + \psi^*.$$

Thus, the period of the emergent jittering solutions is roughly proportional to the delay times the number of oscillators, or the total delay along the ring. As a consequence, even short coupling delays may result in higher-periodical jittering regimes if the number of oscillators is large enough.

The permissibility of short delays may be important for application of the obtained results to real-world networks, for example, neural populations. Coupling delays in neural networks related to signal propagation along axons and the inertness of synapses are typically of the order of milliseconds [46]. Since the typical oscillations frequency in neural network is below 100 Hz, such delays are too small to induce jittering instability by the delayed feedback. However, in closed loop configurations the delays may accumulate and constitute a value larger than the oscillations period. According to recent estimates, the number of synapses to connect any two neurons in the nervous system is from three to seven [47,48]. This suggests that ring motifs of six to 14 neurons are not uncommon. Thus, the emergence of multistable jittering regimes may be expected in such configurations, as well as other types of multistability described previously [49].

The obtained results show that the multijitter instability may appear in networks with pulse delayed interactions. However, since the feed-forward loops are known to possess similar properties to single delay-coupled systems [50], a further objective is a search for similar effects in a wider class of network configurations.

ACKNOWLEDGMENTS

The research was carried out with the financial support of the Russian Science Foundation (Project No. 14-12-01358).

[1] K. T. Judd and K. Aihara, Pulse propagation networks: a neural network model that uses temporal coding by action potentials, Neural Netw. **6**, 203 (1993).
[2] A. T. Winfree, *The Geometry of Biological Time* (Springer, New York, 2001).
[3] E. M. Izhikevich, *Dynamical Systems in Neuroscience: The Geometry of Excitability and Bursting* (MIT Press, Cambridge, MA, 2005).
[4] C. C. Canavier and S. Achuthan, Pulse coupled oscillators and the phase resetting curve, Math. Biosci. **226**, 77 (2010).
[5] L. Glass, M. R. Guevara, J. Belair, and A. Shrier, Global bifurcations of a periodically forced biological oscillator, Phys. Rev. A **29**, 1348 (1984).
[6] B. Ermentrout, Type I membranes, phase resetting curves, and synchrony, Neural Comput. **8**, 979 (1996).
[7] G. B. Ermentrout, B. Beverlin II, T. Troyer and T. I. Netoff, The variance of phase-resetting curves, J. Comput. Neurosci. **31**, 185 (2011).
[8] V. Novicenko and K. Pyragas, Computation of phase response curves via a direct method adapted to infinitesimal perturbations, Nonlinear Dynam. **67**, 517 (2012).
[9] V. V. Klinshov, D. S. Shchapin, and V. I. Nekorkin, Cross-frequency synchronization of oscillators with time-delayed coupling, Phys. Rev. E **90**, 042923 (2014).
[10] I. S. Proskurkin, A. I. Lavrova, and V. K. Vanag, Inhibitory and excitatory pulse coupling of two frequency-different chemical oscillators with time delay, Chaos **25**, 064601 (2015).
[11] P. Goel and B. Ermentrout, Synchrony, stability, and firing patterns in pulse-coupled oscillators, Physica D **163**, 191 (2002).
[12] E. Brown, J. Moehlis, and P. Holmes, On the phase reduction and response dynamics of neural oscillator populations, Neural Comput. **16**, 673 (2004).
[13] K. M. Stiefel, B. S. Gutkin, and T. J. Sejnowski, The effects of cholinergic neuromodulation on neuronal phase-response curves of modeled cortical neurons, J. Comput. Neurosci. **26**, 289 (2009).
[14] Y. Sato, K. Okumura, A. Ichiki, and M. Shiino, Thermal effects on phase response curves and synchronization transition, in *Advances in Neural Networks:ISNN 2011, Lecture Notes in Computer Science*, Vol. 6675, edited by D. Liu, H. Zhang, M. Polycarpou, C. Alippi, and H. He (Berlin, Heidelberg, Springer, 2011), pp. 287–296.
[15] L. Lücken, S. Yanchuk, O. V. Popovych, and P. A. Tass, Desynchronization boost by non-uniform coordinated reset stimulation in ensembles of pulse-coupled neurons, Front. Comput. Neurosci. **7**, 63 (2013).
[16] R. Mirollo and S. Strogatz, Synchronization of pulse-coupled biological oscillators, SIAM J. Appl. Math. **50**, 1645 (1990).
[17] L. F. Abbott and C. van Vreeswijk, Asynchronous states in networks of pulse-coupled oscillators, Phys. Rev. E **48**, 1483 (1993).
[18] C. van Vreeswijk, Partial synchronization in populations of pulse-coupled oscillators, Phys. Rev. E **54**, 5522 (1996).
[19] S. Achuthan and C. Canavier, Phase-resetting curves determine synchronization, phase locking, and clustering in networks of neural oscillators, J. Neurosci. **29**, 5218 (2009).
[20] L. Lücken and S. Yanchuk, Two-cluster bifurcations in systems of globally pulse-coupled oscillators, Physica D **241**, 350 (2012).
[21] R. Zillmer, R. Livi, A. Politi, and A. Torcini, Stability of the splay state in pulse-coupled networks, Phys. Rev. E **76**, 046102 (2007).
[22] H. G. Schuster and P. Wagner, Mutual entrainment of two limit cycle oscillators with time delayed coupling, Prog. Theor. Phys. **81**, 939 (1989).
[23] U. Ernst, K. Pawelzik, and T. Geisel, Delay-induced multistable synchronization of biological oscillators, Phys. Rev. E **57**, 2150 (1998).
[24] V. V. Klinshov and V. I. Nekorkin, Synchronization of time-delay coupled pulse oscillators, Chaos Solitons Fractals **44**, 98 (2011).
[25] S. Yanchuk and P. Perlikowski, Delay and periodicity, Phys. Rev. E **79**, 046221 (2009).
[26] D. V. R. Reddy, A. Sen, and G. L. Johnston, Time Delay Induced Death in Coupled Limit Cycle Oscillators, Phys. Rev. Lett. **80**, 5109 (1998).
[27] S. Heiligenthal, T. Dahms, S. Yanchuk, T. Jüngling, V. Flunkert, I. Kanter, E. Schöll, and K. Wolfgang, Strong and Weak Chaos in Nonlinear Networks with Time-Delayed Couplings, Phys. Rev. Lett. **107**, 234102 (2011).
[28] E. M. Izhikevich, Polychronization: computation with spikes, Neural Comput. **18**, 245 (2006).
[29] O. V. Popovych, S. Yanchuk, and P. A. Tass, Delay- and Coupling-Induced Firing Patterns in Oscillatory Neural Loops, Phys. Rev. Lett. **107**, 228102 (2011).
[30] T. Erneux, *Applied Delay Differential Equations*, Vol. 3 (Springer, New York, 2009).
[31] M. C. Soriano, J. Garcia-Ojalvo, C. R. Mirasso, and I. Fischer, Complex photonics: dynamics and applications of delay-coupled semiconductors lasers, Rev. Mod. Phys. **85**, 421 (2013).
[32] M. Kantner, E. Schöll, and S. Yanchuk, Delay-induced patterns in a two-dimensional lattice of coupled oscillators, Sci. Rep. **5**, 8522 (2015).
[33] V. V. Klinshov, L. Lücken, D. S. Shchapin, V. I. Nekorkin, and S. Yanchuk, Multistable Jittering in Oscillators with Pulsatile Delayed Feedback, Phys. Rev. Lett. **114**, 178103 (2015).
[34] V. V. Klinshov, L. Lücken, D. S. Shchapin, V. I. Nekorkin, and S. Yanchuk, Emergence and combinatorial accumulation of

jittering regimes in spiking oscillators with delayed feedback, Phys. Rev. E **92**, 042914 (2015).

[35] V. V. Klinshov, O. V. Maslennikov, and V. I. Nekorkin, Jittering regimes of two spiking oscillators with delayed coupling, Appl. Math. Nonlin. Sci. **1**, 197 (2016).

[36] G. E. Alexander, M. R. Delong, and P. L. Strick, Parallel organization of functionally segregated circuits linking basal ganglia and cortex, Annu. Rev. Neurosci. **9**, 357 (1986).

[37] M. Courtemanche, L. Glass, and J. P. Keener, Instabilities of a Propagating Pulse in a Ring of Excitable Media, Phys. Rev. Lett. **70**, 2182 (1993).

[38] P. C. Bressloff, S. Coombes, and B. De Souza, Dynamics of a Ring of Pulse-Coupled Oscillators: Group-Theoretic Approach, Phys. Rev. Lett. **79**, 2791 (1997).

[39] R. Ben-Yishai, D. Hansel, and H. Sompolinsky, Traveling waves and the processing of weakly tuned inputs in a cortical network module, J. Comput. Neurosci. **4**, 57 (1997).

[40] M. B. Elowitz and S. Leibler, A synthetic oscillatory network of transcriptional regulators, Nature (London) **403**, 335 (2000).

[41] L. Lücken, J. P. Pade, K. Knauer, and S. Yanchuk, Reduction of interaction delays in networks, Europhys. Lett. **103**, 10006 (2013).

[42] G. B. Ermentrout and N. Kopell, Multiple pulse interactions and averaging in systems of coupled neural oscillators, J. Math. Biol. **29**, 195 (1991).

[43] M. A. Matias and J. Guemez, Transient Periodic Rotating Waves and Fast Propagation of Synchronization in Linear Arrays of Chaotic Systems, Phys. Rev. Lett. **81**, 4124 (1998).

[44] P. Perlikowski, S. Yanchuk, O. V. Popovych, and P. A. Tass, Periodic patterns in a ring of delay-coupled oscillators, Phys. Rev. E **82**, 036208 (2010).

[45] V. V. Klinshov and V. I. Nekorkin, The map with no predetermined firing order for the network of oscillators with time-delayed pulsatile coupling, Commun. Nonlin. Sci. Numer. Simulat. **18**, 973 (2013).

[46] H. Markram, J. Lübke, M. Frotscher, A. Roth, and B. Sakmann, Physiology and anatomy of synaptic connections between thick tufted pyramidal neurones in the developing rat neocortex, J. Physiol. **500**, 409 (1997).

[47] V. Braitenberg and A. Schüz, *Cortex: Statistics and Geometry of Neural Connectivity* (Springer, Berlin, 1998).

[48] G. Buzsáki, *Rhythms of the Brain* (Oxford University Press, New York, 2006).

[49] J. Foss and J. Milton, Multistability in recurrent neural loops arising from delay, J. Neurophysiol. **84**, 975 (2000).

[50] G. Van der Sande, M. C. Soriano, I. Fischer, and C. R. Mirasso, Dynamics, correlation scaling and synchronization behavior in rings of delay-coupled oscillators, Phys. Rev. E **77**, 055202(R) (2008).