Breakdown of order preservation in symmetric oscillator networks with pulse-coupling

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Symmetric networks of coupled dynamical units exhibit invariant subspaces with two or more units synchronized. In time-continuously coupled systems, these invariant sets constitute barriers for the dynamics. For networks of units with local dynamics defined on the real line, this implies that the units' ordering is preserved and that their winding number is identical. Here, we show that in permutation-symmetric networks with pulse-coupling, the order is often no longer preserved. We analytically study a class of pulse-coupled oscillators (characterizing for instance the dynamics of spiking neural networks) and derive quantitative conditions for the breakdown of order preservation. We find that in general pulse-coupling yields additional dimensions to the state space such that units may change their order by avoiding the invariant sets. We identify a system of two symmetrically pulse-coupled identical oscillators where, contrary to intuition, the oscillators' average frequencies and thus their winding numbers are different. © *2011 American Institute of Physics*. [doi:10.1063/1.3589960]

Symmetries are an important feature of network dynamical systems, often constraining their dynamics. One such restriction is, e.g., the forced order conservation of oscillators in fully symmetric systems of time-continuously coupled oscillators.[1,2] Here, we reveal that symmetric networks of dynamical units coupled via the exchange of pulses, such as networks of spiking neurons, circumvent these restrictions, thus increasing the complexity of the dynamical phenomena emerging in such systems. We show that pulse-coupled oscillators may overtake each other, thus breaking the order conservation in contrast to similar time-continuously coupled systems. We explain the mechanisms behind this overtaking phenomenon and discuss its consequences. Intriguingly, we find that identical and symmetrically pulse-coupled oscillators may exhibit n : m locking (n ≠ m), which is impossible for similar systems that are time-continuously coupled. Our results highlight that the nature of discrete-time pulse-coupling plays a distinct role in network dynamical systems, in particular, for synchronization and phase-locking phenomena.

I. IMPACT OF SYMMETRY ON DYNAMICS

Symmetries strongly impact the time evolution of dynamical systems. For instance, in Hamiltonian systems, Noether's theorem[3] states that a symmetry of the action of the system implies an integral of motion, e.g., conservation of momentum, if the system is invariant under translations. In general, a symmetry of a dynamical system is a transformation that keeps the set of all trajectories unchanged. Dynamical systems with symmetries are called equivariant dynamical systems.[4–6] The symmetries in such equivariant systems entail certain properties of their bifurcations (equivariant bifurcation theory). For example, the equivariant branching lemma[5] ensures the existence of specific equilibrium solution branches from the bifurcation point given a certain symmetry of the system. Symmetries also play an important role for the existence and robustness of heteroclinic cycles.[7] Such structures for example enable dynamical computations via switching phenomena along the heteroclinic orbits in models of neuronal networks.[8,9] In systems of ordinary differential equations (ODEs) whose structure is that of a finite number of subsystems (cells) coupled together, also called coupled cell networks,[10] the appearance of cluster states, i.e., states involving groups of synchronized units, often relies on symmetries.[11–14]

In equivariant dynamical systems defined by a set of ODEs, a symmetry implies the existence of a flow-invariant subspace, the fixed-point space of that symmetry. For example, consider a coupled cell network where a certain subset of the cells is symmetric under permutations. Then the subsets of state space with two or more synchronized units, i.e., the polydiagonals, are invariant under the dynamics. As a consequence, these invariant sets form barriers for the dynamics that cannot be crossed, i.e., units cannot overtake. In particular, this implies that the average frequencies of oscillators for which the polydiagonal is flow-invariant are equal[1,2] and oscillators that have an invariant polydiagonal cannot pass each other. This intuitive fact is often used when

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analyzing the dynamics of such symmetric networks in more detail.[10–12]

Similar arguments that ensure order preservation due to symmetries are used in dynamical systems that are not based on ODEs, as, for example, in networks of pulse-coupled units.[14–17] In a pulsed-coupled system, the interaction between units is determined by discrete points in time where the units generate pulses, e.g., due to a threshold crossing. Pulse-coupled systems provide mathematical models for a wide range of natural phenomena, including fireflies interacting by exchanging light flashes,[18,19] chirping crickets,[20] neurons that interact by sending and receiving electrical pulses,[21,22] and tectonic plates that spread mechanical stress to their neighbors during earthquakes.[23] These networks exhibit several new and sometimes counter-intuitive features, including unstable periodic orbit Milnor attractors,[16,24–27] first order multi-operator dynamics instead of linear relaxation,[28,29] finite time synchronization,[15,30] dynamics that exhibit positive finite time Lyapunov exponents and are highly irregular but nevertheless stable,[31–34] and speed limits in response to dynamical perturbations.[35,36]

In this article, we show that in pulse-coupled dynamical systems with full permutation symmetry, the ordering of the coordinates is not preserved, i.e., that the invariant polydiagonals in general do not form barriers to the dynamics and units may pass each other (we also refer to this as "overtaking"). This is in contrast to the results obtained in time-continuously coupled equivariant systems defined via ODEs, and thus special attention has to be paid when applying well-established results for ODEs to pulse-coupled systems.[9,15]

This article is structured as follows: After introducing the basic notations and relevant results that ensure order preservation in symmetric systems defined via ODEs in Sec. II, the crossing of the invariant polydiagonals in general pulse-coupled systems is illustrated in Sec. III. In Sec. IV, we focus on a class of pulse-coupled oscillators that permits a detailed analysis predicting the breakdown of order preservation. In Sec. V, we identify an example of two symmetrically pulse-coupled identical oscillators that exhibit different average frequencies and thus different winding numbers. Finally, we summarize and discuss our results in Sec. VI.

II. SYMMETRIES, SYNCHRONY, INVARIANCE, AND ORDER PRESERVATION

It is well understood that symmetries imply the existence of invariant subspaces: Consider a system of differential equations of the form

$$\frac{d}{dt}x = F(x,t), \tag{1}$$

where $x \in \mathbb{R}^N$ and $F : \mathbb{R}^{N+1} \to \mathbb{R}^N$ is a smooth velocity field that satisfies the Lipschitz condition. Then there exists a flow $\Phi(t, x_0)$ such that $x(t) = \Phi(t, x_0)$ is the unique solution of Eq. (1) starting from initial conditions $x(0) = x_0 \in \mathbb{R}^N$.[37]

If Eq. (1) has a symmetry, i.e., a group Γ of elements $g \in \Gamma$ acting on $\mathbb{R}^N$ that satisfy

$$gF(x,t) = F(gx,t) \quad \text{for all } g \in \Gamma, \tag{2}$$

then the fixed point spaces

$$\mathrm{Fix}(g) = \{x \in \mathbb{R}^N \,|gx = x\}, \tag{3}$$

for $g \in \Gamma$ and all their intersections are invariant under the flow Φ of Eq. (1), e.g.,

$$x_0 \in \mathrm{Fix}(g) \;\Rightarrow\; \Phi(t,x_0) \in \mathrm{Fix}(g) \quad \text{for all} \quad t \ge 0. \tag{4}$$

For instance, a permutation symmetric coupled cell network of N units with states x_i, $i \in \{1, 2, \ldots, N\}$ evolves according to

$$\begin{aligned}
\dot{x}_1 &= f(x_1; \overline{x_2, x_3 \ldots, x_N}),\\
\dot{x}_2 &= f(x_2; \overline{x_1, x_3 \ldots, x_N})\\
&\vdots\\
x_N &= f(x_N; \overline{x_1, x_2, \ldots, x_{N-1}}),
\end{aligned} \tag{5}$$

where the overbar indicates symmetrization in the variables below, i.e., $f(x_1;\overline{x_2,x_3,\ldots,x_N}) = f(x_1;\overline{x_{\sigma_2},x_{\sigma_3},\ldots,x_{\sigma_N}})$ for all permutations of the indices $\sigma \in S_N$. Hence, Eq. (5) has symmetry group $\Gamma = S_N$ and according to Eqs. (3) and (4), all subspaces of two or more synchronized units, i.e., the sets $\{x \in \mathbb{R}^N \,|x_i = x_j,\}$ and their intersections, are flow invariant. Using continuity of trajectories and uniqueness of the flow, these invariant subspaces cannot be crossed and it follows that if $x_i(t) \le x_j(t)$ at time t, then $x_i(t') \le x_j(t')$ for all future times $t' \in [t, \infty)$, i.e., the units preserve their ordering (cf. Fig. 1).

This fact is often utilized when analyzing the dynamics of such networks in more detail.[15,38–40] Often it is equally presumed for pulse-coupled systems.[1,15,40] However, as we

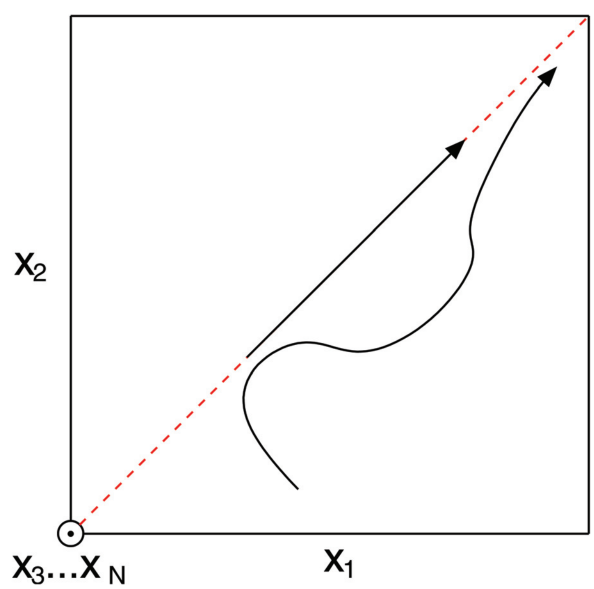

FIG. 1. (Color online) Real-valued units in a permutation-symmetric smooth network dynamical system [Eq. (5)] cannot pass each other because they cannot cross the invariant manifolds (dashed) which are fixed points of the permutation symmetries [Eq. (3)]. A projection of two trajectories (black, solid) onto the x_1 - x_2 plane is sketched, one on the invariant set and one that stays on one side of the invariant manifold.

show in the following, in pulse-coupled systems with full permutation symmetry order preservation may break down.

III. BREAKDOWN OF ORDER PRESERVATION IN PERMUTATION-SYMMETRIC PULSE-COUPLED SYSTEMS

Here, we demonstrate that in pulse-coupled dynamical systems with full permutation symmetry, the order preservation is broken. In a pulse-coupled system, the interaction between individual units is fully determined by discrete events in time at which the units generate pulses. The times at which unit i generates its sth pulse is denoted by t_i^s. In neuronal systems, for example, this could be the spike times of individual neurons. Then, unit i generates a pulse when its state x_i crosses a threshold $x_i\left(t_i^s\right)=\Theta$ from below, $\dot{x}_i\left(t_i^s\right)>0$, and thus the times t_i^s depend on the initial conditions. Mathematically, the velocity field F from Eq. (1) for a pulse-coupled system additionally depends on the pulse generation times t_i^s

$$\frac{d}{dt}x(t)=F\left(x,\left\{t_i^s\right\}_{i\in\{1,\ldots,N\},s\in\mathbb{Z}},t\right). \tag{6}$$

Therefore, there is a fundamental mathematical difference in state space between ODEs and pulse-coupled dynamical systems: In a system of ODEs [Eq. (1)], a state is fully specified by the values x_i, $i\in\{1,\ldots,N\}$, i.e., the system has an N-dimensional state space. On the contrary, a pulse-coupled system [Eq. (6)] at time t in general also depends on the set of all pulse generation times up to time t, $\left\{t_i^s\right\}_{t_i^s\le t}$ and thus its state at time t is fully specified by a tuple

$$y(t)=\left(x(t),\left\{t_i^s\right\}_{t_i^s\le t}\right), \tag{7}$$

that formally has infinite dimension. The additional dimensions that control the change in the velocity field F due to different pulse sequences $\left\{t_i^s\right\}$ enable the units to pass each other, avoiding the invariant sets of the symmetric system.

To illustrate that order preservation is broken in pulse coupled systems, we focus on pulse-coupled oscillators used to model, e.g., spiking neurons.[21,22] In general, the state of each of the N oscillators is specified by a single real variable, the "potential" $V_j(t)$, $j\in\{1,2,\ldots,N\}$, that evolves according to

$$\frac{d}{dt}V_j=G(V_j)+Z(V_j)\sum_{\substack{i=1\\i\neq j}}^{N}\sum_{s\in\mathbb{Z}}\varepsilon_{ji}K(t-t_i^s), \tag{8}$$

where the function $G(V)>0$ specifies the local dynamics, $Z(V)$, determines the response to incoming pulses, $K(t)$ is a causal ($K(t)\equiv 0$ for $t<0$) interaction kernel modeling the shape of the pulses and ε_{ji} is the coupling strength from oscillators i to j. When an oscillator i reaches the potential threshold $V_i\left(t_i^{s-}\right)=V_\Theta:=1$, its potential is reset to $V_i\left(t_i^s\right)=V_0:=0$ and a pulse is generated. If $Z(V)<0$ or $Z(V)>0$ for all V, there is a transformation of variables and coupling strengths to a system [Eq. (8)] with $Z=\text{const.}$[41] Thus, we set $Z(V)=1$ and consider homogenous inhibitory interactions $\varepsilon_{ij}=\varepsilon(1-\delta_{ij})$, $\varepsilon<0$. This makes the system symmetric under permutations of the indices.

Figure 2 illustrates that in this permutation symmetric system, the different oscillators may pass each other, i.e., the ordering is not preserved. Note that the dynamics of the oscillator variables $V_i(t)$ (except at the reset points) is continuous and differentiable and that there is no delay in the coupling. The breakdown of order preservation is thus caused by the pulsatile nature of the coupling.

IV. ANALYTICAL PREDICTION FOR THE BREAKDOWN OF ORDER PRESERVATION

Does pulse-coupling imply the breakdown of order conservation? Is the phenomenon restricted to specific choices of parameters or initial conditions? To access these questions, we analyze a class of pulse-coupled systems that is analytically tractable.

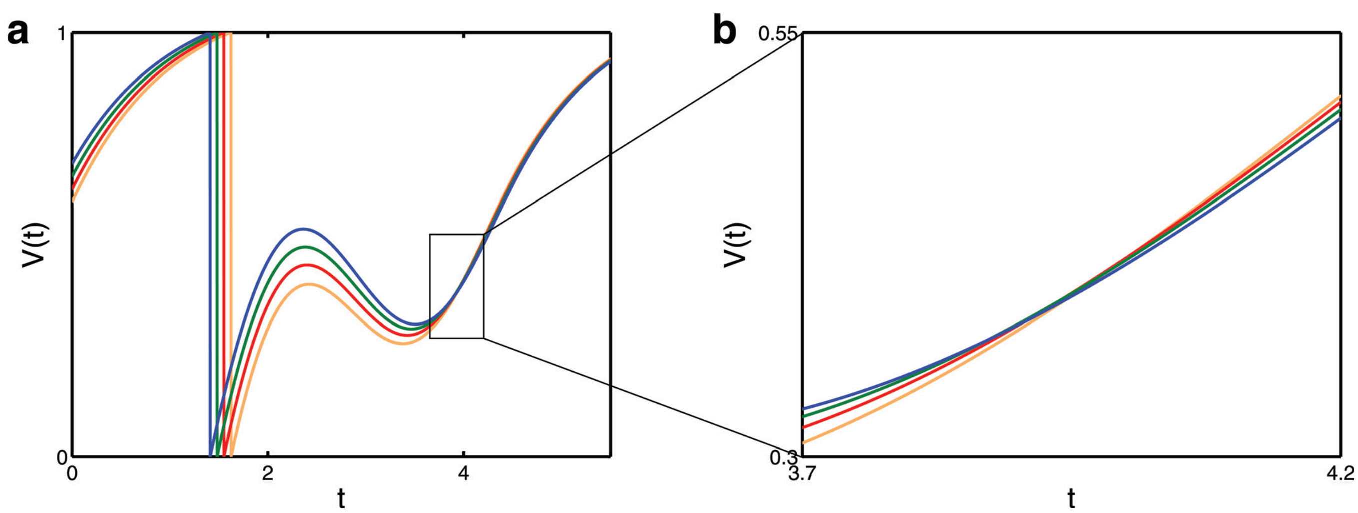

FIG. 2. (Color) Breakdown of order preservation in permutation symmetric pulse-coupled networks: (a) dynamics of $N=4$ pulse-coupled units [Eq. (8)] with $K(t)=\frac{1}{\sigma}\sin^2\left(\frac{\pi}{\sigma}t\right)$ for $t\in[0,\sigma]$ and $K(t)=0$ otherwise, $\sigma=3$, $G(V)=I-V$, $I=1.1$, coupling strength $\varepsilon=-1$, and initial condition near the synchronous state to which the dynamics converges. In the process of synchronization, the units pass each other; (b) magnification.

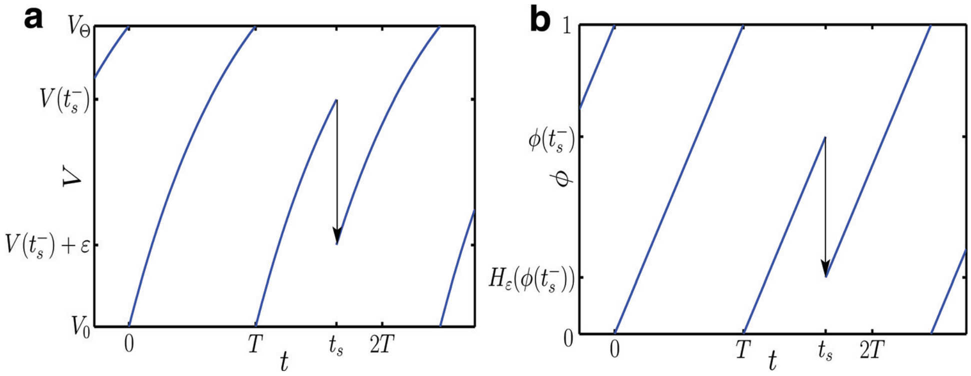

FIG. 3. (Color online) Model. Time evolution [Eq. (8)] of the potential $V(t)$ and the corresponding phase $\phi(t)$ of one oscillator [Eqs. (10) and (11)]: (a) the time evolution of the oscillator's potential, which evolves freely for one period and then receives an inhibitory pulse of strength ε at time t_s causing a potential jump from $V(t_s)$ to $V(t_s)+\varepsilon$; (b) the time evolution of the corresponding phase ϕ that jumps according to the transfer function (12) from $\phi^- = t_s/T$ to $\phi = H_\varepsilon(\phi^-)$.

A. Model and numerical simulations

We focus on pulse-coupled oscillators of the form (8) with an interaction kernel

$$K(t) = \delta(t-\tau_V). \tag{9}$$

Here, a pulse generated at time t is received after a delay time τ_V and then instantaneously increases the potentials of the oscillators. This approximation is valid in the limit where the time scale of the interaction due to the pulses is much faster than the period of intrinsic oscillation.

The system has an equivalent phase description that simplifies the analysis: as $G>0$, the free ($\varepsilon=0$) solution $\tilde{V}(t)$ of Eq. (8) starting with initial condition $\tilde{V}(0)=0$ increases monotonically and reaches the threshold after a time T, i.e., $\tilde{V}(T^-)=1$. This solution defines a bijective map between potential and phase representation

$$U : [\phi_-, 1) \to (-\infty, 1]; \phi \mapsto U(\phi) := \tilde{V}(\phi T),$$

called the rise function. Here, ϕ_- is a lower bound of the phase and possibly $\phi_- = -\infty$, cf. Refs. 32, 33, 42, 43. In the phase representation, the free dynamics simplifies to

$$\frac{d\phi_j}{dt} = 1. \tag{10}$$

When ϕ_i reaches its phase threshold $\phi_i(t^-)=1$, it is reset to $\phi_i(t) := 0$ and a pulse is generated that is received by all other oscillators j after a rescaled delay time $\tau = \tau_{\mathrm{v}}/T$, where it causes an instantaneous phase jump

$$\phi_j(t+\tau) = H_\varepsilon\big(\phi_j((t+\tau)^-)\big) \tag{11}$$

mediated by the interaction function

$$H_\varepsilon(\phi) = U^{-1}(U(\phi)+\varepsilon). \tag{12}$$

The dynamics of single units of this system is illustrated in Figure 3. For later use, we define a pure phase shift by

$$S_\Delta(\phi) = \phi + \Delta.$$

In such network dynamical systems, the synchronous state, where all oscillators have the same phase $\phi_i(t) = \phi_j(t) =: \phi_0(t)$ for all $t \in \mathbb{R}$ and all $i,j \in \{1,\ldots,N\}$, exists due to permutation symmetry and is linearly and asymptotically stable for inhibitory interactions ($\varepsilon < 0$) and concave rise functions ($U'' < 0$).[28,29]

Numerical simulations of such systems suggest that in the process of synchronization oscillators can overtake repeatedly for certain parameters while for others the ordering is conserved (cf. Figure 4). Systematic numerical analysis uncovers that the breakdown of order preservation depends on the system parameters only (cf. Figs. 4 and 5).

B. Analysis

In this subsection, we concentrate on order preservation close to the synchronous state. In the synchronous state $\phi_i(t) = \phi_0(t)$, all pulses are simultaneously sent when the phases reach the threshold, say at time $t=0$ and reset to $\phi_s(0)=0$. All pulses are simultaneously received at time $t=\tau$, leading to a phase jump to $\phi_0(\tau) = H_{(N-1)\varepsilon}(\tau)$. Assume now that the system is close to the synchronous state. Without a loss of generality, we label the oscillators such that initially

$$1 > \phi_1 \geq \phi_2 \geq \ldots \geq \phi_N > 0\,. \tag{13}$$

To study whether some oscillators pass each other, we switch to a different coordinate system $\{\phi_1, \Delta_{1,2}, \Delta_{2,3}, \ldots, \Delta_{N-1,N}\}$ that encodes for the phase differences $\Delta_{i,i+1} = \phi_i - \phi_{i+1}$ between the oscillators i and $i+1$, $i \in \{1,2,\ldots,N-1\}$. Using the ordering [Eq. (13)], we have $\Delta_{i,i+1} \geq 0$. The original phases are recovered from these relative coordinates via $\phi_i = \phi_1 - \sum_{j=1}^{i-1} \Delta_{j,j+1}$. We assume that we are sufficiently close to the synchronous state such that the total phase spread $\Delta_{1,N} := \sum_{i=1}^{N-1} \Delta_{i,i+1}$ satisfies $\Delta_{1,N} < \min\{\frac{\tau}{2}, \frac{1-\tau}{2}\}$, i.e., in this perturbed synchronous state, first all oscillators generate a pulse and afterwards all pulses are received. Assuming that the first pulse is generated at $t=0$ ($\phi_1(0^-)=1$), the second pulse is generated at time $t = \Delta_{1,2}$, etc. In general, the k-th pulse is generated at $t = \sum_{i=1}^{k-1} \Delta_{i,i+1}$, i.e., the ith inter-pulse interval is exactly given by the phase difference $\Delta_{i,i+1}$. Thus, the reception of the individual pulses mediated by the interaction function H_ε alternates with phase shifts mediated by $S_{\Delta_{i,i+1}}$. The reception of the pulses starts at $t=\tau$ and the phases of oscillators i and $i+1$ after reception of all pulses at time $t = \tau + \Delta_{1,N}$ are (cf. Appendix for details)

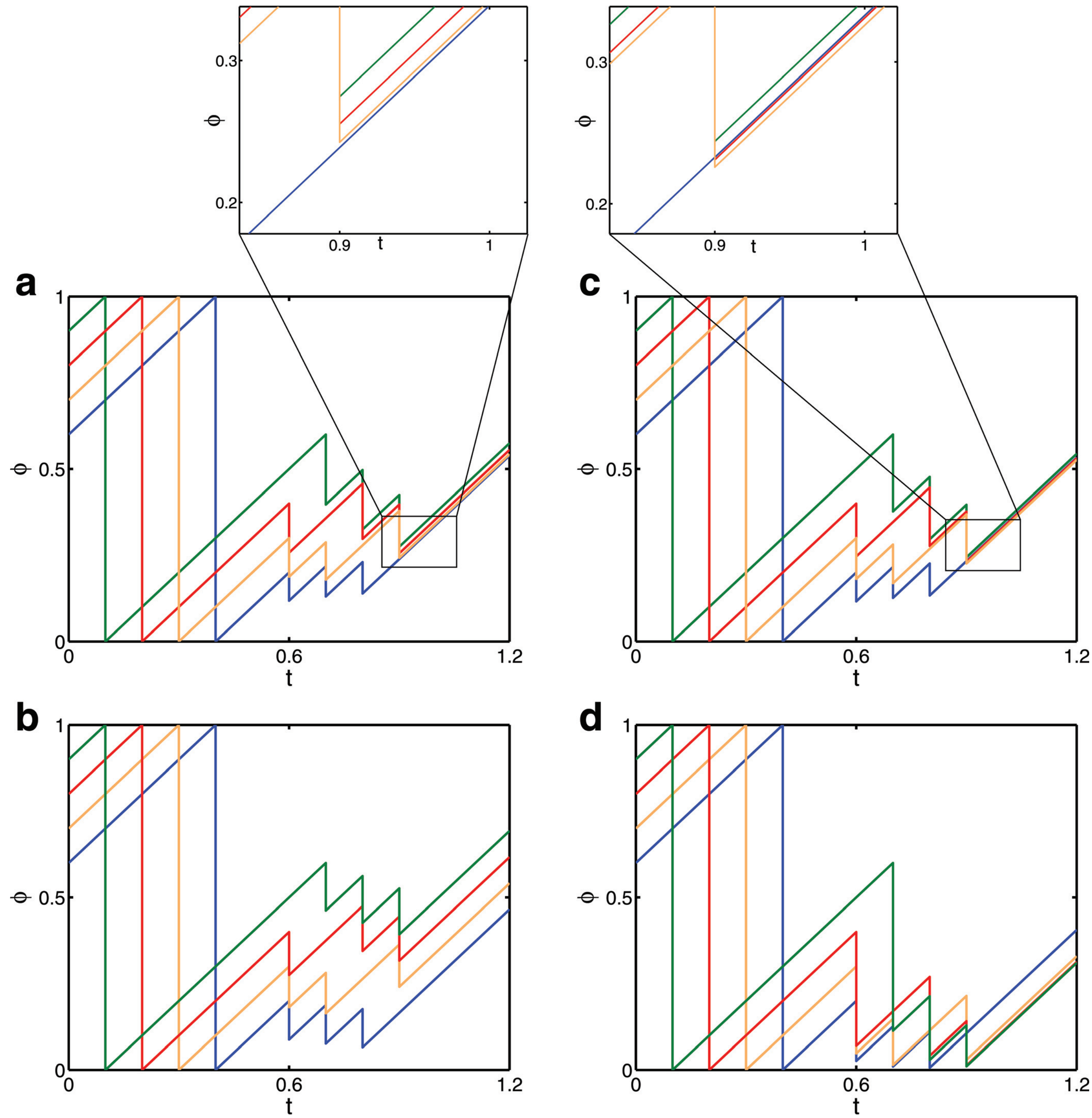

FIG. 4. (Color) Order preservation and its breakdown in the time evolution of a network of $N=4$ pulse-coupled oscillators [Eqs. (10) and (11)] with $\tau=0.5$, $U(\phi)=U_b(\phi)$ [Eq. (21)]. The phases of all oscillators (color-coded) are shown vs. time t. Insets show magnifications as indicated: (a) time evolution for $b=2.7$ and $\varepsilon=-0.13$ with approach to stable synchronous state where the ordering of the oscillators is conserved; (b) similar dynamics that synchronize more slowly for $b=0.5$ and $\varepsilon=-0.13$; (c) time evolution for $b=3.2$ and $\varepsilon=-0.13$ shows that oscillators pass each other; (d) similar dynamics with slower synchronization for $b=3.8$ and $\varepsilon=-0.4$. Notice that in (d) all oscillators exchange their ordering, while in (c) only the blue oscillator overtakes the red and yellow oscillator.

$$
\begin{aligned}
\phi_i(\tau+\Delta_{1,N}) &= H_\varepsilon \circ S_{\Delta_{N-1,N}} \circ \ldots \circ H_\varepsilon \circ S_{\Delta_{i+1,i+2}} \circ H_\varepsilon \circ S_{\Delta_{i,i+1}} \circ \\
&\quad \times S_{\Delta_{i-1,i}} \circ \ldots \circ S_{\Delta_{2,3}} \circ H_\varepsilon \circ S_{\Delta_{1,2}} \circ H_\varepsilon(\phi_i(\tau)) \\
\phi_{i+1}(\tau+\Delta_{1,N}) &= H_\varepsilon \circ S_{\Delta_{N-1,N}} \circ \ldots \circ H_\varepsilon \circ S_{\Delta_{i+1,i+2}} \circ S_{\Delta_{i,i+1}} \circ H_\varepsilon \circ \\
&\quad \times S_{\Delta_{i-1,i}} \circ \ldots \circ S_{\Delta_{2,3}} \circ H_\varepsilon \circ S_{\Delta_{1,2}} \\
&\quad \times \circ H_\varepsilon(\phi_i(\tau)-\Delta_{i,i+1}).
\end{aligned}
\tag{14}
$$

Note that as we exclude the self-coupling, H_ε is missing between $S_{\Delta_{i,i+1}}$ and $S_{\Delta_{i-1,i}}$ for oscillator i, etc. The following dynamics are pure phase shifts which do not change the phase differences. Thus, after one cycle of N pulse generations and receptions, the return map for $\Delta_{i,i+1}$ is given by

$$\Delta^r_{i,i+1} = \phi_i(\tau+\Delta_{1,N}) - \phi_{i+1}(\tau+\Delta_{1,N}).$$

As the $\Delta_{i,i+1}$ are small, we only keep terms linear in $\Delta_{i,i+1}$ in Eq. (14) which yields

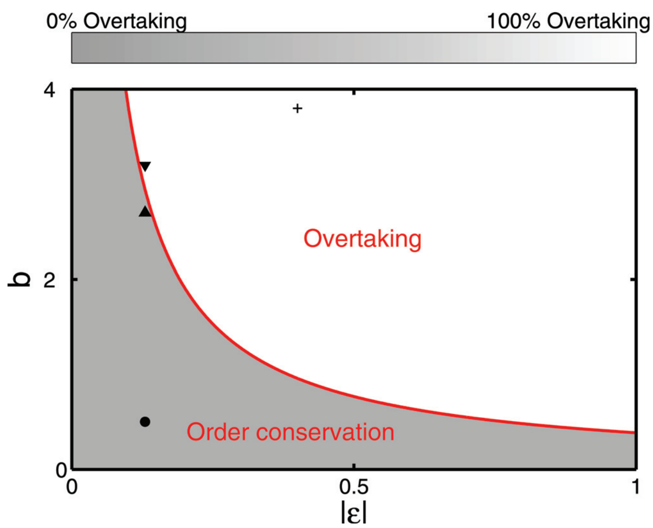

FIG. 5. (Color online) Parameter dependence of the transition between order conservation and its breakdown in b - ε -parameter space of the pulse-coupled network used in Figure 4. For each parameter set (ε, b) ($b \in [0.04, 4.00]$ in steps of $\Delta b = 0.04$, $\varepsilon \in [-1.0, -0.01]$ in steps of $\Delta\varepsilon = 0.01$), the system was initialized 250 times with uniform distributed phases $\phi_i \in [0, 0.1]$. Shown is the percentage of these runs where the ordering is not conserved. The solid red line, given by Eq. (22), indicates the theoretically predicted transition between the regimes where the order is conserved or units pass each other. The parameter values used for Figure 4 for the cases of order conservation (•, ▲) and overtaking (+, ▼) are indicated. Because eigenvalues are close to zero near the transition line, the dynamics synchronize faster for ▲ and ▼.

$$\begin{aligned}\phi_i(\tau + \Delta_{1,N}) \doteq{} & H_{(N-1)\varepsilon}(\tau) + \sum_{k=1}^{i-1} \alpha_k \Delta_{k,k+1} + \sum_{k=i+1}^{N-1} \beta_k \Delta_{k,k+1} \\ & + H'_{(N-i-1)\varepsilon}(H_{i\varepsilon}(\tau))\Delta_{i,i+1}, \\ \phi_{i+1}(\tau + \Delta_{1,N}) \doteq{} & H_{(N-1)\varepsilon}(\tau) + \sum_{k=1}^{i-1} \alpha_k \Delta_{k,k+1} + \sum_{k=i+1}^{N-1} \beta_k \Delta_{k,k+1} \\ & + H'_{(N-i-2)\varepsilon}\left(H_{(i+1)\varepsilon}(\tau)\right)\Delta_{i,i+1} \\ & - H'_{(N-1)\varepsilon}(\tau)\Delta_{i,i+1},\end{aligned} \tag{15}$$

with $\alpha_k = \beta_k - H'_{(N-1)\varepsilon}(\tau)$ and $\beta_k = H'_{(N-k-1)\varepsilon}(H_{k\varepsilon}(\tau))$. Hence for the return map of the phase differences, we obtain

$$\begin{aligned}\Delta^r_{i,i+1} = \Big[& H'_{(N-i-1)\varepsilon}(H_{i\varepsilon}(\tau)) - H'_{(N-i-2)\varepsilon}\left(H_{(i+1)\varepsilon}(\tau)\right) \\ & + H'_{(N-1)\varepsilon}(\tau)\Big]\Delta_{i,i+1}.\end{aligned} \tag{16}$$

Note that in this linear approximation, the phase difference after return $\Delta^r_{i,i+1}$ depends only on the initial phase difference $\Delta_{i,i+1}$ and no other $\Delta_{k,k+1}$, $k \neq i$, i.e., the phase differences $\Delta_{j,j+1}$ provide the coordinates in which the linearized dynamics close to the synchronous state is diagonal and the prefactors

$$\lambda_i = H'_{(N-i-1)\varepsilon}(H_{i\varepsilon}(\tau)) - H'_{(N-i-2)\varepsilon}\left(H_{(i+1)\varepsilon}(\tau)\right) + H'_{(N-1)\varepsilon}(\tau), \tag{17}$$

in Eq. (16) are the corresponding eigenvalues.

If one of these eigenvalues is negative $\lambda_i < 0$, the phase difference $\Delta_{i,i+1}$ changes sign under the return map and thus the ordering of oscillators i and $i+1$ is exchanged. Thus, for order preservation, we must have $\lambda_i > 0$ for all $i \in \{1, 2, \ldots, N-1\}$. Using

$$\frac{dH_\varepsilon(\phi)}{d\phi} = \frac{U'(\phi)}{U'(H_\varepsilon(\phi))} \tag{18}$$

and the group property of the transfer functions $H_{\varepsilon_1} \circ H_{\varepsilon_2}(\phi) = H_{\varepsilon_1+\varepsilon_2}(\phi)$, we obtain the conditions

$$\frac{U'[H_{(i+1)\varepsilon}(\tau)]}{U'[H_{(N-1)\varepsilon}(\tau)]} - \frac{U'[H_{i\varepsilon}(\tau)]}{U'[H_{(N-1)\varepsilon}(\tau)]} < \frac{U'(\tau)}{U'[H_{(N-1)\varepsilon}(\tau)]}. \tag{19}$$

As $U'(\phi) > 0$, we can multiply by the denominator and arrive at the following result:

Proposition 1: Prediction for the Breakdown of Order Preservation: In pulse-coupled oscillator networks of the form in Eqs. (8) and (9), the set of inequalities

$$U'[H_{i\varepsilon}(\tau)] - U'[H_{(i-1)\varepsilon}(\tau)] < U'(\tau) \quad \text{for all } i \in \{1, \ldots, N-1\} \tag{20}$$

constitutes necessary and sufficient conditions for order preservation close to the synchronous state. If one or more of the conditions [Eq. (20)] is violated, oscillators pass each other for sufficiently small perturbations around the synchronous state.

Remark 1: For instance, if Eq. (20) is not fulfilled for $i = i_1$, Δ_{i_1,i_1+1} changes its sign under the return map and thus for oscillators satisfying the initial ordering [Eq. (13)], the (i_1+1)th oscillator will overtake the i_1th oscillator. The derivation [Eqs. (13) and (14)] of Eq. (20) yields an intuitive understanding of this inequality: The term on the right hand side, $U'(\tau)$, accounts for how the initial phase difference $\Delta_{i,i+1}$ changes due to the reception of all pulses. The larger the term, the less the oscillators synchronize which makes it harder for them to pass each other. The two terms on the left hand side arise because unit i does not receive the ith pulse, while unit $i+1$ does not receive the $(i+1)$th pulse as self-coupling is excluded. The difference between these two terms leads to a change in phase difference which if large makes it easier for the $(i+1)$th unit to pass unit i.

Remark 2: It is important to note that conditions (20) ensuring order conservation depend only on U, τ, and ε but not on the perturbation vector itself. Therefore, order preservation and its breakdown are intrinsic properties of the system, at least close to synchrony.

For convex and for concave rise functions, the conditions (20) are monotonic in the sense that once a single condition ($i = N-1$ for concave U or $i = 1$ for convex U) is satisfied, all others are, too. Using the rise function[15]

$$U_b(\phi) = \frac{1}{b}\ln\left[1 + (e^b - 1)\phi\right], \tag{21}$$

which is concave for $b > 0$ and convex for $b < 0$, the conditions (20) for order conservation explicitly become

$$1 < e^{\varepsilon b} + e^{i\varepsilon b} \tag{22}$$

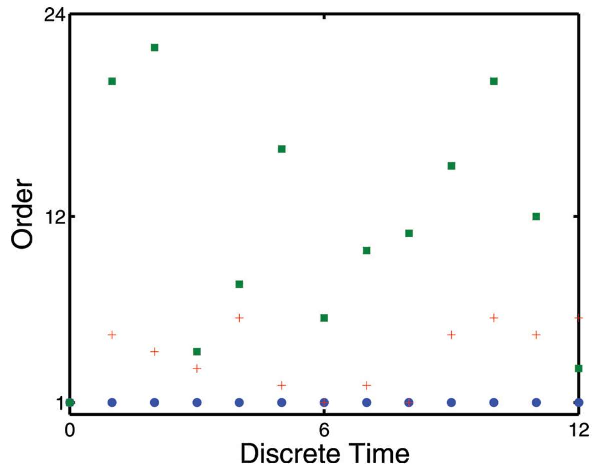

FIG. 6. (Color online) Dynamics of the ordering of the oscillator phases ($N = 4$, $\tau = 0.5$, $\varepsilon = -0.13$). Without loss of generality, we labeled all possible orderings of the oscillators from 1 to $4! = 24$. We start the system close to the synchronous state and plot the ordering index at discrete times just after the reception of all pulses of one cycle (return map) for $b = 2.7$ (•), $b = 3.2$ (+), and $b = 4.0$ (■).

where for $b > 0$, $i = N - 1$, and $b < 0$, $i = 1$. Interestingly, these conditions are independent of the delay τ, because the transfer function for $U = U_b$ has the invariance property $H_\varepsilon(\phi) - H_\varepsilon(\psi) = H_\varepsilon(t + \phi) - H_\varepsilon(t + \psi)$ for all t and ϕ, ψ, $\phi + t$, and $\psi + t$ in the domain of H_ε. This explicitly shows that the delay is not essential for whether or not oscillators overtake.

The explicit prediction [Eq. (22)] for the breakdown of order preservation is illustrated in Figure 5. Condition (22) divides the parameter-space into two regions, one where oscillators pass each other repeatedly and one where the ordering is preserved. Numerical simulations agree very well with our theoretical prediction.

Note that the subset of the eigenvalues λ_i which are negative (i.e., for which indices i the parameter conditions (20) do not hold) determines the possible permutations among the oscillators in one cycle. For instance, Figure 6 shows the dynamics for three different parameter values of b in a $N = 4$ network. It illustrates that with increasing b more and more permutations become possible, increasing the disorder in the system. For $b = 2.7$, all conditions (22) are satisfied, and the ordering of the oscillators is preserved. For $b = 3.2$, condition (22) still holds for $i \in \{1, 2\}$ but not for $i = 3$. Thus, the first three oscillators' ordering is preserved, but the oscillator with the smallest phase can pass the other oscillators and because condition (20) is sufficient for overtaking, it must at least pass the second last oscillator. For $b = 4.0$, the condition is violated for $i \in \{2, 3\}$ and thus only the first two oscillators keep their ordering while the other oscillators overtake.

We remark further that we considered local dynamics converging towards the synchronous state, but in fact we assumed only the existence of a fully synchronous state and not its stability. Thus, in principle, overtaking is possible also during a desynchronization process from an unstable synchronous state. However, in the class of systems studied in this section, the ordering is necessarily conserved close to an unstable synchronous state: For instance, for systems with convex rise function and inhibitory interactions, $\varepsilon < 0$, the synchronous state is unstable and the oscillators locally desynchronize.[44,45] Due to convexity $U'' > 0$, we obtain

$$U'[H_{i\varepsilon}(\tau)] - U'[H_{(i-1)\varepsilon}(\tau)] < 0, \tag{23}$$

for all i, and as $U'(\tau) > 0$, the oscillators cannot pass each other according to Eq. (20).

Let us shortly summarize our results: We found in a large class of pulse-coupled systems that overtaking occurs depending on the parameters but not on the initial conditions, where we derived conditions predicting the breakdown of order preservation analytically to first order approximation. We found that the phenomenon of overtaking is insensitive to parameter changes and thus robust.

V. DIFFERENT AVERAGE FREQUENCIES IN PERMUTATION-SYMMETRIC SYSTEMS WITH PULSE-COUPLING

So far, we have demonstrated that order preservation breaks down in a class of pulse-coupled oscillator networks converging towards the periodic orbit displaying full synchrony. Here, we identify an example where oscillators may also pass each other if their dynamics is not close to synchrony. Interestingly, in this permutation-symmetric network of identical oscillators the combination of desynchronizing dynamics and overtaking leads to different average frequencies of the oscillators.

We consider the system of phase oscillators [Eq. (8)] with $G(\phi) = \omega$ where we substitute V by the phase ϕ. Here, ω is the intrinsic frequency of the oscillators and $Z(\phi)$ may be viewed as their phase response curve.[46] Equation (8) thus reads

$$\frac{d}{dt}\phi_j = \omega + Z(\phi_j)\sum_{i,s}\varepsilon_{ji}K\left(t - t_i^s\right). \tag{24}$$

Similarly to Sec. IV, the phase ϕ_j is defined on the interval $[0, 1)$ and whenever the phase of a unit j reaches the threshold $\phi_j(t_j^{s-}) = 1$, it is reset to $\phi_j(t_j^s) = 0$ and a pulse is generated.

We focus on a system of two identical phase oscillators $N = 2$ coupled symmetrically, $\varepsilon_{ij} = (1 - \delta_{ij})\varepsilon$, with coupling strength $\varepsilon = 11.7$, a phase response

$$Z(\phi) = \sin(2\pi\phi)e^{-3\phi} \tag{25}$$

and a normalized alpha function for the pulse

$$K(t) = \Theta(t)30(\exp(-20t) - \exp(-60t)) \tag{26}$$

(cf. Figure 7).

With this choice of the phase response, the two oscillators do not synchronize and repeatedly pass each other. Figure 8 shows an example where one oscillator generates four pulses during one period of the dynamics while the other one generates only three. More generally, we find that the dynamics of Eq. (24) with a phase response similar to Eq. (25) and strong enough coupling typically converges to a periodic

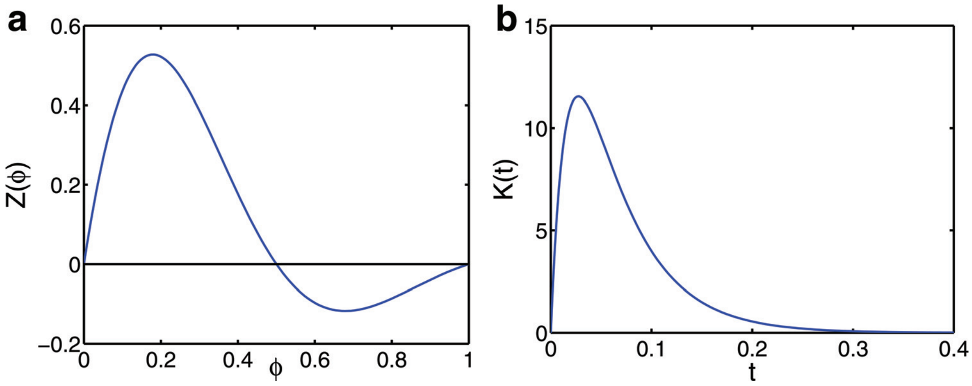

FIG. 7. (Color online) (a) Phase response curve [Eq. (25)] and (b) interaction function [Eq. (26)] used in the simulations shown in Figure 8.

state in which one oscillator generates n pulses while the other oscillator generates m, with $n \neq m$, i.e., the system shows $n : m$ locking. Thus, in this permutation-symmetric network, one of the oscillators has a higher average frequency than the other, and only the initial conditions determine which of the oscillators exhibits the higher frequency and thus a larger winding number.

These findings for pulse-coupled cell networks are in stark contrast to the behavior obtained in similar systems with time-continuous coupling analyzed in Refs. 1 and 2. There it was shown that if the polydiagonals are invariant, the ordering of the oscillators cannot change, and thus all oscillators necessarily have identical average frequencies and equal winding numbers.

We also note that the average frequencies of the oscillators are determined by the initial conditions. Thus, these symmetric pulse-coupled systems are capable of storing information about their initial state in terms of a rate code. Moreover, due to symmetry, there is no bias for one of the frequency-locked states and all inputs are stored in a fully symmetric way.

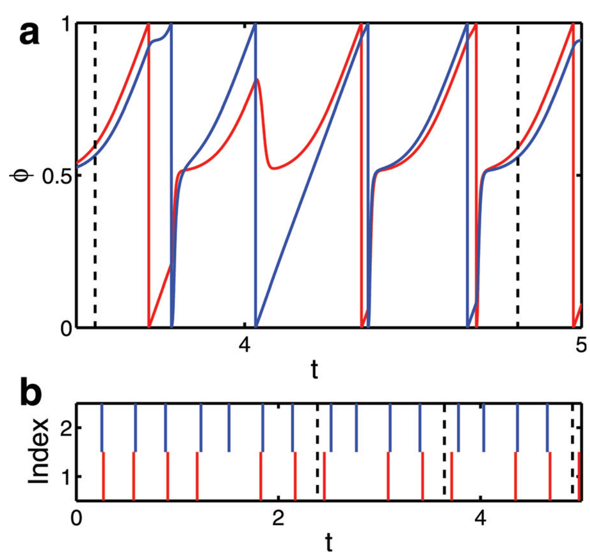

FIG. 8. (Color) Symmetrically pulse-coupled identical oscillators with different average frequencies: (a) dynamics of $N = 2$ phase oscillators [Eqs. (24)–(26)] with $\omega = 3$ and $\varepsilon = 11.7$ numerically integrated using Euler's method with step size $\Delta t = 10^{-4}$. Dashed lines indicate the beginning of one period of a 4 : 3 frequency locked state; (b) pulse generation times of the two oscillators in (a) indicated by vertical bars showing the convergence of the dynamics to the periodic 4 : 3 frequency locked state from initial condition $\phi_1 = 0.2$, $\phi_2 = 0.24$. By permutation symmetry of the network, the exchange of the initial phases leads to 3 : 4 frequency locked state.

The key to obtaining different average frequencies in the symmetric system above is related to the question of how two oscillators in a pulse-coupled system can pass each other and additionally increase their phase difference. The form of the phase response function (25) achieves simultaneously desynchronization and overtaking, as it desynchronizes the two oscillators right after the first oscillator has generated a pulse. This is due to the negative part of $Z(\phi)$ at large ϕ (see Figure 7). When the second oscillator finally reaches the threshold and its phase is reset to zero, the phase velocity strongly increases as the response $Z(\phi)$ becomes very large for ϕ close to zero and thus the oscillator may pass the first oscillator. By then, this oscillator has already achieved a large enough phase where the phase response curve becomes negative again and thus the reception of the pulse forces its phase to be pulled towards the phase ψ, the zero crossing of the phase response $Z(\psi) = 0$. In total, this increases the phase difference between both oscillators while they pass each other.

VI. CONCLUSIONS

Symmetry in dynamical systems forces the existence of sets that are invariant under the dynamics.[10,47] In standard dynamical systems, such as ordinary differential equations defining a smooth flow, trajectories cannot cross such invariant manifolds. For permutation symmetric dynamical systems consisting of one-dimensional units such as homogenous globally time-continuously coupled networks of phase oscillators,[39,48,49] this implies that an initial ordering of the units is conserved for all future times. As a consequence, the oscillators necessarily have identical average frequencies.[1,2] It is quite tempting to apply this intuition also to permutation symmetric systems with pulse-coupling.

However, as shown here, pulse-coupling removes the barrier property of the invariant sets and the oscillators can pass each other. We have demonstrated the breakdown of order preservation in different prototypical model systems. In a particular class of pulse-coupled oscillator networks, the breakdown was explained analytically. We found that order conservation only depends on the system parameters but not on the initial conditions.

The breakdown of order preservation is caused by the pulsatile (discrete-time) coupling. If a trajectory in any dynamical system leads onto an invariant manifold, it will stay on this manifold for all future times. In systems with pulse-coupling, the state space dimension is increased compared to time-continuous coupling and thus trajectories can avoid the lower dimensional invariant manifolds when two units pass each other by moving around them in the additional dimensions. In the lower dimensional phase space that coincides with the time-continuous system, it appears as if the trajectories cross the invariant manifolds.

We stress that inhomogeneous systems without permutation symmetry do not show order preservation in general.[50,51] Here, we analyzed the effect of how pulse-coupling provides a mechanism that breaks order preservation in permutation symmetric systems. Possible other factors that lead to this phenomenon in symmetric systems[1,2] are, e.g., interaction delays that also increase the system's dimension or instantaneous and discontinuous couplings. Also, strong inhibitory coupling in combination with an extended phase representation can lead to overtaking:[1,52] In Ref. 1, the state space of the uncoupled oscillators consists of the ordinary positive phase values $\phi \in S^1 = [0,1]/0 \sim 1$ (0 and 1 are identified) but strong inhibitory coupling causes the phase to decay and can lead to negative phases $\phi < 0$, i.e., the state space is extended by the negative real line $\mathbb{R}^-$ that is attached to S^1 at 0. In this case oscillators that receive strong inhibitory coupling can get trapped in the negative phase part while others pass them on S^1. The mechanism of overtaking revealed in the current work is markedly different: It does not require negative phases and the breakdown of order preservation is solely caused by the pulse-coupling. This may also explain overtaking in other systems with similar types of pulse-coupling as, e.g., in Refs. 53 and 54, where the interaction is determined by the discrete times of threshold crossings from below and above.

Finally, we identified permutation symmetric pulse-coupled oscillator networks where the identical units have different average oscillation frequencies. For two oscillators, we find different $n:m$ frequency lockings with $n \neq m$ and thus non-identical winding numbers. Further, the average frequencies of the individual oscillators in these systems may be varied by varying the initial conditions. Thus, the system is capable of coding information about its initial state via the different rates of the oscillators. Due to the permutation symmetry of the system, the basins of attraction are symmetric as well, such that the information about the initial state is coded in a completely symmetric way. This might have useful applications to systems in engineering and neuroscience when faced with symmetric information sources.

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APPENDIX: RETURN MAP FOR PHASE DIFFERENCES

Here, we calculate the change of the phase differences $\Delta_{i,i+1}$ of the system's dynamics for one cycle, i.e., the time evolution until oscillator 1 has returned to its original phase (cf. Table I and Eq. (14)). Because of the oscillators' simple intermediate dynamics $d\phi_i/dt = 1$, we just consider their state at single event times: the pulse-sending times t_s^i of the single oscillators and the times t_r^i, when the other oscillators

TABLE I. The phases of the N units directly after the events of the sequence $s_1 \to s_2 \to \ldots \to s_N \to r_1 \to r_2 \to \ldots \to r_n$

Event	t	ϕ_1	ϕ_2	...
s_1	0	$1 \to 0$	$1-\Delta_{1,2}$	...
s_2	$\Delta_{1,2}$	$\Delta_{1,2}$	$1 \to 0$	...
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
s_N	$1-\Delta_{1,N}$	$\Delta_{1,N}$	$\Delta_{2,N}$	...
r_1	τ	$\phi_1(\tau) = \tau$	$\phi_2(\tau) = H_\varepsilon(\tau - \Delta_{1,2})$	...
r_2	$\tau + \Delta_{1,2}$	$\phi_1(\tau + \Delta_{1,2}) = H_\varepsilon \circ S_{\Delta_{1,2}}(\phi_1(\tau))$	$\phi_2(\tau + \Delta_{1,2}) = S_{\Delta_{1,2}}(\phi_2(\tau))$	...
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
r_N	$\tau + \Delta_{1,N}$	$\phi_1(\tau + \Delta_{1,N}) = H_\varepsilon \circ S_{\Delta_{N-1,N}}(\phi_1(\tau + \Delta_{1,N-1}))$	$\phi_2(\tau + \Delta_{1,N}) = H_\varepsilon \circ S_{\Delta_{N-1,N}}(\phi_1(\tau + \Delta_{1,N-1}))$	...

Event	t	ϕ_i	...	ϕ_N
s_1	0	$1-\Delta_{1,i}$	...	$1-\Delta_{1,N}$
s_2	$\Delta_{1,2}$	$1-\Delta_{2,i}$	...	$1-\Delta_{2,N}$
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
s_N	$\Delta_{1,N}$	$\Delta_{i,N}$	...	$1 \to 0$
r_1	τ	$\phi_i(\tau) = H_\varepsilon(\tau - \Delta_{1,i})$		$\phi_i(\tau) = H_\varepsilon(\tau - \Delta_{1,N})$
r_2	$\tau + \Delta_{1,2}$	$\phi_i(\tau + \Delta_{1,2}) = H_\varepsilon \circ S_{\Delta_{1,2}}(\phi_i(\tau))$	...	$\phi_N(\tau + \Delta_{1,2}) = H_\varepsilon \circ S_{\Delta_{1,2}}(\phi_N(\tau))$
$\vdots$	$\vdots$	$\vdots$	$\vdots$	$\vdots$
r_N	$\tau + \Delta_{1,N}$	$\phi_i(\tau + \Delta_{1,N}) = H_\varepsilon \circ S_{\Delta_{N-1,N}}(\phi_i(\tau + \Delta_{1,N-1}))$		$\phi_N(\tau + \Delta_{1,N}) = H_\varepsilon \circ S_{\Delta_{N-1,N}}(\phi_N(\tau + \Delta_{1,N-1}))$

receive these pulses. We label these events s_i, when oscillator i sends a pulse, and r_i, when the other oscillators receive the pulse of oscillator i.

To calculate the phases at these times, we first add the time difference between the current and the previous event to an oscillator's phase by applying the shift $S_\Delta(\phi) = \phi + \Delta$ to all oscillators' phases. Here, Δ is determined by the time to the next event, either $\Delta = \min_i\{1-\phi_i\}$ for sending events s_i or $\Delta = \min_i\{\tau - \phi_i\}$ for receiving events r_i. In the case of a pulse-sending event s_i, we reset the phase of oscillator i. If we have a pulse-reception event r_i, we apply the transfer function $H_\varepsilon(\phi)$ to all phases except the phase of oscillator i as there is no self-coupling ($\varepsilon_{ij} = (1-\delta_{ij})\varepsilon$).

Defining $\Delta_{i,j} = \sum_{k=j}^{i-1} \Delta_{k,k+1}$, we start at time $t = 0$ with initial state $\phi_i(0) = 1 - \Delta_{1,i}$. As all $\Delta_{i,i+1} > 0$, oscillator $i = 1$ generates the first pulse, then oscillator $i = 2$, etc. The reception times are locked to the pulse-sending times via the delay $\tau(t_r^i = t_s^i + \tau)$. Using the condition $\Delta_{1,N} < \min\left\{\frac{\tau}{2}, \frac{1-\tau}{2}\right\}$, we have the event sequence

$$s_1 \to s_2 \to \ldots \to s_N \to r_1 \to r_2 \to \ldots \to r_N. \qquad \text{(A1)}$$

At time $t = \tau + \Delta_{1,N}$, all pulses of this sequence have been received. Taken together, this results in the dynamics shown in event Table I.

The remainder of the time evolution until the next pulse generation event is a pure phase shift $S_{\tilde{\Delta}}$ where $\tilde{\Delta} = 1 - \max_i\left\{\phi_i\left(\tau + \Delta_{1,N}\right)\right\}$ which does not change the phase differences $\Delta_{i,i+1}$. We thus arrive at the expression (14) for the phase differences after return.

[1] M. Golubitsky, K. Josić, and E. Shea-Brown J. Nonlinear. Sci. **16**, 201 (2006).
[2] K. Parwani and K. Josić, Chaos **16**, 015115 (2006).
[3] E. Noether, Nachr. König. Ges. Wiss. Göttingen, Math-phys. Kl. **1918**, 235 (1918); E. Noether and M. A. Tavel, Transport. Theory Statist. Phys. **1**, 186 (1971) [English translation].
[4] M. Golubitsky and I. Stewart, *The Symmetry Perspective* (Birkhäuser Verlag, Basel, 2002).
[5] M. Golubitsky, I. Stewart, and D. G. Schaeffer, *Singularities and Groups in Bifurcation Theory*, Vol. II (Springer Verlag, New York, 1988).
[6] P. Chossat and R. Lauterbach, *Methods in Equivariant Bifurcations and Dynamical Systems* (World Scientific, Singapore, 2000).
[7] M. Krupa, J. Nonlinear Sci. **7**, 129 (1997).
[8] P. Ashwin and M. Timme, Nature **436**, 36 (2005).
[9] C. Kirst and M. Timme, Phys. Rev. E **78**, 065201 (2008).
[10] I. Stewart, M. Golubitsky, and M. Pivato, SIAM J. Appl. Dyn. Syst. **2**, 609 (2003).
[11] P. Ashwin and J. Borresen, Phys. Rev. E **70**, 026203 (2004).
[12] P. Aswhin and J. W. Swift, J. Nonlinear Sci. **2**, 69 (1992).
[13] P. Ashwin, G. Orosz, J. Wordsworth, and S. Townley, SIAM J. Appl. Dyn. Syst. **6**, 728 (2007).
[14] C. Kirst, T. Geisel, and M. Timme, Phys. Rev. Lett. **102**, 068101 (2009).
[15] R. E. Mirollo and S. H. Strogatz, SIAM J. Appl. Math. **50**, 1645 (1990).
[16] P. Ashwin and M. Timme, Nonlinearity **18**, 2035 (2005).
[17] P. Goel and B. Ermentrout, Physica D **163**, 191 (2002).
[18] J. Buck and E. Buck, Sci. Am. **234**, 74 (1976).
[19] J. Buck, Q. Rev. Biol. **63**, 265 (1988).
[20] T. J. Walter, Science **166**, 891 (1969).
[21] F. Rieke, D. Warland, R. de Ruyter van Steveninck, and W. Bialek, *Spikes: Exploring the Neural Code* (MIT, Cambridge, USA, 1999).
[22] W. Maass and C.M. Bishop, *Pulsed Neural Networks* (MIT, Cambridge, USA, 1995).
[23] A. V. M. Herz and J. J. Hopfield, Phys. Rev. Lett. **75**, 1222 (1995).
[24] M. Timme, F. Wolf, and T. Geisel, Phys. Rev. Lett. **89**, 154105 (2002).
[25] M. Timme, F. Wolf, and T. Geisel, Chaos **13**, 377 (2003).
[26] H. Broer, K. Efstathiou, and E. Subramanian, Nonlinearity **21**, 13 (2008).
[27] H. Broer, K. Efstathiou, and E. Subramanian, Nonlinearity **21**, 1385 (2008).
[28] M. Timme, F. Wolf, and T. Geisel, Phys. Rev. Lett. **89**, 258701 (2002).
[29] M. Timme and F. Wolf, Nonlinearity **21**, 1579 (2008).
[30] U. Ernst, K. Pawelzik, and T. Geisel, Phys. Rev. Lett. **74**, 1570 (1995).
[31] P. Gong and C. v. Leeuwen, Phys. Rev. Lett. **98**, 048104 (2007).
[32] S. Jahnke, R.-M. Memmesheimer, and M. Timme, Phys. Rev. Lett. **100**, 048102 (2008).
[33] S. Jahnke, R.-M. Memmesheimer, and M. Timme, Front. Comput. Neurosci. **3**, 13 (2009).
[34] R. Zillmer, R. Livi, A. Politi, and A. Torcini, Phys. Rev. E **74**, 036203 (2006).
[35] M. Timme, F. Wolf, and T. Geisel, Phys. Rev. Lett. **92**, 074101 (2004).
[36] M. Timme, F. Wolf, and T. Geisel, Chaos **26**, 015108 (2006).
[37] M.W. Hirsch and S. Smale, *Differential Equations, Dynamical Systems and Linear Algebra* (Academic, New York, USA, 1974), Chap. 8.
[38] H. Kori and Y. Kuramoto, Phys. Rev. E **63**, 046214 (2001).
[39] S. H. Strogatz, Physica D **143**, 1 (2000).
[40] R. Zillmer, R. Livi, A. Politi, and A. Torcini, Phys. Rev. E **76**, 046102 (2007).
[41] L. Abbott and C. van Vreeswijk, Phys. Rev. E **48**, 1483 (1993).
[42] R.-M. Memmesheimer and M. Timme, Phys. Rev. Lett. **97**, 188101 (2006).
[43] R.-M. Memmesheimer and M. Timme, Physica D **224**, 182 (2006).
[44] W. Wu and T. Chen, Nonlinearity **20**, 789 (2007).
[45] A. Zumdieck, M. Timme, T. Geisel, and F. Wolf, Phys. Rev. Lett. **93**, 244103 (2004).
[46] Y. Kuramoto, *Chemical Oscillations, Waves, and Turbulence* (Springer, Berlin, 1984).
[47] I. Stewart, Nature **427**, 601 (2004).
[48] Y. Kuramoto, Prog. Theor. Phys. Suppl. **79**, 223 (1984).
[49] J. A. Acebron, L. L. Bonilla, C. J. P. Vicente, F. Ritort, and R. Spigler, Rev. Mod. Phys. **77**, 137 (2005).
[50] G. B. Ermentrout and N. Kopell, Proc. Natl. Acad. Sci. U.S.A. **95**, 1259 (1998).
[51] J. Karbowski and N. Kopell, Neural Comput. **12**, 1573 (2000).
[52] M. Myongkeun Oh and V. Matveev, J. Comput. Neurosci. **26**, 303 (2009).
[53] D. Somers and N. Kopell, Biol. Cybern. **68**, 393 (1993).
[54] D. Terman, N. Kopell, and A. Bose, Physica D **117**, 241 (1998).