Globally attracting synchrony in a network of oscillators with all-to-all inhibitory pulse coupling

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The synchronization tendencies of networks of oscillators have been studied intensely. We assume a network of all-to-all pulse-coupled oscillators in which the effect of a pulse is independent of the number of oscillators that simultaneously emit a pulse and the normalized delay (the phase resetting) is a monotonically increasing function of oscillator phase with the slope everywhere less than 1 and a value greater than $2\varphi - 1$, where φ is the normalized phase. Order switching cannot occur; the only possible solutions are globally attracting synchrony and cluster solutions with a fixed firing order. For small conduction delays, we prove the former stable and all other possible attractors nonexistent due to the destabilizing discontinuity of the phase resetting at a phase of 0.

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I. INTRODUCTION

The synchronization tendencies of networks of oscillators have been studied intensely in the context of fireflies [1], cardiac cells [2–4], Josephson junctions [5], laser arrays [6], chemical oscillators [7], hybrid dynamical systems [8], pulse-coupled sensor networks [9], neural networks [10], and neutrino flavor oscillations [11]. There are three general approaches to studying synchronization of oscillators [12]: One can assume a form for the oscillator and for the nature of the coupling and derive results for that particular system, or one can use phase resetting theory with the assumption that the coupling is weak, or phase resetting theory with the assumption that the coupling is pulsatile. We make the assumption of pulsatile coupling. We reduce each node in the network to a single variable, its phase φ, and use network interactions consisting of instantaneous phase resetting by the other nodes. Our results generalize to any physical system under the same assumptions of pulse-coupled phase oscillators [1,13–17]. Systems with conduction delays [18,19] are of particular interest in neurobiology and other applications such as laser arrays, electronic circuits, microwave devices, and communications satellites. In some cases, conduction delays can stabilize synchrony [20–22]. We use phase resetting theory [23–25] and stability results based on event-driven maps to prove that in a network of pulse-coupled phase oscillators with a small conduction delay δ, inhibition can be globally synchronizing. The phase of each oscillator increases monotonically at a fixed rate until an input is received, then the phase is instantaneously increased (an advance) or decreased (a delay). This constitutes the hybrid continuous-discrete system:

$$\frac{d\varphi_i}{dt} = 1 - \sum_{j=1}^{j=N-1, j\neq i} f(\varphi_i)\delta(t - t_j - \delta). \qquad (1)$$

An oscillator emits a pulse when its phase φ_i reaches 1, and then its phase is reset to zero. The argument of the Dirac delta function reflects the emission of a pulse by the jth oscillator at times t_j when the phase φ_j reaches 1, and then the receipt of the pulse by oscillator i after a conduction delay equal to the quantity δ. When an oscillator receives a pulsatile input, the timing of the next emitted pulse can be advanced or delayed depending upon of the phase at which it is received. For a free-running oscillator, this implies that the cycle period containing the input is either lengthened or shortened. The phase resetting curve [PRC or $f(\varphi_i)$] for a single isolated oscillator plots the normalized change in the cycle period due to the receipt of a single pulse as a function of the phase.

Much of the literature on pulse-coupled oscillators implicitly defines a PRC, but does not explicitly use the PRC in the derivation of stability results. Hence the application of this literature is limited to oscillators with PRCs that match the implicitly defined ones. For example, Peskin [2] examined a system of two identical pulse-coupled leaky integrate and fire (LIF) oscillators, where for each oscillator i, the time course of the membrane potential is given by $dV_i/dt = S_O - \gamma V_i(t)$. LIF oscillators [26] model the action potential simply as a resetting of the membrane potential from the threshold to a reset potential. The parameter S_O drives repetitive firing if it is greater than or equal to the action potential threshold, and γ is the leak parameter. A LIF oscillator maps onto a phase oscillator because every value of the membrane potential in a repetitively firing LIF model is associated with a unique oscillatory phase within the cycle. Peskin assumed a very simple type of excitatory pulse coupling in which a pulse emitted by one oscillator increased the membrane potential of the oscillator to which it projects by a fixed amount ε or brought the neuron to threshold, whichever was less. This implicitly defines a phase resetting curve (dashed curve in Fig. 1) $f(\phi) = \min[\ln(1 - \gamma\varepsilon S_o^{-1} e^{A\phi})/A, \phi - 1]$, where $A = \ln(S_O/S_O - \gamma)$. The minimum is required for $\varepsilon > 0$ (excitatory coupling) because the phase after a pulse is $\phi - f(\phi)$, and ϕ cannot exceed 1. Using the one-to-one mapping between V and ϕ, a return map can be derived that gives the phase of 1 oscillator immediately after its partner fires, by assuming an alternating firing pattern, then reversing the roles of the two oscillators on each iteration of the map. This map has a unique, unstable fixed point that repels trajectories toward synchronization at a phase of 1, where the coupling term drops out because each neuron is already at threshold when its partner fires; hence synchronization is globally attracting. Peskin's result depends critically on the implicitly defined shape of the PRC, specifically (1) the highly stabilizing region of unit slope as $\phi = 1$ is approached from the left, and (2) the destabilizing negative slope everywhere else, as explained in [21].

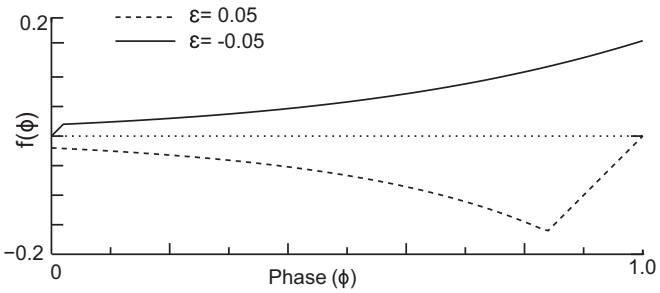

FIG. 1. PRCs for leaky integrate and fire oscillator. $S_O = 1.0$ and $\gamma = 0.9$. These PRC shapes result when an instantaneous change in voltage of magnitude epsilon is applied to an oscillator with a monotonically increasing concave down membrane potential waveform between threshold crossings that result in a reset. Excitatory pulse coupling (dashed lines) and inhibitory pulse coupling (solid lines) each have two regions, a linear region where the slope is 1 due to the requirement to keep the phase between zero and 1, and a region in which the advance or delay increases with phase.

Mirollo and Strogatz [1] generalized these results in two important ways. First, instead of a LIF oscillator, any "concave" membrane potential trajectory with $dV/dt > 0$ and $d^2V/dt^2 < 0$ was allowed. These conditions, coupled with the assumed simple form of the excitatory pulse coupling and the assumption that all oscillators are identical, guarantee that, once established, the firing order is invariant, and that the PRC has the same general shape as for a LIF. This allows for the second major generalization, to a network of N all-to-all pulse-coupled oscillators. Using similar methodology, they proved that all cluster solutions with fixed firing order are unstable, with the very strong result that global synchrony is globally attracting provided their assumptions are met. The equivalence of the maps constructed by Mirollo and Strogatz with those based directly on the PRC is shown in [15].

In order to apply a map strategy [27] to networks of identical neurons with inhibitory pulse coupling, the phase resetting was redefined (see solid curve in Fig. 1) as $f(\phi) = \max[\ln(1-\gamma\varepsilon S_o^{-1}e^{A\phi})/A, \phi]$ where $A = \ln(S_O/S_O - \gamma)$. The maximum is required for $\varepsilon < 0$ (inhibitory coupling) because the phase after a pulse is $\phi - f(\phi)$, and ϕ was not allowed to drop below 0. They showed that two oscillators coupled by inhibition could stably synchronize in the presence of conduction delays whereas excitatory pulse coupling led to a phase lag equal to the conduction delay. In a subsequent paper [28], they simulate identical all-to-all inhibitory pulse-coupled Hodgkin-Huxley neurons with alpha functions with a delay, and get two to three clusters in networks of 50 neurons. It is likely that these clusters would be predicted by the methods presented herein.

No biological networks consist of identical all-to-all coupled networks, but such networks are theoretically more tractable, and may provide useful insights that can be applied to sparsely connected networks of heterogeneous neurons. Some results have been obtained for sparse coupling: For inhibitory pulse coupling with arbitrary coupling, Timme and Wolf [29] showed that synchrony is locally stable provided the synaptic conductances are normalized so that each neuron receives the same amount of total inhibitory conductance, that the implicitly defined phase resetting curve has the appropriate stabilizing shape, and that there is a path through the network that connects every oscillator to every other oscillator. The derivation also included a small delay, and, although it is not noted in the study of Timme and Wolf, this small delay is required [20,21,30] in order to avoid the highly destabilizing discontinuity as a phase of 1 is approached from the left (Fig. 1, solid trace), as proven in this study for networks of N neurons.

The results in the earlier studies described above, as well as other studies of pulse coupling with conduction delays [31], are attributed to the assumed "concavity" of the membrane potential waveform (but see [32] for exceptions), and are also highly dependent on the nonphysiological form assumed for the pulse coupling. The coupling assumption that the phase resetting is dependent only upon the instantaneous value of the membrane potential in the specific way assumed by the authors is not valid in general [33–35]. Physiological PRCs can take forms other than those shown in Fig. 1; for example, they can be sinusoidal for weak coupling near a Hopf bifurcation [34]. Therefore, the most general strategy is to use the phase resetting curve directly as we do in this study, rather than implicitly as in previous studies.

We use an equivalent mapping strategy but constrain the PRC rather than the dynamics of the membrane potential. In our sign convention, a positive resetting value implies a delay in the timing of the next threshold event. We assume a monotonically increasing PRC with $0 < f'(\varphi_i) < 1$ for $\varphi_i \in [0,1)$ to ensure that the firing order, once established, remains constant [13]. Therefore, the only possible solutions are global synchrony and cluster solutions with a fixed firing order. Since the phase resetting is monotonically increasing, and the definition of phase is circular, there is a discontinuity as a phase of 1 is approached from the left. This discontinuity destabilizes synchrony with zero conduction delay.

II. EXISTENCE AND STABILITY CRITERIA FOR CLUSTER SOLUTIONS

We use a single self-connected oscillator as an analog for each synchronous cluster in a splay mode of n clusters, where the self-connection is meant to represent feedback from the cluster in which each oscillator is embedded [Figs. 2(b1) and 2(b2)]. Previously a self-connected neuron has been used as an analog for a coupled neural network [36]. We then use the response of each cluster to input at different phases φ within its cycle, the phase resetting curve, to determine existence and stability criteria for cluster modes. We define $f_{n,\delta}(\varphi)$ as the phase resetting curve (PRC) of a self-coupled oscillator with feedback conductance from $\frac{N}{n}$ oscillators ($\frac{N}{n} - 1$ oscillators if no autapses are allowed), feedback delay δ, and an input from $\frac{N}{n}$ oscillators as an analog for another cluster in the network to generate the PRC [Fig. 2(a1)]. A perturbation simulating the input received from another cluster is applied at each interval t_s after a spontaneous spike, for intervals ranging from zero to the intrinsic period $P_{n,\delta}$ of the self-connected oscillator. The interval between the application of the input and the next spike emitted is called the recovery interval t_r. The sum of t_s and t_r on any given cycle for any given oscillator is equal to the perturbed cycle period [see Fig. 2(a2)], so we define the phase resetting as $f_{n,\delta}(\varphi) = (t_s + t_r - P_{n,\delta})/P_{n,\delta}$. We assume

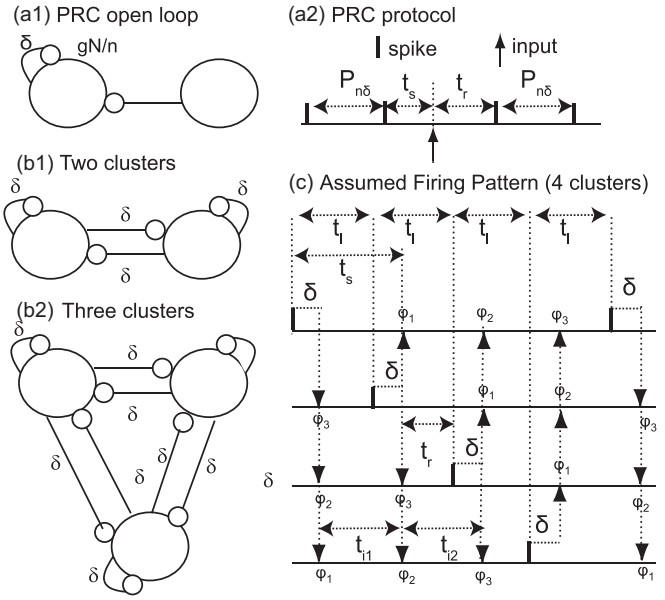

FIG. 2. PRC protocol, cluster logic, and pulse-coupled firing patterns. (a) The PRC is measured (a1) by applying a pulse to a self-connected oscillator (a2) representing a cluster. (b1) In a two-cluster network each cluster receives an input from itself at a delay (which is inside the "black box" used for computing the PRC) and an input from an identical cluster. (b2) The logic is similar for larger clusters. (c) A fixed firing pattern sequence for $n = 4$. A pulse is emitted when a "spike" occurs, and received after a delay δ as an input by the other clusters.

a n-cluster mode in a network of N identical oscillators with equal time lags between spikes and delays short enough that no spikes occur in the interval between when a spike is emitted by one cluster and received by the other(s) [see Fig. 2(c)]. For a firing pattern in a fully connected network [Fig. 2(c)], we redefine the intervals in the network in terms of the phase resetting measured for isolated clusters under the assumption the phase resetting is the same in the closed loop network as in the open loop PRC in Fig. 2(a1):

$t_s = P_{n,\delta}\varphi_1$; $t_{i_i} = P_{n,\delta}\{\varphi_{i+1} - \varphi_i + f_{n,\delta}(\varphi_i)\}$ for $1 < i < n - -1$; $t_r = P_{n,\delta}\{1 - \varphi_{n-1} + f_{n,\delta}(\varphi_{n-1})\}$, where φ_i is the phase of each oscillator immediately before a pulse and $\varphi_i - f_{n,\delta}(\varphi_i)$ is the phase immediately afterwards. Moreover, we can define the following algebraic relationships between the intervals and the delays because each of the following quantities is equal to the time lag t_l interval between spikes in successive clusters [see Fig. 2(b)]:

$$t_s - \delta = t_{i_i} = t_r + \delta.$$

The sum of the time lags (t_l), as well as the sum of the stimulus intervals (t_s), is equal to the network period, which is determined by summing all the resetting received during a cycle, multiplying by the intrinsic period $P_{n,\delta}$, then adding it to the intrinsic period as follows:

$$\sum_{i=1}^{n-1} t_{l_i} = \sum_{i=1}^{n-1} t_{s_i} = \sum_{i=1}^{n-1} (P_{n,\delta}\varphi_i - \delta) = P_{n,\delta}\left[1 + \sum_{i=1}^{n-1} f_{n,\delta}(\varphi_i)\right].$$

Since we have assumed that all time lags are equal, then each oscillator receives its successive inputs at the same phases. Therefore we can write φ_{n-1} in terms of φ_1, because $t_s - \delta = t_r + \delta$ always gives the phase of the first input in terms of the phase at the last input: $\varphi_1 = 1 - \varphi_{n-1} + f_{n,\delta}(\varphi_{n-1}) + 2\delta/P_{n,\delta}$. If intermediate phases exist, the phase at which each intermediate pulse is received can always be written in terms of the phase at which the previous pulse was received, using $t_{i_1} = t_s - \delta$ to give $\varphi_1 - \delta/P_{2,\delta} = \varphi_2 - \varphi_1 + f_{2,\delta}(\varphi_1)$ and $t_{i_i} = t_{i_{i-1}}$ to give $\varphi_i - \varphi_{i-1} + f_{n,\delta}(\varphi_{i-1}) = \varphi_{i+1} - \varphi_i + f_{n,\delta}(\varphi_i)$. Thus all phases can be written in terms of φ_{n-1} which provides a closed form solution for this phase for each equal time lag n-cluster mode. This solution is easily separated into a left-hand side that depends on the phase resetting, and a right-hand side that does not. The left-hand side is $g_{n,\delta}(\varphi_{n-1}) = (n-1)f_{n,\delta}(\varphi_{n-1}) - \sum_{i=1}^{n-2} f_{n,\delta}(\varphi_i)$, where the sum is only needed for $n > 2$. The right-hand side is $n\varphi - n + 1 - \frac{n\delta}{P_{n,\delta}}$. Equations (2)–(4) give the solutions for clusters where $n = 2$, 3, and 4, respectively.

$$f_{2,\delta}(\varphi_1) = 2\left(\varphi_1 - \frac{\delta}{P_{2,\delta}}\right) - 1, \tag{2}$$

$$2f_{3,\delta}(\varphi_2) - f_{3,\delta}\left[1 - \varphi_2 + f_{3,\delta}(\varphi_2) + \frac{2\delta}{P_{3,\delta}}\right] = 3\left(\varphi_2 - \frac{\delta}{P_{3,\delta}}\right) - 2, \tag{3}$$

$$\begin{aligned} &3f_{4,\delta}(\varphi_3) - f_{4,\delta}\left[1 - \varphi_3 + f_{4,\delta}(\varphi_3) + \frac{2\delta}{P_{n,\delta}}\right] \\ &- f_{4,\delta}\left\{2 + \frac{3\delta}{P_{4,\delta}} - 2\varphi_3 + 2f_{4,\delta}(\varphi_3)\right. \\ &\left. - f_{4,\delta}\left[1 - \varphi_3 + f_{4,\delta}(\varphi_3) + \frac{2\delta}{P_{4,\delta}}\right]\right\} = 4\left(\varphi_3 - \frac{\delta}{P_{4,\delta}}\right) - 3. \end{aligned} \tag{4}$$

The value of the phase φ^*_{n-1}, at which the last input within its cycle is received by a cluster, is given by the intersection at which $g_{n,\delta_j,j}(\varphi^*{}_{n-1,j}) = n\varphi^* - n + 1 - \frac{n\delta}{P_{n,\delta_j}}$; see the dashed lines labeled $n = 2, 3$, or 4 in Fig. 3 where $\delta = 0$. Figure 3 uses a linear PRC with a slope of 0.1 to illustrate a case in which the delay is zero, and the phase of the last inputs for the $n = 2$, 3, and 4 cluster modes (open circles) falls on the monotonically rising part of the curve and not in the discontinuity as a phase of 1 is approached from the left. The functions $g_{n,\delta_j,j}(\varphi_{n-1,j})$ were calculated for a constant PRC (note that it may be weaker for smaller clusters with fewer oscillators emitting each pulse). Values of $\varphi_i > \varphi_{n-1}$ violate the assumption of the firing pattern and were eliminated from the calculation of $g_{n,\delta_j,j}(\varphi_{n-1,j})$ when they occurred. Negative values of φ were allowed after a pulse, but not at the time a pulse was received because the PRC is undefined in this instance. Moreover, failure of the phase to recover to a positive value between inputs would lead to suppression of firing in any case.

A constant firing order is guaranteed for monotonically increasing PRCs with a slope that is everywhere less than or equal to 1 [13]. However, firing patterns with constant order but unequal time lags cannot be analyzed by the graphical method

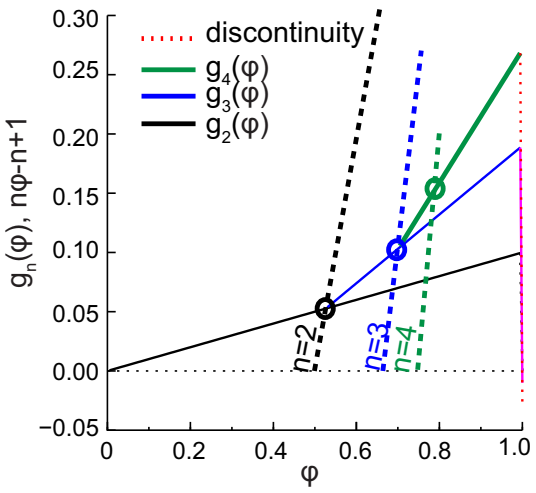

FIG. 3. Graphical method. The phase of the last input (φ_n^*, indicated by the open circles) received by each cluster in an n-cluster mode with no delay falls at the intersection of these two functions described in the text.

in Fig. 3, because the entire analysis is based on the assumption of equal time lags. In Fig. 4, phases φ_{ji} are indexed not only by firing order i but also by oscillator j since each oscillator receives inputs at a different set of phases. There is no fixed relationship between the phases on successive time lags. If one time lag t_{l_j} in the unequal time lags case is shorter than the time lag t_l in the corresponding equal time lag n-cluster mode, then the phase of the stimulus interval defined by that lag must be less than the 1 in the equal intervals case, $\varphi_{j,1} < \varphi_1$. The

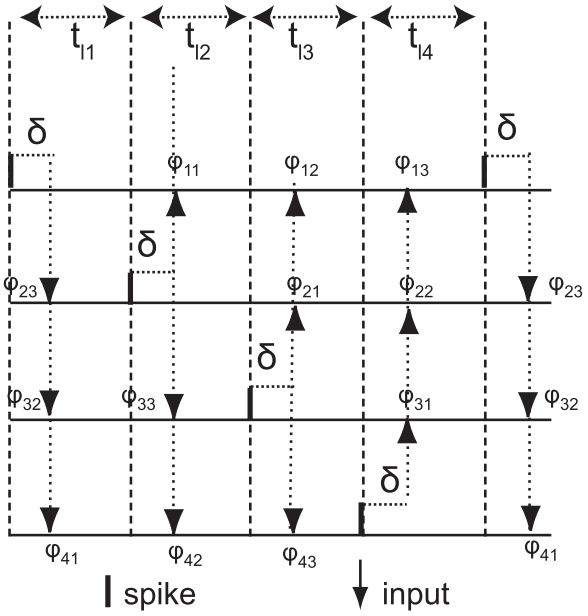

FIG. 4. Generalization to unequal time lags. For each time lag, there is a clear relationship between the four phases defined in relationship to this lag by the definitions of the stimulus, recovery, and intermediate intervals. However, unless the lags are equal, there is no fixed relationship between phases at which inputs are received in adjacent time lag intervals.

phase of the last input in the corresponding equal time lag is given by $\varphi_{n-1} - f(\varphi_{n-1}) = 1 - \varphi_1 + 2\delta/P_{n\delta}$, whereas for the shorter unequal time lag it is $\varphi_{j+1,n-1} - f(\varphi_{j+1,n-1}) = 1 - \varphi_{j1} + 2\delta/P_{n\delta}$. The constraint that $0 < f'(\varphi) < 1$, combined with $\varphi_{j,1} < \varphi_1$, implies that $\varphi_{j+1,n-1} > \varphi_{n-1}$.

Next we need to show that there is always one time lag in the unequal time lag mode that is shorter than the lags in the equal time lag mode. For $n = 2$, it is clear that no unequal times lags modes can exist for a monotonically increasing PRC, because the constraint that both oscillators receive the same amount of phase resetting $f(\varphi_1) = f(\varphi_2)$ to achieve the same network period cannot be satisfied. For $n > 2$, we will first assume that all times lags are indeed longer than those in the equal time lags, and prove by contradiction that this cannot be true.

The assumption that $\varphi_{j1} - \delta/P_{n,\delta} > \varphi_1 - \delta/P_{n,\delta}$ implies that $\varphi_{j1} > \varphi_1$ and by the same logic used above, that $\varphi_{j+1,n-1} < \varphi_{n-1}$. The assumption that $\varphi_{j,i+1} - \varphi_{ji} + f_{n,\delta}(\varphi_{ji}) > \varphi_{i+1} - \varphi_i + f_{n,\delta}(\varphi_i)$ implies that $\varphi_{j,i+1} > \varphi_{i+1}$ provided that $\varphi_{j,i} > \varphi_i$. Since $\varphi_{j+1,n-1} < \varphi_{n-1}$ and $\varphi_{j+1,n-1} > \varphi_{n-1}$ cannot both be true, a contradiction is reached. Therefore at least one oscillator in the unequal time lags mode always receives an input at a larger phase than the phase at which the last input is received in the corresponding equal time lags mode. This result has important implications for global stability; see below.

III. STABLE SYNCHRONY BUT NO TWO-CLUSTER SOLUTION

We are particularly interested in conditions that guarantee both that global synchrony is stable and that the two-cluster mode does not exist. Again, we assume $f_{2,\delta}(\varphi)$ is positive and monotonically increasing for $\varphi \in [0,\varphi_D)$ except for a discontinuity at $\varphi_D = 1$ causing an effectively infinite local negative slope as a phase of 1 is approached from the left, which is maximally destabilizing. Local, or asymptotic, stability is analyzed by determining whether a perturbation to an oscillatory solution with constant phasic relationships will increase or decrease with time. In general, we assume a steady phase locked mode in which oscillator j receives inputs from the other $n-1$ clusters at a phase of $\varphi_{i,j}^*$ where $i \in [1,n-1]$, and further assume that each phase is perturbed by $\Delta\varphi_{i,j}[k]$ on cycle k. We then construct a discrete linear system (map) of how these perturbations evolve in time. A discrete system is unstable if any single eigenvalue has an absolute value greater than 1. Synchrony with $\delta = 0$ is always unstable because according to [20,37] perturbing the synchrony by slightly perturbing the firing pattern of half the neurons in a synchronous cluster yields the eigenvalue $\lambda = [1 - f_{2,0}(0^+)][1 - f_{2,0}(1^-)]$ or $\lambda = [1 - f_{2,0}(0^+)][1 - f_{2,0}(1^-)]$, either of which results in instability due to an eigenvalue with an effectively infinite absolute value as a phase of 1 is approached from the left. In a synchronous mode with $\delta > 0$, for small $\delta > 0$ each cluster receives the input from the other cluster at a phase of $\frac{\delta}{P_{n,\delta}} = \varphi_S$, and treating two clusters as two oscillators, the delay switches the form of the eigenvalue to $\lambda = 1 - 2f_{2,0}(\frac{\delta}{P_{n,\delta}})$ [20]. Thus a PRC slope at the input phase of $0 < f'(\varphi_S) < 1$ guarantees stability of global synchrony, provided the stimulus interval is less than the network period, that is, for $\delta < P_{n,\delta}$. Phase

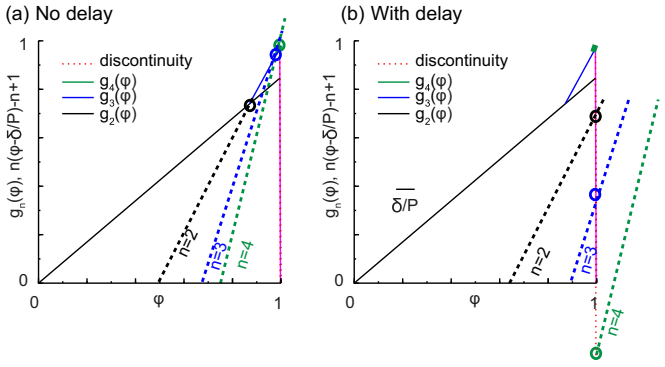

FIG. 5. How delays destroy cluster modes. The intersection of the g functions with the dashed lines labeled with $n = 2$, 3, or 4 gives the phase of the last input for cluster modes. (a) With no delay and a linear PRC with slope 0.85, cluster modes 2, 3, and 4 are stable. (b) A normalized delay shown by the labeled bar shifts all lines to the left, destroying all cluster modes and leaving virtual (or ghost) repellers in their wake. This particular PRC with the illustrated delay guarantees that global synchrony is globally attracting; see text.

resetting due to delayed feedback from within the same cluster need not be considered in the analysis, because it was already incorporated into the oscillator for which the phase resetting is calculated. Now that we have established the conditions for which synchrony is stable, we examine criteria for the stability of the two-cluster mode.

As described above, the intersection point $g_{2,\delta}(\varphi_1) = 2(\varphi_1 - \frac{\delta}{P_{2,\delta}}) - 1$ determines the phase $\varphi_1^* = \varphi_{\rm AP}$ at which and input is received by each cluster in the antiphase mode. Stability of the two-cluster mode can be calculated by treating the two clusters as two oscillators, provided synchrony within each cluster is stable [37]; otherwise a more complicated analysis applies [38]. Since we are only interested in cases in which synchrony is stable, this caveat is not relevant. The two-cluster solution is stable if the absolute value of the eigenvalue $\lambda = [1 - f_{2,\delta}(\varphi_{\rm AP})]^2$ is less than 1 for both zero delays and short delays [16], which implies stability for $0 < f'_{2,\delta}(\varphi_{\rm AP}) < 2$ and $\varphi_{\rm AP} < \varphi_D$. Note: This stability criterion holds while the conduction delay δ is less than the time lag t_l between successive spikes in different neurons in Figs. 2(b) and 4; otherwise the assumed pattern of updating the phases in the matrix above is invalidated. In brief, the effect of a pulse in one oscillator will take more than one cycle to affect the timing of a spike in the same oscillator for longer delays. However, firing patterns in which a spike in one oscillator takes more than one cycle to affect the firing of another spike in the same oscillator via feedback through the network are in general less stable than those in which feedback is received within a single cycle [20], so in practice the magnitude of the delay should not have an upper limit. In any case, we are interested in cases in which the two-cluster mode does not exist.

Since we have already constrained $0 < f'_{n,\delta}(\varphi) < 1$, it is clear that in order to destroy the cluster mode, we must have $\varphi_{\rm AP} = \varphi_D$. Figure 5 illustrates how to destroy the two-cluster mode using delays. For example, for a linear PRC, $f_{2,\delta}(\varphi) = m_{\rm PRC}\varphi$ and $\varphi_D = 1$, and a two-cluster mode is guaranteed to be stable for $\frac{\delta}{P_{2,\delta}} < \frac{1-m_{\rm PRC}}{2}$. Conversely, the two-cluster mode is guaranteed to be nonexistent for $\frac{1-m_{\rm PRC}}{2} < \frac{\delta}{P_{2,\delta}} < 1$. Figure 5(a) shows a linear PRC with a slope of 0.85 with a stable two-cluster mode indicated by the black open circle. If we assume the size of the cluster does not affect the PRC, the three- and four-cluster modes are also stable because the phase at which the last input is received in each cycle falls on the monotonically increasing part of the PRC. Note that increasing the slope from 0.1 in Fig. 3 to 0.85 in Fig. 5 greatly reduces the range in which the g functions with indices greater than 2 are defined because of the requirement that the value of the phase at which the last input is received must be greater than the calculated values of the phases at which earlier inputs are received. Adding a normalized delay greater than 0.075 shifts the $n = 2$ line to the right by 0.15, the $n = 3$ line by 0.225, and the $n = 4$ line by 0.3, causing all these modes to be destabilized. In the next section we will prove that for stability to be globally attracting under our assumptions, it is sufficient to show the two-cluster mode does not exist while global synchrony remains stable.

IV. GLOBALLY ATTRACTING SYNCHRONY

Here we consider cases in which synchrony is stable but the two-cluster mode does not exist, that is, cases for which the PRC is monotonically increasing with $0 < f'_\delta(\varphi) < 1$, and $f_\delta(\varphi) > 2\varphi - 1$ for $\varphi \in [0,1)$ in order to prove that synchrony is globally attracting under certain assumptions. We drop the subscript n on the PRC because we now assume that the effect of a pulse is independent of the number of oscillators that simultaneously emit a pulse so that $f_{n,\delta}(\varphi) = f_{n-1,\delta}(\varphi)$ [1,13]. This assumption is exact if the PRC for a single pulse is saturated. The assumption that the PRC is independent of cluster size allows the generalization of the analysis to include all clusters of unequal size in the analysis for each n. This assumption can be weakened as described below.

For two clusters, $g_{2,\delta}(\varphi_{n-1})$ is simply the PRC parametrized by the internal conduction delay. However, as explained above, a more complicated expression applies for larger numbers of clusters:

$$g_{n,\delta}(\varphi_{n-1}) = f_\delta(\varphi_{n-1}) + \sum_{i=1}^{n-2} \{f_\delta(\varphi_{n-1}) - f_\delta(\varphi_i)\}. \qquad (5)$$

Note that $f_\delta(\varphi)$ is only defined for $\varphi_{n-1} > \varphi_i$ for $i < n-1$. From Figs. 2(b) and 4 it is clear the phase of the oscillator receiving the last input of its cycle must be greater than the phase of any other oscillator both before and after its last input is received, because in the absence of additional inputs, this oscillator fires next. Recall that we assume $f_\delta(\varphi)$ is monotonically increasing for $\varphi \in [0,\varphi_D)$ except for a discontinuity at $\varphi = \varphi_D$, causing an effectively infinite local negative slope at $\varphi = \varphi_D$. Then the terms in brackets in Eq. (5) are positive by monotonicity, which implies that $g_{n,\delta}(\varphi) > g_{2,\delta}(\varphi)$, as illustrated in Figs. 3 and 5. Then $g_{n,\delta}(\varphi)$ also becomes discontinuous at $\varphi = \varphi_D$, where $\varphi_D = 1$. For the $n = 2$ case [21], the value of φ at the intersection of the line $(y = 2\varphi - 1)$ with $f_\delta(\varphi)$ [which is also in this case $g_{2,0}(\varphi)$] determines the phase of an input from the other cluster in an antiphase two-cluster solution with no delay. For the linear PRC shown in Fig. 3(a), the only intersection is at $\varphi_D = 1$,

where the slope is maximally destabilizing, so there are no stable two-cluster solutions at zero delay. In general, there are no stable two-cluster solutions if $2\varphi - 1 < g_{2,0}(\varphi)$ for $\varphi \in [0,1)$. Furthermore, since $\varphi < 1$, then $(\varphi - 1) < 0$, and $n(\varphi - 1) < 2(\varphi - 1)$ as is also clear from the observation that the $n = 3$ and $n = 4$ lines are always below the $n = 2$ line at every value of φ in Figs. 3 and 5. Thus $n\varphi - n + 1 < 2\varphi - 1 < g_{2,0}(\varphi) < g_{n,0}(\varphi)$ for $\varphi \in [0,1)$.

The above inequality states that an absence of stable two-cluster equal time lag solutions implies that there are no stable cluster solutions for any n at zero delay. The inequality can be extended to finite delays as follows:

$$n\left(\varphi - \frac{\delta}{P_{n,\delta}}\right) - (n-1) < 2\left(\varphi - \frac{\delta}{P_{2,\delta}}\right) - 1 < g_{2,\delta}(\varphi) < g_{n,\delta}(\varphi) \quad \text{for } \varphi \in [0,1),$$

if $P_{n,\delta}$ is equal to $P_{2,\delta}$, meaning that the effect of a pulse from the other oscillators within the same cluster is also independent of the number of oscillators within a cluster. These results hold strictly for the delays smaller than the time lags labeled t_{l_i} in Figs. 2(b) and 4. As explained above, longer delays will not be stabilizing, so again, in practice the magnitude of the delay should not have an upper limit. The assumption that $f_{n,\delta}(\varphi)$ is independent of cluster size can be weakened to simply require that the decrease in strength of $f_{n,\delta}(\varphi)$ with cluster size must be smaller than the sum of the bracketed terms in Eq. (5) for the inequality $g_2(\varphi) < g_n(\varphi)$ to hold.

Moreover, if the equal cluster solutions do not exist because $\varphi_{n-1} = \varphi_D$, then unequal modes that are perturbations of these modes, as shown in Fig. 4, cannot exist either because there are no possible phases greater than 1. Since $0 < f'(\varphi) < 1$ for $\varphi_i \in [0,1)$, global synchrony is stable for delays greater than zero. Combining the stability of the synchronous solution with the lack of existence of any cluster solution, synchrony is globally attracting for delays above the minimum required to destabilize the two-cluster mode. Numerical simulations [39] suggest that these results hold for sparsely connected networks unless both the connectivity is very strong and the delays are very short, on the order of the jitter induced by sparse connectivity [40].

V. CONCLUSIONS

We have shown that conduction delays, which are of interest in many fields, can stabilize global synchrony in a network of oscillators mediated by inhibition. Under the assumptions that the PRC is independent of cluster size and is monotonically increasing, with $0 < f'(\varphi) < 1$ and $f(\varphi) > 2\varphi - 1$ for $\varphi_i \in [0,1)$, synchrony is globally attracting for all conduction delays greater than zero. Other PRCs can be shown to lead to globally attracting synchrony above a minimum delay that is greater than zero. Our results may be of particular interest in biology and neuroscience because a linear PRC with a slope near 1 is characteristic of a nearly constant latency to the next spike after a strong inhibition, for example, in neurons with Hodgkin's type 2 excitability [41] that exhibit postinhibitory rebound [42]. Inhibition at chemical synapses does not act simply as an injected hyperpolarizing current; instead it depends on the reversal potential (E_{syn}) of the ion carrying the current through the neurotransmitter-gated channels $I_{\text{syn}} = g_{\text{syn}}(V_{\text{post}} - E_{\text{syn}})$, where I_{syn} is the current; g_{syn} is the conductance and is the membrane potential of the postsynaptic neuron. Thus for strong inhibition, the membrane potential approaches the hyperpolarized value of E_{syn} and I_{syn} approaches zero. A strong inhibition may completely reset the phase such that the value of the phase after a pulse is approximately constant no matter the phase at which the pulse is applied. Therefore the phase resetting becomes a linear function of the phase with a slope of 1. We are most interested in monotonically increasing PRCs whose slope always remains slightly less than 1.

We have focused on using the measured PRC in the context of event-related maps and pulsatile coupling. As mentioned in the Introduction, there are other approaches which often require knowledge of the equations that characterize the evolution of the dynamical system, so they are not generalizable to systems for which the equations are unknown. One such method to calculate the stability of synchrony and cluster states uses the evaporation Lyapunov exponents [43,44] that characterize the evolution of perturbations in transversal directions. For example, Olmi *et al.* [45] use an event-driven discrete-time map to determine the interspike interval of the splay mode, using logic similar logic to ours. They then utilize Floquet theory and the evaporation exponent to determine the stability of synchrony and splay modes with equal time lags. Their analysis implicitly assumes that an excitatory synaptic current simply speeds up the oscillator whereas an inhibition slows down the oscillator, and that the magnitude of the phase resetting effect is determining by simply integrating the current. Another line of research uses the assumption of weak coupling in which the magnitude of the resetting scales linearly with the amplitude of the perturbation, which is not a good approximation for strong coupling [37]. For example, Pazó and Montbrió [46] focused on pulse-coupled oscillators using a Winfree model [47] based on the concept of an infinitesimal PRC with a sinusoidal shape, which characterizes the response of an oscillator that results from a Hopf bifurcation to weak perturbations [34], and is associated with Hodgkin's type 2 excitability [48,49]. They were able to reduce an N-dimensional system of oscillators with a heterogeneous frequency distribution to only two ordinary differential equations. Both studies are elegant, but clearly do not apply to the noninfinitesimal PRCs with the shapes we study here, nor to the biological instantiation of this type of PRC in networks of oscillators with Hodgkin's type 2 excitability that exhibit postinhibitory rebound in response to strong saturating inhibitory input. The master stability function [50] (MSF) is an elegant method that is often applied in physics because it separates the network properties from the dynamical properties of individual oscillators. This method also requires one to assume a form for the dynamic system, such as a normalized SNIPER (Saddle-Node Infinite Period) bifurcation, Fitzhugh-Nagumo or Stuart-Landau [51]. Moreover, the derivation of the master stability function assumes linear coupling between the state variables of the oscillators; diffusive coupling is an example of linear coupling. There are two types of connectivity between neurons: electrical synapses and chemical synapses. With an appropriate choice of coupling function, diffusive coupling is a good approximation

of electrical, but not synaptic, coupling. Electrical coupling is not delayed and only exists between neurons within the same brain area. Chemical synapses are better approximated by assuming that the effect of each input is pulsatile. Since coupling between neurons in the mammalian nervous system is in general mediated by chemical synapses [52], the PRC-based approach used in this study provides an alternate approach to studying synchronization, and may be most applicable to biological neural networks. Unlike the MSF approach, the method we present is applicable to cluster states that have unequal time lags between oscillators. Moreover, since we assume that the PRC in response to a particular synaptic perturbation can be measured, our approach does not require knowledge of the equations describing the intrinsic oscillatory dynamics, which are very complex for physiological neurons [53]. Under the assumption of weakly coupled oscillators [54–56], the infinitesimal PRC (response to a brief, weak input) is used to characterize the intrinsic dynamics, and the synaptic dynamics are considered separately, but here we have combined the two types of dynamics by using the PRC in response to the specific synaptic perturbations received in the intact network.

The results presented here complement those using similar methods to analyze pulse-coupled systems of oscillators with conduction delays that have examined, under different assumptions of PRC shape, the basins of attraction for synchrony [57], cluster solutions [58], the destabilization of synchrony [18], and solutions for no predetermined firing order [59]. Although our results were obtained for all-to-all coupling, they can be generalized to sparsely coupled networks with the caveat that jitter induced by sparse connectivity [29,40] can increase the minimum delay required for global synchrony [39].

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