Dynamics of a Ring of Pulse-Coupled Oscillators: Group Theoretic Approach

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We use group-theoretic methods to analyze phase-locking in a ring of identical integrate-and-fire oscillators with distributed delays. It is shown how certain phase-locked solutions emerge through symmetry breaking bifurcations as some characteristic delay of the system is varied. The reduction to a phase-coupled model in the weak coupling regime is discussed.   [S0031-9007(97)04283-X]

The dynamics of coupled oscillator arrays has been the subject of much recent experimental and theoretical interest. Example systems include Josephson junctions [1,2], lasers [3], oscillatory chemical reactions [4], heart pacemaker cells [5], central pattern generators [6], and cortical neural oscillators [7]. In many applications the oscillators are identical, dissipative, and the coupling is symmetric. Under such circumstances one can exploit the symmetry of the system to determine generic features of the dynamics such as the emergence of certain classes of solutions due to symmetry breaking bifurcations. Group-theoretic methods have been used to study both small amplitude oscillators on a ring near a Hopf bifurcation [8], and weakly coupled oscillators under phase averaging [9]. Symmetry arguments have also been used to construct central pattern generators for animal gaits [10] and to establish the existence of periodic orbits in Josephson junction series arrays [11]. Most work to date on the role of symmetry in coupled oscillator arrays has assumed that the interactions between elements of the array are smooth. On the other hand, many biological oscillators communicate with impulses as exemplified by the so-called integrate-and-fire model [12]. This latter model has recently sparked interest within the physics community due to connections with stick-slip models and self-organized criticality [13]. In Ref. [12], it was rigorously proved that globally coupled integrate-and-fire oscillators always synchronize in the presence of excitatory coupling. However, more biologically realistic models have spatially structured patterns of excitatory or inhibitory connections, and delayed couplings. It is an important issue to determine how the dynamics of pulse-coupled oscillators depends on the distribution of delays and the range of interactions. As we shall show here, the analysis of such systems is considerably facilitated by exploiting the underlying symmetries of the system.

In this Letter we use group-theoretic methods to analyze the dynamics of a ring of N identical integrate-and-fire oscillators with delayed interactions. In particular, we derive conditions for the existence of periodic, phase-locked solutions in which every oscillator fires with the same frequency; the latter is determined self-consistently.

This set of conditions is invariant under the action of the spatiotemporal symmetry group $\mathbf{D}_N \times \mathbf{S}^1$, where $\mathbf{D}_N$ is the group of cyclic permutations and reflections in the ring and $\mathbf{S}^1$ represents constant phase shifts in the direction of the flow. We classify the symmetries of the periodic solutions and indicate how this may be used to construct bifurcation diagrams. We also show how our results reduce to those of a corresponding phase-coupled model in the weak coupling regime.

Consider a circular array of N identical pulse-coupled integrate-and-fire oscillators labeled $n = 1, \ldots, N$. Let $U_n(t)$ denote the state of the nth oscillator at time t. Suppose that $U_n(t)$ satisfies the set of coupled equations

$$\frac{dU_n(t)}{dt} = -U_n(t) + I + \epsilon \sum_{m=1}^{N} W_m \hat{E}_{n+m}(t) \quad (1)$$

supplemented by the reset conditions $U_n(t^+) = 0$ whenever $U_n(t) = 1$. (All subscripts n, m are taken modulo N). The input is $\hat{E}_m(t) = \int_0^\infty P(\tau)E_m(t - \tau)\,d\tau$, where $E_m(t)$ represents the sequence of pulses transmitted from the mth oscillator at time t and $P(\tau)$ represents a distribution of delays. Neglecting the shape of an individual output pulse, the resulting spike train is $E_n(t) = \sum_{j=-\infty}^{\infty} \delta(t - T_j^n)$, where T_j^n is the jth firing time of the nth oscillator. We shall assume that $W_m \geq 0$ and $W_m = W_{N-m}$ for all m so that the network has symmetric excitatory connections. It then follows that the underlying symmetry of the ring of coupled oscillators is $\mathbf{D}_N$. (In the special case of global coupling, W_m independent of m, the symmetry is given by the full permutation group).

One may interpret Eq. (1) as a simple model of nerve tissue in which the distribution $P(\tau)$ incorporates certain important aspects of neural processing such as axonal transmission delays [14], synaptic processing [15], and dendritic processing [16]. For concreteness, we shall consider only the first two features by taking $P(\tau) = g(\tau - \tau_d)\theta(\tau - \tau_d)$, where $g(\tau) = \alpha^2 \tau \exp(-\alpha\tau)$ is the so-called α function representing the shape of a postsynaptic potential and τ_d is a discrete transmission delay. Here $\theta(x) = 1$ if $x \geq 0$ and is zero otherwise. A simplifying assumption of the model is that there is no

correlation between W_m and the delays τ. (An example of space-dependent delays is considered elsewhere [16].)

Suppose that we restrict our attention to periodic solutions of Eq. (1) in which every oscillator fires with the same fixed period T (phase-locking). The state of each oscillator can then be characterized by a constant phase $\phi_n \in \mathbb{R}\backslash\mathbb{Z}$. We shall represent the set of N phases by the vector $\Phi = (\phi_1, \ldots, \phi_N) \in \mathcal{M}^N$, where $\mathcal{M}^N$ denotes the N torus. The firing times of the nth oscillator are $T_j^n = (j - \phi_n)T$. Generalizing the analysis of two integrate-and-fire oscillators in Ref. [15], we integrate Eq. (1) over the interval $t \in (-T\phi_n, T - T\phi_n)$ and incorporate the reset condition by setting $U_n(-\phi_n T) = 0$ and $U_n(T - \phi_n T) = 1$. This leads to the result

$$1 = (1 - e^{-T})I + \epsilon \sum_{m=1}^{N} W_m K(\phi_{n+m} - \phi_n) \quad (2)$$

for $n = 1, \ldots, N$, where

$$K(\phi) = e^{-T} \int_0^T e^{t'} \hat{g}(t' + \phi T - \tau_d)\, dt' \quad (3)$$

with $\hat{g}(t) = \sum_{j=0}^{\infty} g(t + jT)$; that is,

$$\hat{g}(t) = \frac{\alpha^2 e^{-\alpha t}}{1 - e^{-\alpha T}}\left[t + \frac{T e^{-\alpha T}}{(1 - e^{-\alpha T})} \right] \quad (4)$$

for $0 \le t < T$; $\hat{g}(t)$ is extended outside this range by taking it to be a periodic function of t.

The system of Eqs. (2) is invariant under the action of the group $\Gamma = \mathbf{D}_N \times \mathbf{S}^1$. That is, if $\Phi = (\phi_1, \ldots, \phi_N)$ is a solution of Eqs. (2) then so is $\sigma\Phi$ for all $\sigma \in \Gamma$. We can take the generators of $\mathbf{D}_N$ to be $\{\gamma_1, \gamma_2\}$ with $[\gamma_1\Phi]_n = \phi_{n+1}$ and $[\gamma_2\Phi]_n = \phi_{N-n+2}$. The additional $\mathbf{S}^1$ symmetry, which corresponds to constant phase shifts $\phi_n \to \phi_n + \delta$, is a consequence of the fact that Eqs. (2) depend only on phase differences. It follows that any solution of Eqs. (2) will determine Φ (up to an arbitrary phase shift) and the period $T = T(\Phi)$ such that $T(\sigma\Phi) = T(\Phi)$ for all $\sigma \in \Gamma$.

The existence of an underlying symmetry group allows one to systematically explore the different classes of solutions to Eqs. (2) and the bifurcations that can occur as some system parameter is varied. In order to develop this issue further, it is useful to introduce a few simple definitions from group theory. [For a general account of symmetries in bifurcation theory see [8]. The more specific case of the group $\mathbf{D}_N \times \mathbf{S}^1$ within the context of coupled (phase) oscillators is discussed in Ref. [9]]. The symmetries of any particular solution Φ form a subgroup called the *isotropy* subgroup of Φ defined by $\Sigma_\Phi = \{\sigma \in \Gamma: \sigma\Phi = \Phi\}$. More generally, we say that Σ is an isotropy subgroup of Γ if $\Sigma = \Sigma_\Phi$ for some $\Phi \in \mathcal{M}^N$. The *fixed-point subspace* of an isotropy subgroup Σ, denoted by Fix(Σ), is the set of points $\Phi \in \mathcal{M}^N$ that are invariant under the action of Σ, Fix(Σ) = $\{\Phi \in \mathcal{M}^N: \sigma\Phi = \Phi$ for all $\sigma \in \Sigma\}$. Finally, the *group orbit* through a point Φ is $\Gamma\Phi = \{\sigma\Phi: \sigma \in \Gamma\}$. If Φ is a solution to Eqs. (2) then so are all other points of the group orbit.

One can now restrict the search for solutions of Eqs. (2) to those that are fixed points of a particular isotropy subgroup Σ. The isotropy subgroups and fixed-point spaces of $\mathbf{D}_N \times \mathbf{S}^1$ are listed in Table 2 of Ref. [9]. It can be shown that the fixed-point spaces consist of m blocks of k adjacent oscillators where $mk = N$ runs through all binary factorizations of N. The phases $\phi_1, \ldots, \phi_k$ determine the state of the system, and the dimension of the fixed-point space is the number of independent phases within this block. If dim Fix(Σ) = d then the N equations of (2) reduce to d independent equations, one of which determines the period T. In particular, if $d = 1$ then a solution is guaranteed to exist by the underlying symmetry. Examples of these maximally symmetric solutions are the *in-phase* solution, $\phi_n = \phi$ for all n, and *traveling wave* solutions, $\phi_n = \phi + n\beta$ with $\beta = n_b/N$, $n_b = 1, \ldots, N - 1$, where ϕ is an arbitrary phase. For even integers N one also has alternating solutions of the form $(\phi, \overline{\phi}, \phi, \overline{\phi}, \ldots)$, where $\overline{\phi} = \phi + 1/2$. Maximally symmetric solutions typically bifurcate into solutions that have an isotropy group with $d > 1$ as some system parameter is varied (spontaneous symmetry breaking). Such a parameter could be a characteristic length or time scale, for example, the range of interactions, the discrete time delay τ_d, or the inverse rise time α for oscillator response. We shall illustrate some of these ideas with a few simple examples; a more detailed analysis will be presented elsewhere [17].

First consider the case of two coupled integrate-and-fire oscillators [18]; the underlying symmetry group is $\mathbf{Z}_2 \times \mathbf{S}^1$. Equations (2) can be written for $N = 2$ as the pair of equations $1 = (1 - e^{-T})I + \epsilon K(\pm\phi)$, where $\phi = \phi_1 - \phi_2$. These equations reduce to one independent equation (that determines the period T) for the in-phase solution $\phi = 0$ (or equivalently $\phi = 1$) and the antiphase solution $\phi = 1/2$. Both of these solutions are guaranteed to exist by the symmetry of the problem. In Fig. 1, we show how an additional pair of solutions $\{\phi, 1 - \phi\}$ with $0 < \phi < 1/2$ bifurcates from the antiphase solution as the parameter α is varied, and for a range of values of the coupling ϵ. (The fact that $1 - \phi$ is a solution when ϕ is a solution is again a consequence of the underlying symmetry; that is, they lie on the same group orbit.) In the case of two integrate-and-fire oscillators one can derive a simple condition for the dynamical stability of phase-locked solutions [15]: a solution ϕ^* is stable provided that $\partial K_-(\phi)/\partial\phi|_{\phi=\phi^*} > 0$, where $K_-(\phi) = K(\phi) - K(-\phi)$.

As a more complicated example, we show in Fig. 2 a bifurcation diagram for a ring of four oscillators with uniform nearest neighbor coupling ($W_m = \delta_{m,1} + \delta_{m,N-1}$). Again we find that solutions with $d > 1$ bifurcate from maximally symmetric solutions as the parameter α is varied. For $N \ge 2$ the linear stability of the phase-locked solutions can be determined by considering small perturbations of the firing times, $T_j^n = (j - \theta_n)T + \delta_j^n$ [17].
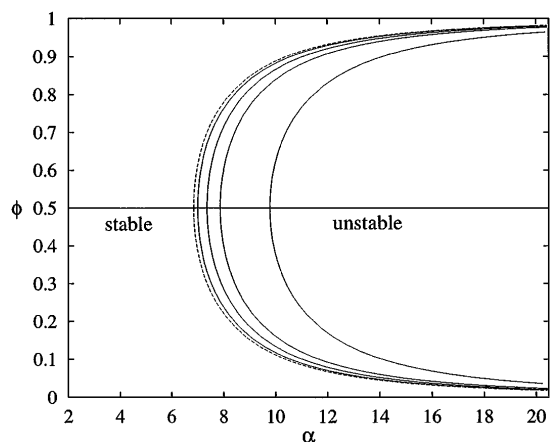
FIG. 1. Relative phase in the IF model as a function of the distributed delay parameter α is shown with solid lines for $\epsilon = 0.01, 0.05, 0.1, 0.25$ with $t_d = 0$ and $I = 2$. In each case the antiphase state undergoes a pitchfork bifurcation at a critical value of α (which increases with ϵ) where it becomes unstable and two additional stable solutions $\phi, 1 - \phi$ are created. The dashed curves show the bifurcation branches in the limiting case of the weakly coupled phase-interaction picture.

However, the spectrum of the resulting linear map for the δ_j^n is infinite dimensional due to the presence of delays. Hence, proving stability analytically is generally not feasible and one must rely on numerical simulations. The latter shows, for example, that the traveling wave solution of Fig. 2 is unstable for small α but is stable beyond the bifurcation point A.
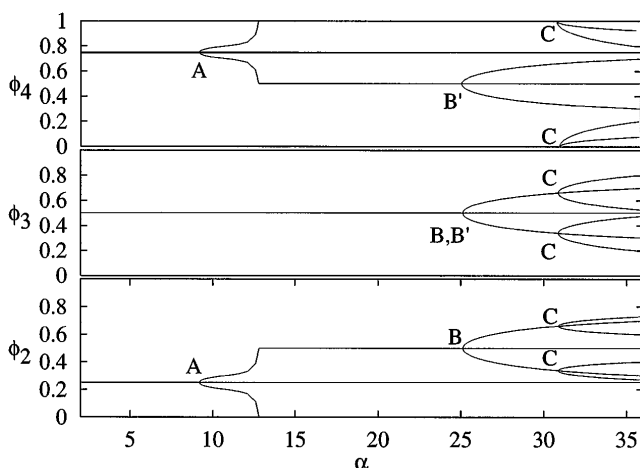

FIG. 2. Relative phases of a ring of four IF neurons with nearest neighbor coupling illustrating bifurcations to isotropy groups with $d > 1$ as α is increased ($t_d = 0.14$, $I = 2$, and $\epsilon = 0.05$). The phase ϕ_1 is fixed to be zero. At the point A a pair of $d = 2$ states of the form $(0, \phi, 1/2, \phi d1;)$ bifurcates from a traveling wave state $\phi_n = n/4$. At the point B' a pair of $d = 2$ states of the form $(0, 0, \phi, \phi)$ bifurcates from the state $(0, 0, 1/2, 1/2)$ and similarly at point B a pair of the form $(0, \phi, \phi, 0)$ bifurcates from $(0, 1/2, 1/2, 0)$. At the points C there are bifurcations from $d = 2$ states $(0, \phi, \phi, 0)$ to $d = 4$ states $(0, \phi_2, \phi_3, \phi_4)$.

We shall now show how in the weak coupling limit the phase-locked solutions of the pulse-coupled model converge to corresponding solutions of a phase-coupled model obtained from the former by an averaging procedure. (This feature is illustrated in Fig. 1). As a slight generalization, we shall assume that in the absence of coupling ($\epsilon = 0$) each oscillator evolves according to $dU_n/dt = f(U_n)$ for some smooth function f, with the period of oscillations given by $T_0 = \int_0^1 du/f(u)$. If $f(U) = -U + I$ as in Eq. (1), then $T_0 = \ln[I/(I - 1)]$ with $I > 1$. Following Ref. [15], we introduce the phase variable $\psi_n(t)$ according to (mod 1) $\psi_n(t) + t/T_0 = \Psi(U_n(t)) \equiv T_0^{-1} \int_0^{U_n(t)} du/f(u)$. Under such a transformation Eq. (1) becomes

$$\frac{d\psi_n(t)}{dt} = \epsilon F(\psi_n(t) + t/T_0) \sum_{m=1}^{N} W_m \hat{E}_{n+m}(t), \quad (5)$$

where $F(z) = 1/[T_0 f(\Psi^{-1}(z))]$ for $0 \le z < 1$ and $F(z + j) = F(z)$ for all $j \in \mathbb{Z}$. When $\epsilon = 0$, the phase variable $\psi_n(t)$ is constant in time and all oscillators fire with period T_0. Now suppose that the oscillators are weakly coupled (ϵ small). To a first approximation, each oscillator still fires with period T_0 but now the phases $\psi_n(t)$ slowly drift according to Eq. (5). Therefore, the firing times may be approximated by $T_j^n = (j - \psi_n(t))T_0$ such that the right-hand side of Eq. (5) becomes a periodic function of t with period T_0. We can then average Eq. (5) over a single period to obtain the phase equations

$$\frac{d\psi_n(t)}{dt} = \epsilon \sum_{m=1}^{N} W_m H[\psi_n(t) - \psi_{n+m}(t)], \quad (6)$$

where H is the phase interaction function

$$H(\psi) = \frac{1}{T_0} \int_0^{\infty} P(\tau) F[\psi + \tau/T_0] d\tau. \quad (7)$$

Equation (6) immediately shows that delays in the propagation of signals between pulse-coupled neurons reduce to phase shifts in the corresponding phase-coupled model. Also note that the system of equations is invariant under the symmetry group $\Gamma = \mathbf{D}_N \times \mathbf{S}^1$.

Proceeding along similar lines to our analysis of the pulse-coupled model, we consider phase-locked solutions of the form $\psi_n(t) = \phi_n + \Omega t$, where ϕ_n is a constant phase and Ω is an $O(\epsilon)$ contribution to the effective frequency of the oscillators; that is, $1/T = 1/T_0 + \Omega$. Substitution into Eq. (6) leads to the set of equations

$$\Omega = \epsilon \sum_{m=1}^{N} W_m H[\phi_n - \phi_{n+m}] \quad (8)$$

for $n = 1, \ldots, N$. As in the analysis of the analogous system of Eqs. (2), we can exploit the underlying symmetry to construct bifurcation diagrams for phase-locked solutions. Note, however, that these solutions are now independent of the coupling ϵ; the coupling only affects the value of the frequency Ω. In order to make a direct comparison with the previous pulse-coupled model we

set $f(U) = -U + I$. Then $F(z) = e^{T_0 z}/[I T_0]$, $H(\phi) = e^{T_0} K_0(-\phi)/[I T_0^2]$, where K_0 satisfies Eq. (3) with T replaced by T_0, and Eqs. (2) reduce to Eqs. (8) to first order in ϵ (see Fig. 1). Thus phase-locked solutions of the pulse-coupled model converge to those of the phase-coupled model in the limit $\epsilon \to 0$. The following stability result also holds [17]: for any finite N and for sufficiently small ϵ, if there exists a stable or unstable (hyperbolic) phase-locked solution of the phase-coupled model then there exists a corresponding solution of the pulse-coupled model of the same stability type.

The stability of phase-locked solutions can be determined analytically for any finite N. Set $\psi_n(t) = \phi_n + \Omega t + \theta_n(t)$ and expand Eq. (6) to first order in θ:

$$\frac{d\theta_n}{dt} = \sum_{m=1}^{N} J_{nm}[\theta_n - \theta_m], \qquad (9)$$

where $J_{nm} = \epsilon W_{m-n} H'[\phi_n - \phi_m]$. The Floquet exponents of a periodic orbit are simply given by the eigenvalues of the Jacobian matrix $\hat{J}_{nm} = J_{nm} - \delta_{nm} \sum_{k=1}^{N} J_{nk}$. One of these eigenvalues is always zero, and the corresponding eigenvector points in the direction of the flow, that is $(1, 1, \ldots, 1)$. The periodic solution will be stable provided that all other eigenvalues have a negative real part. As a simple example, consider traveling wave solutions $\psi_n(t) = n\beta + \Omega t$, where $\beta = n_b/N$, $n_b = 1, \ldots, N - 1$. The fact that J_{nm} now depends on $m - n$ (mod N) means that the eigenvectors of the Jacobian matrix are of the form $\theta_n(t) = e^{\lambda_p t + 2\pi i n p}$, $p = k/N$, $k = 0, 1, \ldots, N - 1$ and the eigenvalues λ_p satisfy

$$\lambda_p = \epsilon \sum_{m=1}^{N} [1 - e^{2\pi i p m}] W_m H'[-m\beta]. \qquad (10)$$

A traveling wave solution will be stable provided that Re $\lambda_p < 0$ for all $p \neq 0$. (The stability of traveling wave solutions in a number of different coupled oscillator models has been investigated in Ref. [19]).

Phase-locked solutions of the phase-coupled model bifurcate whenever there exists more than one eigenvalue with zero real part (nonhyperbolic solutions). If one or more real eigenvalues cross the imaginary axis then the bifurcating branches correspond to other phase-locked solutions as discussed previously. However, as we shall show elsewhere, in the case of an odd number of oscillators in the ring it is also possible for Hopf bifurcations to occur leading to quasiperiodic behavior. Establishing the existence of quasiperiodic (and perhaps chaotic) behavior in the underlying pulse-coupled model is less straightforward and is the subject of future work.

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