Synchronization Induced by Temporal Delays in Pulse-Coupled Oscillators

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We derive return maps and phase diagrams to identify mechanisms of synchronization of pulse-coupled oscillators and emphasize the importance of temporal delays and inhibitory coupling. Optimum synchronization between two oscillators is obtained for *inhibitory* coupling, where delays give rise to stable in-phase synchronization; those with excitatory coupling only synchronize with a phase lag. In large ensembles of globally coupled oscillators the delayed interaction leads to new collective phenomena like synchronization in multistable clusters of common phases for inhibitory coupling; for excitatory coupling a mechanism of emerging and decaying synchronized clusters prevails.

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Synchronization of coupled oscillators is a widespread phenomenon occurring in physics [1], chemistry [2], and biology [3]. Theoretical efforts toward a mathematical description of synchronization were stimulated considerably by the discovery of synchronized firing activity of neurons in the central nervous system [4,5]. Here the synchronization of neurons is believed to represent the binding of object features, a problem of outstanding significance for information processing in the brain [6]. Abstracting from biophysical details, neurons belong to an important class of oscillators characterized by a pulselike interaction, i.e., where the coupling consists in the transmission of a short pulse from an oscillator to its partners. For an understanding of the general principles underlying synchronization phenomena, it is useful to consider abstract oscillator models which subsume various existing models under very general assumptions and can be treated conveniently. Assuming such a model, Mirollo and Strogatz [7] have proved rigorously that globally pulse-coupled oscillators always synchronize with zero phase difference. This result pertains only to excitatory couplings, in realistic applications, however, one is also confronted with inhibitory couplings, which are abundant, e.g., in the central nervous systems and whose importance for synchronization was pointed out recently [8]. Furthermore, in most applications the transmission of a pulse requires a finite propagation time. It is an important question, how synchronization over long distances can be achieved when such temporal delays prevail (like in the visual cortex [9]).

In the present Letter we want to identify general mechanisms of synchronization in cases where delays and also inhibitory couplings are present. We demonstrate that even in the presence of delays a return map can be determined analytically for two coupled oscillators. The return map proves to be very useful for understanding synchronization phenomena and deriving phase diagrams from its basins of attraction. In particular, while one might have expected that inhibitory coupling tends to prevent synchronization or admits out-of-phase synchronization only, we find that the presence of delays and even *arbitrarily small delays* leads to stable in-phase synchronization. For excitatory coupling, on the other hand, the presence of delays causes the synchronization to get out of phase by a finite time lag. Thus, if stable in-phase synchronization is required in the presence of transmission delays, we conclude that this can be achieved best by inhibitory coupling. We believe that this mechanism explains the precise synchronization in populations of flashing fireflies [10], and may turn out to be substantial for feature binding in the brain by ensuring synchronization of distant neurons. The return maps also serve to understand our numerical results on the collective dynamics of many globally coupled oscillators. For inhibitory coupling the delayed interaction gives rise to *multistable* clusters synchronized in common phases. The network as a whole then oscillates at a multiple of the single oscillator frequency, a fact which was also observed experimentally in the hippocampus of the rat [11]. For excitatory couplings we report a new phenomenon of spontaneous emergence and decay of synchronized clusters.

Considering pulse-coupled oscillators, an individual oscillator i may be described by a smooth function $f(\Phi_i)$ which is concave down and monotonically increasing [$f' > 0$, $f'' < 0$, $f(0) = 0$, $f(1) = 1$]. f plays the role of an amplitude and $\Phi_i \in [0, 1]$ is a phase [7], which in the case of vanishing input from other oscillators corresponds to the normalized time elapsed since the last firing of i. These mathematical conditions including the concavity condition are fulfilled by many models of relaxation oscillators; as a simple example we only mention that leaky integrate-and-fire neurons without mutual interaction obey the differential equations

$$\frac{df_i}{dt} = -c_1 f_i + c_2 \quad \text{for } i = 1, \ldots, N. \tag{1}$$

When f reaches a threshold $f_s := 1$, the oscillator fires and Φ_i and f are reset to zero. Caused by the firing, the amplitudes $f(\Phi_j)$ of all the other oscillators are raised (excitatory couplings) or lowered (inhibitory couplings) by an amount $\epsilon = \epsilon^*(N-1)^{-1}$, where ϵ^* denotes the normalized coupling strength ($\epsilon^* \in [0, 1]$). The coupling

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to the oscillators j may be represented equivalently by an increase or decrease in phase $\Delta\Phi_j$

$$\Phi_j + \Delta\Phi_j = f^{-1}(\min[f(\Phi_j) + \epsilon, 1]), \quad (2a)$$

$$\Phi_j + \Delta\Phi_j = f^{-1}(\max[f(\Phi_j) - \epsilon, 0]), \quad (2b)$$

where Eqs. (2a) and (2b) refer to excitatory and inhibitory coupling, respectively. We point out that the concavity of f is responsible for the dependence of $\Delta\Phi_j$ on Φ_j, the larger the phase Φ_j, the larger the phase shift $\Delta\Phi_j$. In the present Letter we focus on the effect of a finite transmission delay $\tau < 0.5$ in this model, which represents the (normalized) time a pulse needs to travel from one to another oscillator.

In the case of two oscillators ($N = 2$, $\epsilon = \epsilon^*$) with phases Φ_A and Φ_B, a return map $\Phi^{k+1} = R(\Phi^k)$ can be defined by considering the phase difference $\Phi^k := \Phi_B(t_k) - \Phi_A(t_k) = \Phi_B(t_k)$ for times t_k when oscillator A fires [$\Phi_A(t_k) = 0$]. Performing a detailed but straightforward mathematical analysis one can determine R analytically for all $f(\Phi)$ obeying the above conditions. Because of the delay a number of 0 to 2 pulses can be emitted without being received at time $t = t_k$. For this reason and for the min and max conditions in Eqs. (2a) and (2b), the derivation of R requires numerous case distinctions and will therefore be published elsewhere [12]. For brevity we only give the graphs of R in Figs. 1(a) and 2(a). For these figures we have chosen

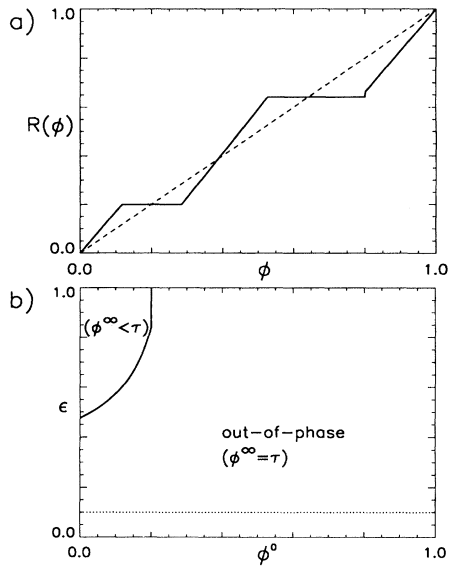

FIG. 1. (a) Return map R for excitatory coupling of strength $\epsilon = 0.1$ with delay $\tau = 0.2$. Two stable fixed points lead to asymptotic out-of-phase synchronization with phase difference $\Phi^\infty = \tau$. (b) Phase diagram determining the asymptotic behavior in dependence of the coupling strength ϵ and the initial phase difference Φ^0. Out-of-phase synchronization with phase lag τ is stable everywhere apart from the upper left corner where synchronization with phase lag smaller than the delay is possible. The dotted line denotes the parameter value ϵ of the particular return map shown in (a).

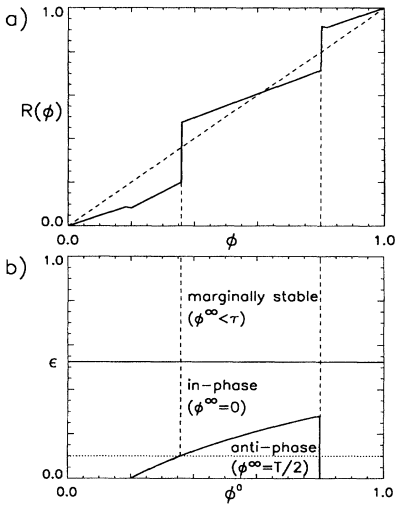

FIG. 2. (a) The return map R for inhibitory coupling with $\epsilon = 0.1$ and $\tau = 0.2$ shows two stable fixed points giving rise to in-phase ($\Phi^\infty = 0$) or antiphase ($\Phi^\infty = T/2$) synchronization. The respective basins of attraction determine the phase diagram (b) as indicated by the dashed lines for the particular value of ϵ under consideration. For intermediate values of ϵ, the oscillators always fire simultaneously. Large ϵ leads to marginally stable synchronization with phase lag $\Phi^\infty \leq \tau$.

$f(\Phi)$ to be $f(\Phi) = b^{-1}\ln[1 + (e^b - 1)\Phi]$ with $b = 3$, whereby R becomes piecewise linear. Qualitatively the return maps do not change for other admitted choices of $f(\Phi)$. Iteration of R gives us the time evolution Φ^k and in particular the asymptotic phase difference $\Phi^\infty := \lim_{k\to\infty}\Phi^k$. As was shown rigorously in [7], excitatory coupling without delay always leads to in-phase synchronization ($\Phi^\infty = 0$). Here, for a finite delay τ, the return map has two stable fixed points at τ and $f^{-1}(1 - \epsilon) - \tau$ [Fig. 1(a)], where in both cases the oscillators synchronize with a phase lag $\Phi^\infty = \tau$. Investigating the return map for all parameters $\epsilon \in [0, 1]$, $\tau \in [0, 0.5]$, and $\Phi^0 \in [0, 1]$ we can analytically derive a phase diagram [Fig. 1(b)]. It gives the asymptotic behavior in dependence of ϵ and the initial phase Φ^0, while the dependence on τ shows no additional features. Out-of-phase synchronization with $\Phi^\infty = \tau$ is stable for all parameter values apart from the upper left corner [above $\epsilon = 1 - f(\tau)$], where synchronization with phase lag smaller than τ is possible depending on Φ^0, but in-phase synchronization remains forbidden except for $\Phi^0 = 0$.

For inhibitory coupling the delay leads to three scenarios depending on the inhibition strength ϵ. For $\epsilon < 1 - f(2\tau)$, the return map has two stable fixed points at $\Phi = 0$ and $\Phi = 1 + \tau - f^{-1}[f(\Phi + \tau) + \epsilon]$ as shown in Fig. 2(a). The oscillators therefore synchronize either in phase $\Phi^\infty = 0$ or in antiphase $\Phi^\infty = T/2$, depending on their initial configuration Φ^0, where $T = T(\epsilon)$ denotes the average period between two firing events of one oscillator. The phase diagram Fig. 2(b) is obtained from

the respective basins of attraction (dashed lines) as the particular value of ϵ (dotted line) considered in the return map is varied. For $1 - f(2\tau) < \epsilon < f(\tau)$, the second fixed point disappears and the two oscillators always synchronize with zero phase. Still larger values $\epsilon > f(\tau)$ give rise to marginally stable synchronization with variable phase lag $\Phi^\infty \in [0, \min\{\tau, f^{-1}(\epsilon) - \tau\}]$, similarly as for excitatory couplings. The remarkable mechanism of in-phase synchronization ($\Phi^\infty = 0$) caused by the delay is directly related to the concavity of f. Consider a time t_k where two pulses have been emitted but not been received yet. This is always the case for Φ^0 smaller than the delay τ. After receipt of the two pulses the oscillators have lowered their amplitudes $f(\Phi_A)$ and $f(\Phi_B)$ by ϵ. The phase reset of the oscillator with the larger absolute phase is larger than the phase reset of the other oscillator such that the phase difference is decreased successively, whenever this happens. It is important to note that this analysis only depends on the function f being monotonically increasing, concave down and smooth, and not on a specific oscillator model.

Such models may be rather simple like integrate-and-fire oscillators or more complex like the Hodgkin-Huxley neuron. Nevertheless, many of them may be subsumed under these rather general assumptions such that we may expect the same synchronization mechanisms to occur [13]. As an example we mention coupled McGregor neurons [14], for which our simulations showed the same phenomenology of delay-induced clustering [15]. For more detailed oscillators and more complex interactions, however, our phase description is only approximate [16] and in general might apply only in the limit of weak interaction.

For $N > 2$ oscillators we can describe the state of the system by a vector $\mathbf{\Pi}$ containing the phases Φ_i and the times τ_i elapsed since the last spike of each oscillator i, $\mathbf{\Pi}(t) := \{\Phi_1, \ldots, \Phi_N, \tau_1, \ldots, \tau_N\}$, if one oscillator cannot spike twice during a time $t = \tau$. Choosing a reference oscillator j, we can construct a time-discrete function R_N, the N-dimensional return map, which maps $\mathbf{\Pi}(t_k)$ onto $\mathbf{\Pi}(t_{k+1})$, where t_k is the time when oscillator j fires for the kth time

$$R_N : \mathbf{\Pi}(t_k) \mapsto \mathbf{\Pi}(t_{k+1}) = R_N(\mathbf{\Pi}(t_k)). \quad (3)$$

In the case of $N = 2$ oscillators, R_2 equals R if we demand that $\Phi_2 = \tau_2$ at t_k (for $\Phi_2 < \tau$), $R(\Phi) := R_2(\mathbf{\Pi})$. The function R then is one dimensional and does not depend on τ_2. For a given f, the dynamics of the phases Φ_i can be written as

$$d\Phi_i/dt = \omega_0 + \omega(\Phi_i), \quad (4)$$

where ω_0 is a constant phase shift, $\omega(\Phi_i)$ denotes an instantaneous phase velocity which for small ϵ becomes

$$\omega(\Phi_i) = \pm\epsilon/f'[\Phi_i(t)] \sum_j^N \delta(t - \tau - t_j*), \quad (5)$$

where the + and − signs refer to excitatory and inhibitory couplings, respectively, and t_j* is the time when oscillator j has fired last. Starting with $\mathbf{\Pi}(0)$, one can calculate $\mathbf{\Pi}(t_k)$ analytically in an iterative procedure.

Our numerical results for the time evolution of $N = 100$ oscillators with excitatory couplings exhibit a clustering [Fig. 3(a)] with spontaneous synchronization and desynchronization. To probe for stability a small amount of noise was added. Stable clusters of synchronous oscillators are formed, but become unstable after a time. Apparently a cluster destabilizes when the neighboring cluster has desynchronized. This behavior might be related to the fact that the fixed point of R at $\Phi = 0$ is unstable while the fixed point at $\Phi = \tau$ is stable [Fig. 1(a)]. Single clusters seem to be unstable but serve to stabilize others.

In contradistinction to the former case, we find (multi)stable clustering for inhibitory couplings [Fig. 3(b)]. Despite random initialization stable clusters of synchronized oscillators are formed. The average number N_c of clusters follows the power law $N_c \simeq \tau^{-1}$ as a function of the delay (Fig. 4). Solutions with less than N_c clusters and even the fully synchronized solution where all the oscillators fire simultaneously are stable, too. This behavior is analogous to the existence of several stable fixed points and basins of attraction of R [Fig 2(a)] which lead either to in-phase or antiphase synchronization. The fixed points of R_N act as attractors or repellors, synchronizing those oscillators that are in

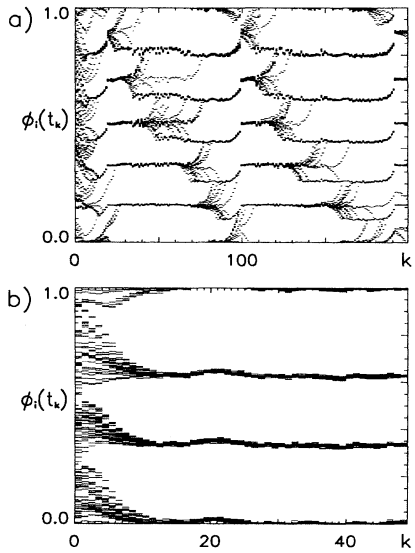

FIG. 3. (a) Stroboscopic picture of the time evolution of the phases of $N = 100$ oscillators with excitatory couplings ($\tau = 0.15$, $\epsilon = 0.2$) displaying the emergence and decay of synchronized clusters. k counts the periods of a fixed but arbitrary reference oscillator. (b) Same as (a) for inhibitory couplings and $\tau = 0.2$, $\epsilon = 0.2$. The delayed interaction leads to stable clustering in three different phases depending on the delay. The network frequency increases almost by a factor of 3.

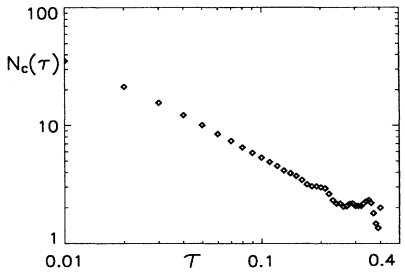

FIG. 4. The average number of stable clusters nearly follows a power law $N_c \sim \tau^{-1}$ as a function of the delay τ shown here for $\epsilon = 0.2$.

the same basin of attraction. The number N_c of clusters is determined approximately by the mean firing period T divided by the size l_A of the basin of attraction of R at $\Phi = 0$: $N_c \simeq T/l_A$. Stable clustering leads to new effects for the overall network firing activity where the individual spiking events are summed up. Assuming M stable clusters, the network as a whole fires at a multiple of the single frequency $f_{\text{Net}} = M/T$. This might be an explanation of the frequency doubling and tripling found in the hippocampus of the rat [11], a system in which inhibition dominates and where single neurons fire with a maximum frequency of 100 Hz, while measurements of the network activity have detected oscillations of 200 and 300 Hz, respectively. We have checked that the phenomenon of multistable clustering described above is robust against the fluctuations of the delay times among the oscillators.

In the limit of large populations of oscillators, we can describe the high dimensional dynamics by a nonlinear delayed inhomogeneous partial differential equation for the density of phases [2]:

$$\partial\rho/\partial t = -\partial(\omega\rho)/\partial\Phi\,, \tag{6}$$

with periodic boundary conditions $\dot{\rho}(0,t) = \dot{\rho}(1,t)$. Here, $\rho(\Phi,t)d\Phi$ is the portion of all oscillators with phases in $[\Phi, \Phi + d\Phi]$ at time t. According to the discrete dynamics [Eq. (4)], the phase velocity ω depends on the firing history $\rho(0, t-\tau)$, on the phase Φ, and on the coupling strength ϵ

$$\omega = \omega_0 \pm \epsilon\, /f'(\Phi)\rho(0, t-\tau)\,. \tag{7}$$

Synchronized clusters are represented by peaks in ρ and numerical evaluations of Eq. (6) show the same phenomenology as the discrete dynamics. It should be noted here that Eqs. (6) and (7) complement previous approaches to synchronization of pulse-coupled oscillators [2,17,18] where the effects of variable phase velocity were not taken into account. Extending Eq. (6), a probabilistic firing of the oscillators can be included by adding a term $-p_f\rho$ to the right-hand side as discussed in Refs. [2,19]. Here, p_f is a rate function depending on the phase and the previous activity of the network.

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