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Partial synchronization in populations of pulse-coupled oscillators

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I study the long-term behavior of populations of nonlinear oscillators with all-to-all, noninstantaneous, pulse coupling. With fast enough excitatory coupling both the fully synchronized and the asynchronous state are unstable. In this case individual units fire quasiperiodically even though the network as a whole shows a periodic firing pattern. The behavior of networks with three or more units is different in this regard from that of two-unit networks. With inhibitory coupling the network can break up into a variable number of fully synchronized clusters. For fast inhibition the number of clusters tends to be large, while the number of clusters is smaller for slow inhibition. [S1063-651X(96)09310-5]

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I. INTRODUCTION

Most studies of the temporal organization of populations of nonlinear oscillators concentrate either on synchronous activity [1] or on the asynchronous state [2]. However, many model networks of nonlinear oscillators have regions in parameter space in which the population evolves neither to an asynchronous state nor to a fully synchronized state. These partially synchronized states are usually discussed in the presence of noise [3,4] or inhomogeneities [5,6]. Yet many networks of identical nonlinear oscillators can evolve to stable partially synchronized states, even in the absence of noise. In this paper we will look in detail into the behavior of such networks.

In a previous paper [7] we considered a population of integrate-and-fire oscillators, with all-to-all coupling, and determined the conditions under which the asynchronous state is stable. Here the long-time behavior of such a network with parameter values for which the asynchronous state is unstable is studied. We find that these parameter values do not typically lead to fully synchronized states but rather to partial synchrony.

The paper is organized as follows. In Sec. II the model is outlined. Section III briefly describes previous work on two-unit systems [8] and its implications for larger networks. In networks of two oscillators with excitatory coupling, the units fire periodically in the partially synchronized state. In Sec. IV I show that this is not true for networks with three or more units. It is shown that for networks with three or more units the partially synchronized state is characterized by quasiperiodically firing units.

Sections V–VIII deal with large excitatory networks. Section V briefly summarizes the analysis of the asynchronous state developed in Ref. [7]. Section VI discusses numerical simulations of large networks with parameter values for which the asynchronous state is unstable. I show that the network evolves to a partially synchronous state in which the firing rate fluctuates periodically. This state is analyzed in Sec. VII. Section VIII describes the quasiperiodic behavior of individual units in this state.

Section IX discusses large networks with inhibitory coupling. Depending on the speed of the coupling, the network can break up in two or more clusters, with all oscillators belonging to a cluster in complete synchrony [9,5,10]. The exact number of clusters into which the network breaks up depends on the initial condition. In Sec. X we evaluate the results of our study and consider the implications for populations of more biologically realistic model neurons.

II. MODEL

The model consists of N identical oscillators that are uniformly coupled to all other oscillators. Oscillator i is described by a voltagelike variable x_i that runs between zero and one. The evolution of x_i is given by the equation

$$\frac{dx_i}{dt}=F(x_i)+gE_i(t). \tag{2.1}$$

The function F determines the behavior of the oscillator in the absence of coupling. It can be an arbitrary positive-definite function. The second term in Eq. (2.1) describes the coupling. g is the coupling strength, with $g>0$ for excitatory coupling and $g<0$ for inhibitory coupling. $E_i(t)$ is a dynamical variable that characterizes the inputs from the other oscillators.

Equation (2.1) determines the behavior of x_i in the range between 0 and 1. When x_i reaches the threshold $x_i=1$, the cell is said to fire. This firing immediately resets x_i to zero and increments the coupling variable $E_j(t)$ for $j\neq i$ by a single pulse response. I will set the response for a single pulse equal to an α function

$$E_j(t)\rightarrow E_j(t)+\frac{\alpha^2}{N-1}(t-t_0)e^{\alpha(t_0-t)}. \tag{2.2}$$

Here t_0 is the time at which oscillator i fires.

Except for Secs. III and IV I work in the large-N limit. In this limit I will not remove the self-coupling from Eqs. (2.1) and (2.2). We then have $E_j(t)=E(t)$ for all j with $E(t)$ incremented by

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$$E(t)\to E(t)+\frac{\alpha^2}{N}(t-t_0)e^{\alpha(t_0-t)}. \tag{2.3}$$

This is equivalent to a mean-field approximation.

The results we obtain for this model also hold for a more general model in which the input in cell i depends on the state variable x_i. In this model the state variables satisfy

$$\frac{dx_i}{dt}=F(x_i)+G(x_i)E_i(t), \tag{2.4}$$

with $G>0$ for excitatory coupling and $G<0$ for inhibitory coupling. This is because a transformation of the state variable $x_i\to g\int_0^{x_i}dx/G(x)$, with $g^{-1}=\int_0^1 dx/G(x)$, will transform Eq. (2.4) into Eq. (2.1). So without loss of generality we can assume that the coupling is independent of x_i.

Another way the model can be generalized is by describing the pulse response by a difference of exponentials rather than by an α function. This amounts to replacing Eq. (2.2) by

$$E_i(t)\to E_i(t)+\frac{\alpha_1\alpha_2}{(\alpha_1-\alpha_2)(N-1)}\left(e^{\alpha_1(t_0-t)}-e^{\alpha_2(t_0-t)}\right). \tag{2.5}$$

One regains the α function by taking the limit $\alpha_1\to\alpha_2=\alpha$. Since models with a difference of exponentials rather than an α function as response to a single pulse exhibit qualitatively the same behavior and their analysis is essentially the same, this generalization is not considered here.

III. TWO-OSCILLATOR SYSTEM

To understand the behavior of a system with a large number of oscillators it is often helpful to know how a two-unit system evolves. Here we will give a short description of a two-oscillator system. A more detailed analysis can be found in [8].

We will limit our discussion to a system for which the state variables satisfy the equations

$$\frac{dx_i}{dt}=X_0-x_i+gE_i(t), \tag{3.1}$$

with $i=1,2$ and $X_0>1$. The coupling variable E_1 is given by

$$E_1(t)=\sum_i^{t_{2,i}<t}\alpha^2(t-t_{2,i})e^{\alpha(t_{2,i}-t)}, \tag{3.2}$$

where $t_{2,i}$ is the set of times at which cell 2 fires. A simular equation holds for E_2.

It turns out that both for excitatory coupling and for inhibitory coupling that is not too strong the system evolves to a state in which the oscillators fire periodically. We assume that unit 1 fires at times $t=nT$ and unit 2 at $t=(n+\phi)T$, for some period T and phase difference ϕ between 0 and 1. Then

$$E_1(t)=E_T(t-\phi T),\quad E_2(t)=E_T(t), \tag{3.3}$$

with

$$E_T(t)=\frac{\alpha^2}{1-e^{-\alpha T}}\left(\frac{Te^{-\alpha T}}{1-e^{-\alpha T}}+t\right)e^{-\alpha t} \tag{3.4}$$

for $0\leqslant t<T$ and $E_T(t+T)=E_T(t)$.

Using Eq. (3.2), with $x_1(0^+)=0$, one can show [8] that $x_1(T^-)$ satisfies

$$x_1(T^-)=X_0(1-e^{-T})+ge^{-T}\int_0^T dt e^t E_T(t-\phi T). \tag{3.5}$$

Since unit 1 fires again at time T, $x_1(T^-)$ has to satisfy $x_1(T^-)=1$.

Using $x_2(\phi T^+)=0$, $x_2((\phi+1)T^-)$ can be written as

$$\begin{aligned}x_2((\phi+1)T^-)&=X_0(1-e^{-T})+gE^{-T}\int_0^T dt e^t E_T(t+\phi T)\\&=1+ge^{-T}\int_0^T dt e^t[E_T(t+\phi T)\\&\quad -E_T(t-\phi T)].\end{aligned} \tag{3.6}$$

This has to be equal to 1 also.

The requirement that both $x_1(T^-)$ and $x_2((\phi+1)T^-)$ are equal to 1 can be satisfied only for a few values of ϕ. As Eq. (3.6) shows, the two values for ϕ that one expects from symmetry arguments, $\phi=0$ and $\phi=1/2$, are always solutions. For small α these are the only solutions. As α is increased, one reaches a bifurcation point $\alpha=\alpha_{\rm cr}$. At this point there is a pitchfork bifurcation of the $\phi=1/2$ solution. Beyond this point there are two extra solutions $\phi_1<1/2$ and $\phi_2=1-\phi_1$ in which the units are partially synchronized. As α is increased ϕ_1 goes to 0 asymptotically; the cells get closer and closer to synchrony (see Fig. 1).

Stability analysis shows [8] that for excitatory coupling the antisynchronous state $\phi=1/2$ is stable for $\alpha<\alpha_{\rm cr}$. For $\alpha>\alpha_{\rm cr}$ the antisynchronous state is no longer stable, while the two partially synchronized solutions ϕ_1 and ϕ_2 are stable. The synchronous solution $\phi=0$ is always unstable.

For inhibitory coupling the synchronized solution is always stable. The antiphase state is unstable for $\alpha<\alpha_{\rm cr}$ and stable for $\alpha>\alpha_{\rm cr}$. The two other solutions for $\alpha>\alpha_{\rm cr}$ are unstable for inhibitory coupling [8].

One can show that for a more general description, in which X_0-x_i in Eq. (3.2) is replaced by $F(x_i)$, the situation does not change qualitatively as long as $F>0$ and $dF/dx<0$. Then there is also always an in-phase and an antiphase solution and a pitchfork bifurcation of the antiphase state at some value $\alpha_{\rm cr}$, while for $\alpha>\alpha_{\rm cr}$ there are two extra, partially synchronized, solutions. For excitatory coupling the antisynchronous state is still the only stable solution if $\alpha<\alpha_{\rm cr}$ and for $\alpha>\alpha_{\rm cr}$ the partially synchronized solutions are the only stable solutions. For inhibitory coupling the synchronous state is always stable, while the antisynchronous state changes from unstable for slow coupling to stable for fast coupling.

In a two-unit system with excitatory coupling we have antisynchronous firing for slow coupling. As the time constant for the coupling is decreased past the critical value the units will fire more and more in synchrony. However, there

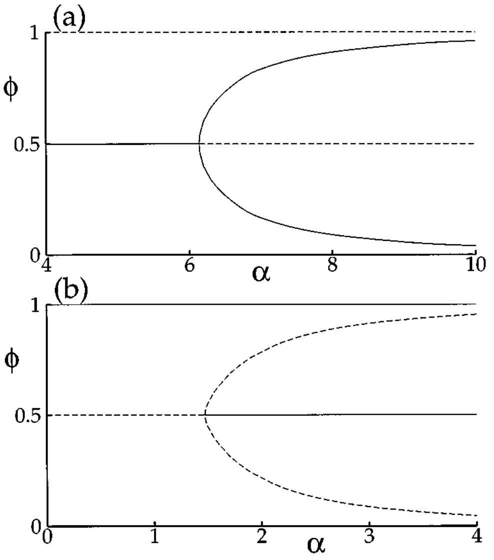

FIG. 1. Phase difference in a periodically firing two-unit system. The phase difference ϕ between the units is plotted against the coupling rate constant. Solid lines, stable solution; dashed lines, unstable solution. (a) For excitatory coupling. $\phi = 1/2$ is stable for $\alpha < \alpha_{\mathrm{cr}}$. For $\alpha > \alpha_{\mathrm{cr}}$ the partially synchronized solutions are stable. All other states are unstable. (b) Inhibitory coupling. The in-phase solution is always stable, while the antiphase solution is stable for $\alpha > \alpha_{\mathrm{cr}}$. All other solutions are unstable.

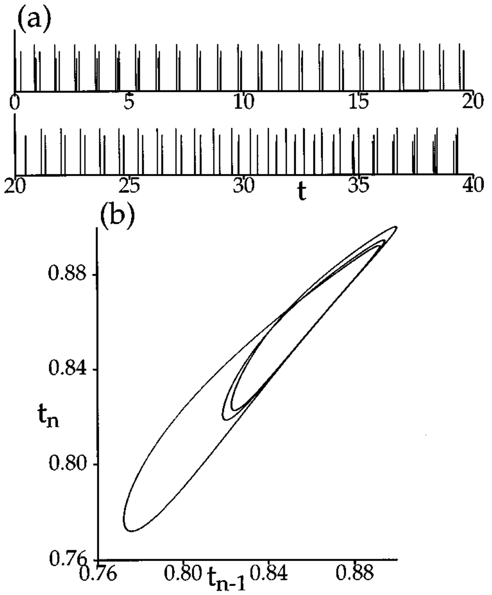

FIG. 2. (a) Time of firing of each cell plotted for a three-oscillator network for a time interval after the transients have died out. To facilitate the distinction between the three cells, the spikes are drawn to different height for the different oscillators. Notice that the firing pattern between $t = 0$ and $t = 5$ closely resembles the firing pattern between $t = 34.5$ and $t = 39.5$, though the role of the units is changed. This indicates quasiperiodic behavior. In this simulation, $F(x) = 1.3 - x$, $g = 0.4$, and $\alpha = 9.0$. (b) Interspike interval t_n, plotted against the previous interspike interval. The points lie on a curve that makes three loops before it repeats itself.

will never be complete synchronization. If a system with two oscillators does not reach complete synchrony, one expects large networks also to be only partially synchronized. One also expects the synchrony to increase as α is increased.

For inhibitory coupling the synchronous state is the only stable state in a two-oscillator network with slow coupling. It seems likely that in large networks with slow inhibitory coupling the oscillators will also fully synchronize. For faster coupling a two-cell network can be either in synchrony or in antisynchrony. In a large network the synchronous state is therefore probably still stable, but one expects there to be another stable state in which the cells have broken up in two clusters, so that each unit is in synchrony with the other units in its cluster and in antisynchrony with the units in the other cluster. One might also expect that if the coupling is speeded up even more there are stable states in which the oscillators have broken up in more than two clusters.

In Sec. V I will show that large excitatory networks evolve to a partially synchronized state if the coupling rate constant exceeds a critical value and that above this critical value the level of synchrony increases with the rate constant. In Sec. IX it is shown that the units in inhibitory networks break up in clusters, with a tendency to have a large number of clusters if the coupling rate constant is larger. This confirms the intuition we have gained from two-neuron networks.

IV. A FEW NEURONS

In excitatory networks with just two oscillators, the cells fire in antisynchrony if the coupling time constants are large, while for faster coupling the cells partially synchronize. This leads one to suspect that in networks with N oscillators, the system will evolve to an asynchronous state, with the units firing $360/N$° out of phase if the coupling is slow, while for faster coupling the units will fire in a partially synchronized pattern.

To test this expectation I performed numerical simulations for networks of three units satisfying Eqs. (2.1) and (2.2) with $F(x) = X_0 - x$, for different values of X_0, g, and α. X_0 was always chosen larger than 1 and g always between 0 and 1 so as to ensure continuous firing with finite rates.

For all choices of X_0 and g the network evolved to a state in which the oscillators were 120° out of phase, regardless of the initial conditions, for sufficiently small α. When α was increased past a critical value this was no longer the case and the spike trains evolved to a complicated pattern. Figure 2 shows an example.

In Fig. 2(a) the firing times for a network with $X_0 = 1.3$, $g = 0.4$ and $\alpha = 9.0$ are shown. To facilitate the identification of the three units the spikes are drawn to different heights for different cells. The spikes of the three units tend to be clustered, indicating that the network is partially synchronized, but the cells no longer fire periodically. This is in marked contrast to two-unit networks, in which the units fire periodically in the partially synchronized state. Figure 2(b) shows a plot of the interspike interval of a unit t_n against the previous interspike interval, t_{n-1}. All points lie on a closed curve, consisting of three loops. That these points all lie on a closed curve indicates that the units fire quasiperiodically.

To understand why, in a two-unit network, the oscillators fire periodically in the partially synchronized state, while they fire quasiperiodically in a three-unit network, I will study the bifurcation from the asynchronous state in some detail.

I will analyze an N oscillator system in which the state variables x_i obey the equation

$$\frac{dx_i}{dt}=X_0-x_i+gE_i(t), \tag{4.1}$$

with E_i given by Eq. (2.2). In the asynchronous state, unit i fires at times $t=[n+(i-1)/N]T$, where T is the period with which the oscillators fire and n is an integer. The coupling function $E_i(t)$ is given by

$$\begin{aligned} E_i(t)&=\frac{1}{N-1}\sum_{\substack{j\neq i\\ n}} E_s\left(t+\left[n-\frac{j-1}{N}\right]t\right)\\ &\equiv\frac{1}{N-1}\sum_{j\neq i} E_T\left(t-\left[\frac{j-1}{N}\right]T\right). \end{aligned} \tag{4.2}$$

Here we used $E_s(t)\equiv\alpha^2 t\exp(-\alpha t)$ to denote the α function.

To investigate the stability of this state we assume that the times at which the cells fire are slightly perturbed. Unit i fires at times $t=[n+(i-1)/N]T+\delta_{n,i}$. We require that the perturbations are consistent with Eqs. (4.1) and (2.2). If $\delta_{n,i}$ is given for $n<n_0$, one can calculate $x_1(t)$ for $t\leqslant n_0T+\delta_{n_0,1}$. At $t=n_0T+\delta_{n_0,1}$ cell 1 fires again, therefore the $x_1(n_0T+\delta_{n_0,1})$ must be 1. This determines $\delta_{n_0,1}$. Once $\delta_{n_0,1}$ is known, $\delta_{n_0,2}$ can be determined, etc. The antisynchronous state is stable if for all i and j, $\delta_{n,i}-\delta_{n,j}\rightarrow 0$ for $n\rightarrow\infty$. (If $\delta_{n,i}$ converges to δ for all i the whole system is translated in time by an amount δ, but the N oscillators will still fire asynchronously.)

If the perturbations are small one can write $\delta_{n,i}=\lambda^n\delta_i$. The asynchronous state is stable if apart from the solution $\lambda=1$ and $\delta_i=\delta$ all solution have $|\lambda|<1$. At $\alpha=\alpha_{\mathrm{cr}}$ the asynchronous state becomes unstable and one or more solutions with $|\lambda|<1$ for $\alpha<\alpha_{\mathrm{cr}}$ will switch to solutions with $|\lambda|>1$ for $\alpha>\alpha_{\mathrm{cr}}$. For $\alpha=\alpha_{\mathrm{cr}}+\delta\alpha$, with $0<\delta\alpha\ll 1$, one can, in general, have either one real eigenvalue and $|\lambda|>1$ with $|\lambda|\leqslant 1$ for all other eigenvalues or two complex-conjugate eigenvalues with $|\lambda|>1$ and $|\lambda|\leqslant 1$ for all other eigenvalues.

The behavior of the network past the transition point depends on how the asynchronous state becomes unstable. If there is one real eigenvalue $\lambda=1+\epsilon$, with $0<\epsilon\ll 1$ for $\alpha=\alpha_{\mathrm{cr}}+\delta\alpha$, the system undergoes a pitchfork bifurcation at the critical point. This can be a sub- or supercritical pitchfork bifurcation. If the bifurcation is subcritical there is no stable solution close to the asynchronous state past the critical point. If the bifurcation is supercritical there is a stable solution close to the asynchronous state past the critical point. In this solution unit i fires at time $t=[n+(i-1)/N]T+\Delta_i$ for some small Δ_i. So if past the critical point the system is slightly perturbed from the asynchronous state, the perturbations will evolve to $\delta_{n,i}\rightarrow\Delta_i$ for large n. The oscillators will no longer fire antisynchronously, but they will still fire periodically past the bifurcation point.

If past the critical point the system has two complex-conjugate eigenvalues for which $|\lambda|=1+\epsilon$, the network undergoes a sub- or supercritical Hopf bifurcation. In a subcritical Hopf bifurcation, like in the subcritical pitchfork bifurcation, there is no stable solution close to the asynchronous state past the critical point. In a supercritical Hopf bifurcation there is a stable solution past the critical point. In this solution the perturbation around the asynchronous state varies periodically. In this case small perturbations of $\delta_{0,i}$ of the asynchronous state will evolve to $\delta_{n,i}\rightarrow\Delta_i\cos(n\phi+\psi_i)$ for $n\rightarrow\infty$. In this case the interspike interval is modulated periodically and the cells fire quasiperiodically.

I will not analyze whether the system undergoes a super- or subcritical bifurcation. Simulations show for excitatory networks of any size that close to the transition point that the system stays close to the asynchronous state. Thus we can assume that there is a supercritical bifurcation. We have to determine whether it is a supercritical Hopf bifurcation or a supercritical pitchfork bifurcation.

So to understand why in a two-unit network the partially synchronized state is periodic, while it is quasiperiodic in a three-unit network, we have to show why at the critical value in a two-cell network one of the eigenvalues goes through 1, while this does not happen in a network with three units.

We will first analyze a two-unit network. In the asynchronous state cell 1 fires at times $t=nT$ and cell 2 at $t=(n+1/2)T$. The period is given by

$$X_0(1-e^{-T})+ge^{-T}\int_0^T dte^tE_T(t-T/2)=1. \tag{4.3}$$

The coupling strength is chosen small enough so that the rate of the units does not increase without bound. If we start the units in antiphase, but with a slightly smaller (or larger) period than the period found in Eq. (4.3), the network should evolve to to a state with the rate given by Eq. (4.3). This will happen only if

$$\frac{\partial}{\partial T}\left[x_0(1-e^{-T})+ge^{-T}\int_0^T dte^t\sum_n E_s(t+(n-1/2)T)\right]<0 \tag{4.4}$$

or

$$\begin{aligned} &X_0-1+gE_T(-T/2)+ge^{-T}\sum_n (n-1/2)\\ &\quad\times\int_0^T dte^t\dot{E}_s(t+(n-1/2)T)<0. \end{aligned} \tag{4.5}$$

Here I have used $\dot{E}$ to denote dE/dt.

When the system is perturbed the units fire at times $t=[n+(i-1)/2]T+\delta_{n,i}$. The perturbation results in a change in the coupling functions E_i. To lowest order in $\delta_{n,i}$, E_1 changes to

$$E_1(t)=E_T(t-T/2)-\sum_n \delta_{n,2}\dot{E}_s(t-(n+1/2)T). \tag{4.6}$$

For E_2 one finds an analogous expression. Setting $x_1(nT+\delta_{n,1})=0$ one finds

$$x_1((n+1)T+\delta_{n+1,1})$$
$$=X_0(1-e^{-T-\delta_{n+1,1}+\delta_{n,1}})+ge^{-T-\delta_{n+1,1}+\delta_{n,1}}$$
$$\times\int_0^{T+\delta_{n+1,1}-\delta_{n,1}}dte^tE_1(t+nT+\delta_{n,1}). \qquad (4.7)$$

By assumption $x_1((n+1)T+\delta_{n+1,1})=1$. Therefore, to lowest order in $\delta_{n,i}$

$$(\delta_{n+1,1}-\delta_{n,1})\left[X_0e^{-T}-ge^{-T}\int_0^T dte^tE_T\left(t-\frac{T}{2}\right)\right.$$
$$\left.+gE_T\left(-\frac{T}{2}\right)\right]+\delta_{n,1}\left[ge^{-T}\int_0^T dte^t\dot{E}_T\left(t-\frac{T}{2}\right)\right]$$
$$=ge^{-T}\sum_m\delta_{m,2}\int_0^T dte^t\dot{E}_s(t+(n-m-\tfrac{1}{2})T). \qquad (4.8)$$

A similar equation hold for $\delta_{n+1,2}$.

Solutions of these equations can be written in the form $\delta_{n,i}=\lambda^n\delta_i$. The state is stable if for every solution $|\lambda|<1$ or $\lambda=1$, and $\delta_1=\delta_2$. To make the set of consistency equations more transparent we introduce variables $C_2(\lambda)$, defined as

$$C_2(\lambda)=(\lambda-1)\left[X_0-1+gE_T\left(-\frac{T}{2}\right)\right]$$
$$+ge^{-T}\int_0^T dte^t\dot{E}_T\left(t-\frac{T}{2}\right), \qquad (4.9)$$

and $S(\lambda,\phi)$ defined as

$$S(\lambda,\phi)=ge^{-T}\sum_n\lambda^{-n}\int_0^T dte^t\dot{E}_s(t+(n-\phi)T). \qquad (4.10)$$

With these two variables the consistency equations can be written as

$$C_2(\lambda)\delta_1=S(\lambda,\tfrac{1}{2})\delta_2, \quad C_2(\lambda)\delta_2=S(\lambda,\tfrac{1}{2})\lambda\delta_1. \qquad (4.11)$$

These equations have two sets of solutions, one with $\delta_2=\sqrt{\lambda}\delta_1$ and $C(\lambda)=\sqrt{\lambda}S(\lambda,1/2)$ and one with $\delta_2=-\sqrt{\lambda}\delta_1$ and $C(\lambda)=-\sqrt{\lambda}S(\lambda,1/2)$. Here we use $\sqrt{\lambda}$ to denote the square root of the (possibly complex) λ with argument greater than $-\pi/2$ and less than or equal to $\pi/2$. Since

$$C_2(1)=ge^{-T}\int_0^T dte^t\dot{E}_T\left(t-\frac{T}{2}\right)=S\left(1,\frac{T}{2}\right), \qquad (4.12)$$

the first set always has a solution $\lambda=1$. In this case $\delta_1=\delta_2$, so this is the solution in which both oscillators fire a time δ_1 later but still in antisynchrony. This is the translationally invariant solution. The antisynchronous state is unstable if there are other solutions with $|\lambda|\geqslant 1$. The network will continue to fire periodically if, for α slightly larger than $\alpha_{\rm cr}$, there is a solution with $\lambda=1+\epsilon$, with $0<\epsilon\ll 1$. There cannot be such a solution with $\delta_2=\sqrt{\lambda}\delta_1$ since

$$\frac{\partial}{\partial\lambda}[C_2(\lambda)-\sqrt{\lambda}S(\lambda,1/2)]_{\lambda=1}$$
$$=X_0-1+gE_T(-T/2)-ge^{-T}\sum_n(n-1/2)$$
$$\times\int_0^T dte^t\dot{E}_s(t+(n-1/2)T). \qquad (4.13)$$

According to Eq. (4.5), this is always negative, so $C_2(1+\epsilon)\neq\sqrt{(1+\epsilon)}S(1+\epsilon,1/2)$ for small ϵ. If there is a solution with $\lambda=1+\epsilon$ for α just past the critical point, this has to be a solution with $\delta_2=-\sqrt{(1+\epsilon)}\delta_1$. Thus, at $\alpha=\alpha_{\rm cr}$ there is a solution with $C_2(1)=-S(1,1/2)$ or $S(1,1/2)=0$. In [8] it was shown that the bifurcation does indeed occur at the value of α for which $S(1,1/2)=0$. There it was also shown that for $\alpha=\alpha_{\rm cr}+\delta\alpha$, with $0<\delta\alpha\ll 1$ there is a solution with $\lambda=1+\epsilon>1$. Since λ is real at the point where the antisynchronous state becomes unstable, the system will evolve to a state with $\delta_{n,1}\rightarrow\Delta_1$ and $\delta_{n,2}\rightarrow\Delta_2\neq\Delta_1$. In this state the cells still fire periodically.

To study the stability of the asynchronous state in a three-cell network we assume that cell i, with $i=1,2,3$, fires at times $t=[n+(i-1)/2]T+\delta_{n,i}$, with $\delta_{n,i}$ small. Requiring that the $\delta_{n,i}$'s are consistent leads, for $\delta_{n,i}=\lambda^n\delta_i$, to the equations

$$C_3(\lambda)\delta_1=\frac{1}{2}[S(\lambda,\tfrac{1}{3})\delta_2+S(\lambda,\tfrac{2}{3})\delta_3],$$

$$C_3(\lambda)\delta_2=\frac{1}{2}[S(\lambda,\tfrac{1}{3})\delta_3+S(\lambda,\tfrac{2}{3})\lambda\delta_1],$$

$$C_3(\lambda)\delta_3=\frac{1}{2}[S(\lambda,\tfrac{1}{3})\lambda\delta_1+S(\lambda,\tfrac{2}{3})\lambda\delta_2], \qquad (4.14)$$

with $C_3(\lambda)$ defined as

$$C_3(\lambda)=(\lambda-1)\left\{X_0-1+\frac{g}{2}\left[E_T\left(-\frac{1}{T}\right)+E_T\left(-\frac{2}{3}T\right)\right]\right\}$$
$$+\frac{g}{2}e^{-T}\int_0^T dte^t\left[\dot{E}_T\left(t-\frac{1}{3}T\right)+\dot{E}_T\left(t-\frac{2}{3}T\right)\right]. \qquad (4.15)$$

$S(\lambda,\phi)$ is defined as above. The consistency equations (4.14) have three sets of solutions. If we define $\lambda^{1/3}$ as the cube root of λ for which the argument is between $-\pi/3$ and $\pi/3$, these sets have solutions with $\delta_3=\lambda^{1/3}e^{2k\pi i/3}\delta_2=(\lambda^{1/3})^2e^{4k\pi i/3}\delta_1$ and $C_3(\lambda)=[\lambda^{1/3}e^{2k\pi i/3}S(\lambda,1/3)+(\lambda^{1/3})^2e^{4k\pi i/3}S(\lambda,2/3)]/2$, with k equal to 0 for the first set, 1 for the second set, and 2 for the last set. A solution in the second set with $\lambda=\lambda_0$ has a complex-conjugate solution in the third set with $\lambda=\lambda_0$.

Since $C_3(1)=[S(1,1/3)+S(1,2/3)]/2$ the first set has a solution with $\lambda=1$ and $\delta_1=\delta_2=\delta_3$, corresponding to the asynchronous solution that is translated in time. Analogous to the two-unit network one can show that there is no solution with $\lambda=1+\epsilon$, with $\delta_3=\lambda^{1/3}\delta_2=(\lambda^{1/3})^2\delta_1$ for $\alpha=\alpha_{\rm cr}+\delta\alpha$. The asynchronous solution can bifurcate in the same manner as the antisynchronous solution in a two-cell network if for some α the second and third sets have solutions with $\lambda=1$. The second and third sets have $\lambda=1$ as a solution if $S(1,1/3)+S(1,2/3)=e^{2\pi i/3}S(1,1/3)+e^{4\pi i/3}S(1,2/3)$ or, equivalently, $S(1,1/3)=0$ and $S(1,2/3)=0$. But these two integrals are generally not 0 for the same value of α. Therefore if α is increased there is no critical value $\alpha_{\rm cr}$ at which the second and third sets of solutions will give an eigenvalue $\lambda=1$.

Therefore, beyond this critical value we will not have a real eigenvalue $\lambda=1+\epsilon$, but instead two eigenvalues $\lambda=(1+\epsilon)e^{\pm i\psi}$. Since these eigenvalues are complex, the stable state past the transition point will be very different. For $\alpha=\alpha_{\rm cr}+\delta\alpha$, with $0<\delta\alpha\ll 1$, the displacement in the time at which the cell k fires $\delta_{n,k}$ will evolve to $\delta_{n,k}\rightarrow{\rm Re}(e^{[n\psi+(k-1)\pi/3]i}\Delta)$ for some (complex) value of Δ. The interspike interval t_n between two consecutive firings of the first cell is given by

$$t_n=T+\delta_{n,1}-\delta_{n-1,1}=T+A\cos(n\psi+\psi_0), \tag{4.16}$$

with $A=|\Delta(e^{i\psi}-1)|$. So for each n the pair $(t_{n-1},t_n)=(T+A\cos[(n-1)\psi+\psi_0],T+A\cos(n\psi+\psi_0))$ lies on the ellipse $\gamma:\theta\mapsto(T+A\cos(\theta-\psi),T+A\cos(\theta))$, with $0\leq\theta<2\pi$. The interspike interval varies periodically, showing that the oscillators fire quasiperiodically. In the plot of t_n against t_{n-1} in Fig. 2(b) the points do not lie on an ellipse as prediced by the linearized theory. This is not surprising since α is quite far from the critical value, so that higher-order terms in $\delta_{n,i}$ have to be taken into account.

Let us summarize these results. In a two-unit network the antisynchronous state shows a bifurcation, with one of the eigenvalues going through 1, for the value of α at which a single condition $S(1,1/2)=0$ is met. Since this eigenvalue is real the oscillators continue to fire periodically past the bifurcation point. In a three-cell network the eigenvalue of the mode that becomes unstable is equal to 1 only if, for the same α two conditions are satisfied: $S(1,1/3)=0$ and $S(1,2/3)=0$. In general, this will not be the case and there will be a bifurcation with complex eigenvalues for the modes that become unstable. This leads to quasiperiodically firing in the partially synchronized state.

One can do the same analysis for networks with four or more units. Then one will also find that at least two conditions have to be met for the same α to have an eigenvalue $\lambda=1$ at the bifurcation point. As in three cell networks both conditions will generally not be satisfied for the same α and the eigenvalues will be complex, so that the cells will fire quasiperiodically past the bifurcation point. So in contrast to two-oscillator networks, networks with three or more units will have partially synchronized states in which the cells fire quasiperiodically.

This analysis is confirmed by simulations with networks of 4–7 units. In Fig. 3 the interspike interval t_n is plotted against the previous interspike interval t_{n-1} for networks with 4–7 oscillators. All other parameters are as in Fig. 2. In a three-unit network the point (t_{n-1},t_n) traced out a curve that consisted of three loops. In a four-cell network a four-loop curve is formed, but three of these loops are much smaller than the fourth loop. For networks with five units, the small loops become even smaller and vanish as the number of units in the network is increased. For larger networks the points (t_{n-1},t_n) lie on a curve that consists of a single curve. [See also Fig. 7(b).]

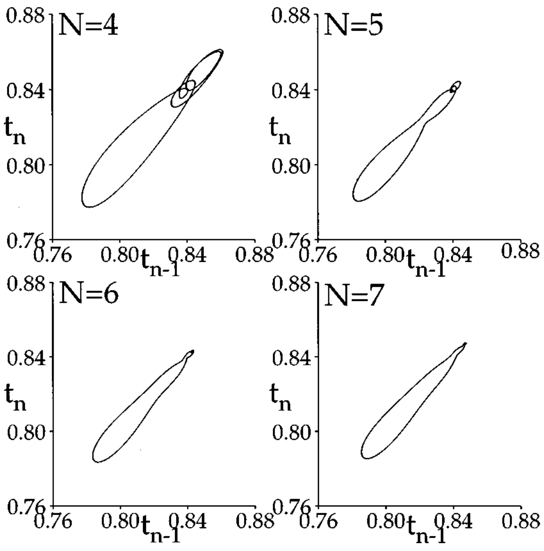

FIG. 3. Interspike interval t_n plotted against the previous interspike interval t_{n-1} in networks with four to seven oscillators. For the four-call network the points lie on a curve that has four loops, three small loops and one large one. As the number of cells is increased, the small loops shrink, leaving only a single loop in larger networks.

The fact that the plot of t_n against t_{n-1} becomes ''simpler'' as N is increased suggests that the behavior of the network in the large-N limit is simpler than the behavior of networks with a few oscillators. In Secs. V–VIII we will study large excitatory networks.

V. LARGE ASYNCHRONOUS NETWORKS

In a previous paper [7] we studied the asynchronous state in the large-N limit. Here I will briefly summarize the methods and findings relevant for the study of networks with parameter values for which the asynchronous state is not stable.

For large networks the asynchronous state is characterized by a coupling variable E that is constant $E(t)=E_0$. If in this state the oscillators fire with a frequency R, it follows from Eq. (2.3) that $E_0=R$. With $E(t)$ constant the rate R can be calculated from Eq. (2.1). Combining these two equations, we find that E_0 has to satisfy

$$\frac{1}{E_0}=\int_0^1\frac{dx}{F(x)+gE_0}. \tag{5.1}$$

For continuous $F>0$ this equation always has a solution for $g<1$.

For the analysis of the asynchronous state it is convenient to change variables from x_i to a phase variable

$$y_i=\int_0^{x_i}\frac{E_0dx}{F(x)+E_0}, \tag{5.2}$$

which ranges from 0 to 1 and satisfies the equation

$$\frac{dy_i}{dt}=E_0+\Gamma(y_i)\epsilon(t), \tag{5.3}$$

where

$$\Gamma(y)=\frac{gE_0}{F(x)+gE_0}, \quad \epsilon(t)=E(t)-E_0. \tag{5.4}$$

The state of the full population is described by a density function $\rho(y,t)$ and flux $J(y,t)$ defined by

$$\rho(y,t)=\frac{1}{N}\sum_i \delta(y-y_i(t)),$$

$$J(y,t)=[E_0+\Gamma(y)\epsilon(t)]\rho(y,t). \tag{5.5}$$

These satisfy the continuity equation

$$\frac{\partial}{\partial t}\rho(y,t)=-\frac{\partial}{\partial y}J(y,t) \tag{5.6}$$

for $0<y<1$ and the boundary condition

$$J(0,t)=J(1,t). \tag{5.7}$$

The flux though $x=1$, $J(1,t)$, is the population firing rate.

The asynchronous solution is given by $\rho(y,t)=1$ and $J(y,t)=E_0$. To determine the stability of this solution one expands around it, writing

$$J(y,t)=E_0+j(y,t) \tag{5.8}$$

and using Eq. (5.5) to express ρ in terms of j and ϵ. The stability against small fluctuations is examined by expanding ρ to first order in j and ϵ. In this approximation the continuity equation (5.6) becomes

$$\frac{\partial j}{\partial t}=\Gamma(y)\frac{d\epsilon}{dt}-E_0\frac{\partial j}{\partial y}. \tag{5.9}$$

With the fluctuation in the firing rate $j(1,t)$ we can rewrite Eq. (2.3) for the coupling variable ϵ as

$$\left(\frac{d}{dt}+\alpha\right)^2\epsilon(t)=\alpha^2 j(1,t). \tag{5.10}$$

Solutions of the linearized equations (5.9) and (5.10) will have time dependence $\exp(\lambda t)$. Using this we can calculate the eigenvalue spectrum [11]. (References [12,2,13] use similar methods.) With Eq. (5.9) $j(y,t)$ can be written as

$$j(y,t)=\frac{\epsilon(t)\lambda}{E_0}\left[\int_0^y dy'\Gamma(y')e^{\lambda y'/E_0}+C_\lambda\right]e^{-\lambda y/E_0}. \tag{5.11}$$

C_λ is determined by the boundary condition Eq. (5.7)

$$C_\lambda=(e^{\lambda/E_0}-1)^{-1}\int_0^1 dy\Gamma(y)e^{\lambda y/E_0}. \tag{5.12}$$

By substituting this into Eq. (5.10) we have that the eigenvalues λ have to satisfy the eigenvalue equation

$$E_0(\lambda+\alpha)^2(e^{\lambda/E_0}-1)=\alpha^2\lambda\int_0^1 dy\Gamma(y)e^{\lambda y/E_0}. \tag{5.13}$$

This eigenvalue equation has infinitely many solutions. In limiting cases, for example weak coupling, the eigenvalues can be determined by perturbation expansion [7]. Away from these limits the eigenvalues have to be determined numerically.

For small coupling there is one doubly degenerate eigenvalue $\lambda\approx-\alpha$ that determines the stability of the network against fluctuations in the firing rate of the whole network. The other eigenvalues are approximated by $\lambda_n\approx 2\pi ni/E_0$ and have eigenfunctions $j_n(y)\approx C_n\exp(2\pi ny)$. These eigenvalues determine the stability of the network against the modes of fluctuation that tend to synchronize the oscillators into $|n|$ different clusters.

For excitatory coupling the asynchronous state is never stable if $F(1)>F(0)$. If $dF/dx<0$ there is a critical value $\alpha_{\rm cr}$ for the coupling rate constant so that for $\alpha<\alpha_{\rm cr}$ the asynchronous state is stable, while the asynchronous state is unstable for $\alpha>\alpha_{\rm cr}$. At the bifurcation point $\alpha=\alpha_{\rm cr}$ the two eigenvalues λ_1 and λ_{-1} are purely imaginary. All other eigenvalues have a negative real part.

For inhibitory coupling $g<0$, the asynchronous state is always unstable if $dF/dx<0$. For small α all complex eigenvalues have a positive real part. As α is increased the real part of the two eigenvalues λ_1 and λ_{-1} change sign. As the coupling time constant is decreased further additional modes become stable.

For inhibitory coupling the higher modes are all unstable. If the system starts close to the asynchronous state, the higher modes will initially grow exponentially. So the final state of the system can depend on the initial conditions [14]. In Sec. IX I will show that this is indeed the case. In contrast, for excitatory coupling the higher modes are stable, suggesting that the final state of the system does not depend on the details of the initial conditions. In the next section we will see that this is also true.

VI. PARTIAL SYNCHRONY IN LARGE NETWORKS

In the preceding section we saw that for large excitatory networks, the asynchronous state switches from stable for α smaller than some critical value $\alpha_{\rm cr}$ to unstable for α larger than this critical value. Two complex-conjugate eigenvalues for perturbations of the asynchronous state have a real part that goes from negative for $\alpha<\alpha_{\rm cr}$ to positive for $\alpha>\alpha_{\rm cr}$. These eigenvalues have a nonzero imaginary part and the real part of the eigenvalues $\mathrm{Re}(\lambda)$ has a nonzero derivative with respect α_i. All other eigenvalues have strictly negative real parts for α close to the critical point $\alpha_{\rm cr}$. At $\alpha=\alpha_{\rm cr}$ the system undergoes a Hopf bifurcation [15,16].

Hopf bifurcation theory tells us that for a parameter α that induces a bifurcation, there is a periodic solution for parameters in the neighborhood of the bifurcation point. The amplitude of this periodic solution vanishes when the parameter reaches the critical point. We can have one of two kinds of Hopf bifurcations: (i) the subcritical Hopf bifurcation, in which case there is a *unstable* periodic solution for $\alpha < \alpha_{\text{cr}}$, or (ii) the supercritical Hopf bifurcation with a *stable* periodic solution for $\alpha > \alpha_{\text{cr}}$.

If the Hopf bifurcation is supercritical, the behavior of the network changes continuously when the rate constant changes past the critical value. If the Hopf bifurcation is subcritical the change is discontinuous. Since for excitatory coupling a system with two oscillators has a stable firing pattern with the cells firing nearly antisynchronously just past the bifurcation point, we expect a large network also to change continuously. Thus, in a large network we expect a supercritical Hopf bifurcation.

I investigated the behavior of the system for parameter values at which the asynchronous state is unstable, using computer simulations with 100 oscillators. The units satisfy Eq. (2.1) with $F(x) = X_0 - x$. At $t = 0$ the oscillators were given random values x_i. The self-coupling was not removed, E satisfies Eq. (2.3) and is initialized at $E = 0$. The firing rate for a finite population of N oscillators is estimated in the following manner. Suppose a cell fires at time t_i, the last cell that fired before this cell fired at t_{i-1}, and the next one will fire at t_{i+1}. Then there is a time interval $(t_{i+1} - t_{i-1})/2$ around time t_i in which one cell fires. We take the firing rate $J(1,t)$ at time t_i to be

$$J(1,t_i) = \frac{2}{N(t_{i+1} - t_{i-1})}. \tag{6.1}$$

In the simulations we let the system evolve from $t = 0$ to $t = 45\,000$, to make sure that all the transients have died out. We plot the firing rate for the next ten time units. Figure 4 shows the firing rate for systems with $X_0 = 1.3$ and $g = 0.4$. The firing rate is shown for different values of α. Using these parameters, the eigenvalue Eq. (5.13) tells us that the asynchronous state is unstable for $\alpha > \alpha_{\text{cr}} = 8.34 \pm 0.01$. For $\alpha < \alpha_{\text{cr}}$ the firing rate is indeed constant. For α just larger than α_{cr} the firing rate has a small periodic perturbation. If one increases α the firing rate oscillates with an increasing amplitude and the system becomes more synchronized. This gradual growth the amplitude of a periodic firing rate is exactly what one expects from a supercritical Hopf bifurcation.

To quantify the level of synchronization we introduce an order parameter $m(t)$ defined as

$$m(t) = \left| \int_0^1 dy \rho(y,t) e^{2\pi i y} \right|. \tag{6.2}$$

If the system is in the asynchronous state $[\rho(y,t) = 1]$ the order parameter is zero, while for a completely synchronized system the order parameter equals one. For $\alpha > \alpha_{\text{cr}}$ we have a partially synchronized system that fires periodically. If $J(1,t)$ is periodic, ρ and J are periodic for all values of y, so ρ can be written as $\rho(y,t) = \Sigma_k \rho_k(y) \exp(ik\omega t)$ for some value of ω. With the definition $\rho_{k,n} = \int_0^1 dy \rho_k(y) \exp(-2\pi n i y)$, the order-parameter can be written as

$$m(t) = \left| \sum_k \rho_{k,-1} e^{ik\omega t} \right|. \tag{6.3}$$

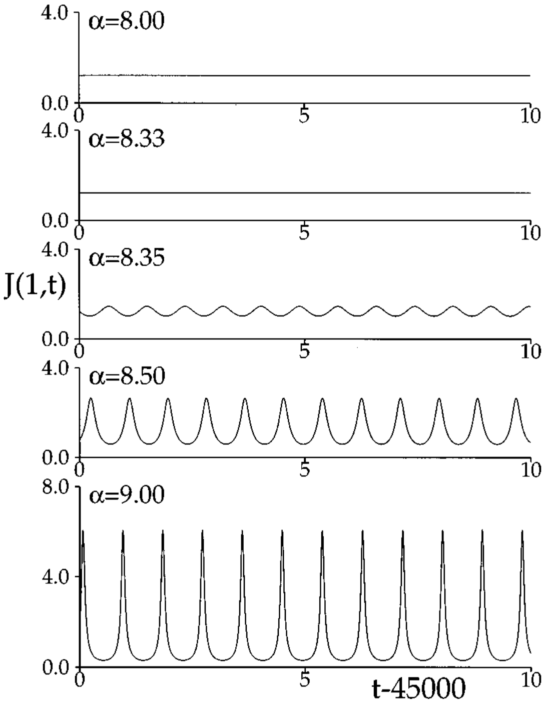

FIG. 4. Firing rate $J(1,t)$ for different coupling time constants for a system of 100 oscillators with $X_0 = 1.3$ and $g = 0.4$. For $\alpha = 8.0$ and 8.33 the asynchronous state is stable and the firing rate is constant. For $\alpha = 8.35$ the asynchronous state is no longer stable and a small periodic perturbation appears. For $\alpha = 8.5$ and $\alpha = 9.0$ the amplitude of the oscillations in the firing rate increases.

In general m will vary periodically for a partially synchronized system. We characterize the level of synchronization of the system by $\overline{m}$, the temporal average of $m(t)$. We determined $\overline{m}$ as function of α for a system with parameters as in Fig. 4. In Fig. 5 $\overline{m}$ is plotted against $1/\alpha$. As α is increased past the transition point, $\overline{m}$ increases rapidly. Then $\overline{m}$ levels off and $\overline{m}$ goes to 1 asymptotically as α goes to infinity. The system thus reaches total synchronization asymptotically.

The simulations were repeated with different random initial conditions, for different values of α up to 8 times. Up to

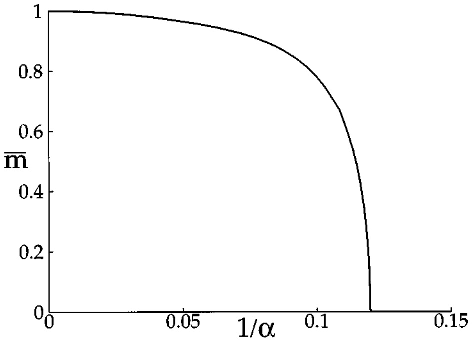

FIG. 5. Order parameter $\overline{m}$ that characterizes the level of synchronization as a function of $1/\alpha$ for a system with $N = 100$, $X_0 = 1.3$, and $g = 0.4$. For α larger than the critical value, $\overline{m} = 0$ and the system is in the asynchronous state. Past the transition point $\overline{m}$ increases and the level of synchronization in the system increases. As $1/\alpha$ reaches 0, $\overline{m}$ goes to 1. The system goes asymptotically to complete synchronization for increasing α.

a phase factor these gave the same firing rates. Simulations with $X_0 = 1.2$ and $X_0 = 1.5$ gave analogous results, as did simulations for different values of g.

VII. CLOSE TO THE TRANSITION POINT

Finding the stable periodic solution is not easy. For parameters close to the bifurcation point, we can use the fact that this solution stays close to the steady-state solution $J = E_0$ and write the solution as an expansion in j and ϵ. In this section I will describe how j and ϵ depend on $\delta\alpha$ for $\alpha = \alpha_{\mathrm{cr}} + \delta\alpha$, with $0 < \delta\alpha \ll 1$.

It is clear from Fig. 5 that the order parameter $\overline{m}$ and therefore j and ϵ are not analytical functions of α at $\alpha = \alpha_{\mathrm{cr}}$ and hence their dependence on α cannot be written as a Taylor expansion around $\alpha = \alpha_{\mathrm{cr}}$. We will show that, analogous to many physical phenomena near a phase transition [17], j and ϵ can, for $\alpha = \alpha_{\mathrm{cr}} + \delta\alpha > \alpha_{\mathrm{cr}}$, be written as an expansion in $\delta\alpha$ with a critical exponent c

$$j(y,t) = (\delta\alpha)^c [J(y,t) + J'(y,t)(\delta\alpha)^d + \cdots] \tag{7.1}$$

and

$$\epsilon(t) = (\delta\alpha)^c [E(t) + E'(t)(\delta\alpha)^d + \cdots], \tag{7.2}$$

with $d > 0$. Since $\overline{m}$ vanishes as $\delta\alpha$ goes to zero, while $d\overline{m}/d\alpha$ diverges, the critical exponent c must between 0 and 1.

In Appendix A it is shown that $j(y,t)$ can be written as $j(y,t) = \Sigma_n j_n(y) \exp(in\omega t)$, where

$$j_n(y) = (\delta\alpha)^{|n|/2} [j_n^0(y) + (\delta\alpha)^{1/2} j_n^1(y) + \cdots] \tag{7.3}$$

for $n \neq 0$ with j_n^k independent of $\delta\alpha$ and $j_0(y)$ is of order $\delta\alpha$. The angular frequency ω is to lowest order given by the absolute value of imaginary part of the eigenvalues $(\lambda_{\pm 1})$ whose real part goes through zero at the critical point. Simular results hold for $\epsilon(t)$.

Thus, close to the transition point the average firing rate $J(1,t)$ will oscillate periodically with an angular frequency that is close to $|Im(\lambda_{\pm 1})|$, while the amplitude of the oscillations will grow as $(\delta\alpha)^{1/2}$ as α exceeds the critical value α_{cr} by an amount $\delta\alpha$. Therefore the critical exponent is $c = 1/2$.

It should be noted that in the derivation of the critical exponent in the Appendix I did not make any special assumptions about the function Γ. Therefore the procedure outlined above will work for any model that has the following properties. (i) The model can be reduced to a model in which the state of cell i can be described by a variable y_i that obeys Eq. (5.3) for some function $b\Gamma$. (ii) The model has a stable asynchronous state for an region of coupling rate constants. (iii) The model has a stable static solution that has a supercritical Hopf bifurcation at the edge of that region.

Whether the asynchronous state is stable for a given function $\Gamma(y)$ can be determined by solving the eigenvalue Eq. (5.13). The eigenvalues of the modes that become unstable at the edge of the region of stability will determine whether or not there is a Hopf bifurcation at this edge. But it will not tell you whether this Hopf bifurcation is super- or subcritical. The procedure outlined in the Appendix for the determination of the critical exponent in a supercritical Hopf bifurcation can actually be used to determine whether the bifurcation is sub- or supercritical. If the bifurcation is subcritical, this procedure will not work. Specifically Eq. (16) will give a *negative* value for $e_{-1}e_1 = |e_1|^2$ if the Hopf bifurcation is subcritical. So to determine whether the system has a sub- or supercritical Hopf bifurcation one can use the procedure outlined above to calculated $e_1 e_{-1}$. If $e_1 e_{-1}$ is positive the bifurcation is supercritical and just past the critical point there is a periodic firing pattern that is close to the asynchronous firing pattern. If $e_1 e_{-1}$ is negative the bifurcation is subcritical and the firing pattern changes discontinuously at the critical point.

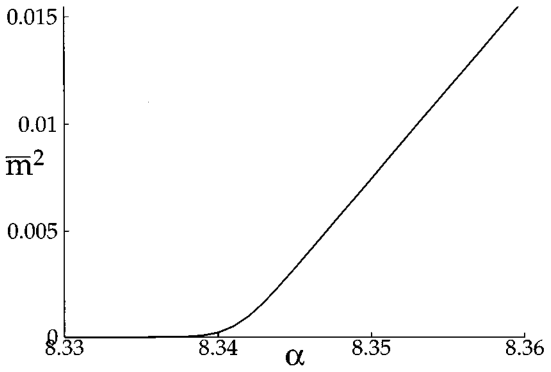

FIG. 6. $\overline{m^2}$ as a function of α. A linear graph for $\alpha > \alpha_{\mathrm{cr}}$ indicates a critical exponent of 1/2. The smooth change in slope at $\alpha = \alpha_{\mathrm{cr}}$ is caused by the transients that have not yet died out due to the divergence of the relaxation time at the transition point.

The critical exponents can also be determined using numerical simulations. As before I used a system consisting of 100 cells, with $F(x) = X_0 - x$. The parameters were the same as in Sec. VI. For values of α ranging from 8.25 to 8.60 the order parameter $\overline{m}$ was determined. The system started at $t = 0$ with random initial values for x_i. We assumed that at $t = 45\,000$ the system had reached its steady state. The order parameter was determined by calculating $m = |N^{-1}\Sigma_i \exp(2\pi i y_i)|$ every time one of the cells fired for the next 200 time units and averaging these values.

For $\alpha = \alpha_{\mathrm{cr}} + \delta\alpha$, with $0 < \delta\alpha \ll 1$, $j(y,t)$ and $\epsilon(t)$ are to lowest order proportional to $(\delta\alpha)^{1/2}$. Therefore $\delta\rho = \rho - 1$ is of order $(\delta\alpha)^{1/2}$, so that $\overline{m}$ is proportional to $(\delta\alpha)^{1/2}$. Thus if $\overline{m^2}$ is plotted against α, one should theoretically get 0 for $\alpha < \alpha_{\mathrm{cr}}$ and a straight line with positive slope through $(\alpha_{\mathrm{cr}},0)$ for $\alpha > \alpha_{\mathrm{cr}}$.

Figure 6 shows the results for our simulations. Not too close to the phase transition the simulation does agree with the theory. Near α_{cr} the simulation does not give the predicted result. This is not surprising since at the critical value the linearized theory has an eigenvalue with a vanishing real part, so that the relaxation time goes to infinity as one approaches α_{cr}. Thus, even at $t = 45\,000$ the simulations will not have lost all initial transients.

VIII. INDIVIDUAL CELLS IN THE PERIODIC SOLUTION

For $\alpha > \alpha_{\mathrm{cr}}$, the stable solutions for ρ, J, and E are periodic. It would be natural to guess that individual cells also behave periodically. Yet one can show that individual oscillators cannot fire periodically in this solution. It is instructive to prove this first in the special case where $F(x)$ is given by $F(x)=X_0-x$. After that I will show that it is true in other cases also, at least close to the transition point.

Suppose that all units fire periodically with period T. Then $J(1,t)=J(1,t+T)$ and $E(t)=E(t+T)$. In that case either the cells are all synchronized in a finite number of groups or $E(t)$ is constant, at least for a part of the period. Namely, if we assume that the cells are not synchronized in a finite number of groups, there is a time interval $\langle t_0,t_1\rangle$, with $0\leqslant t_0<t_1\leqslant T$ in which $J(1,t)\neq 0$. So that for every t in this interval there is a cell i with $x_i(t)=0$. For this cell the state variable a time T later is given by

$$x_i(t+T)=X_0(1-e^{-T})+ge^{-T}\int_0^T dt' e^{t'}E(t+t')=1, \tag{8.1}$$

since the cell fires with period T. We can rewrite this as

$$\int_0^T dt' e^{t'}E(t+t')=g^{-1}(e^T-X_0(e^T-1)). \tag{8.2}$$

The right-hand side of this equation is independent of t. So if we take the derivative of the left-hand side with respect to t we should have 0. But using partial integration and the periodicity of E, we can also write

$$\begin{aligned}\frac{\partial}{\partial t}\int_0^T dt' e^{t'}E(t+t')&\\ =\int_0^T dt' e^{t'}E'(t+t')&\\ =e^T E(t+T)-E(t)-\int_0^T dt' e^{t'}E(t+t')&\\ =(e^T-1)E(t)-g^{-1}(e^T-X_0(e^T-1)).&\end{aligned} \tag{8.3}$$

Setting this equal to 0 we have, for $t_0<t<t_1$,

$$E(t)=g^{-1}\left(\frac{1}{1-e^{-T}}-X_0\right), \tag{8.4}$$

independent of t.

Since with excitatory coupling the system undergoes a supercritical Hopf bifurcation if α is increased past the critical value α_{cr}, close to the transition point, $J(1,t)$ will differ only a small amount from E_0 and therefore $J(1,t)>0$ for all t. Thus it would follow that if the cells fire periodically, $E(t)$ is constant. But if E is constant, $J(1,t)$ has to be constant also, and this is in contradiction with the theory. Therefore, close to the transition point, the cells *do not* fire periodically, even though macroscopic quantities ρ, J, and E behave periodically. The simulations indecate that for any finite α, $J(1,t)>0$ for all t, so for any $\alpha>\alpha_{\mathrm{cr}}$ the units do not fire periodically.

That the oscillators do not fire periodically for any $F>0$ with $dF/dx<0$ can be seen in the following way. If the self-coupling term is not removed, so that $E_i(t)=E(t)$ for all i, Eq. (2.1) implies that all other cells fire exactly once between two consecutive firings of one cell. Assume that cell fires at time t and fires again at time $t+f(t)$. Since $\int_{t_0}^{t_1}dt' J(1,t')$ is the fraction of units that fire between time t_0 and time t_1, $f(t)$ satisfies

$$\int_t^{t+f(t)} dt' J(1,t')=1. \tag{8.5}$$

If individual neurons fire periodically with period T, $f(t)=T$. But in this case $J(1,t)$ is also periodic with period T. So the integral of $J(1,t)$ over one period should be 1. For a synaptic rate constant close to the transition point $\alpha=\alpha_{\mathrm{cr}}+\delta\alpha$, we have to lowest order $J(1,t)=E_0+j_1^{(0)}\sqrt{\delta\alpha}\cos(\omega_{\mathrm{cr}}t+\phi)$, so that $T=2\pi/\omega_{\mathrm{cr}}$ and

$$\int_t^{t+T} dt' J(1,t')=\frac{2\pi E_0}{\omega_{\mathrm{cr}}}. \tag{8.6}$$

Thus, if the cells fire periodically ω_{cr} has to satisfy $\omega_{\mathrm{cr}}=2\pi E_0$. Therefore at the critical point there should be eigenvalues $\lambda=\pm\omega_{\mathrm{cr}}i=\pm 2\pi E_0 i$. Substituting this in the eigenvalue Eq. (5.13) one finds that this is equivalent to $\int_0^1 dy\Gamma(y)\exp(\pm 2\pi yi)=0$. But if $dF/dx<0$, $d\Gamma/dy>0$, so that

$$\begin{aligned}\int_0^1 dy\Gamma(y)\sin(2\pi y)&=\int_0^{1/2}dy[\Gamma(y)-\Gamma(1-y)]\sin(2\pi y)\\ &<0.\end{aligned} \tag{8.7}$$

Therefore $\int_0^1 dy\Gamma(y)\exp(2\pi yi)\neq 0$, but has a negative imaginary part. So close to the critical point $J(1,t)$ cannot satisfy $\int_t^{t+T}dt' J(1,t')=1$ and therefore the cells do not fire periodically.

This is also in agreement with numerical simulations. For example, with $F(x)=1.3-x$ and $g=0.4$ we have, for $\alpha=\alpha_{\mathrm{cr}}$, $E_0=1.221$ and $\omega_{\mathrm{cr}}=7.363$, so $2\pi E_0/\omega_{\mathrm{cr}}=1.042$. Thus, during one period the average cell fires a little more than 1.04 times, for α just larger than α_{cr}. In the simulations discussed in Sec. VI I found that as α is increased and the system becomes more synchronized, $\int_t^{t+T}dt' J(1,t')$ decreases asymptotically to 1 with increasing α.

Figure 7(a) shows the times at which one of the neurons fires after the network has settled in partially synchronized state. The data in this figure are taken from a simulation with $\alpha=9.0$, $F(x)=1.3-x$, and $g=0.4$. The top of the figure shows the network firing rate $J(1,t)$; below that the time at which one of the cells fires is indicated. The time at which the cell fires shifts a little bit relative to the peak in the network firing rate each time the cell fires. The cell fires slightly faster than the network rate peaks. The neuron does not fire exactly periodically; for example, around $t=13$ the interspike interval is shorter than around $t=2$. Since the neurons do not fire exactly periodically, the time between the firing of the neuron shown here and the next one can vary; this interval is short when the firing coincides with a peak in the network firing rate and longer when the firing rate is low.

If the system has settled in a periodic firing pattern with $\int_t^{t+T}dtJ(1,t)\neq 1$ the time between two consecutive firings of one neuron, the interspike interval t_n, can take any value

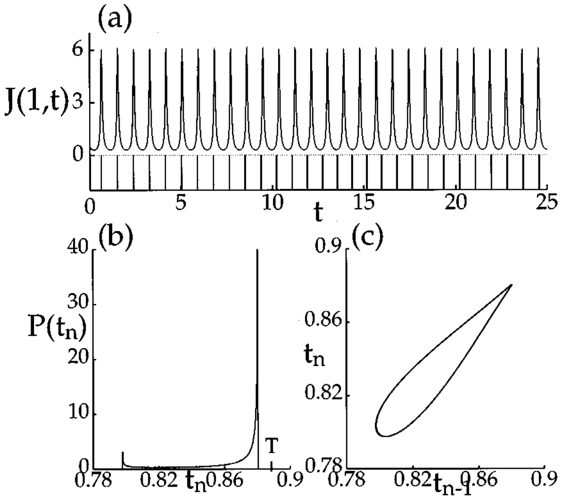

FIG. 7. (a) Network firing rate and the spike times of one of the neurons. The fire rate (upper trace) varies periodically. The times when the neuron fires, indicated below, slowly shifts with respect to the peak of the firing rate. The neuron does not fire periodically. (b) The probability distribution of the interspike interval t_n has its maximum values at the extreme values of t_n. The largest possible value t_n can take is less than the period T with which the network oscillates. (c) Interspike interval t_n plotted against the previous interspike interval t_{n-1} of the same cell.

between some values $t_{n,\min}$ and $t_{n,\max}$, determined by Eq. (8.5). If after some randomly chosen time t we record the time between the next two spikes for one of the neurons, we will have some probability $P(t_n)dt_n$ to record an interval between t_n and t_n+dt_n, with $P(t_n)\neq 0$ for $t_{n,\min}\leq t_n<t_{n,\max}$. One can show that $P(t_n)\to\infty$ for $t_n\to t_{n,\max}$ and $t_n\to t_{n,\min}$.

In Fig. 7(b) the probability distribution of the interspike interval t_n is plotted for the same simulation used in Fig. 7(a). The distribution has two local maxima. There is a large maximum at $t_n=t_{n,\max}$ and a much smaller one at $t_n=t_{n,\min}$. The probability distribution was determined by measuring 2000 consecutive interspike intervals and binning these in bins of size $(t_{n,\max}-t_{n,\min})/50$. Notice that this gives a finite value for $P(t_{n,\max})$ and $P(t_{n,\min})$. This does not contradict that $P(t)\to\infty$ for $t\to t_{n,\max},t_{n,\min}$, since while $P(t_n)$ diverges at these values the integral of P over a bin of finite size converges.

The shape of the interspike interval distribution in this partially synchronized system is clearly different from that of the interspike interval distribution of oscillators that are incompletely synchronized due to noise, in a network that would synchronize completely in the absence of noise. In such a network one expects an interspike interval distribution with a peak for some intermediate value of the interval and tails that fall off at both ends.

If an oscillator fires at some time τ_{n-1}, the next time this cell fires $\tau_n=\tau_{n-1}+t_{n-1}$, with $t_{n-1}=f(\tau_{n-1})$ determined by Eq. (8.5). The next time after that this cell fires at time $\tau_{n+1}=\tau_n+t_n$, with t_n given by $t_n=f(\tau_n)=f(\tau_{n-1}+f(\tau_{n-1}))$. Thus, if one plots t_n against t_{n-1} for any oscillator, this point will be on the curve $\gamma{:}t\mapsto(f(t),f(t+f(t)))$. Since $J(1,t)$ is periodic with period T, $f(t)$ is periodic with period T. Therefore $\gamma(t+T)=\gamma(t)$ and the curve γ traces a closed loop.

Figure 7(c) shows a plot of t_n against t_{n-1} for the 2000 time intervals used to determine P above. All points are indeed on a closed curve as expected.

As we have seen, the coupling function E is periodic, but individual oscillators do not fire with an average frequency that is equal to the frequency with which E varies, or a simple fraction of that frequency. We therefore expect the cells to behave quasiperiodically. This quasiperiodic behavior is indeed consistent with the firing pattern observed in Fig. 7(c). Since the curve γ traces a single loop, we can conclude that the cells fire quasi-periodically with their state characterized by two frequencies.

Is it surprising that in the partially synchronized state individual units behave quasiperiodically, while the macroscopic quantities vary periodically with time? Let us compare this with the asynchronous state. In the asynchronous state the units behave periodically. There is a function $f(x)$ with period 2π so that the state variables x_i can be described by

$$x_i(t)=f(\omega(t-t_i)) \tag{8.8}$$

for some ω. The values of t_i are distributed in such a way that the density

$$\rho(x,t)\equiv N^{-1}\sum_i \delta(x-f(\omega(t-t_i))) \tag{8.9}$$

is independent of time. In other words, the values of t_i are uniformly destributed between 0 and $2/\pi/\omega$.

In the partially synchronized state individual oscillators behave quasiperiodically. There is a function $F(x,y)$ that is periodic both in x and y, with period 2π, so that for the state variable x_i of oscillator i we can write, if t is large enough,

$$x_i(t)=F(\omega_1(t-t_i),\omega_2(t-t_i)), \tag{8.10}$$

with appropriately chosen ω_1 and ω_2. Remarkable about the network is that the values of t_i are distributed in such a way that the density $\rho(x,t)=N^{-1}\Sigma_i\delta(x-F(\omega_1(t-t_i),\omega_2(t-t_i)))$ is periodic rather than quasiperiodic in time. In summing the contributions of all units to the density one of the periods that determine the quasiperiodic behavior of the individual cells is averaged out. For example, the values of t_i could be uniformly distributed between 0 and $2\pi/\omega_1$.

So both in the asynchronous state and in the partially synchronized state one needs one more frequency to describe the states of the individual units than is needed to describe variables ρ, J, and E. In both states the time offsets t_i are distributed so that they cancel this extra frequency in the macroscopic variables.

IX. INHIBITION

We now turn our attention to large networks of oscillators with inhibitory coupling. In a system with two oscillators the synchronous state is always stable, while the antisynchronous state is unstable for slow coupling (α small) and stable for fast coupling (α large). This leads one to suspect that in large networks there is always a locally stable synchronous solution and that for faster coupling there is a stable state in which the oscillators are synchronized in two or more clusters.

That the completely synchronized state is locally stable can be shown as follows. In the synchronized state all oscillators fire a time $t=nT$. The state variable x_i is the same for all cells; $x_i(t)=x_{\rm net}(t)$ and $x_{\rm net}$ satisfies

$$\frac{x_{\rm net}}{dt}=F(x_{\rm net})+gE_T(t), \tag{9.1}$$

with $F'=dF/dx<0$, $g<0$, and $E_T(t)=\Sigma_n E_s(t+nT)$. The cells fire at $t=0$ so that $x_{\rm net}(0)=0$. Solving Eq. (9.1) one finds $x_{\rm net}(t)$ for $0<t<T$ and the period T is determined by $x_{\rm net}(T)=1$.

Suppose that at $t=0$ oscillator i is perturbed so that its state variable is shifted to $x_i(0)=\xi$, with $|\xi|\ll 1$. The other cells are not perturbed so that in the large-N limit the coupling variable E will be unperturbed for $t>0$. Thus $x_j(t)=x_{\rm net}(t)$ for $j\neq i$. Let $x_i(t)$ be given by $x_i(t)=x_{\rm net}(t)+\xi(t)$ with $\xi(0)=\xi$. The system is stable for small single-cell perturbations if $|\xi(T)|<|\xi(0)|$ for all $|\xi(0)|\ll 1$. We will only consider the case $\xi>0$ since showing stability for the case $\xi<0$ is completely analogous.

If $\xi>0$ oscillator i will reach the threshold $x=1$ before the rest of the network. The network reaches the threshold at time $t=T$, and cell i at $t=T'<T$. For $0<t<T'$, ξ obeys to lowest order

$$\frac{d\xi}{dt}=F(x_{\rm net}+\xi)-F(x_{\rm net})=F'(x_{\rm net})\xi, \tag{9.2}$$

here we have used F' for dF/dx. To lowest order $\xi(T')$ satisfies

$$\begin{aligned}\xi(T')&=\xi(0)\exp\left(\int_0^{T'}dtF'(x_{\rm net}(t))\right)\\&=\xi(0)\exp\left(\int_0^{T}dtF'(x_{\rm net}(t))\right).\end{aligned} \tag{9.3}$$

Since $x_{\rm net}(T)=1$ and $dx_{\rm net}(T)/dt=F(1)+gE_T(T)$ we also have to lowest order

$$\xi(T')=1-x_{\rm net}(T')=(T-T')[F(1)+gE_T(T)]. \tag{9.4}$$

Thus $T-T'$ satisfies

$$T-T'=\xi(0)\frac{\exp(\int_0^T dtF'(x_{\rm net}(t)))}{F(1)+gE_T(T)}. \tag{9.5}$$

At time T' the state variable x_i is reset to zero $x_i(T'^{+})=0$, so at time T

$$\begin{aligned}\xi(T)&=x_i(T)=(T-T')[F(0)+gE_T(T)]\\&=\xi(0)\frac{F(0)+gE_T(T)}{F(1)+gE_T(T)}\exp\left(\int_0^T dtF'(x_{\rm net})\right).\end{aligned} \tag{9.6}$$

To show that the synchronous state is stable we have to prove that

$$\int_0^T dtF'(x_{\rm net}(t))<\ln\left(\frac{F(1)+gE_T(T)}{F(0)+gE_T(T)}\right). \tag{9.7}$$

With $|g|$ small enough so that $F(x_{\rm net}(t))+gE_T(t)>0$ for all t, we can write

$$\int_0^T dtF'(x_{\rm net})=\int_0^1 dx\frac{F'(x)}{F(x)+gE_T(t(x))}. \tag{9.8}$$

For E_s given by an α function $E_T(t)>E_T(T)$ for $0<t<T$. Since $g<0$ and $F'<0$ Eq. (9.8) is bounded by

$$\begin{aligned}\int_0^T dtF'(x_{\rm net}(t))&<\int_0^1 dx\frac{F'(x)}{F(x)+gE_T(T)}\\&=\ln\left(\frac{F(1)+gE_T(T)}{F(0)+gE_T(T)}\right).\end{aligned} \tag{9.9}$$

If the coupling is stronger, so that $dx_{\rm net}/dt\leq 0$ on some interval $t_0\leq t\leq t_1$, with $0\leq t_0<t_1<T$, one can find a t_2 and t_3 so that $dx_{\rm net}/dt>0$ for $0\leq t\leq t_2$ and $t_3\leq t\leq T$, and $x_{\rm net}(t_2)=x_{\rm net}(t_3)$. Since $F'<0$ we can write

$$\begin{aligned}\int_0^T dtF'(x_{\rm net})&<\int_0^{t_2}dtF'(x_{\rm net})+\int_{t_3}^T dtF'(x_{\rm net})\\&=\int_0^{x_{\rm net}(t_2)}dx\frac{F'(x)}{F(x)+gE_T(t)}\\&\quad+\int_{x_{\rm net}(t_3)}^1 dx\frac{F'(x)}{F(x)+gE_T(t)}\\&<\int_0^1 dx\frac{F'(x)}{F(x)+gE_T(T)}.\end{aligned} \tag{9.10}$$

Therefore the inequality (9.7) also holds for stronger inhibitory coupling. The synchronous state is stable against small single-oscillator perturbations.

We will now briefly outline how one analyzes the stability of a state in which the cells are synchronized in two clusters. The stability analysis has two components. First one assumes that all oscillators are synchronized in two groups that fire periodically. A fraction η_A of the cells fire at time $t=nT$, while a fraction $\eta_B=1-\eta_A$ fire at time $t=(n+\phi)T$. The coupling variable E is then

$$E(t)=\eta_A E_T(t)+\eta_B E_T(t-\phi T). \tag{9.11}$$

In the case where $F(x)$ is given by $F(x)=X_0-x$, one has for group A, with $x_A(0)=0$,

$$\begin{aligned}x_A(T)&=X_0(1-e^{-T})+ge^{-T}\\&\quad\times\int_0^T dte^{t}[\eta_A E_T(t)+\eta_B E_T(t-\phi T)]=1.\end{aligned} \tag{9.12}$$

For group B one finds, since $x_B(\phi T)=0$,

$$x_B((1+\phi)T)=X_0(1-e^{-T})+ge^{-T}\times\int_0^T dte^t[\eta_A E_T(t+\phi T)+\eta_B E_T(t)]=1. \tag{9.13}$$

These equations always have a solution with $\phi=0$ and at least one other solution. For example, with $\eta_A=1/2$ there is always a solution with $\phi=1/2$. Just as in the two-oscillator system one will find two more solutions if α exceeds a critical value. Below this critical value the solution with $\phi=1/2$ is unstable, while above the critical value $\phi=1/2$ gives a stable solution. For $\eta_A\neq 1/2$ there is also one (unstable) solution with $\phi\neq 0$ for small α and three solutions with $\phi\neq 0$, one of which is stable, for large values of α. Thus if one analyzes the system under the constraint that all oscillators are synchronized in two groups, these groups can fire with a fixed phase difference, if the coupling time constants are small enough.

Next one can show that the two-cluster state is also stable for small perturbations of single cells. Since this can be done more or less analogously to the small single-oscillator perturbation in the completely synchronized state given above we will not show this here.

The completely synchronous solution is always stable. However, if one decreases the coupling time constants past some critical value, there are also stable solutions in which the oscillators synchronize in two clusters. One can show that if the time constants are decreased even more, states with three synchronized clusters also become stable. Reducing the time constants even further yields stable solutions with even more clusters. If α is very large the system has a lot of stable states. The state into which the system will evolve will depend on the initial conditions. This is in contrast to a system with excitatory coupling, in which the final state of the system is independent of the initial conditions.

I did computer simulations on a system with 100 oscillators. As before, I used model oscillators for which $F(x)=1.3-x$. The coupling strength g was set to $g=-0.4$. At $t=0$ the state variables x_i were given random initial values between 0 and 1. $E(0)$ and $dE(0)/dt$ were initially set to zero. We let the system evolve until a periodic firing pattern was reached, making sure that all transient had died out. Figure 8 shows the value for the state variable x_i for all cells just before one of the oscillators starts to fire, in a simulation for which $\alpha=4.0$ at a time $t>10\,000$. To make it easier to see the clusters, the cells were renumbered so that $x_1\leqslant x_2\leqslant\cdots\leqslant x_{100}$. The system is clearly broken up into three different clusters with 25, 37, and 38 oscillators, respectively.

I did simulations for α ranging from 1.5 to 5.0. For each value of α we did ten simulations, each with different initial conditions. After the transients had died out the number of clusters M was determined. Table I shows for each value of α the number of times with which the system evolved into an M-cluster state. There is clearly a trend towards a state with a larger number of clusters as α increases.

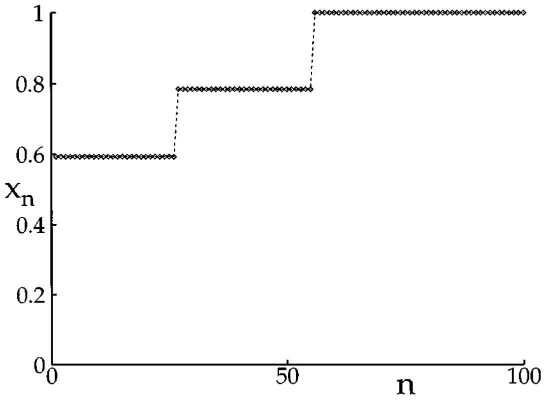

FIG. 8. State variables x_i for a simulation in a system of 100 oscillators with $F(x)=1.3-x$, $g=-0.4$, and $\alpha=4.0$. The cells were renumbered so that $x_1\leqslant x_2\leqslant\cdots\leqslant x_{100}$. The state variable x_i is plotted against i at some time $t>10\,000$, just before one of the clusters fires. The system is clearly broken up into three clusters.

TABLE I. Number of clusters M into which the system breaks up for different values of α. For each value of α ten simulations were performed, each with different randomly chosen initial conditions. The table shows for each α how many of these simulations evolved into a system with M clusters. For small α the system always completely synchronizes ($M=1$ for all simulations). As α increases the number of clusters into which the system evolves tends to increases.

$\alpha \setminus M$	1	2	3	4
1.5	10	0	0	0
2.0	6	4	0	0
2.5	0	9	1	0
3.0	0	10	0	0
3.5	0	4	6	0
4.0	0	2	8	0
4.5	0	1	9	0
5.0	0	1	4	5

X. DISCUSSION

In a network of integrate and fire cells, in which the coupling is modeled by an α function, we find that, for excitatory coupling, the networks evolves to the asynchronous state if the coupling time constants are slow enough. When the speed of the coupling is increased, the network starts to synchronize. For finite time constants the network does not reach complete synchrony, even though the network consists of identical oscillators and the system is completely noiseless. If the network consists of more than two units, the cells fire quasiperiodically in the partially synchronized state. In large networks the average firing rate of the network varies periodically in this state, even though individual cells are quasiperiodic.

With inhibitory coupling the network synchronizes completely if the coupling is slow. With faster coupling the network breaks up into two or more completely synchronized clusters. The average number of clusters that is formed increases as the coupling time constant decreases, though the exact number of clusters that is formed depends on the initial conditions. For a network with a large but finite number of oscillators the number of clusters that are formed will eventually approach the number of cells. The final state is then indistinguishable from the asynchronous state.

Thus with inhibitory coupling the system goes from completely synchronized for slow coupling to an essentially asynchronous state for fast coupling, by the formation of an increasing number of completely synchronized clusters. This should be contrasted with excitatory coupling. There the network is completely synchronized if the coupling is infinitely fast and asynchronous if the time constants exceed some critical value. The transition from a synchronous to an asynchronous system is accomplished by the broadening of one cluster rather than by breaking up into ever more clusters.

We find these properties for populations of very simple nonlinear oscillators. An interesting question is whether this behavior is also found in networks of more complicated oscillators, for example, in networks of realistic neurons. Some studies have been done on the thalamic reticular nucleus [9,5,10,18–20], in which channel-based models of the neurons were used. In the thalamic reticular nucleus the cells have inhibitory coupling, either through fast $GABA_A$ or slow $GABA_B$ synapses. These studies found that with the slow inhibitory $GABA_B$ coupling all cells synchronize completely, while with the fast $GABA_A$ coupling the cells synchronized in two or more groups. This agrees with what our simple model predicts.

We do not know of any study that shows large populations of conductance-based model neurons behaving as our simple network with excitarory connections. However, systems of two identical Hodgin-Huxley model neurons with excitatory coupling fire completely asynchronously when the coupling is slow, while they partially synchronize for faster synapses, as we showed in Sec. III. However, if the synaptic time constant is of the order of the spike duration, the neurons completely synchronize. This leads one to expect that large populations of Hodgkin-Huxley-type neurons with slow excitatory synapses will evolve to the asynchronous state, while for faster synapses the network will partially synchronize, with individual neurons firing quasiperiodically. Large networks of these cells will probably also synchronize for small but finite synaptic time constants, in contrast to networks of intergrate and fire neurons.

ACKNOWLEDGMENTS

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APPENDIX A: CRITICAL EXPONENT

In this appendix the critical exponent is determined. Since ϵ is small, the density ρ can be written as a converging series

$$\rho(y,t)=\frac{E_0+j(y,t)}{E_0+\Gamma(y)\epsilon(t)}$$
$$=\left(1+\frac{1}{E_0}j(y,t)\right)\sum_{k=0}^{\infty}\left(\frac{-\Gamma(y)\epsilon(t)}{E_0}\right)^k. \tag{A1}$$

The solution is periodic in time, so we can write j and e as Fourier series $j(y,t)=\Sigma_n j_n(y)\exp(in\omega t)$ and $e(t)=\Sigma_n\epsilon_n\exp(in\omega t)$, where ω has to be determined.

The density $\rho(y,t)=\Sigma_n\rho_n(y)\exp(in\omega t)$ can be written as

$$\rho(y,t)=1+\frac{1}{E_0}\sum_n\left(j_n(y)-\epsilon_n\Gamma(y)+\sum_{j=2}^{\infty}S_{n,j}(y)\right)e^{in\omega t}, \tag{A2}$$

with the jth-order term in ϵ_n and $j_n(y)$

$$S_{n,j}(y)=\sum_{\substack{n_1,\ldots,n_j\\ n_i=n}}\prod_{k=1}^{j-1}\epsilon_{n_k}[j_{n_j}(y)-\epsilon_{n_j}\Gamma(y)]\left(\frac{-\Gamma(y)}{E_0}\right)^{j-1}. \tag{A3}$$

From the continuity Eq. (5.6) it follows that

$$in\omega\left(j_n(y)-\epsilon_n\Gamma(y)+\sum_{j=2}^{\infty}S_{n,j}(y)\right)=-E_0\frac{d}{dy}j_n(y). \tag{A4}$$

Since $S_{n,j}(y)$ depends on $j_k(y)$ for all k there is no simple solution for $j_n(y)$ for $n\neq 0$. Only for $n=0$ is there an explicit solution with $j_0(y)$ constant.

For $n\neq 0$ the $j_n(y)$'s can be written implicitly as

$$j_n(y)=\frac{in\omega}{E_0}\left[\int_0^y dy'\left(\epsilon_n\Gamma(y')-\sum_{j=2}^{\infty}S_{n,j}(y)\right)\right.$$
$$\left.\times e^{in\omega y'/E_0}+C_n\right]e^{-in\omega y/E_0}. \tag{A5}$$

From the boundary condition $j(0,t)=j(1,t)$ it follows that

$$C_n=\frac{1}{e^{in\omega/E_0}-1}\int_0^1 dy\left(\epsilon_n\Gamma(y)-\sum_j S_{n,j}(y)\right)e^{in\omega y/E_0}. \tag{A6}$$

From Eq. (5.13) for the coupling variable one has $(in\omega+\alpha)^2\epsilon_n=\alpha^2 j_n(1)$. So $j_0(y)=\epsilon_0$ and

$$A_n(\omega,\alpha)\epsilon_n=-in\omega\alpha^2\sum_j\int_0^1 dyS_{n,j}(y)e^{in\omega y/E_0} \tag{A7}$$

for $n\neq 0$. Here we have used

$$A_n(\omega,\alpha)\equiv E_0(in\omega+\alpha)^2(e^{in\omega/E_0}-1)$$
$$-in\omega\alpha^2\int_0^1 dy\Gamma(y)e^{in\omega y/E_0}. \tag{A8}$$

Since $j_n(y)$ and ϵ_n vanish if $\delta\alpha$ goes to 0, j_n and ϵ_n will be of order $(\delta\alpha)^{c_n}$ for some positive constant c_n. Since j_{-n} is the complex conjugate of j_n we have $c_{-n}=c_n$. The simulations show that j_1 and j_{-1} dominate for small $\delta\alpha$, so we assume $c_n>c_1\equiv c$ for $n\neq -1,1$.

With $\omega=\omega_{\mathrm{cr}}+\delta\omega$ and $\delta\omega\rightarrow 0$ if $\delta\alpha\rightarrow 0$, we write $A_n(\omega,\alpha)$ as

$$A_n(\omega,\alpha)=A_n(\omega_{\rm cr},\alpha_{\rm cr})+\frac{\partial A_n}{\partial\omega}\,\delta\omega+\frac{\partial A_n}{\partial\alpha}\,\alpha+\cdots. \tag{A9}$$

For $n=1$ we have from Eq. (A7), to lowest order of $\delta\alpha$,

$$\left[A_1(\omega_{\rm cr},\alpha_{\rm cr})+\frac{\partial A_1}{\partial\omega}\,\delta\omega+\frac{\partial A_1}{\partial\alpha}\,\delta\alpha\right]\epsilon_1 =-i\omega_{\rm cr}\alpha_{\rm cr}^2\int_0^1 dy\sum_j S_{1,j}(y)e^{i\omega_{\rm cr}y/E_0}. \tag{A10}$$

It is easy to see that $S_{n,j}=O((\delta\alpha)^{jc})$ for $j=|n|+2k$ (with $k=0,1,2,\ldots$) and $S_{n,j}=o((\delta\alpha)^{jc})$ otherwise. Therefore the right-hand side of of Eq. (A10) is of order less than $(\delta\alpha)^{2c}$. But if $A_1(\omega_{\rm cr},\alpha_{\rm cr})\neq 0$ the right-hand side is of order $(\delta\alpha)^{c}$. So we have $A_1(\omega_{\rm cr},\alpha_{\rm cr})=0$.

This is exactly the eigenvalue equation (5.13) for small perturbations about the asynchronous solution, with $\lambda=i\omega_{\rm cr}$. Equation (5.13) has infinite many solutions, but only two of them $\lambda=\pm i\omega_{\rm cr}$ are purely imaginary. For $n\neq -1,1$ we therefore have $A_n(\omega_{\rm cr},\alpha_{\rm cr})\neq 0$.

Since for $n=\pm 2$ the left-hand side of Eq. (A7) is of order $(\delta\alpha)^{c_2}$, while the right-hand side is at most of order $(\delta\alpha)^{2c}$, $c_{-2}=c_2\geqslant 2c$. Using this one next shows that $c_{-3}=c_3\geqslant 3c$, etc. Thus one shows that, for $n\neq 0$, $c_n\geqslant |n|c$.

We can determine ϵ_0 by observing that $\int_0^1 dy\rho(y,t)=1$. With the continuity equation (5.6) we have, for $n\neq 0$, $\int_0^1 dy\rho_n(y)=[j_n(0)-j_n(1)]/in\omega=0$. Therefore

$$\int_0^1 dy\rho_0(y)=1+\frac{1}{E_0}\left(\epsilon_0\int_0^1 dy[1-\Gamma(y)] -\sum_{j=2}^{\infty}\int_0^1 dyS_{0,j}(y)\right)=1 \tag{A11}$$

or, since $\Gamma(y)<1$,

$$\begin{aligned}\epsilon_0&=\left(1-\int_0^1 dy\Gamma(y)\right)^{-1}\sum_j\int_0^1 dyS_{0,j}(y)\\ &=-\left(1-\int_0^1 dy\Gamma(y)\right)^{-1}\\ &\quad\times\left\{\frac{\epsilon_{-1}}{E_0}\int_0^1 dy[j_1(y)-\epsilon_1\Gamma(y)]\Gamma(y)+\frac{\epsilon_1}{E_0}\int_0^1 dy\right.\\ &\quad\left.\times[j_{-1}(y)-\epsilon_{-1}\Gamma(y)]\Gamma(y)\right\}\\ &\quad+\text{(higher order terms)}.\end{aligned} \tag{A12}$$

For j_n, to the lowest order in $\delta\alpha$,

$$j_n(y)=\epsilon_n\frac{in\omega_{\rm cr}}{E_0}\left(\int_0^y dy'\Gamma(y')e^{in\omega_{\rm cr}y'/E_0}+k_n\right)e^{-in\omega_{\rm cr}y/E_0}, \tag{A13}$$

with k_n determined by the boundary condition. Thus, to lowest order $\epsilon_0=\epsilon_1\epsilon_{-1}K_0$, where K_0 can be determined using Eqs. (A12) and (A13).

Since ϵ_0 is of order $(\delta\alpha)^{2c}$ and ϵ_n is of order $(\delta\alpha)^{|n|c}$ or smaller, from Eq. (A7) ϵ_2 is given to lowest order by $\epsilon_2=\epsilon_1^2K_2$. K_2 is a complex constant that can be calculated from Eqs. (A7) and (A13) for $n=2$.

We now return to Eq. (A10) for ϵ_1. The right-hand side has only terms of the order $(\delta\alpha)^{3c}$ or higher. The terms of order $(\delta\alpha)^{3c}$ can all be written as the product of $\epsilon_{-1}\epsilon_2$, $\epsilon_0\epsilon_1$, or $\epsilon_{-1}\epsilon_1^2$ and some constants that can be determined using Eq. (A13). Using the results for ϵ_0 and ϵ_2 we derived above, one finds that the right-hand side of Eq. (A7) can be written as $\epsilon_{-1}\epsilon_1^2K_1$, where K_1 is a complex constant.

With $A_1(\omega_{\rm cr},\alpha_{\rm cr})=0$ we have

$$\frac{\partial A_1}{\partial\omega}\,\delta\omega+\frac{\partial A_1}{\partial\alpha}\,\delta\alpha=\epsilon_{-1}\epsilon_1K_1, \tag{A14}$$

with $\delta\omega=\omega'(\delta\alpha)^{c_\omega}$. The right-hand side of this equation is of order $(\delta\alpha)^{2c}$. If $c_\omega<1$ the left-hand side is of order $(\delta\alpha)^{c_\omega}$, so that $c=c_\omega/2$ and $\omega'(\partial A_1/\partial\omega)=e_{-1}e_1K_0$, while for $c_\omega>1$, the left-hand side is of order $\delta\alpha$ and therefore $c=1/2$ and $e_{-1}e_1K_0=\partial A_1/\partial\alpha$. But since $e_{-1}e_1$, $\delta\alpha$, and ω' are all real, while $\partial A/\partial\omega$, $\partial A/\partial\alpha$, and K_1 are complex, these will in general not be valid solutions. Therefore, for the generic case, we will have $\delta\omega=\omega'\delta\alpha$. In that case, with $\epsilon_1=e_1(\delta\alpha)^{1/2}$ and $\epsilon_{-1}=e_{-1}(\delta\alpha)^{1/2}$,

$$e_{-1}e_1=\frac{1}{K_1}\frac{\partial A_1}{\partial\omega}\,\omega'+\frac{1}{K_1}\frac{\partial A_1}{\partial\alpha}. \tag{A15}$$

With real solutions

$$e_{-1}e_1=\frac{\operatorname{Im}\left(\dfrac{\partial A/\partial\alpha}{\partial A/\partial\omega}\right)}{\operatorname{Im}\left(\dfrac{K_1}{\partial A/\partial\omega}\right)} \tag{A16}$$

and

$$\omega'=-\frac{\operatorname{Im}\left(\dfrac{1}{K_1}\dfrac{\partial A_1}{\partial\alpha}\right)}{\operatorname{Im}\left(\dfrac{1}{K_1}\dfrac{\partial A_1}{\partial\omega}\right)}. \tag{A17}$$

We have shown that $\epsilon_{\pm 1}$ and $j_{\pm 1}$ are of order $(\delta\alpha)^{1/2}$, while all others are proportional to $\delta\alpha$ to some higher power. Therefore, an expansion of j or ϵ in $\delta\alpha$ using a critical exponent c, as in Eqs. (7.1) and (7.2), has 1/2 as lowest power in $\delta\alpha$. Thus the critical exponent is 1/2. Notice that this procedure determines ϵ_1 only up to a phase factor $e^{i\phi}$, so that ϵ_n is determined up to a factor $e^{in\phi}$. This is to be expected since a translation of the time coordinate $t\rightarrow t+\delta t$ transforms ϵ_n as $\epsilon_n\rightarrow\epsilon_n e^{in\omega\delta t}$.

To summarize, since $j(y,t)$ is periodic in t, it can be written as

$$j(y,t)=\sum_n j_n(y)e^{in\omega t}. \tag{A18}$$

The angular frequency ω is given to first order in $\delta\alpha$ by $\omega = \omega_{\mathrm{cr}} + \omega' \delta\alpha$. Here ω_{cr} is the imaginary part of that eigenvalue of the transients of the asynchronous solution at $\alpha = \alpha_{\mathrm{cr}}$ for which $\mathrm{Re}(\lambda) = 0$. The Fourier components $j_n(y)$ of $j(y,t)$ can be expanded in $\delta\alpha$ as

$$j_n(y) = (\delta\alpha)^{|n|/2}[j_n^{(0)}(y) + j_n^{(1)}(y)(\delta\alpha)^{1/2} + \cdots] \tag{A19}$$

for $n \neq 0$, while $j_0(y)$ is of order $\delta\alpha$. Therefore we have that j is of order $\delta\alpha^{1/2}$, so that the critical exponent c is $\frac{1}{2}$.

[1] R.E. Mirollo and S.H. Strogatz, SIAM J. Appl. Math. **50**, 1645 (1990).

[2] S.H. Strogatz and R.E. Mirollo, J. Stat. Phys. **63**, 613 (1991).

[3] A. Arenas and C.J. Pérez Vicente, Physica A **201**, 614 (1993).

[4] Y. Kuramoto, Physica D **50**, 15 (1991).

[5] D. Golomb and J. Rinzel, Physica D **72**, 259 (1994).

[6] A.T. Winfree, J. Theor. Biol. **16**, 15 (1967).

[7] L.F. Abbott and C. van Vreeswijk, Phys. Rev. E **48**, 1483 (1993).

[8] C. van Vreeswijk, L.F. Abbott, and G.B. Ermentrout, J. Comp. Neurosci. **1**, 303 (1994).

[9] A. Destexhe, D. Contreras, T.J. Sejnowski, and M. Steriade, Neuroreport **5**, 2217 (1994).

[10] D. Golomb, X.-J. Wang, and J. Rinzel, J. Neurophysiol. **72**, 1109 (1994).

[11] A. Treves, Network **4**, 259 (1993).

[12] D. Golomb, D. Hansel, B. Shraim, and H. Sompolinsky, Phys. Rev. A **45**, 3516 (1993).

[13] S. H. Strogatz and R. E. Mirollo, Phys. Rev. E **47**, 200 (1993).

[14] J.D. Murray, *Mathematical Biology* (Springer, New York, 1989), p. 548.

[15] B.D. Hassard, N.D. Kazarinoff, and X.-J. Wang, *Theory and Application of Hopf Bifurcation* (Cambridge University Press, Cambridge, 1981).

[16] J.E. Marsden and M. McCracken, *The Hopf-Bifurcation and its Application* (Springer, New York, 1976).

[17] E.M. Fisher, Rep. Prog. Phys. **30**, 615 (1967).

[18] S.H. Strogatz and R.E. Mirollo, J. Phys. A **21**, L699 (1988); Physica D **31**, 143 (1988).

[19] X.-J. Wang and J. Rinzel, Neuroscience **53**, 899 (1992).

[20] X.-J. Wang and J. Rinzel, Neural Comp. **4**, 84 (1992).