PHYSICAL REVIEW E VOLUME 48, NUMBER 5 NOVEMBER 1993

Clustering and slow switching in globally coupled phase oscillators

D. Hansel
Centre de Physique Théorique CNRS, Ecole Polytechnique, 91128 Palaiseau CEDEX, France

G. Mato
Racah Institute of Physics, Hebrew University, 91904 Jerusalem, Israel

C. Meunier
Centre de Physique Théorique CNRS, Ecole Polytechnique, 91128 Palaiseau CEDEX, France
(Received 17 May 1993)

We consider a network of globally coupled phase oscillators. The interaction between any two of them is derived from a simple model of weakly coupled biological neurons and is a periodic function of the phase difference with two Fourier components. The collective dynamics of this network is studied with emphasis on the existence and the stability of clustering states. Depending on a control parameter, three typical types of dynamics can be observed at large time: a fully synchronized state of the network (one-cluster state), a totally incoherent state, and a pair of two-cluster states connected by heteroclinic orbits. This last regime is particularly sensitive to noise. Indeed, adding a small noise gives rise, in large networks, to a slow periodic oscillation between the two two-cluster states. The frequency of this oscillation is proportional to the logarithm of the noise intensity. These switching states should occur frequently in networks of globally coupled oscillators.

PACS number(s): 05.45.+b, 05.90.+m, 87.10.+e

I. INTRODUCTION

The dynamics of coupled nonlinear oscillators can be described in the limit of weak interaction by phase models. For a free oscillator a single phase variable that indicates its position on the limit cycle can be naturally defined. When interactions between oscillators are switched on, this phase description is *a priori* no longer sufficient, as amplitude effects alter, or even destroy, the limit cycles. However, if the coupling is weak enough, such effects can be neglected, and the original coupled system can be replaced by phase oscillators coupled by an effective interaction [1]. The situation where the oscillations of the single units emerge through a normal Hopf bifurcation has been widely studied. In this case, the effective phase interaction reduces to a single Fourier mode. Obviously, this does not exhaust all the richness of phase models. In the context of neural modeling, for instance, more complicated interactions must be considered [2,3]. In [3] we showed that phase interactions with several Fourier modes were needed to account for synaptic couplings [4] between Hodgkin-Huxley (HH) neurons [5], with nontrivial consequences on the dynamics of a pair of coupled neurons.

We study here the phase dynamics of a large network for an interaction with two Fourier modes inspired by [3]. This interaction depends on a parameter α that controls the competition between an attractive contribution and a repulsive contribution. Depending on α, we find that besides the fully synchronized state in which all the oscillators are phase locked with zero phase shift and the totally incoherent state (these states can also be found for a single mode phase interaction), the network can reach less trivial states at large time. The first type consists of stable n-cluster states ($n > 1$) [6–10] where the network spontaneously breaks into n macroscopic subgroups inside which the oscillators are locked in phase. A second type consists of pairs of *unstable* two-cluster states connected by heteroclinic orbits.

In a large range of the parameter α, random initial conditions lead at large time to states of the network belonging to this second class. Adding a small noise has a remarkable consequence: a slow collective dynamics emerges and the system switches back and forth between the two connected two-cluster states. In large networks, this switching is periodic with a period depending logarithmically on the intensity of the noise. This phenomenon is similar to the effects reported in the context of Gauss-Lotka-Volterra species dynamics [11] and rotating-convection experiments [12–14].

II. THE MODEL

We consider a network of N globally coupled identical phase oscillators evolving in time according to

$$\frac{d\phi_i}{dt} = \omega + g\frac{1}{N}\sum_{j=1}^{N}\Gamma(\phi_i - \phi_j) + \eta_i(t). \qquad (1)$$

The phase of oscillator i ($i = 1, ..., N$) is ϕ_i, $0 \le \phi_i < 2\pi$. In the absence of coupling, each unit is moving around its limit cycle at frequency ω. The function Γ characterizes the interaction between the oscillators and the coupling constant g is positive. The uncorrelated noise $\eta_i(t)$ is local and Gaussian with variance σ^2. One

1063-651X/93/48(5)/3470(8)/$06.00

can assume that $g = 1$ without loss of generality provided that σ, ω and the time are properly rescaled.

In the following we consider a simple model defined by

$$\Gamma(x) = -\sin(x+\alpha) + r\sin(2x), \tag{2}$$

where α takes values in $[-\pi, \pi]$ and $1/2 > r > 0$. It should be noted that, except for $\alpha = 0$, the dynamics of the network described by (1) and (2) does not derive from an energy function. It should also be remarked that the dynamical equations display the obvious symmetry: $\alpha \to -\alpha$, $\phi_i \to -\phi_i$ (for all $i = 1, ..., N$). Hence we may restrict our attention to $0 \le \alpha \le \pi$. For $\alpha < \pi/2$, the first term in Γ corresponds to a "ferromagnetic" interaction that tends to lock two coupled oscillators in phase. On the other hand, the second term favors out-of-phase locking. The parameter α controls the competition between these two terms. Denoting by Δ the phase shift between the two oscillators, one easily shows that for $\alpha < \alpha_c = \arccos(2r)$ the only stable state corresponds to in-phase locking. At $\alpha = \alpha_c$ it loses its stability and a bifurcation to an out-of-phase locking [with $\Delta \neq 0$ and satisfying $\Gamma(\Delta) = \Gamma(-\Delta)$] occurs. One expects that such a competition between the attractive part and the repulsive part of the interaction will give rise to nontrivial patterns of synchronization in large networks. The effects reported in this paper exist for all values of r $(0 < r < \frac{1}{2})$ and do not depend qualitatively on its precise numerical value. To be more specific, numerical results will be given for $r = 1/4$ $(\alpha_c = \pi/3)$, which corresponds to a truncation of the phase interaction we have calculated for HH neurons [3], keeping two modes in the Fourier expansion.

All the numerical results presented below were obtained by integrating Eqs. (1) and (2) with $N = 100$ using an order-four Runge-Kutta integration scheme. Finite size effects have been investigated by comparing results with $N = 100$ and $N = 400$. The coupling was fixed at $g = 1$ and the free frequency was $\omega = 5$. The state of the network was studied as a function of both the control parameter α and the intensity of the noise. Initial conditions were chosen randomly, with uniform distribution between 0 and 2π. The indices of the neurons were rearranged so that at time $t = 0$, $\phi_i(0) < \phi_j(0)$ for $i < j$. The time step was set at $dt = 0.01$ after carefully checking its influence on the simulations.

III. DETERMINISTIC DYNAMICS OF THE NETWORK

A. The network dynamics at large time

In this section we investigate the noiseless case considering first the dynamical states reached by the network at large time for random initial conditions and various values of α.

For $\pi/2 \le \alpha \le \pi$ the system converges to an incoherent state, i.e, the distribution function of the phases at any time is $P(\phi, t) = \frac{1}{2\pi}$ up to finite-size fluctuations. As a consequence, the interaction term is of order $O(1/\sqrt{N})$ for all the oscillators and they are rotating independently at constant frequency ω. This is in perfect agreement with the stability analysis of the incoherent state for a system described by (1) and (2).

For $0 < \alpha \le \pi/3$ the typical result that we obtain is displayed in Fig. 1, where the successive times at which the oscillators cross 2π are shown. The oscillators move periodically with constant frequency Ω_1 and are all locked in phase. The dependence of Ω_1 on α was found to agree with the analytic expression given in the Appendix. The transition at $\pi/3$ corresponds to the limit of stability of this one-cluster state.

For $\pi/3 < \alpha < \pi/2$ the situation is different. Numerical integration of Eqs. (1) and (2) indicates that starting from random initial conditions, the system eventually converges to a state constituted of two macroscopic groups of oscillators, the masses of which are in general different. In each group of this *two-cluster state*, the oscillators are locked in phase and rotate at constant frequency Ω_2. The fraction of oscillators in the group in advance will be denoted by p and the dephasing, constant in time, between this group and the other group will be denoted by Δ. Note that by convention Δ is positive. An example of a two-cluster state is displayed in Fig. 2 for $\alpha = 1.25$. In the following, the two-cluster state with $m = Np$ and dephasing Δ will be denoted by (p, Δ).

Many such two-cluster states exist (see Appendix), differing by the fraction of oscillators in each of the groups and by the dephasing between the two groups. We have investigated the possible selection of a particular pattern in the large-N limit. This was done by integrating (1) and (2) with 100 initial conditions to evaluate the distribution of p and Δ in the final state. Two values of α have been studied: $\alpha = 1.25$ and $\alpha = 1.1$. For $\alpha = 1.25$,

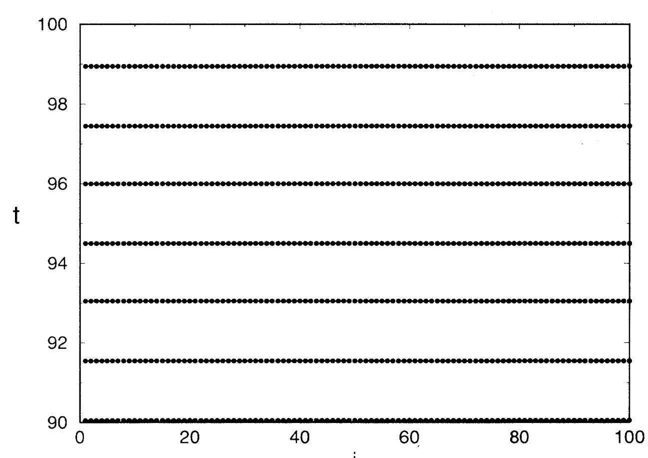

FIG. 1. Times at which the phase of each oscillator crosses 2π. The time unit corresponds to 7 ms for a system of HH neurons with an injected current of 50 μA/cm^2 and coupled with a synaptic interaction of 1 mS/cm^2. (See [3] for the other parameters of the model.) The abscissa corresponds to the labeling of the oscillators, after appropriate ordering of the initial condition (see Sec. II). Same conventions are used in the following figures.

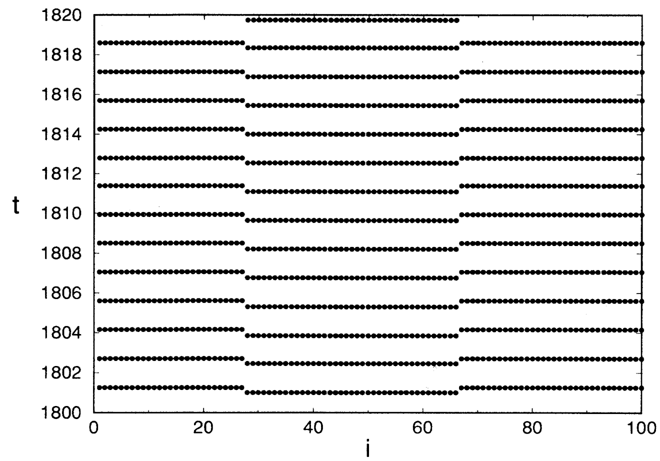

FIG. 2. Times at which the phase of each oscillator crosses 2π, for $\alpha = 1.25$ and $\sigma = 0$.

the histogram of p for $N = 100$ has an average $p_* = 0.59$ and a width $v = 0.09$ for $N = 100$. For $N = 400$ the corresponding numbers are $p_* = 0.58$ and $v = 0.04$. This indicates that the system selects two-cluster states with a particular fraction $p \simeq 0.59$ up to finite-size effects. Corresponding to this value of p, Eq. (13) predicts three possible values of Δ: $\Delta_1 = 2.7$, $\Delta_2 = 1.14$, and $\Delta_3 = 0.7$. However, the histogram of Δ obtained in our simulations (for $N = 400$) is monomodal around an average value of $\Delta_* = 1.15$ and it has a variance 0.2. This suggests that the state ($p = 0.59, \Delta = 1.14$) is selected by the dynamics at large time and large N.

For $\alpha = 1.1$, which is closer to the transition than $\alpha = 1.25$, finite-size effects were stronger. For $N = 400$ the histogram for p has an average value of $p_* = 0.66$ and the variance was $v = 0.08$. Moreover, the distribution of Δ was very broad (variance of 0.4) and we were unable to conclude about the selection of a particular state in the vicinity of the transition.

In this range of α, we have also found that the network can also converge to cluster states with more than two clusters (in particular stable three-cluster states in which the network is broken into three subpopulations) [15]. However, these configurations have very small basin of attractions in comparison to the two-cluster states, and to be observed the initial conditions have to be tuned to the vicinity of these configurations. Similarly, choosing initial conditions near a two-cluster state with $p \neq p_*$ (but with similar stability properties, see Appendix), it is found that the system converges to a state with such value of p. It is nevertheless interesting to find a great variety of attractors in spite of the high degree of symmetry of the global coupling. Similar phenomena have been previously found in other networks of globally coupled units [6–10].

The existence and stability analysis of the various cluster states can be easily performed. Results of this analysis are given in the Appendix. Applying these results to the states found in our simulations, one finds that the two-cluster states to which the system "converges" at large time are always *linearly unstable*. This is an *a priori* paradoxical situation that is clarified in the next two sections.

B. The heteroclinic connection

In this section we show numerically that two-cluster states are paired by heteroclinic orbits. More precisely, we show that the state (p, Δ) is connected to a state $(1-p, \Delta')$, where p (respectively, $1-p$) and Δ (respectively, Δ') satisfy Eq. (13).

For the sake of concreteness let us consider the case $\alpha = 1.25$ and the two-cluster state (p_*, Δ_*) defined in the preceding section. (Similar arguments can be repeated for other observed two-cluster states and for other values of α without qualitative changes.)

In order to show that a heteroclinic structure connects the state (p_*, Δ_*) to another two-cluster state $(1-p_*, \Delta'_*)$, we consider trajectories that start at $t = 0$, from a point in the vicinity of the state (p_*, Δ_*) and that lies on its unstable manifold $M_u(p_*, \Delta_*)$. Numerically integrating the equations of motion one finds that the network converges without oscillating to the state $(1-p_*, \Delta'_*)$ where $\Delta'_* = 0.70$. Note that this value satisfies Eq. (13). The time of convergence is found to depend logarithmically on the amplitude of the initial deviation. This fact shows that trajectories connect the state (p_*, Δ_*) to the state $(1-p_*, \Delta'_*)$. These trajectories belong to both the unstable manifold of (p_*, Δ_*) and to the stable manifold $(1-p_*, \Delta'_*)$. By symmetry, similar trajectories from $(1-p_*, \Delta'_*)$ to (p_*, Δ_*) exist. This entails that heteroclinic cycles connect the two two-cluster states (p_*, Δ_*) and $(1-p_*, \Delta'_*)$. It is important to note that in the two states (p_*, Δ_*) and $(1-p_*, \Delta'_*)$ the mass of the largest group is the same.

The large-N limit is not necessary to find heteroclinicity. Actually heteroclinic connections exist for $N > 3$. In the case $N = 4$ the dynamics depends only on the *differences* of the phases $\phi_2 - \phi_1, \phi_3 - \phi_1, \phi_4 - \phi_1$. Moreover, by dimensionality argument, only one heteroclinic orbit exists for $N = 4$ and it can be visualized in a three-dimensional space. Figure 3 shows the heteroclinic orbit for $\alpha = 1.25$ and $p = 1/2$.

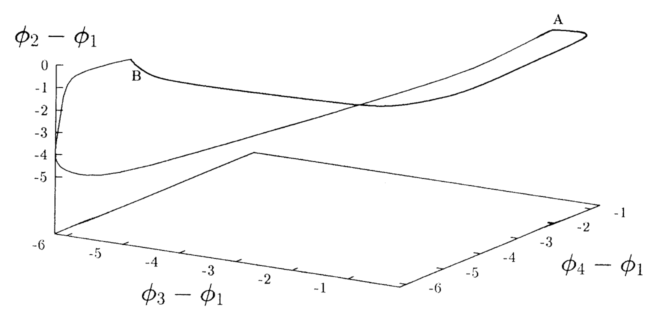

FIG. 3. The heteroclinic connection for $\alpha = 1.25$, $p = 1/2$, and $N = 4$. The symbols A, B indicate the locations of the two two-cluster states, the unstable manifolds of which are also displayed.

C. Stability of the heteroclinic connection

In order to solve the apparent paradox of Sec. III A where two-cluster states are found at large time even when they are linearly unstable, a crucial remark concerns the transients observed when starting near a two-cluster state (p, Δ) (see Fig. 4 for an illustration). Before stabilizing, the system oscillates several times between this state and the state $(1-p, \Delta')$. The number of observed oscillations depends on the numerical integration accuracy (typically three or four oscillations). The time needed to leave one two-cluster state and to evolve to the other state increases at each oscillation. Most of this time is spent in the vicinity of the two-cluster states and the transition between the neighborhood of these two states is very fast. Moreover, at each oscillation the time spent near the two-cluster states increases [16]. An example of such a transient behavior is depicted in Fig. 4. Numerically one has $T_{n+1}/T_n \approx 1.4$, where T_n is the nth sojourn time near a two-cluster state.

The existence of these heteroclinic trajectories allows us to understand the apparent stability of the two-cluster states observed for $\alpha > \pi/3$. We consider an initial condition that differs from the two-cluster state (p, Δ) by a distance of order $\epsilon_0 \ll 1$ along the direction with eigenvalue λ_u (unstable direction) and a distance of order 1 along direction with eigenvalue $-\lambda_s$ (stable direction). The effect of a component along the direction with eigenvalue λ_3 will be considered below. (See the Appendix for the definition of the eigenvalues and eigenvectors.) Linearizing the equations, we find that the unstable perturbation x_u grows according to

$$x_u \sim \epsilon_0 \exp(\lambda_u t). \tag{3}$$

After a time $T_0 \sim -\frac{1}{\lambda_u} \ln \epsilon_0$ it will be of order 1 and nonlinear effects will start to be important. At the same time the stable perturbation x_s [that is decreasing according to $x_s \sim \exp(-\lambda_s t)$] will have decayed to a value of order:

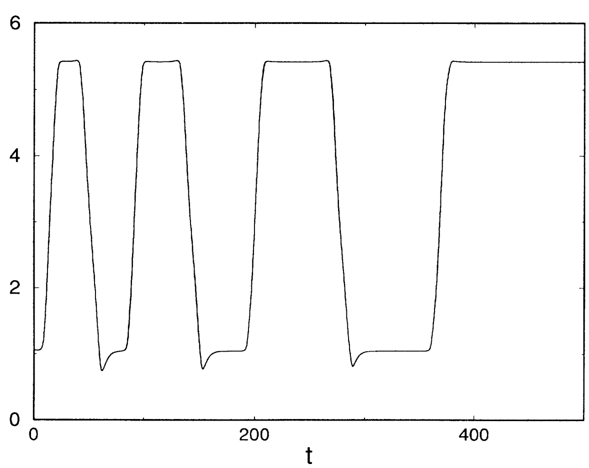

FIG. 4. Difference δ (rad) between the average phases of the two clusters as a function of time. The initial condition corresponds to a small random perturbation around the two-cluster state ($\alpha = 1.25, p = 0.57, N = 100$).

$$\epsilon_1 \sim \epsilon_0^{\lambda_s/\lambda_u}. \tag{4}$$

At that time a rapid motion along the orbit and towards the state $(1-p, \Delta')$ will occur. This "reconnection" is the result of nonlinear effects but due to its brevity it affects very little the distance to the heteroclinic orbit. Now we can reiterate the argument but this time around the state $(1-p, \Delta')$. The distance to the fixed point in the unstable direction is now of order $\epsilon_0^{\lambda_s/\lambda_u}$ while the distance in the stable direction is of order 1. The time needed to escape from the two-cluster state is

$$T_1 \sim -\ln \epsilon_1/\lambda_u' \sim T_0(\lambda_s/\lambda_u'), \tag{5}$$

where the eigenvalues λ_s' and λ_u' now refer to the fixed point $(1-p, \Delta')$.

The eigenvalues λ_s' and λ_u' differ from λ_s and λ_u since the masses of the two clusters are not, in general, the same. After escaping from the state $(1-p, \Delta')$ the system will come back again in the vicinity of the state (p, Δ) deviating from it on the unstable direction by $\epsilon_2 \approx \epsilon_0^{\gamma}$ where

$$\gamma = \frac{\lambda_s \lambda_s'}{\lambda_u \lambda_u'}. \tag{6}$$

If the exponent γ is larger than 1, the perturbation will be reduced after one cycle.

After $2n$ switchings (n cycles) the time spent around the fixed point and the distance to it will be

$$T_n \sim T_0(\lambda_s/\lambda_u)^n(\lambda_s'/\lambda_u')^n, \tag{7}$$

$$\epsilon_n \sim \epsilon_0^{(\lambda_s/\lambda_u)^n(\lambda_s'/\lambda_u')^n}. \tag{8}$$

For example, for $\alpha = 1.25$ and $p_* = 0.59$ one finds $\lambda_s = 0.436, \lambda_u = 0.315, \lambda_s' = 0.391, \lambda_u' = 0.297$ corresponding to $\gamma = 1.82$. The escape time from state (p_*, Δ_*) to the state $(1-p_*, \Delta_*')$ increases therefore at each cycle by a factor of 1.46 to be compared with Fig. 3 where $T_{n+1}/T_n \approx 1.4$.

What are the effects of an initial condition with a component along the direction with the third eigenvalue (denoted by η)? Near the fixed point this perturbation will evolve according to $\eta \propto \exp(\lambda_3 t)$. Next, the system will switch to the other state. Assuming as before that this is a fast movement, and that the perturbation along the third manifold is independent from the other ones (as is observed in the numerical simulations), it is possible to show that after one cycle the perturbation in this direction will have changed by a factor $\exp[(\lambda_3 + \lambda_3')T]$, where λ_3' refers to the state $(1-p, \Delta')$. If $\lambda_3 + \lambda_3' < 0$, the perturbation will decay to zero. In all the two-cluster states that were obtained in our simulations this condition was always verified.

One can wonder what happens at the transition point $\alpha = \pi/3$. Numerical integration of the equations indicates that at that point the typical state reached by the system is the one-cluster state in which all the oscillators are in phase. The one-cluster state is marginal for that value of α. It should be noted that even below this transition, some two-cluster states do exist and the lin-

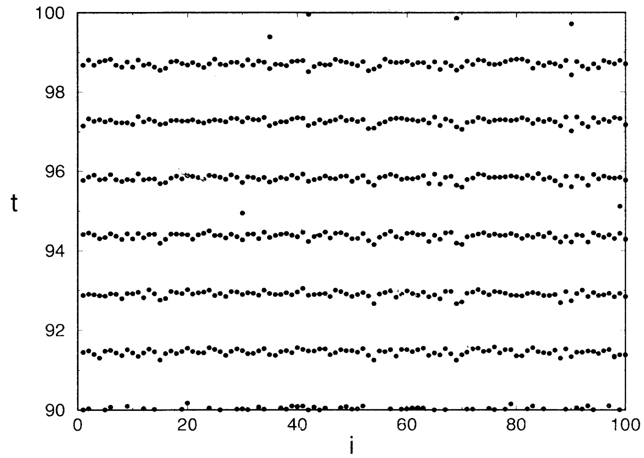

FIG. 5. Times at which the phase of each oscillator crosses 2π, for $\alpha = 0.85$ and $\sigma = 0.000\,22$.

ear stability analysis around these states reveals exactly the same characteristics as above the transition (provided that $0.70 \leq \alpha < \pi/3$). However, any trajectory starting in the vicinity of such a two-cluster state ends on the one-cluster state, at variance with what is found above the transition.

IV. DYNAMICS OF LARGE NETWORKS WITH SMALL NOISE

In this section we investigate the effects of a small noise on the dynamics of large networks. For $\alpha < \pi/3$, the dynamics is not much modified, as illustrated in Fig. 5. The one-cluster state is now replaced by a highly coherent state: the distribution of the phases is peaked with a width of order $O(\sigma)$. This is in contrast with the situation for $\pi/3 < \alpha < \pi/2$ where introducing a small noise changes dramatically the behavior of the system. To the overall periodic and global motion of the clusters at frequency Ω_2, a slower motion is superimposed that exchanges the two clusters (see Fig. 6). We call this situation a *switching state*. A noticeable fact is that *only* one cluster is destroyed at a time. After complete destruction this cluster is rebuilt in such a way that the order of the clusters is inverted. The process then repeats itself but this time with the other cluster.

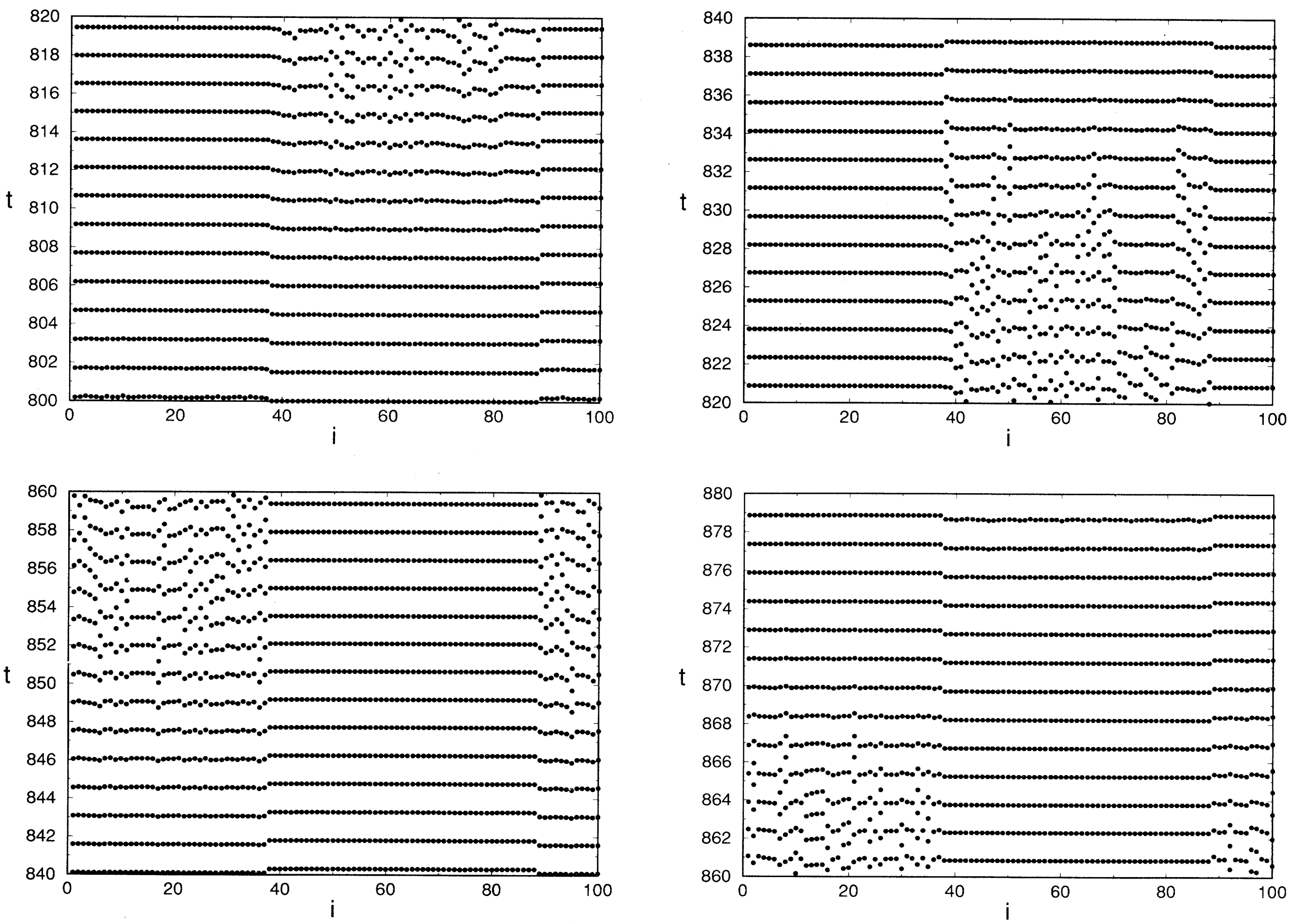

FIG. 6. Times at which the phase of each oscillator crosses 2π, for $\alpha = 1.25$ and $\sigma = 0.000\,22$. Each of the four frames displays the evolution during 20 units of time of the system.

A good way to analyze the behavior of the system is to consider the two complex order parameters defined by

$$Z_1(t) = \frac{1}{N}\sum_{j=1}^{N} \exp\left[i(\phi_j - \omega t)\right], \quad (9)$$

$$Z_2(t) = \frac{1}{N}\sum_{j=1}^{N} \exp\left[2i(\phi_j - \omega t)\right], \quad (10)$$

that can be used to rewrite the equations of motion. In Fig. 7 we have plotted the moduli, r_1 and r_2 of these two complex numbers. These two quantities display a periodic time evolution after the transients have died out, as confirmed by their Fourier spectra (not shown). The period of this collective effect depends essentially on the noise level. Fig. 8, that displays the switching period versus the noise variance, shows a clear logarithmic dependence.

It is also important to note that the switching phenomenon disappears when the noise is increased past a critical value σ_c. The system then reaches a stationary state characterized by a distribution of the phases with one broad peak. For $\alpha = 1.25$ the transition occurs for $\sigma_c \simeq 0.011$. Finally, the switching state is also destroyed if α is increased too much. For $\alpha > \alpha_c = \pi/2$ the system reaches at large time the incoherent state. This can be checked by looking at the order parameter that eventually decays to zero.

Generalizing the picture of Sec. III B to the noisy case, one can understand the noise-induced switching. The noise perturbs constantly the system giving rise to a deviation from the deterministic trajectory with a nonzero component along the unstable manifold. If the variance of the noise is σ^2, this deviation will be of order σ. For finite N, the switching between the two two-cluster states is aperiodic. However, for large N the fluctuations of the switching time are of order $\frac{1}{\sqrt{N}}$. This is due to the large dimension (of order N) of the unstable manifolds of the fixed points: a central limit theorem can be invoked for the norm of the deviation. Therefore, in the limit $N \to \infty$ the switching becomes strictly periodic. Linearizing the dynamics around the fixed points, we find that the time it takes for the system to perform a cycle is given by

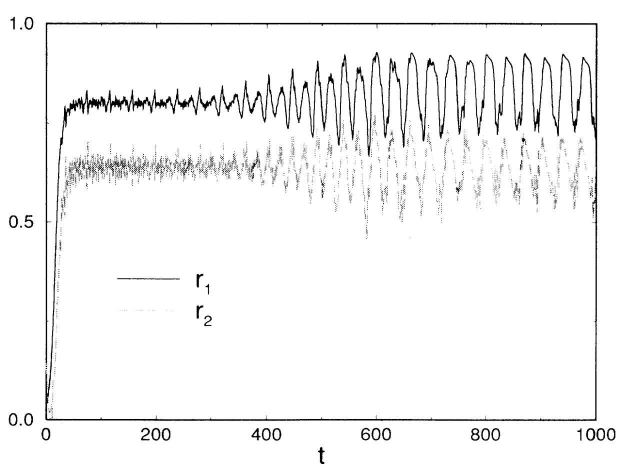

FIG. 7. Order parameters r_1 and r_2 versus time for $\alpha = 1.25$ and $\sigma = 0.000\,22$.

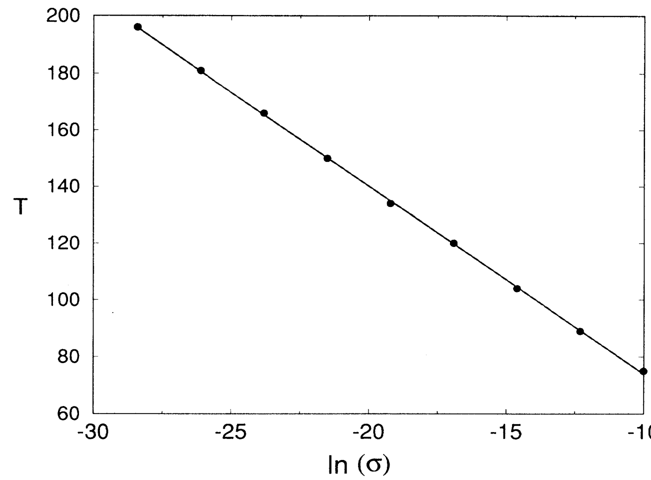

FIG. 8. Period T of a cycle versus $\ln\sigma$ for $\alpha = 1.25$. The line is a linear fitting of the data.

$$T \sim -\left(\frac{1}{\lambda_u} + \frac{1}{\lambda'_u}\right)\ln\sigma. \quad (11)$$

The value of the slope obtained for $\alpha = 1.25$ is -6.54, in good agreement with the slope obtained from Fig. 8, that is approximately -6.6.

V. CONCLUSIONS

Most studies on networks of coupled phase oscillators have concentrated on cases where only one Fourier mode is included in the interaction. This situation is representative of a large class of coupled oscillators at weak coupling, namely oscillators near a Hopf bifurcation. However, more complicated interactions can be commonly found in other contexts. The model we have studied here involves an interaction with two Fourier components; it corresponds to a simplified model of interacting conductance-based neurons. At variance with the one-Fourier-mode case, that network can reach at large time many attractors. Among them we have been mostly interested in attractors of the cluster type.

We have seen that, for a large range of the parameters, the asymptotic dynamics of the network is governed by a pair of two-cluster states, related by a symmetry, and connected by heteroclinic orbits. The system is strongly affected by the noise, which provokes the emergence of a slow dynamics through network effects. In large networks, this dynamics takes the form of a periodic oscillation, the frequency of which is proportional to the logarithm of the amplitude of the noise. This switching phenomenon is also observed in small systems (from $N = 4$) but only in the limit of large N does it become really periodic. In the noiseless limit the period of the oscillations increases exponentially with time.

Several interesting questions remain to be solved or understood.

(1) The system can display a great variety of cluster states. Numerical integration indicates that among these, two particular two-cluster states are selected at least far from the transitions at $\pi/3$ and $\pi/2$. Is there any simple argument that would allow us to understand this selection?

(2) Heteroclinic orbits are *a priori* structurally unstable. However, we have tested the robustness of the heteroclinic structure with respect to small perturbations that preserve the symmetry of the global coupling. In all the cases considered we have found no qualitative changes of the dynamics. This apparent robustness of the heteroclinic junction needs to be confirmed. One can think that it could be related to the high degree of symmetry of the interaction that constrains strongly the dynamics. It has been recently shown that some globally coupled phase oscillators can possess a large number of constants of motion [of order $O(N)$] and even can be fully integrable in special cases [18]. Has the model we have studied $O(N)$ constants of motion also? This could shed some light on the stability of heteroclinicity in our model.

(3) A third question raised by the present work concerns the generality of the observed phenomena in the framework of globally coupled phase models beyond the one-parameter family of models studied here. The existence of various stable clustering regimes is commonly expected as soon as one considers interactions with more than one-Fourier mode. The generality of the switching state is much less obvious. However, we have checked that adding additional Fourier components to the Γ function, or even including in the dynamics terms that do not depend on the difference of phases, does not change the behavior qualitatively, as long as these changes are not too large [17].

(4) The phase model we have studied here corresponds to the weak-coupling limit of a network of Hodgkin-Huxley oscillators coupled synaptically. The dynamics of each of these oscillators is described by four highly nonlinear equations of motion. Moreover, the synaptic form of the interaction makes the stability analysis of the possible asymptotic dynamics very difficult (even for the fully synchronized state). The phase reduction is much more convenient to study and one can wonder whether it can also give some insight into the dynamics of the original model beyond the weak coupling limit. We found by numerical integration that the original network of globally coupled Hodgkin-Huxley neurons displays similar heteroclinic structures and noise-induced slow oscillations for coupling strength that are beyond the weak coupling limit.

ACKNOWLEDGMENTS

We thank P. Collet, B. Shraiman, H. Sompolinsky, and M. Tsodyks for many useful discussions. We thank V. Hakim for pointing Refs. [12] and [13] to our attention. We thank D. Golomb, S. Seung, M. Tsodyks, and X. J. Wang for a careful reading of the manuscript. Part of the work of G.M. was supported by the Centre de Physique Théorique, Ecole Polytechnique. D.H acknowledges the very warm hospitality of Racah Institute of Physics and Center for Neural Computation of the Hebrew University.

APPENDIX

We study here the existence and the stability of the incoherent state of the one-cluster and of the two-cluster states. States with n clusters can also exist, but they will not be considered. We assume that $g = 1$ and $r = 1/4$.

Incoherent state. In the incoherent state the oscillators are uniformly distributed on $[0, 2\pi]$. This state exists for all α and all intensity of the noise. Kuramoto [1] has studied the stability of incoherent states for a general phase interaction. Applying his results to our case, one finds that it is unstable for

$$\sigma^2 < \cos\alpha. \tag{A1}$$

In particular, at zero noise the incoherent state is unstable for $\alpha < \pi/2$ and stable for $\alpha > \pi/2$. This is in agreement with the fact that we did not observe a stable incoherent state except for $\alpha > \pi/2$.

One-cluster state. The state in which the N oscillators are phase-locked with zero phase shift exists for any value of α. The frequency of the oscillation is $\Omega_1 = \omega + \Gamma(0)$. One easily shows that it is stable for $\alpha < \pi/3$ and loses stability at $\alpha = \pi/3$. This is in agreement with the fact that random initial conditions lead to the one-cluster state for $\alpha < \pi/3$.

Two-cluster state. We consider a two-cluster solution in which the two clusters contain, respectively, Np and $N(1-p)$ units. Inside each group the oscillators are fully phase locked and synchronized and the dephasing between the groups is constant in time and equal to Δ. The relation between p and Δ can be simply obtained from the equation of motion:

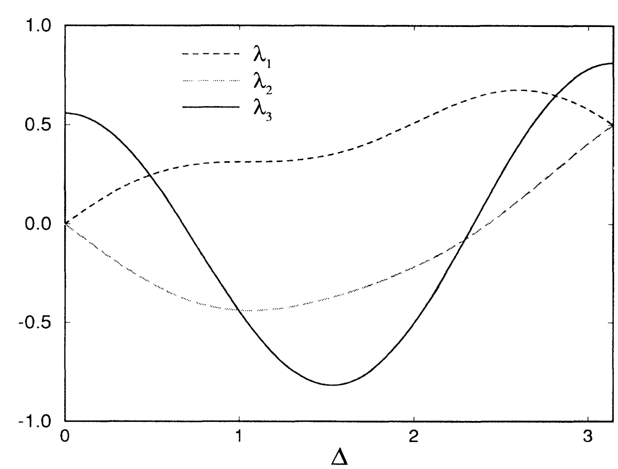

FIG. 9. Eigenvalues of the two-cluster states as a function of Δ for $\alpha = 1.25$.

$$p = \frac{\Gamma(0) - \Gamma(\Delta)}{2\Gamma(0) - \Gamma(\Delta) - \Gamma(-\Delta)}. \quad \text{(A2)}$$

For a given value of α, two-cluster states exist with p ranging from $1-p_{\max}$ to $p_{\max}$. For instance, for $\alpha = 1.25$, $p_{\max} = 0.68$. For a given p in this interval, there are in general three solutions corresponding to three possible (p, Δ) states. In the frame rotating at frequency $\Omega_2 = p\Gamma(0) + (1-p)\Gamma(\Delta)$, the two-cluster state (p, Δ) becomes a fixed point and the stability analysis of this state can be performed straightforwardly for a general $\Gamma(\phi)$. The eigenvalues of the stability matrix are

$$\lambda_1 = p\Gamma'(0) + (1-p)\Gamma'(\Delta), \quad \text{(A3)}$$

$$\lambda_2 = (1-p)\Gamma'(0) + p\Gamma'(-\Delta), \quad \text{(A4)}$$

$$\lambda_3 = p\Gamma'(\Delta) + (1-p)\Gamma'(-\Delta), \quad \text{(A5)}$$

with multiplicity $Np - 1$, $N(1-p) - 1$ and 1. One last eigenvalue (with multiplicity 1) is 0 that relates to the invariance with respect to translation along the limit cycle (shift of time). The eigenvalues λ_1 and λ_2 correspond to fluctuations inside each one of the two clusters and λ_3 corresponds to a fluctuation in the distance between the two clusters while keeping their structure intact. In Fig. 9 we have plotted the three eigenvalues versus Δ. We can see everywhere that at least one of the eigenvalues λ_1 and λ_2 is positive. This means that two-cluster states are *never stable.* In the cases in which one of them is positive and the other negative, the positive one will be denoted by λ_u, and the negative, by $-\lambda_s$.

---

[1] Y. Kuramoto, *Chemical Oscillations, Waves and Turbulence* (Springer, New York, 1984).

[2] E. R. Grannan, D. Kleinfeld, and H. Sompolinsky, Neural Computation **4**, 550 (1993).

[3] D. Hansel, G. Mato, and C. Meunier, Europhys. Lett. **23**, 367 (1993).

[4] E. R. Kandel, S. A Siegelbaum, and J. H. Schwartz, *Synaptic Transmission*, in *Principles of Neuroscience*, edited by E. R Kandel, J. H. Schwartz, and T. M. Jessell (Elsevier, New York, 1991).

[5] A. L. Hodgkin and A. F. Huxley, J. Physiol. (London) **117**, 500 (1952).

[6] K. Kaneko, Physica D **54**, 137 (1990).

[7] V. Hakim and W. J. Rappel, Phys. Rev. A **46**, R7347 (1992).

[8] N. Nakagawa and Y. Kuramoto, Prog. Theor. Phys. **89**, 313 (1993).

[9] D. Golomb, D. Hansel, B. Shraiman, and H. Sompolinsky, Phys. Rev. A **45**, 3516 (1992).

[10] D. Hansel and H. Sompolinsky (unpublished).

[11] R. M. May and W. J. Leonard, SIAM J. Appl. Math. **29**, 243 (1975).

[12] F. H. Busse and K. E. Heikes, Science **208**, 173 (1980).

[13] Y. Tu and M. C. Cross, Phys. Rev. Lett. **69**, 2515 (1992).

[14] E. Knobloch and M. Silber, Physica D **63**, 213 (1993).

[15] While we were completing this paper, we received an article by Okuda [Physica D **63**, 424 (1993)]. In this work the author claims that in order to have n-cluster states in a network of phase oscillators, it is indispensable to have a mode of order n in the Fourier expansion of the phase interaction. The argument of the author seems to us doubtful since it is based on a linear stability analysis in cases where marginality occurs. Moreover, in our model we are able to find stable three-cluster states for suitable initial conditions although the interaction contains only modes 1 and 2.

[16] The observation that the system oscillates between the two alternative two-cluster states and spends more and more time near each one may seem in contradiction with the fact that the histogram of Δ (Sec. III A) is monomodal. This histogram was obtained starting from random initial conditions. In order to solve this apparent paradox, we suggest that the basin of attraction of one of the two-cluster states is actually much bigger than the basin of attraction of the other. As a consequence the network enters into the oscillatory regime nearer to one of the cluster states. Then, the system performs oscillations and eventually converges due to the finite precision of the computer. The number of these oscillations depends barely on the initial conditions, since it varies only logarithmically with the deviation from the two-cluster states at the beginning of these oscillations. Therefore the system is expected to end almost always in the same final state.

[17] Okuda describes in a footnote of his paper [Physica D **63**, 424 (1993)] a phenomenon that seems similar to the one we have described in Part 3. He also suggests an interpretation in terms of heteroclinicity. This provides some indication of the generality of our results.

[18] S. Watanabe and S. H. Strogatz, Phys. Rev. Lett. **70**, 2391 (1993).