Learning-rate-dependent clustering and self-development in a network of coupled phase oscillators

Ritwik K. Niyogi[1,2] and L. Q. English[1]
[1]*Department of Physics and Astronomy, Dickinson College, Carlisle, Pennsylvania 17013, USA*
[2]*Program in Neuroscience and Department of Mathematics, Dickinson College, Carlisle, Pennsylvania 17013, USA*
(Received 2 September 2009; published 30 December 2009)

We investigate the role of the learning rate in a Kuramoto Model of coupled phase oscillators in which the coupling coefficients dynamically vary according to a Hebbian learning rule. According to the Hebbian theory, a synapse between two neurons is strengthened if they are simultaneously coactive. Two stable synchronized clusters in antiphase emerge when the learning rate is larger than a critical value. In such a fast learning scenario, the network eventually constructs itself into an all-to-all coupled structure, regardless of initial conditions in connectivity. In contrast, when learning is slower than this critical value, only a single synchronized cluster can develop. Extending our analysis, we explore whether self-development of neuronal networks can be achieved through an interaction between spontaneous neural synchronization and Hebbian learning. We find that self-development of such neural systems is impossible if learning is too slow. Finally, we demonstrate that similar to the acquisition and consolidation of long-term memory, this network is capable of generating and remembering stable patterns.

DOI: 10.1103/PhysRevE.80.066213 PACS number(s): 05.45.Xt, 87.19.lm, 87.19.lj, 05.65.+b

I. INTRODUCTION

Spontaneous mass synchronization has been observed in several biological systems, such as in the synchronous flashing of fireflies [1,2], the chirping of crickets [3], and in the pacemaker cells in the cardiovascular system [4]. Within the nervous system, synchronous clustering has been reported in networks of neurons in the visual cortex [5], olfactory bulb [6], central pattern generators [7–10] as well as in those involved in generating circadian rhythms [11]. Neuronal synchronization has been attributed to play a role in movement [12], memory [13], and epilepsy [14,15]. It is clear that in all these examples the structure of the neural network must play a crucial role in its function. The adaptive development of the network structure takes place through the modifications of synaptic connections, governed by underlying neural learning mechanisms. Such synaptic modifications are posited to constitute the neural basis of learning and the consequent acquisition of long term memory [16,17].

In the nervous system, a neuron integrates inputs from other neurons and generates outputs in the form of action potentials or spikes when its membrane potential exceeds an electrophysiological threshold. In particular, tonically spiking neurons are observed to "fire" spikes at regular intervals with a particular time period. Although the dynamics of single neurons are essential, complex cognitive phenomena emerge from the interactions of many neurons. In a given neuronal network, neurons that make synaptic connections influence one another through either excitation or inhibition.

Collective synchronization in natural systems has been previously modeled by representing them as networks of coupled phase oscillators [18–23]. These studies assumed a preimposed static network structure and connectivity. In particular, the influential Kuramoto Model [20] relied on global, all-to-all connectivity in which each oscillator affected every other oscillator equally.

Recent theoretical efforts have studied how a network may develop in accordance with neural learning mechanisms in relation to the dynamics of synchronous cluster formation [21,24–27]. Neurophysiological studies have shown that a synapse is strengthened if the presynaptic neuron repeatedly causes the postsynaptic neuron to fire, leading to the long term potentiation (LTP) of the synapse [28,29]. Symmetrically, long term depression (LTD) occurs when the postsynaptic neuron does not fire when the presynaptic neuron does. Experimental findings suggest further that learning may not depend solely on the rate of spikes at a synapse but on the relative timing of pre- and postsynaptic spikes [30–33]. According to the Hebbian theory [34], the strength of the synapse between two neurons is enhanced if they are simultaneously coactive. In this work, we represent the relative time between spikes in the pre- and postsynaptic neurons as the relative phase of a pair of coupled oscillators, and in this way the phase of an oscillator may be used to represent the time between two spikes generated by a given tonically spiking neuron. The intrinsic frequency, the frequency of an oscillator independent of any influence from other oscillators, shall represent the natural firing-rate of a neuron in a network [35,36].

Phase oscillator models with slow time-varying coupling have previously been capable of displaying associative memory properties, while revealing parameter regimes for which both synchronized and unsynchronized clusters are stable [21,26]. We explore how synchronization and learning mutually affect one another for both slow and fast learning rates. Similar recent models have assumed homogeneous networks with equal intrinsic frequencies [24]. We show, however, that an oscillator network develops stable synaptic couplings that depend on the relative intrinsic frequencies and on the learning rate, as well as on the initial network state. The paper is organized as follows: in Sec. II we introduce the model endowed with dynamic connectivity. In Secs. III and IV we focus on the scenario when the network learns quickly and slowly, respectively. We extend our findings to the scenario when the network starts out without any connec-

tions and self-develops due to the mutual interaction of synchronization and learning in Sec. V. We summarize our findings and provide perspectives in Sec. VI.

II. MODEL

The Kuramoto Model [20] considers a system of limit-cycle oscillators moving through the phases of their cycles based on each oscillator's intrinsic frequency and its interaction with other oscillators,

$$\frac{d\phi_i}{dt} = \omega_i + \frac{1}{N}\sum_{j=1}^{N} K_{ij}F(\phi_j - \phi_i), \tag{1}$$

where $\phi_i \in [0,2\pi)$ is the phase of the ith oscillator and ω_i is its intrinsic frequency. The intrinsic frequencies ω_i can be drawn from a probability distribution $g(\omega)$, which is assumed to be unimodal and symmetrically distributed around its mean. K is an $N \times N$ matrix of coupling coefficients, and F is a coupling function with a period of 2π. Following Kuramoto [20], we assume $F(\phi)=\sin(\phi)$. In order to measure the degree of synchronization, a global order parameter, r, is defined as

$$re^{i\psi}(t) = \frac{1}{N}\sum_{j=1}^{N} e^{i\phi_j(t)}. \tag{2}$$

It represents the centroid of the phases with $r(t)$ corresponding to the coherence in phases and $\psi(t)$ representing the mean phase. Another convenient measure of synchronization is given by $r^2 \in [0,1]$, the square of the modulus of the order parameter.

If we assume constant and identical coupling coefficients, then $K_{ij}=K$ for all i,j. This is known as the globally coupled Kuramoto Model. Assuming such coupling, Eq. (1) becomes

$$\frac{d\phi_i}{dt} = \omega_i + \frac{K}{N}\sum_{j=1}^{N} \sin(\phi_j - \phi_i). \tag{3}$$

The Kuramoto Model then reduces to a mean-field model. Any particular oscillator is sensitive only to the mean, global properties of the entire system of oscillators, making the detailed configuration of coupled oscillators irrelevant. It can be shown [37] that the degree of synchronization becomes nonzero (in a second-order phase transition) when $K > K_c$ where K_c is a critical coupling. If the distribution $g(\omega)$ of intrinsic frequencies is Gaussian, with a standard deviation σ, then

$$K_c = \frac{2}{\pi g(0)} = \sqrt{\frac{8}{\pi}}\sigma. \tag{4}$$

It should be noted that due to rotational symmetry in the model, $g(\omega)$ can always be shifted so that its peak occurs at $\omega=0$. The system of coupled oscillators reaches an average degree of synchronization that is independent of initial conditions, whether the oscillators started out completely in phase or distributed over the unit circle [38].

Instead of assuming a constant, preimposed connectivity and coupling matrix, we wish to investigate how this network develops through neural learning mechanisms and affects synchronous cluster formation, and vice versa. The learning mechanisms discussed above can be represented by dynamically varying coupling coefficients according to the rule

$$\frac{dK_{ij}}{dt} = \epsilon[G(\phi_i - \phi_j) - K_{ij}]. \tag{5}$$

Choosing $G(\phi)=\alpha\cos(\phi)$ renders Eq. (5) roughly equivalent to the Hebbian learning rule. Note that ϕ_i and ϕ_j are simultaneously coactive if they are in phase and hence representative of LTP. When they are in antiphase, that is, $\phi_i-\phi_j=\pi$, the condition is representative of LTD. Note that with this choice, $G(\phi)$ is odd with respect to $\phi=\pi/2$, which means that there is a symmetry between growth and decay of synaptic strengths.

We define α to represents a *learning enhancement factor*. It amplifies the amount of learning if two neurons are coactive. When the *learning rate* ϵ is small, synaptic modification is slow. In this case, synchronized clusters are formed which are usually stable with respect to external noise [26], although we discuss below how the stability depends on α. Since such stabilization, as in the Hopfield model [39], is reflective of long-term associative memory formation [40], such a representation would be expected to yield an important perspective on the mechanisms of learning.

Combining the models of spontaneous synchronization and Hebbian learning, our joint dynamical system is represented by

$$\frac{d\phi_i}{dt} = \omega_i + \frac{1}{N}\sum_{j=1}^{N} K_{ij}\sin(\phi_j - \phi_i) \tag{6}$$

$$\frac{dK_{ij}}{dt} = \epsilon[\alpha\cos(\phi_i - \phi_j) - K_{ij}]. \tag{7}$$

The K_{ij} in Eq. (7) is a saturating term which prevents coupling coefficients from increasing or decreasing without bound. A hard bound such as restricting $|K_{ij}| \leq 1$ as in [25] can effectively limit the steady state values of the coupling coefficients to one of the two hard bounds. Although such restrictions can account for the memorization of binary data, a soft bound such as the saturating term we enlist here can allow the network to possess more diverse connectivity. It should be noted that the number of parameters appearing in Eqs. (6) and (7) could be reduced by means of rescaling time and absorbing ϵ. However, since both ϵ and α are meaningful from a neurophysiological perspective, we choose to leave the equations in their present form.

Whereas previous work focused on slow learning [21,26], we explore the network's behavior for both fast- and slow-learning scenarios. We observe qualitatively different behaviors depending on the values of ϵ and α. Particularly, we observe that there is a critical value of the learning rate below which a single synchronous cluster is formed as in the original Kuramoto Model in Eq. (3). Above this critical value, two synchronous clusters emerge (see Fig. 4). We define a new order parameter, r_2, as

$$r' e^{i\psi'(t)} = \frac{1}{N}\sum_{j=1}^{N} e^{i2\phi_j(t)},$$

$$r_2^2 = |r' - r|^2. \tag{8}$$

The subtraction of the degree of synchronization for a single cluster r is necessary since r' is large also for the single cluster configuration; r_2 is designed to pick out the dipole moment of the distribution (i.e., two clusters).

As we will show, the dynamics of the system depends on whether the learning rate parameter ϵ is large or small compared to some critical ϵ_c. For fast learning, $\epsilon > \epsilon_c$, the coupling coefficients can adjust themselves rapidly enough according to Eq. (7) that they follow the "fixed point" $\alpha\cos(\phi_i - \phi_j)$ adiabatically as it oscillates before a synchronized state has manifested. For slow learning, $\epsilon < \epsilon_c$, the coupling coefficients cannot follow the oscillation, and thus they can only depart consistently from the initial values once a synchronized state has established itself.

To estimate the magnitude of ϵ_c, we have to compare the rate at which Eq. (7) can change with the frequency of the term $\cos(\phi_i - \phi_j)$. It is clear that Eq. (7) would asymptotically approach a static fixed point with a time constant of $\tau_1 = 1/\epsilon$. On the other hand, $\cos(\phi_i - \phi_j)$ is expected to oscillate at a frequency of $|\omega_i - \omega_j|$, and so on average $\tau_2 = \pi/2\sigma$ is the time it takes for two oscillators starting in phase to have moved $\pi/2$ out of phase where they do not influence their mutual coupling coefficient any longer. Setting these two time scales equal to one another yields,

$$\epsilon_c = \frac{2\sigma}{\pi}. \tag{9}$$

In our study, $\sigma = 0.1$, so that $\epsilon_c \approx 0.064$. It should be noted that the argument above only holds when the starting coupling coefficients of the network satisfy $K_{ij}(0) > K_c \approx 0.16$ [see Eq. (4)]. Below K_c, the system cannot attain global synchronization at all in the slow-learning regime.

III. FAST LEARNING

Situations where memorization of specific details is necessary involve fast learning. Hippocampal conjunctive coding in particular is believed to involve such rapid, focused learning [41]. Note that fast learning according to Eq. (9) does not imply that learning dynamics is faster than individual synaptic dynamics, which would be unrealistic. Instead, learning dynamics is faster only compared to the relative synaptic dynamics between two neurons, but it is still much slower than individual synaptic spike dynamics. In our joint dynamical system, when $\epsilon > \epsilon_c$, the coupling coefficients can follow the "fixed point" and so $K_{ij}^* = \alpha\cos(\phi_i - \phi_j)$. Substituting K_{ij}^* into Eq. (6) then yields,

$$\frac{d\phi_i}{dt} = \omega_i + \frac{\alpha}{2N}\sum_{j=1}^{N} \sin[2(\phi_j - \phi_i)]. \tag{10}$$

Multiplying both sides of Eq. (10) by 2 and defining $\phi_i' = 2\phi_i$ and $\omega_i' = 2\omega_i$ yields,

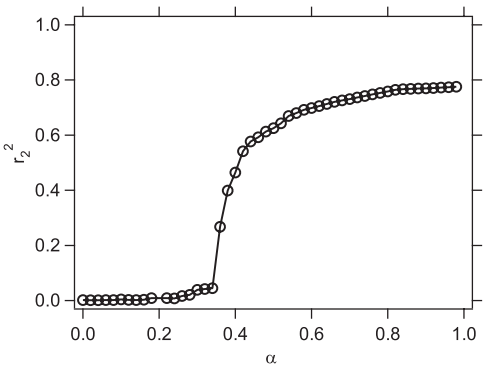

FIG. 1. Two-cluster synchronization r_2^2 as a function of the learning enhancement factor α when the initial phases of oscillators are uniformly distributed over the circle. $\epsilon > \epsilon_c$ was set at a large value of 1. A second-order phase transition is observed at $\alpha_c = 2K_c = 0.32$ for Gaussian intrinsic frequency distribution of standard deviation $\sigma = 0.1$.

$$\dot{\phi}_i' = \omega_i' + \frac{\alpha}{N}\sum_{j=1}^{N} \sin(\phi_j' - \phi_i'). \tag{11}$$

This is equivalent to the global Kuramoto Model in Eq. (3), except that the phases are now in double angles. We would therefore expect to find a critical value of the learning enhancement factor, α_c, at which a second-order phase transition to synchronization occurs. Under our previous assumptions for $g(\omega)$,

$$\int_{-\infty}^{\infty} g(\omega)d\omega = 1 = \int_{-\infty}^{\infty} g'(\omega')d\omega', \tag{12}$$

it follows that

$$g'(\omega) = \frac{g(\omega)}{2}. \tag{13}$$

Accordingly, comparing with Eq. (4),

$$\alpha_c = \frac{2}{\frac{\pi g(0)}{2}} = 2K_c \tag{14}$$

In order to verify the value of α_c, we performed a series of numerical simulations. All simulations in this study employed an Euler time step of $\Delta t = 0.1$; all results shown started with initial oscillator phases spread out over the entire unit circle. In Fig. 1, ϵ was set to 1.0, so that $\epsilon > \epsilon_c = 0.064$, and the network consisted of 500 oscillators. Intrinsic frequencies ω_i were drawn from a Gaussian distribution with mean $\mu = 0$ and standard deviation $\sigma = 0.1$. In this case, according to Eq. (4), $K_c \approx 0.16$. We then varied the value of α from 1 toward 0 and obtained a bifurcation diagram relating the average eventual degree of synchronization to the learning enhancement factor. We observe a second-order phase transition in α for the joint system similar to that of the original Kuramoto model with global all-to-all coupling. Critically, this phase transition occurs at $\alpha_c = 0.32 = 2K_c$, veri-

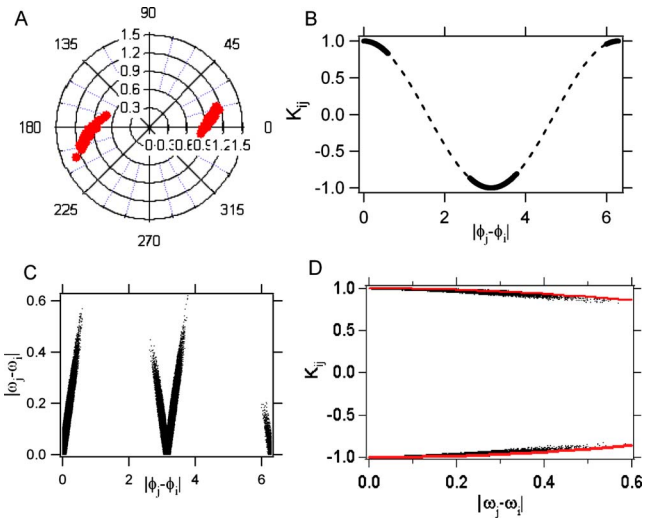

FIG. 2. (Color online) Fast Learning ($\epsilon > \epsilon_c$) with $\alpha = 1 > \alpha_c$. (A) Polar plot of the distribution of oscillators. Two stable clusters are formed. (B) Final K_{ij} as a function of the final relative phases $|\Delta\phi_{ij}|$. The thick line represents the data from simulations, dashed curve is the theoretical prediction: $K^*_{ij} = \alpha \cos(\phi_i - \phi_j)$. (C) Relative intrinsic frequencies $|\Delta\omega_{ij}|$ as a function of final relative phases $|\Delta\phi_{ij}|$. (D) Final K_{ij} as a function of relative intrinsic frequencies $|\Delta\omega_{ij}|$. Black dots represent data from simulations, the solid curve corresponds to the theoretical fit.

fying the theoretical prediction. This critical value is robust with respect to varying initial conditions of the phase distribution $\phi_i(0)$ and connectivity $K_{ij}(0)$.

When $\alpha > \alpha_c$, $\epsilon > \epsilon_c$, and all oscillators do not start out in phase, two clusters are formed, which remain 180° apart from each other in mean phase as shown in Fig. 2(A). Here, the intrinsic oscillator frequencies are displayed along the radial axis. Analyzing the phase-plane we obtain four fixed points for the joint dynamics of Eqs. (6) and (7). Two of them are stable, corresponding to $\phi_j - \phi_i = 0$ and $\phi_j - \phi_i = \pi$. Thus, stable states for this system occur when pairs of oscillators are either synchronized or antisynchronized with each other, leading to the formation of the two antisynchronized clusters. The other steady states, corresponding to a relative phase of $\frac{\pi}{2}$ and $\frac{3\pi}{2}$, are unstable. It follows that for the stable steady states,

$$K^*_{ij} = \alpha \cos(\phi_i - \phi_j) \approx \pm \alpha \tag{15}$$

with $K^*_{ij} \approx \alpha$ within a synchronized cluster and $K^*_{ij} \approx -\alpha$ between two antisynchronized clusters. As seen in Fig. 2(B), the final steady-state values of the coupling coefficients for the two clusters, observed in the simulations, are in excellent accordance with the prediction of Eq. (15). The final values of the coupling coefficients K_{ij} can also be correlated against the initial relative intrinsic frequencies of oscillators $\Delta\omega_{ij} = |\omega_i - \omega_j|$. Here it is useful to first relate the relative intrinsic frequencies of the oscillators to their final relative phases [Fig. 2(C)]. Within a cluster, we can calculate the slope of this relationship. The scatter-plot relating the final steady-state value of the coupling coefficients to the relative intrinsic frequencies of oscillators also depicts the formation of

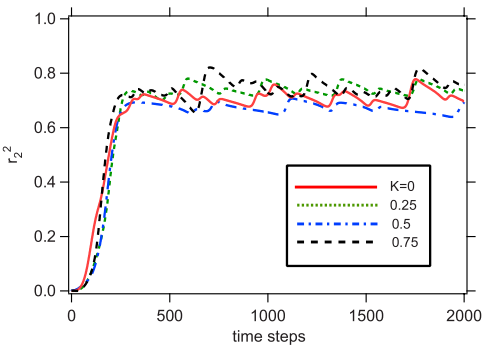

FIG. 3. (Color online) The time evolution of the two-cluster order parameter, r_2, when $\alpha > \alpha_c$ and ϵ is large (fast learning) for different initial coupling strengths $K(0)$. α was fixed at 0.5, $\epsilon = 1$ and $K(0)$ was varied from 0, 0.25, 0.5 and 0.75. r_2 attains the same final value regardless of the initial coupling strengths.

two clusters [Fig. 2(D)]. Using the slope of the line in Fig. 2(C) together with the cosine fit in Fig. 2(B), we can again match the scatter plot very well.

In the fast learning scenario, the strength of the initial network coupling has no effect on the eventual network structure (one or two clusters formed) or degree of synchronization. As shown in Fig. 3, regardless of whether we start the network without connections, with coupling coefficients $K(0) < \alpha$, $K(0) = \alpha$, or $K(0) > \alpha$, the two-cluster order parameter, r_2, always attains the same eventual value. In contrast to the original Kuramoto model of Eq. (3), here the degree of synchronization does depend on the initial relative phases of the oscillators and on the value of α. When $\alpha > \alpha_c$ and all oscillators start out in phase, that is, $\phi_i(0) = 0$ for $i = 1, 2, \ldots, N$, then only a single synchronized cluster is formed (the second cluster being viable but unpopulated), and a relatively large value of r^2 is observed, while r_2^2 tends toward 0. As discussed above, if $\alpha < \alpha_c$ then no synchronization can manifest.

IV. SLOW LEARNING

In neuroscience, the ability of abstracting generalizable properties from specific details is believed to involve slow learning mediated by the neocortex [41]. In our model of coupled phase oscillators, slow learning occurs when $\epsilon < \epsilon_c$. Qualitatively, since there is very little change in Eq. (7), $K_{ij} \approx K_{ij}(0) = K > K_c$ on an intermediate time scale. Substitution of this approximate condition into Eq. (6) recovers the globally coupled Kuramoto Model given by Eq. (3). In this case, only a single synchronized cluster should form, and this result is easily verified by simulations.

Whether this single cluster remains stable over long time scales depends on the value of α. If α is chosen too low, an interesting phenomenon occurs whereby a cluster initially forms but at long times disintegrates again. The eventual disintegration is due to the decrease of the coupling coefficients at longer times below a value needed to sustain synchronization.

Figure 4 summarizes the transition from a one-cluster state to a two-cluster state as ϵ is increased above the critical

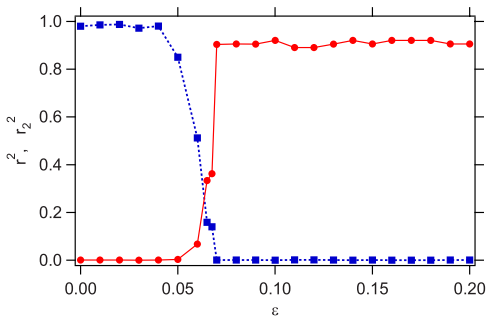

FIG. 4. (Color online) One- and two-cluster synchronization as a function of ϵ when $K(0)=0.75$. $\alpha>\alpha_c$ was set at a large value of 1. The dotted line (with squares) and the solid line (with circles) represent the average eventual degree of synchronization for a single cluster r^2 and that for two clusters r_2^2, respectively. Each data point was computed by simulating a network of 250 oscillators for 5000 time steps and averaging over the last 1000 time steps.

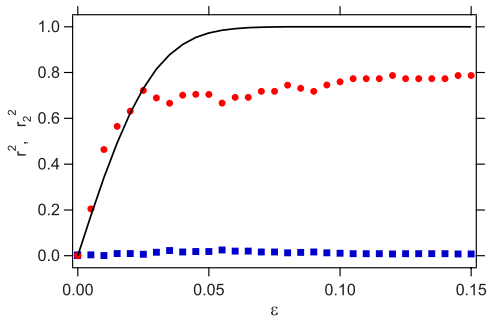

FIG. 5. (Color online) Two-cluster synchronization r_2^2 as a function of learning rate ϵ when $K(0)=0$. Circles represent the numerical result for r_2^2 (computed as in Fig. 4). The solid line represents the predicted percentage of synchronized pairs. Squares depict the mean degree of sync for one cluster r^2.

value. The dotted trace depicts r^2 and the solid trace r_2^2. The transition from a one-cluster state at small learning rates to a two-cluster state for fast learning is evident. A starting value of $K_{ij}(0)=0.75>K_c$ was used in the simulations shown, but other values of $K(0)$ were tested as well. Note that the transition between the one-cluster and two-cluster state occurs at the predicted $\epsilon_c=0.064$ separating slow and fast learning, thus verifying the prediction of Eq. (9).

V. SELF-DEVELOPMENT

We now consider the intriguing case of $K_{ij}(0)=0$ for all i,j. This means that we start the joint system out with no connections between oscillators in order to observe how a connective structure may self-develop in this model. In neuroscience terms, we study whether parts of the nervous system can develop from the time of conception through the mutual interaction of spontaneous neural synchronization and Hebbian learning in order to perform their rich repertoire of functions.

Let us investigate the role of the learning rate ϵ in the self-development of synchronized clusters. For this purpose, the learning enhancement factor, α, is set to a value well above $\alpha_c=2K_c$ found earlier (see Fig. 1). We would like to find the conditions that allow two oscillators that are near in phase at some instant of time to become entrained to one another. It is clear that in order for this to happen,

$$\int_0^{T/4} \dot{K}dt \geq K_c, \quad \text{with}$$

$$K \approx \epsilon\alpha \cos(\Delta\omega t). \tag{16}$$

T denotes the time it would take for the unsynchronized oscillator pair to diverge in phase by 2π and thus meet again; i.e., $T=2\pi/\Delta\omega$. Note that the distribution of frequency differences of oscillator pairs is also normally distributed, but with a standard deviation increased by a factor of $\sqrt{2}$.

This condition implies that the two oscillators cannot be any further apart in intrinsic frequency than $\Delta\omega=\epsilon\alpha/K_c$. Thus, a first estimation of the percentage of oscillator pairs which are able to synchronize is given by the following function of ϵ:

$$\int_{-\Delta\omega}^{\Delta\omega} g(\omega)d\omega = \text{erf}(y),$$

$$y = \frac{\epsilon\alpha}{2\sigma K_c}. \tag{17}$$

This relationship suggests that the degree of synchronization should depart roughly linearly from the origin as ϵ is raised from zero, indicating the absence of a phase transition in this case. This prediction is confirmed by numerical simulations. Figure 5 shows the computed one- and two-cluster order parameters, r^2 and r_2^2, as a function of ϵ. We observe that the one-cluster state does not occur for any value of ϵ; it is "frozen" out for the initial condition $K(0)=0$. In contrast, the two-cluster state gradually turns on as ϵ is increased from zero.

In order to characterize the coupling coefficients that result from a self-assembled network further, let us examine the case $\epsilon=0.05$ (and $\alpha=1$, as before). Figure 6 depicts a scatter plot of the final coupling coefficients between all pairs of oscillators. We observe that the distribution falls into two distinct groups. The synchronized (and antisynchronized) oscillator pairs fall into the top and bottom arches. For the unsynchronized oscillators, an envelope (see green line in the figure) can be derived as follows:

Since for this subpopulation, $d\phi_i/dt \approx \omega_i$, after substitution into Eq. (7), we obtain the first-order nonhomogeneous differential equation

$$\dot{K}_{ij} + \epsilon K_{ij} = \epsilon\alpha \cos(\phi_i - \phi_j) = \epsilon\alpha \cos(|\Delta\omega_{ij}|t), \tag{18}$$

with solutions of

$$K_{ij}(t) = \frac{\alpha}{\sqrt{1+\left(\frac{|\Delta\omega_{ij}|}{\epsilon}\right)^2}} \cos(|\Delta\omega_{ij}|t + \delta), \tag{19}$$

where δ is a phase offset. Thus, for unsynchronized oscillators, the relation between the coupling coefficients attained

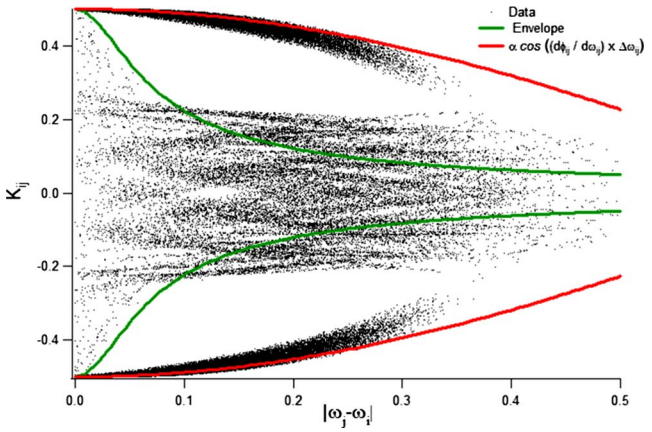

FIG. 6. (Color online) Final coupling coefficients, K_{ij}, in a self-developed network plotted against $|\Delta\omega_{ij}|$. Black dots represent simulation results with $N=250$ oscillators, $\alpha=1$, $\epsilon=0.05$. Pairs of unsynchronized oscillators remain within an envelope while other oscillators form two synchronized clusters in antiphase with each other.

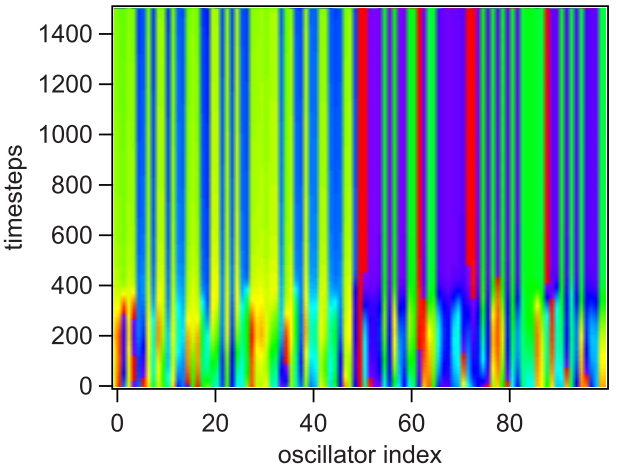

FIG. 7. (Color online) The learning rate is abruptly changed from $\epsilon=0.1$ to $\epsilon=0.01$ at a time step of 1000. The color indicates the oscillator phase relative to the middle oscillator (50). Once a stable pattern is established with fast learning, it does not change when the learning rate is reduced below ϵ_c.

and the relative intrinsic frequencies remains within an envelope (Fig. 6, green trace) that is expressed by the amplitude term in Eq. (19). For synchronized oscillators, the previous relationship holds (red line).

Whereas previous research demonstrated the ability of slow-learning coevolving networks to possess associative memory properties and learn binary patterns [24,26], here we provide a mechanism whereby the network generates and learns more diverse patterns even if learning is fast. Figure 7 illustrates what happens when the learning rate ϵ is changed abruptly from a high to a low value. This discontinuity happens at $t=1000$ in the figure. The color in this density plot indicates the phase of the 100 oscillators relative to the middle one. We see that once fast learning establishes a stable pattern, the switch to slow learning does not alter this pattern. Stable learning of this kind has been put forward as a neurally plausible mechanism for the consolidation of declarative memories [41]. In addition, in some connectionist models [42], short-term or temporary memory has been modeled with fast weight dynamics; this fast learning can then interact with older associations formed by slower learning processes.

VI. CONCLUSION

In summary, we have explored the mutual effects of spontaneous synchronization and Hebbian learning in a neuronal network, focusing specifically on the role of the learning rate. Our work predicts qualitatively different behaviors of the network depending on whether learning is fast or slow. Specifically, unless the network is in a pre-existing state of phase synchrony, when learning is fast, it evolves into two antisynchronized clusters as long as a learning enhancement factor, α, is larger than a critical value. We found that $\alpha_c=2K_c$. Furthermore, when learning is fast and $\alpha>\alpha_c$,the network always organizes itself into an all-to-all coupling structure with two clusters, regardless of its initial connectivity.

Fast temporal synchronization of groups of neurons has been identified as one possible mechanism underlying the cognitive process of *binding* [43–47]. Here, the bundling of multiple representations of a single object (such as its shape and its color) into a coherent entity is seen as encoded in the correlations or anticorrelations between groups of neurons. Anticorrelation, in particular, has been posited to play a role in *segmentation* or applications where neurons must spontaneously subdivide into several distinct groups (without accidental interferences) on short time-scales [48]. Conversely, temporal binding has been discussed as a basis for rapid synaptic plasticity [44]. Our study demonstrates that clustering and anticorrelation among initially disconnected neurons can emerge rapidly in the context of a Hebbian learning model.

We also predict a critical value in the learning rate, ϵ_c, below which learning can be thought of as slow. In this regime, for sufficiently strong initial couplings, only one synchronized cluster forms. This synchronized cluster is stable and is maintained only if α is greater than its critical value. Otherwise, the network attains a state of synchrony but in the long-term returns to a state of disorder.

Finally, we extended our analysis to the case when a network starts out without any connections (or with sufficiently weak connections). We demonstrated that the degree of synchronization varies continuously with the learning rate and no phase transition is observed. Here when the learning rate is too slow, the network remains in an unsynchronized state indefinitely. Thus, our model predicts that if learning is too slow, a neuronal network cannot self-develop through the mutual interactions of neural synchronization and Hebbian learning. In such a case, pre-existing couplings, or pre-existing synapses, which are sufficiently strong, are necessary for the neuronal network to self-develop.

[1] J. Buck, Q. Rev. Biol. **63**, 265 (1988).
[2] J. Buck and E. Buck, Sci. Am. **234**, 7485 (1976).
[3] T. J. Walker, Science **166**, 891 (1969).
[4] D. Michaels, E. Matyas, and J. Jalife, Circ. Res. **61**, 704 (1987).
[5] H. Sompolinsky, D. Golomb, and D. Kleinfeld, Phys. Rev. A **43**, 6990 (1991).
[6] R. F. Galán, N. Fourcaud-Trochmé, G. B. Ermentrout, and N. Urban, J. Neurosci. **26**, 3646 (2006).
[7] N. Kopell and G. B. Ermentrout, Commun. Pure Appl. Math. **39**, 623 (1986).
[8] K. A. Sigvardt and T. L. Williams, Semin. Neurosci. **4**, 37 (1992).
[9] R. H. Rand, A. H. Cohen, and P. J. Holmes, in *Neural Control of Rhythmic Behavior*, edited by A. H. Cohen (Wiley, New York, 1988).
[10] F. Cruz and C. M. Cortez, Physica A **353**, 258 (2005).
[11] C. Liu, D. R. Weaver, S. H. Strogatz, and S. M. Reppert, Cell **91**, 855 (1997).
[12] M. Cassidy *et al.*, Brain **125**, 1235 (2002).
[13] W. Klimesch, Int. J. Psychophysiol **24**, 61 (1996).
[14] K. Lehnertz, Int. J. Psychophysiol **34**, 45 (1999).
[15] F. Mormann, K. Lehnertz, P. David, and C. E. Elger, Physica D **144**, 358 (2000).
[16] L. F. Abbott and S. B. Nelson, Nat. Neurosci. **3**, 1178 (2000).
[17] E. Shimizu, Y. P. Tang, C. Rampon, and J. Z. Tsien, Science **290**, 1170 (2000).
[18] D. Cumin and C. P. Unsworth, Physica D **226**, 181 (2007).
[19] H. Kori and Y. Kuramoto, Phys. Rev. E **63**, 046214 (2001).
[20] Y. Kuramoto, *Chemical Oscillations, Waves and Turbulence* (Springer-Verlag, Berlin, 1984).
[21] Y. L. Maistrenko, B. Lysyansky, C. Hauptmann, O. Burylko, and P. A. Tass, Phys. Rev. E **75**, 066207 (2007).
[22] D. Pazo, Phys. Rev. E **72**, 046211 (2005).
[23] L. S. Tsimring, N. F. Rulkov, M. L. Larsen, and M. Gabbay, Phys. Rev. Lett. **95**, 014101 (2005).
[24] T. Aoki and T. Aoyagi, Phys. Rev. Lett. **102**, 034101 (2009).
[25] Q. Ren and J. Zhao, Phys. Rev. E **76**, 016207 (2007).
[26] P. Seliger, S. C. Young, and L. S. Tsimring, Phys. Rev. E **65**, 041906 (2002).
[27] Y. K. Takahashi, H. Kori, and N. Masuda, Phys. Rev. E **79**, 051904 (2009).
[28] T. V. P. Bliss and T. Lomo, J. Physiol. (London) **232**, 331 (1973).
[29] T. V. P. Bliss and A. R. Gardener-Medwin, J. Physiology **232**, 357 (1973).
[30] G. Q. Bi and M. M. Poo, J. Neurosci. **18**, 10464 (1998).
[31] G. Q. Bi and M. M. Poo, Annu. Rev. Neurosci. **24**, 139 (2001).
[32] H. Markram *et al.*, Science **275**, 213 (1997).
[33] G. M. Wittenberg and S. S. H. Wang, J. Neurosci. **26**, 6610 (2006).
[34] D. O. Hebb, *The Organization of Behavior* (Wiley, New York, 1949).
[35] B. Hutcheon and Y. Yarom, Trends Neurosci. **23**, 216 (2000).
[36] R. R. Llinas, Science **242**, 1654 (1988).
[37] S. H. Strogatz, Physica D **143**, 1 (2000).
[38] L. Q. English, Eur. J. Phys. **29**, 143 (2008).
[39] J. J. Hopfield, Proc. Natl. Acad. Sci. U.S.A. **79**, 2554 (1982).
[40] J. Hertz, A. Krogh, and R. G. Palmer, *Introduction to the Theory of Neural Computation* (Westview Press, Boulder, CO, 1991).
[41] J. L. McClelland, B. L. McNaughton, and R. C. O'Reilly, Psychol. Rev. **102**, 419 (1995).
[42] G. E. Hinton and D. C. Plaut, Proceedings of the 9th Annual Conference Cognitive Science Society (unpublished).
[43] A. M. Treisman and G. Gelande, Cogn. Psychol. **12**, 97 (1980).
[44] C. Von der Malsburg, Curr. Opin. Neurobiol. **5**, 520 (1995).
[45] A. M. Treisman, Curr. Opin. Neurobiol. **6**, 171 (1996).
[46] C. Von der Malsburg, Neuron **24**, 95 (1999).
[47] A. K. Engel and W. Singer, Trends Cogn. Sci. **5**, 16 (2001).
[48] C. von der Malsburg and J. Buhmann, Biol. Cybern. **67**, 233 (1992).