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STABLE PERIODIC SOLUTIONS TO DISCRETE AND CONTINUUM ARRAYS OF WEAKLY COUPLED NONLINEAR OSCILLATORS*

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This paper is dedicated to the memory of Charles Amick.

Abstract. The existence and stability of periodic solutions to spatially distributed arrays of neural oscillators is analyzed. Conditions are found that guarantee that phase-locked patterns are orbitally stable. These conditions allow the solutions to be extended as some parameter varies. For continuum arrays with some differentiability conditions, it is shown that locking is lost when certain phase gradients become unbounded. Numerical methods are used to show that the results apply to realistic synaptically coupled oscillating neural networks. In particular, it is shown that synchronized solutions cannot generally be expected even if the neurons are identical.

Key words. oscillators, phase locking, stability, neural networks

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1. Introduction. Coupled oscillators arise in many areas of biology, particularly in neural modelling. Oscillatory activity is seen in most cortical tissue; for example, as epileptic activity in the hippocampus [TM] and as coherent high-frequency oscillations in the cat's visual cortex during cognitive tasks [GS]. Spatial patterns of oscillator activity control the motor patterns of many species, such as the swimming central pattern generator of the lamprey [CHR]. All of these oscillatory patterns are generated by neurons that communicate via synapses that can be chemical or electrical. There have been numerous recent efforts aimed at modelling the behavior of these systems of coupled oscillators. These models can be quite abstract [SGK] or based on detailed anatomy [TM].

Very general equations involving large numbers of coupled nonlinear oscillators present an intractable problem for mathematical analysis. However, if the interactions between the separate oscillating units are "weak," then we can apply the method of averaging to reduce the model to a system of phase equations [EK1], [EK3]. "Weak" coupling, while sufficient, is not necessary for averaging to be a valid approach (see [EK3]). In the phase equation approach, each oscillator is represented by a single variable lying on S^1. The interactions between two connected oscillators depend only on the *difference* between the two phases of the oscillators. The dependence on the difference is a consequence of the averaging and is not dependent on the particular form of the coupling. This property is fundamental in obtaining any kind of analytic insight into the properties of the coupled system. The most general form the equations take is

$$\frac{d\theta_j}{dt} = H_j(\theta_1 - \theta_j, \ldots, \theta_N - \theta_j), \qquad j = 1, \ldots, N, \tag{1.1}$$

where H_j is a periodic function of each of its N arguments. A *phase-locked* solution to (1.1) is one for which $d\theta_j/dt = \Omega$, where Ω is a constant, called the ensemble

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frequency. In neural network applications of this theory, H_j has a more specific and simple form,

$$(1.2)\qquad H_j(\theta_1-\theta_j,\dots,\theta_N-\theta_j)=\omega_j+\sum_{k=1}^{N}H_{jk}(\theta_k-\theta_j).$$

Here $H_{jk}(\phi)$ is a periodic function. The parameter ω_j represents inhomogeneities in the network from external inputs or local differences between cells. The coupling functions H_{jk} vanish if there is no synapse from neuron k to neuron j.

Equations (1.1), (1.2) are discrete, but, for large numbers of oscillators, it is often desirable to proceed to some continuum limit. The obvious continuum limit for densely connected networks of the form (1.1), (1.2) is

$$(1.3)\qquad \frac{\partial\theta}{\partial t}=\omega(x)+\int_0^1 H(x,y,\theta(y,t)-\theta(x,t))\,dy.$$

This paper is devoted to finding conditions that guarantee the existence of phase-locked solutions to (1.1), (1.2) and the continuum analogue (1.3). A solution to (1.1), (1.2), or (1.3) is *phase-locked* if there exists a solution of the form $\theta_j(t)\equiv\Omega t+\bar\theta_j$ for (1.1), (1.2) and of the form $\theta(x,t)\equiv\Omega t+\bar\theta(x)$ for (1.3). Ω is a constant, and the barred variables are independent of time. We use a continuation argument from a known phase-locked solution based on the implicit function theorem. The conditions that enable continuation of a branch of solutions via the implicit function theorem also allow us to prove asymptotic stability. Our principal requirement for continuation and stability is that the derivative of H with respect to its third argument is positive for all interactions in the continuum model. For the discrete case, we only require nonnegativity and some connectedness requirements of an associated graph. Under conditions in which we cannot show that the implicit function theorem holds, we use a result of Rabinowitz to prove the existence of a global branch of solutions to (1.3). This theorem allows us to characterize the behavior as phase locking is lost.

Many mathematical papers have addressed the question of phase locking in arrays of coupled nonlinear oscillators, but none to the present degree of generality. Most of the results concern either local coupling (nearest neighbor) [EK1], [KE], [CHR] or "all-to-all" coupling [E1], [Ku], [SM]. There have been a few results on "multiple" (beyond nearest neighbor) coupling, but these have been restricted to either discrete models with restricted coupling [KEZ] or models in a very simple geometry such as the circle [E2]. The following describes some of these prior results. Our methods and results can be applied to most of these situations. Additionally, where our methods apply, they also imply the stability of the locked solutions. What is lost is the precise quantitative description of solutions that comes with decreased generality.

Kiemel [Ki] has studied locking in the case of multiple coupling for systems in which $\omega_j=\omega$, a constant, and

$$(1.4)\qquad H_{jk}(\phi)=a_{jk}h(\phi+2\pi(j-k)/N),$$

where $h(\phi)$ is a fixed periodic function with $h(0)=0$ and $h'(0)>0$. He calls this form of coupling "tuning" since one set of solutions to (1.1)–(1.3) is the travelling wave $\theta_j=\omega+2\pi j/N$. Thus the system is tuned to have a travelling wave solution. Kiemel uses the implicit function theorem for some examples of (1.4) to show how the travelling wave is altered by perturbations away from perfect tuning. One of his most striking results is the sensitivity of nearest neighbor coupling ($a_{jk}=0$ for $k\neq j\pm1$).

In [KEZ], the following example of (1.1), (1.2) is considered:

$$\frac{d\theta_j}{dt} = \omega_j + \sum_{k=-m}^{m} c_k H(\theta_{j+k} - \theta_j), \tag{1.5}$$

for all j such that $1 \leq j \pm m \leq N$. For the remaining values of j, terms such that $j + k \notin [1, N]$ are deleted from the sum. It is shown that, for m *fixed* and $N \to \infty$, phase-locked solutions to (1.5) satisfy

$$\Omega = \chi(x) + f(\Theta_x) + O(1/N), \tag{1.6}$$

where $0 < x < 1$, $\Theta(j/N) = \theta_j$, and $\chi(j/N) = \omega_j$. The function $f(\phi)$ is given by

$$f(\phi) = \sum_{k=-m}^{m} c_k H(k\phi).$$

The solutions to (1.6) are proved to be good approximations to those of (1.5) as long as j is not near 1 or N. The key point to note is that, in proceeding to the continuum limit, the number of neighbors to which an oscillator is connected remain fixed at m. Thus the limiting model is equivalent to nearest neighbor coupling, since interactions remain infinitesimally localized ($m/N \to 0$ as $N \to \infty$.) However, suppose that the number of connections between oscillators scales as N, that is, $m = \sigma N$, where $0 < \sigma \leq 1$. Suppose that, in addition, $c_k = C(k/N)$ for some continuous function $C(x)$. Then, in the limit as $N \to \infty$, (1.6) tends to the continuum equation

$$\Omega = \chi(x) + \int_{-\sigma}^{\sigma} C(y)\mu(x+y)H(\theta(x+y) - \theta(x))dy, \tag{1.7}$$

where $\mu(z) = 1$ if $0 \leq z \leq 1$ and is zero otherwise. More generally, suppose that the coupling functions H_{jk} in (1.2) tend to a function, $H(x, y, \phi)$ as $N \to \infty$. Then, (1.1), (1.2) tend to the continuum limit (1.3). A more direct derivation of (1.3), (1.7) from continuum models of neural networks is provided in the Appendix.

There are few results on continuum phase equations. In [E1] we consider the "all-to-all" case

$$\frac{\partial\theta}{\partial t} = \omega(x) + \int_0^1 \sin(\theta(y,t) - \theta(x,t) + \xi)\, dy. \tag{1.8}$$

Special properties of the sine function along with the symmetry of "all-to-all" coupling enable us to obtain closed-form phase-locked solutions. Some continuum rings are analyzed in [E2]. Amick [Am] studied a problem with distance dependent coupling,

$$\Omega = \int_0^1 \exp(-|x-y|)\sin(\theta(y,t) - \theta(x,t) + \xi)\, dy. \tag{1.9}$$

He showed that there is a branch of phase-locked solutions, $(\theta(x), \Omega, \xi)$ containing $(0, 0, 0)$ for all ξ in some interval around $\xi = 0$. Furthermore, as the endpoints of this interval are approached, $|\theta'(x)| \to \infty$ as $x \to 0^+$. His techniques make special use of the properties of the sine functions and the fact that the exponential kernel $\exp(-|x-y|)$ allows him to convert (1.9) to a differential equation. Phase locking in a continuous space reaction-diffusion equation is considered in [ET] for a special form of kinetics.

Section 2 contains the bulk of the mathematical results for the continuum equations; we prove the existence and stability of phase-locked solutions to (1.3). We allow there to be a parameter in these equations and show how phase locking can be lost for (1.3) as the parameter passes a critical value. The ideas are reminiscent of maximum principle arguments. We apply a theorem of Rabinowitz in situations where we are unable to use the implicit function theorem.

The existence and stability of solutions to the discrete problems (1.1), (1.2) are contained in §3, where some extensions of the results in §2 are proved. In particular, we weaken the connectivity requirements of the oscillators and obtain asymptotic stability of the locked solutions.

Section 4 consists of several numerical experiments showing the forms of solutions to a simple problem of the form derived in the Introduction and in the Appendix. We also numerically demonstrate the theory in §3 that shows how locking is lost. Comparisons are made to unaveraged neural networks that show that the averaging assumptions do not drastically alter the qualitative behavior of the phases.

We directly derive continuum equations from continuum neural networks using formal perturbation theory in the Appendix.

2. Existence theory for continuum models. In this section, we prove the main result on continuum models for coupled nonlinear oscillators. Our approach is to use a homotopy argument to move off a solvable example of (1.3). We initially use the implicit function theorem, which gives both uniqueness and, as a by-product, some stability results. Once we can no longer use the implicit function theorem, we transform the problem to one for which a global bifurcation result of Rabinowitz applies. This allows us to see how phase-locked solutions can break down.

Since we are interested in phase-locked solutions, we consider

$$\Omega = \omega(x, \lambda) + \int_0^1 H(\lambda, x, y, \theta(y) - \theta(x))\, dy. \tag{2.1}$$

Thus we seek phase-locked solutions to (1.3) that are dependent on a parameter λ. We assume that when $\lambda = 0$ there is a solution and we wish to continue this solution by a homotopy off the "trivial" problem. We can consider λ to be a parameter defining, e.g., connectivity, frequency differences, or the shape of the coupling function.

As an example, we continue off the "all-to-all" case

$$\Omega = \lambda\omega(x) + \int_0^1 (1 - \lambda + \lambda k(x, y))H(\theta(y) - \theta(x))\, dy. \tag{2.2a}$$

When $\lambda = 0$, a particular solution is

$$\theta(x) = C, \qquad \Omega = H(0),$$

where C is any constant. Thus a possible solution is the synchronous one (no phase differences) when all oscillators are coupled to all others and there are no inhomogeneities in the medium. The constant solution is not the only solution; there can be many others (e.g., wavelike solutions of the form $\theta(x) = 2\pi kx$ for k an integer).

As another example, consider system (1.9) solved by Amick [Am]

$$\Omega = \int_0^1 e^{-|x-y|} \sin(\theta(y) - \theta(x) + \lambda)\, dy. \tag{2.2b}$$

When $\lambda = 0$, $\theta(x) = C$, $\Omega = 0$ solves (2.2b).

The continuous analogue of tuning provides yet another solvable problem,

$$\Omega = \omega(\lambda, x) + \int_0^1 k(x,y)H(\theta(y) - \theta(x) + 2\pi(x-y)(1-\lambda))\,dy, \tag{2.2c}$$

where $H(0) = 0$ and $\omega(0,x) = \omega_0$. When $\lambda = 0$, the "trivial" solution is $\theta(x) = 2\pi x$ and $\Omega = \omega_0$.

Our final example, below, is another perturbation of "all-to-all" coupling that we discuss in detail in §4:

$$\Omega = \omega(\lambda, x) + \int_0^1 H(\lambda(x-y), \theta(y) - \theta(x))\,dy. \tag{2.2d}$$

Clearly, when $\lambda = 0$, (2.2d) has a solution $\theta(x) = C$ and $\Omega = H(0,0)$.

Our main task is to find easily computable conditions that guarantee that the implicit function theorem is applicable so that the given branch of solutions can be extended.

The first theorem of this section follows.

THEOREM 2.1. *Let $\theta_0(x)$ denote the solution when $\lambda = 0$. Suppose that H is a continuous function of x and y, continuously differentiable with respect to θ and λ. Suppose that $\omega(\lambda, x)$ is continuous and differentiable with respect to λ. Define a functional $G(u, \lambda)$ by*

$$G(\theta, \lambda) = \inf_{x,y} H_\theta(\lambda, x, y, \theta_0(x) - \theta_0(y)).$$

Suppose that $G(\theta, 0) > 0$. Then there is an interval $(0, \hat{\lambda})$ for which there is a locally unique branch of solutions to (2.1), $(\theta_\lambda(x), \Omega_\lambda)$. Furthermore, if $\bar{\lambda}$ is the supremum of $\hat{\lambda}$, then

$$\liminf_{\lambda \to \bar{\lambda}} G(\theta, \lambda) \le 0.$$

If $G(\theta, \lambda) > 0$, then $\theta(x)$ is asymptotically stable.

To prove Theorem 2.1, we recast (2.1) as a map on a Banach space. We can dispense with the parameter Ω by noting that if (2.1) is to hold for all x it must hold for $x = 0$; thus we replace Ω by

$$\omega(\lambda, 0) + \int_0^1 H(\lambda, 0, y, \theta(y) - \theta(0))\,dy.$$

Any equation for the phases that depends only on the *difference* of phases has an infinite family of solutions obtained by adding a C to each $\theta(x)$. This corresponds to the time translation invariance of solutions to an autonomous differential equation. Thus we can redefine the variables $\theta(x)$ by subtracting $\theta(0)$, and so we assume that $\theta(0) = 0$. Consider the space $\mathcal{B} = \{\theta(x) \in C^0[0,1], \theta(0) = 0\}$ and define the map F on $\mathcal{B}$ as follows:

$$\begin{aligned} F(\lambda, \theta(x)) =& \lambda(\omega(\lambda, x) - \omega(\lambda, 0)) \\ &+ \int_0^1 H(\lambda, x, y, \theta(y) - \theta(x)) - H(\lambda, 0, y, \theta(y))\,dy. \end{aligned} \tag{2.3}$$

It is clear that F maps $\mathcal{B}$ into itself and that, if we can solve $F(\lambda, \theta(x)) = 0$, we have solved (2.1). By definition, $F(0, \theta_0(x)) = 0$.

The proof of Theorem 2.1 uses the implicit function theorem to continue the branch. To apply this, we must show that the Frechet derivative of F, $DF(\lambda_0, \theta_0(x))$, is injective and surjective on $\mathcal{B}$. We first need a technical lemma.

LEMMA 2.1. *Suppose that $a(x,y) > 0$ for all $(x,y) \in [0,1]$ and that*

$$(\mathcal{L}\theta)(x) \equiv \int_0^1 a(x,y)(\theta(y) - \theta(x))\, dy - \int_0^1 a(0,y)\theta(y) dy = 0. \tag{2.4}$$

If $\theta(0) = 0$, then $\theta(x) \equiv 0$.

Proof. Let $c = \int_0^1 a(0,y)\theta(y)\, dy$ where $\theta(x)$ is a solution to $\mathcal{L}\theta = 0$. We first prove that $c = 0$. Let x^* be a value of x, where $\theta(x)$ takes a maximum value θ^*. From (2.4), we find that

$$\begin{aligned} c = &\int_0^1 a(x^*,y)\theta(y)\, dy - \theta^* \int_0^1 a(x^*,y)\, dy \\ \leq &\theta^* \int_0^1 a(x^*,y)\, dy - \theta^* \int_0^1 a(x^*,y)\, dy = 0 \end{aligned}$$

since $a(x,y) \geq 0$. The same argument can be applied to the value x_*, where $\theta(x)$ takes a minimum value θ_* to show that $c \geq 0$. Thus $c = 0$. Note that this proof depends only on the nonnegativity of $a(x,y)$, and strict positivity is not necessary.

Since any solution must have $c = 0$, then we must have that

$$\int_0^1 a(x,y)(\theta(y) - \theta(x))\, dy = 0.$$

Again letting x^* be a value at which $\theta(x)$ takes a maximum, we see that

$$\int_0^1 a(x^*,y)(\theta(y) - \theta^*)\, dy = 0,$$

but $\theta(y) - \theta^* \leq 0$ and $a(x^*,y) > 0$, so that the integral can vanish if and only if $\theta(y) - \theta^* \equiv 0$. Since $\theta(0) = 0$, however, this implies that $\theta^* = 0 = \theta(x)$, and we are done.

The next lemma uses the implicit function theorem to obtain local existence and uniqueness around a value of the parameter λ_0 for which a solution is known.

LEMMA 2.2. *Suppose that there is a solution, $F(\lambda_0, \theta_0(x)) = 0$ and that*

$$H_\theta(\lambda_0, x, y, \theta_0(y) - \theta_0(x)) > 0 \quad \textit{for all } x, y.$$

Then there is an open interval of values of λ containing λ_0 for which there is a unique solution to $F(\lambda, \theta(x))$ nearby to $\theta_0(x)$.

Proof. The Frechet derivative of F at $\lambda_0, \theta_0(x)$ is

$$(\mathcal{L}_0\theta)(x) = \int_0^1 a_0(x,y)(\theta(y) - \theta(x))\, dy - \int_0^1 a_0(0,y)\theta(y)\, dy,$$

where

$$a_0(x,y) = H_\theta(\lambda_0, x, y, \theta_0(y) - \theta_0(x)).$$

The implicit function theorem can be used if we show that this operator is injective and surjective. It suffices to do the same for $I - K$, where

$$(K\theta)(x) = \left(\int_0^1 a_0(x,y)\,dy\right)^{-1} \int_0^1 \{a_0(x,y) - a_0(0,y)\}\theta(y)\,dy.$$

K is compact, so it suffices to show that the only solution to $\theta(x) = (K\theta)(x)$ is $\theta(x) = 0$. However, this is assured by Lemma 2.1.

Remark. To show the operator is surjective, it is necessary to rewrite it as a compact perturbation of the identity. Thus we have transformed it from the form of Lemma 2.1.

To study the discrete spectrum of the linearized equation, we will show that all eigenvalues ν must lie in the plane $\Re\nu < 0$.

LEMMA 2.3. *Let ν be such that*

$$\nu u(x) = \int_0^1 a(x,y)(u(y) - u(x))\,dy, \tag{2.5}$$

where $a(x,y) > 0$. Then $\Re\nu \leq 0$, and, if $\Re\nu = 0$, then $\nu = 0$. Furthermore, $\nu = 0$ is a simple eigenvalue corresponding to the constant solution $u(x) = C$.

Proof. We can rewrite the eigenvalue equation as

$$(\nu + \int_0^1 a(x,y)\,dy)u(x) = \int_0^1 a(x,y)u(y)\,dy.$$

Taking absolute values, we obtain the following inequality:

$$\left|\nu + \int_0^1 a(x,y)\,dy\right| \left|u(x)\right| \leq u^* \int_0^1 \left|a(x,y)\right|\,dy,$$

where $u^*$is the maximum value of $\left|u(x)\right|$. Setting $x = x^*$, the value at which u takes its maximum, we obtain

$$\left|\nu + \int_0^1 a(x^*,y)\,dy\right| \leq \int_0^1 \left|a(x^*,y)\right|\,dy.$$

Because $a(x,y) > 0$, this inequality implies that $\Re\nu \leq 0$. Now, letting $v(x) = u(x) - u(0)$, the eigenvalue problem becomes

$$\nu v(x) = \int_0^1 a(x,y)(v(y) - v(x))\,dy - \int_0^1 a(0,y)v(y)\,dy,$$

with $v(0) = 0$. The eigenvalues are the same as those of (2.5) except that zero is no longer an eigenvalue from Lemma 2.1. Thus the zero eigenvalue is simple and corresponds to the constant phase-shift solution $u(x) = C$.

The continuous spectrum is generally more difficult to find, but, for the present problem, we can prove the following lemma.

LEMMA 2.4. *Consider the linear operator*

$$Lu = -b(x)u + \int_0^1 K(x,y)u(y)dy.$$

Suppose that $b(x) > 0$ *and* $K(x,y)$ *is continuous and bounded. Then, if* ν *is in the continuous spectrum,* $\Re\nu < 0$.

Proof. The continuous spectrum is the set of values of ν for which $(L-\nu)u \equiv L_\nu u$ is not invertible. Suppose that ν is not an eigenvalue, so that L_ν is one-to-one. Suppose that ν is chosen so that $b(x)+\nu \neq 0$ for all $x \in [0,1]$. Then, we can divide by $b(x)+\nu$ and obtain a new operator

$$\hat{L}u \equiv u - \frac{1}{\nu + b(x)} \int_0^1 K(x,y)u(y)dy.$$

Since ν is not an eigenvalue of this operator, $\hat{L}$ is one-to-one. Since it is a compact perturbation of the identity and is injective, it is also surjective. Now suppose that $\Re\nu \geq 0$ and ν is in the continuous spectrum and is not an eigenvalue. Since it is in the continuous spectrum, L_ν is not invertible, which implies that $\hat{L}$ is also not invertible. However, this implies that either $\nu + b(x) = 0$ for some x or ν is an eigenvalue. Since ν is not an eigenvalue, we must conclude that $\nu + b(x) = 0$ for some value of x. Since $\Re\nu \geq 0$ and $b(x) > 0$, we obtain the required contradiction.

Proof of Theorem 2.1. Lemma 2.2 allows us to continue the the branch of solutions as long as $H_\theta(\lambda, x, y, \theta(y) - \theta(x)) > 0$. Suppose that we can continue the solution up to, but no further than, $\lambda = \hat{\lambda}$ and suppose that

$$\inf_{x,y} H'(\hat{\theta}(y) - \hat{\theta}(x)) > 0.$$

Then, from Lemma 2.2, we can continue beyond $\hat{\lambda}$, which contradicts our assertion that $\hat{\lambda}$ is the endpoint. Thus as $\lambda \to \hat{\lambda}$ we must have the phase difference between the two oscillators approach a point such that the derivative of H with respect to θ is nonpositive. The discrete spectral results follow from Lemma 2.3. The continuous spectral results follow from Lemma 2.4 after identifying $b(x)$ with $\int_0^1 a_0(x,y)dy$, which is, by hypothesis, positive. By Theorems 11.20 and 11.22 in Smoller [Sm], the fact that the spectrum lies in the left half plane implies that the solution is asymptotically stable.

Remark. There is nothing in the proof of the theorem or the lemmas that requires us to restrict our attention to one-dimensional domains. Any bounded connected region in $\mathbf{R}^n$ is permissible. The crucial part of the theory is the invertibility of the Frechet derivative at a solution. Thus we obtain the following trivial extension of Theorem 2.1.

THEOREM 2.3. *Let* $\mathcal{D}$ *be a bounded simply connected region in* $\mathbf{R}^n$. *Suppose that* $H(\lambda, x, y, \theta(y)-\theta(x))$ *is a continuous scalar function on* $\mathbf{R}\times\mathcal{D}\times\mathcal{D}\times\mathcal{B}$ *and differentiable with respect to* θ *and* λ. *Suppose that* $\omega(\lambda, x)$ *is continuous in* x *and* λ *and differentiable with respect to* λ. *Define* $G(u,\lambda)$ *by*

$$G(\theta, \lambda) = \inf_{x,y} H_\theta(\lambda, x, y, \theta_0(x) - \theta_0(y))$$

Suppose that $G(\theta, 0) > 0$ *Then there is an interval* $(0, \hat{\lambda})$ *for which there is a locally unique branch of phase-locked solutions to* (1.3), $(\theta_\lambda(x), \Omega_\lambda)$. *Furthermore,*

$$\liminf_{\lambda \to \hat{\lambda}} G(\theta, \lambda) \leq 0.$$

If $G(\theta,\lambda) > 0$, *then the solution* $\theta(x)$ *is asymptotically stable.*

Remark. In the Appendix, we show that local diffusion adds terms to (2.1) that have the form (A.12). The presence of these terms does not affect the results of Lemma 2.1 if $\alpha > 0$. Thus it may be that we can also continue the more general equations described by the addition of (A.12). The stability results present a problem unless $\beta \equiv 0$, which is a very nongeneric case.

Suppose that we wish to continue beyond $\hat{\lambda}$. We cannot necessarily continue the solution by the implicit function theorem since we cannot prove invertibility (although it may in fact occur). However, with some additional restrictions, we can apply a more general result for which the spectral results and local uniqueness may possibly be violated. Our proof of Theorem 2.1 requires that $G > 0$, but numerical results indicate that this is not a necessary condition. Indeed, in some of the examples in §4, we construct phase-locked solutions for which $G < 0$. This possibility motivates our next result, where we require differentiability of H with respect to x.

We use a global continuation theorem of Rabinowitz. Let $\mathcal{E} = \mathbf{R} \times \mathcal{B}$, where $\mathcal{B}$ is a Banach space. Let $\mathcal{E}^\mu = \mathbf{R}^\mu \times \mathcal{B}$, where $\mu = \{+,-\}$. A *continuum* $\mathcal{C}$ is a closed connected set in a subset of $\mathcal{E}$. We say a continuum $\mathcal{C}$ meets infinity if $\mathcal{C}$ is not bounded.

THEOREM (Rabinowitz [Ra, Thm. 2.2). *Let $T : \mathcal{E} \mapsto \mathcal{B}$ be a continuous compact operator and suppose that $T(0,u) = 0$ for all $u \in \mathcal{B}$. Let $\mathcal{S}$ denote the solution set to*

$$u = T(\lambda, u).$$

Then $\mathcal{S}$ contains a pair of continua $\mathcal{I}^+$, $\mathcal{I}^-$ lying in $\mathcal{E}^+$, $\mathcal{E}^-$, respectively, and meeting $(0,0)$ and ∞.

To apply this to our problem, differentiate the map $F(\lambda,\theta)$ defined by (2.3) with respect to x and rearrange to obtain

$$\left(\int_0^1 H_\theta(\lambda,x,y,\theta(y)-\theta(x))\,dy\right)\theta_x(x) = \int_0^1 H_x(\lambda,x,y,\theta(y)-\theta(x))\,dy + \omega_x(\lambda,x). \tag{2.6}$$

Define

$$\eta(\lambda,x) \equiv \int_0^1 H_\theta(\lambda,x,y,\theta(y)-\theta(x))\,dy. \tag{2.7}$$

As long as $\eta > 0$,we can divide and integrate once with respect to x to obtain

$$\theta(x) = \int_0^x \left[\omega_s(\lambda,s) + \int_0^1 H_s(\lambda,s,y,\theta(y)-\theta(s))\,dy\right]/\eta(\lambda,s)\,ds \equiv T(\lambda,\theta(x)). \tag{2.8}$$

$T(\lambda,\theta(x))$ is a continuous, compact operator as long as $\eta(\lambda,x) > 0$. We need one additional assumption, namely,

$$T(0,\theta) = 0 \quad \text{for all } \theta \in \mathcal{B}. \tag{2.9}$$

Examples (2.2a) and (2.2d) satisfy (2.9). Rabinowitz's theorem implies that a global branch of solutions exists for λ positive and negative. Either the trivial branch can be continued for all λ or $\theta(\lambda,x)$ becomes unbounded in some way.

To see what might happen to this branch, return to (2.6). For λ sufficiently small, $\eta(\lambda,x) > 0$, since the integrand is strictly positive. However, as λ increases, there may come a point for which H_θ goes through zero and becomes negative. As λ continues to increase, the phases split farther and farther apart until, for some value of x, say $\tilde{x}$, there is a value of λ, say $\tilde{\lambda}$, such that

$$\lim_{x \to \tilde{x}} \eta(\tilde{\lambda}, x) \to 0.$$

If the right-hand side of (2.6) does not vanish, then the derivative of $\theta(x)$ must become unbounded as $x \to \tilde{x}$ at $\lambda = \tilde{\lambda}$. Thus we have the following extension of Theorem 2.1.

THEOREM 2.3. *Suppose that $H(\lambda, x, y, \phi)$ and $\omega(\lambda, x)$ are continuously differentiable with respect to x and ϕ. Suppose that $\omega_x(0, x) = 0$ and $H_x(0, x, y, \phi) = 0$. Then a solution branch exists for all λ in a possibly infinite interval, $[0, \lambda_{\max})$ as long as $\eta(\lambda, x) > 0$. If $\lambda_{\max} < \infty$ and*

$$\int_0^1 H_x(\lambda_{\max}, x, y, \theta(y) - \theta(x))\, dy + \omega_x(\lambda_{\max}, x) \equiv R(\theta, x, \lambda)$$

has a fixed sign for all x, then there is a value of x, say $x_{\max}$ such that

$$\lim_{x \to x_{\max}} |\theta_x(\lambda_{\max}, x)| \to \infty.$$

Remark. The class of problems for which we can guarantee that R is of fixed sign include the all-to-all coupling case with a strictly monotone variation in frequency. Amick shows that $\theta_x(\lambda, x)$ tends to ∞ as $x \to 0$ at a critical value of λ for problem (2.2b). We have no proof that these solutions are stable, although the numerical results in the next section seem to show that stability exists for all values of λ for which existence holds.

3. Existence and asymptotic stability for discrete models. In this section, we prove the existence and stability of locked solutions to equations of the form (1.1), (1.2). The methods parallel those of §2, but, due to the discrete nature of the problem, we cannot use the Rabinowitz theorem. However, we can broaden the hypotheses for which the implicit function theorem holds and also obtain asymptotic stability.

Consider the following discrete analogue of (2.1):

$$\Omega = \omega(\lambda, j) + \sum_{k=1}^{N} H(\lambda, j, k, \theta_k - \theta_j), \qquad j = 1, \ldots, N. \tag{3.1}$$

Suppose that for $\lambda = \lambda_0$ we have a solution to (3.1), θ_j^0. Define a_{jk} by

$$a_{jk} = H_\theta(\lambda_0, j, k, \theta_k^0 - \theta_j^0). \tag{3.2}$$

The analogue of Theorem 2.1 holds for the discrete equations (3.1) as long as $a_{jk} > 0$. However, this is much too strong an assumption; it is violated, for example, by a chain of nearest neighbor oscillators. Thus we would like to let $a_{jk} = 0$ for some pairs j, k. This arises in cases for which two oscillators are not directly connected but rather are coupled indirectly through other units.

We will generalize Lemma 2.1 to extend to this case, and the analogue of Theorem 2.1 will be proved. Rather than requiring direct connections between oscillators, we allow oscillators to connect to only a few other ones. We must first make precise the meaning of indirect interactions. Since the proof of the crucial lemma depends on the positivity of all connections impinging on an oscillator, we generalize this concept. Suppose that oscillator i influences oscillator j, which in turn influences oscillator k. Then we say that oscillator i *indirectly* influences k. This says that $a_{ij}a_{jk} \neq 0$. More generally, we define the notion of indirect influence as follows.

DEFINITION. Oscillator k *indirectly influences* oscillator j if there exists a finite sequence $i_1, \ldots, i_n$ such that $a_{i_1 k} a_{i_2 i_1} \cdots a_{j i_n} \neq 0$.

This definition has a nice graph theoretic interpretation. Assign each oscillator a node and directed connections between the nodes j and k if oscillator j receives a connection from k. The direction of the connection is from j to k. If it is possible to get from any one node to every other node (i.e., each oscillator is indirectly influenced by every other oscillator), then we say that the network is *completely indirectly connected.*

The main result of this section is the following theorem.

THEOREM 3.1. *Suppose that* (3.1) *has a solution* θ_j^0 *for* $\lambda = 0$ *and suppose that* $a_{jk} = H_\theta(\lambda, j, k, \theta_k^0 - \theta_j^0) \geq 0$. *Suppose that the matrix* a_{jk} *is completely indirectly connected. Then, there is a unique branch of solutions containing* θ_j^0 *for all* $\lambda \in (0, \hat{\lambda})$. *If* $a_{jk} \geq 0$, *then this solution is orbitally asymptotically stable.*

Remark. We have relaxed the strict positivity assumptions of Theorem 2.1 and also obtained asymptotic stability. Otherwise, the theorem is identical to its continuum analogue.

The proof of this theorem parallels that of the continuum case, but, for completeness and ease of reading, we will independently present most of the proof. As in §2, the crucial result is a lemma proving the linearized equations are invertible. Thus we must prove the following lemma.

LEMMA 3.1. *Consider the following linear equation:*

$$0 = \sum_{k=1}^{N} a_{jk}(\theta_k - \theta_j) - \sum_{k=1}^{N} a_{1k}\theta_k, \tag{3.3}$$

with $\theta_1 = 0$. *Suppose that the* $a_{jk} \geq 0$ *and suppose that the graph of* (a_{jk}) *is completely indirectly connected. Then the only solution is* $\theta_k = 0$ *for all* k.

Proof. As in Lemma 3.1, we first prove that

$$S_1 \equiv \sum_{k=1}^{N} a_{1k}\theta_k = 0.$$

The proof is completely analogous. Let j^* denote the value of j for which θ_j is maximal. Then, (3.3) implies that

$$S_1 = \sum_{k=1}^{N} a_{j^*k}(\theta_k - \theta_{j^*}) \leq 0$$

since $a_{j^*k} \geq 0$. Letting j_* denote the value of j for which θ_j is minimal implies that $S_1 \geq 0$. Thus $S_1 = 0$.

We must now prove that

$$0 = \sum_{k=1}^{N} a_{jk}(\theta_k - \theta_j) \tag{3.4}$$

and

$$\theta_1 = 0$$

imply that $\theta_k = 0$. Let j^* be an index corresponding to a maximum of the solution $(\theta_1, \ldots, \theta_N)$, say $\theta_{j^*} = u^*$. If $a_{j^*k} > 0$ for all k, we are done, since this implies that all of the θ_k must be equal, otherwise the sum in (3.4) would be positive. For at least one value of k, we must have $a_{j^*k} > 0$, otherwise the node j^* would be disconnected from the rest of the network. For each k that satisfies $a_{j^*k} > 0$, we must have $\theta_k = \theta^*$, otherwise the sum in (3.4) would be positive. Let l be some arbitrary index and let $i_1, \ldots, i_n$ be a sequence of indices such that $a_{i_1 l} a_{i_2 i_1} \cdots a_{j^* i_n} > 0$. Then $\theta_{i_n} = \theta^*$, since θ_{i_n} is directly connected to θ_{j^*}. Continuing in this manner, we have $\theta_{i_{n-1}} = \theta_{i_n} = u^*$, and so on. Thus $\theta_l = \theta^*$. However, $\theta_1 = 0$ by definition, so this implies that all $\theta_k = 0$.

LEMMA 3.2. *Consider the following eigenvalue equation:*

$$\nu\theta_j = \sum_{k=1}^{N} a_{jk}(\theta_k - \theta_j). \tag{3.5}$$

Suppose that $a_{jk} \geq 0$ and that the matrix (a_{jk}) is completely indirectly connected. Then $\Re\nu \leq 0$ and if $\Re\nu = 0$, then $\nu = 0$. Furthermore, $\nu = 0$ is a simple eigenvalue corresponding to the constant solution $\theta_k = C$

Proof. Let $y_1 = \theta_1$ and $y_j = \theta_j - \theta_1$. Then (3.5) becomes

$$\nu y_1 = \sum_{k=2}^{N} a_{1k} y_k \tag{3.6a}$$

and

$$\nu y_j = -a_{j1} y_j + \sum_{k=2}^{N} a_{jk}(y_k - y_j), \tag{3.6b}$$

for $j = 2, \ldots, N$. Thus the eigenvalues are the simple zero from (3.6a) and the eigenvalues of the $(N-1) \times (N-1)$ matrix defined by (3.6b). An application of the Gersgorin circle theorem to (3.6b) shows that the eigenvalues are contained in the union of the disks defined by

$$\left| \nu + \sum_{k=1}^{N} a_{jk} \right| \leq \sum_{k=2}^{N} |a_{jk}| \tag{3.7}$$

for $j = 1, \ldots, N$. Since $a_{jk} \geq 0$, we can remove the absolute value signs in the right-hand sum. All of these lie in the left half plane and intersect at $\nu = 0$. Thus there is a possible zero eigenvalue. However, writing (3.6b) as

$$\nu y_j = \sum_{k=1}^{N} a_{jk}(y_k - y_j)$$

and setting $y_1 = 0$, we see from Lemma 3.1 that this implies all $y_j = 0$. Thus the only zero eigenvalue is the simple one corresponding to $\theta_k = C$.

Proof of Theorem 3.1. As we did in §2, we rewrite (3.1) as

$$0 = \omega(\lambda, j) - \omega(\lambda, 1) + \sum_{k=1}^{N} H(\lambda, j, k, \theta_k - \theta_j) - H(\lambda, 1, k, \theta_k - \theta_1) \tag{3.8}$$

for $j = 1, \ldots, N$. We seek solutions in the finite-dimensional subspace defined by setting $\theta_1 = 0$. The linearization of (3.8) is precisely the equation in Lemma 3.1. The assumptions on the connectivity and nonnegativity of the coefficients a_{jk} guarantee that the linearized equations have no nontrivial solutions, so that the implicit function theorem implies that there is a unique branch of solutions in some open interval containing $\lambda = 0$. In particular, there is a $\hat{\lambda} > 0$ such that there is a unique branch of solutions for $\lambda \in (0, \hat{\lambda})$. The asymptotic stability follows from Lemma 3.2.

Typically, if $a_{jk} = 0$, then it vanishes identically for all phase-shifts and values of the parameter λ, since this means that there is no physical connection between the two oscillators. If a_{jk} is positive and then tends to zero as the λ changes, loss of stability or existence of solutions can follow. For the case of nearest neighbor coupling in a one-dimensional chain, if $a_{j,j\pm 1}$ vanishes for some index j, then locking is lost.

4. Numerical and analytic examples.

4.1. Discrete systems. Consider a chain of length $N+1$ of the following form:

$$\begin{aligned} \frac{d\theta_j}{dt} =& \lambda j + h_1(\theta_{j+1} - \theta_j) + h_1(\theta_{j-1} - \theta_j) \\ &+ h_2(\theta_{j+2} - \theta_j) + h_2(\theta_{j-2} - \theta_j), \end{aligned} \tag{4.1}$$

where the appropriate terms are deleted at $j = 0, 1, N-1, N$, and $h_j(\phi) = c_j \sin j\phi$. If $c_1 > 0$ or $c_2 > 0$, then, when $\lambda = 0$ the synchronous solution, $\theta_j = 0$ is a stable solution. As λ increases, the phases spread out until a critical value of λ is reached and locking is lost. When $c_2 = 0$, we can explicitly calculate the value of the phaselags between nearest neighbors (see [EK1]), as follows:

$$\sin(\theta_{j+1} - \theta_j) = \lambda j(N + 1 - j)/2. \tag{4.2}$$

It is clear that locking is lost when the right-hand side exceeds 1 for some value of j. The stability results in §3 imply that solutions to (4.2) for which $\cos(\theta_{j+1} - \theta_j) > 0$ are stable. At the critical value of $\lambda = N(N+1)/8$, the local phase-difference of the center oscillators ($j = j^*$) is $\pi/2$, which implies that $a_{j^*,j^*+1} = c_1 \cos(\theta_{j^*+1} - \theta_{j^*}) = 0$. The two halves of the chain are disconnected, so that the matrix from §3, a_{jk}, is no longer indirectly connected. For any λ greater than the critical value, no phase-locked solutions exist. Stable phase-locked solutions exist up to that value of λ and cease to exist for larger values. Thus, for nearest neighbor coupling, our existence theory is as strong as possible.

For nonnearest neighbor coupling, $c_2 > 0$. We must solve (4.1) numerically in this case. We find that, as λ increases, locking is lost when linearized system obtains a zero eigenvalue. This occurs for a value of λ exceeding that for which one of the a_{jk} becomes negative. In particular, when $N = 10, c_1 = c_2 = 1$, and $\lambda \approx .1835$, the linearized system has a zero eigenvalue. However, the phaseshift between the fourth and the sixth oscillators exceeds $\pi/2$, and so $a_{46} = a_{64} < 0$. In other words, our method and theorems do not allow us to continue beyond the point where some value of a_{jk} becomes negative, but, in fact, the solutions do exist beyond this point. (For the present problem, the value of λ for which a_{46} vanishes is $\lambda \approx .18$, so that we have not missed a large interval of λ.)

Another discrete chain problem that has recently been analyzed in detail (Ermentrout and Kopell [EK4]) has the form

$$\frac{d\theta_j}{dt} = \sin(\theta_{j+1} - \theta_j) + \sin(\theta_{j-1} - \theta_j), \qquad j = 1, \ldots, 2m, \quad j \neq m, m+1. \tag{4.3}$$

For $j = m$, a term of the form $-\lambda \sin(\theta_{2m} - \theta_m)$ is added, and, for $j = m+1$, $-\lambda \sin(\theta_1 - \theta_{m+1})$ is added. This represents a chain of nearest neighbor coupled oscillators with connections bewteen the ends and the middle. Consider the existence of the trivial solution $\theta_j = 0$. For $\lambda = 0$, $a_{jk} \geq 0$, so that the results of §3 imply that there is a small interval $[0, \lambda)$ for which this is a locally unique solution. When $\lambda \equiv 0$, it also a stable solution. However, for any $\lambda > 0$, the terms $a_{m+1,1}$ and $a_{m,2m}$ are both negative, so that neither stability nor local uniqueness is guaranteed. For (4.3) it is easy to show that a bifurcation occurs at $\lambda = O(1/m)$, and a new small amplitude branch arises from the synchronized solution. Since our present results are independent of the length of the chain, it is clear that, for arbitrarily small $\lambda > 0$, we can find a chain length $N = 2m$ such that the synchronized state is unstable and such that there are other small phase-locked solutions nearby. Our stability results are as good as possible given their generality.

The reader should note that the results in §3 imply only local uniqueness and stability; global uniqueness and stability of phase-locked solutions is very difficult to prove. For example, consider a ring of oscillators coupled with nearest neighbor coupling

$$\Omega = \omega + h(\theta_{j+1} - \theta_j) + h(\theta_{j-1} - \theta_j), \qquad j = 0, \ldots, N-1,$$

where $h'(0) > 0$ and $j \pm 1$ is taken modulo N. The synchronized state $\theta_j = 0$, $\Omega = 2h(0) + \omega$ is stable and locally unique. However, if N is large enough, the solution $\theta_j = 2\pi j/N$, $\Omega = \omega + h(2\pi/N) + h(-2\pi/N)$ is also stable.

We have recently (Ermentrout and Paulett [EP]) proved the existence of nonzero phase-locked solutions to the two-dimensional array of diffusively coupled oscillators

$$\theta'_{jk} = \omega + \sum_{n,m} \sin(\theta_{nm} - \theta_{jk} + \phi) - \sin(\phi),$$

when $\phi = 0, n = j \pm 1$, and $m = k \pm 1$. Our proof also shows that the lags between neighbors are always less than $\pi/2$. Thus Theorem 3.1 enables us to conclude that these are asymptotically stable solutions and that there is a branch of solutions containing $\phi = 0$.

4.2. Continuum chains. We will show some examples of the behavior of continuous chains of oscillators as existence is lost. The first problem we consider is exactly solvable, so that we can compare the results to those of the theorems in §2. Consider the following:

$$\frac{\partial \theta}{\partial t} = \lambda \omega(x) + \int_0^1 \sin(\theta(y,t) - \theta(x,t))\, dy. \tag{4.4}$$

We suppose that the mean value of $\omega(x)$ is zero. Then, it is easy to show that

$$\sin(\theta(x)) = \lambda \omega(x)/I \equiv \mu(x), \tag{4.5}$$

where

$$I = \int_0^1 \cos(\theta(x))\,dx = \int_0^1 \sqrt{1-(\lambda\omega(x)/I)^2}\,dx.$$

This latter equation is just an implicitly defined nonlinear scalar equation for the quantity I. Note that I plays the role of $\eta(\lambda, x)$ defined by (3.7). Let $\bar{x}$ be the value of x at which $|\omega(x)|$ is maximal. Since $I < 1$, this means that there is a value of λ such that $|\mu(\bar{x})| = 1$. Since $\theta'(x) = 1/\sqrt{(1-\mu(x)^2)}$, we see immediately that the derivative of θ becomes unbounded as $x \to \bar{x}$ at the critical value of λ. If we numerically solve (4.4) for λ beyond criticality, then phase-locked solutions are not found; rather, the medium splits into regimes that drift apart in phase and have different average frequencies. The reader should note that the continuum model (4.4) is not like the large N limit of discrete oscillators with random frequencies analyzed by Kuramoto and others [Ku], [E1], [SM]. Here, we implicitly assume a one-dimensional geometry along which the frequency varies in a continuous manner.

Next, we show that it is impossible to obtain phase locking in a unidirectional all-to-all synaptically coupled system

$$\frac{\partial\theta}{\partial t} = \int_0^x F(\theta(y,t)-\theta(x,t))\,dy. \tag{4.6}$$

Here, F is any continuously differentiable periodic function, with $F(0) \neq 0$. This model is like the "all-to-all" case, but oscillators receive inputs only from those below them. Phase-locked solutions must satisfy

$$\Omega = \int_0^x F(\theta(y)-\theta(x))\,dy. \tag{4.7}$$

Setting $x = 0$ shows that $\Omega = 0$. Differentiate (4.7) with respect to x, to obtain

$$0 = F(0) + \int_0^x F'(\theta(y)-\theta(x))\,dy.$$

Finally, set $x = 0$, which implies that $F(0) = 0$, a contradiction. This is not surprising, for the points that are close to $x = 1$ receive inputs from many more oscillators than do those near $x = 0$. Since synaptic inputs effectively raise or lower the local frequency, the oscillators have drastically different levels of excitation.

A perturbation from the "all-to-all" provides another example where the phase gradient tends to infinity as the homotopy parameter increases. Consider the following model:

$$\frac{\partial\theta}{\partial t} = \int_0^1 \exp(-\lambda|x-y|)\sin(\theta(y,t)-\theta(x,t)+\phi)\,dy. \tag{4.8}$$

When $\lambda = 0$, this system has all-to-all coupling, and, as long as $|\phi| < \pi/2$, the synchronized solution $\theta(x,t) = \sin(\phi)t$ is asymptotically stable. Amick [Am] considers the existence of solutions for this problem when $\lambda = 1$ and ϕ is allowed to vary. Here, we are interested in the behavior as λ increases away from zero. For small λ, we can use the implicit function theorem to obtain the following perturbed solution:

$$\theta(x,t) = -\lambda\big(t\sin(\phi)/3 + \tan(\phi)(x^2-x)\big).$$

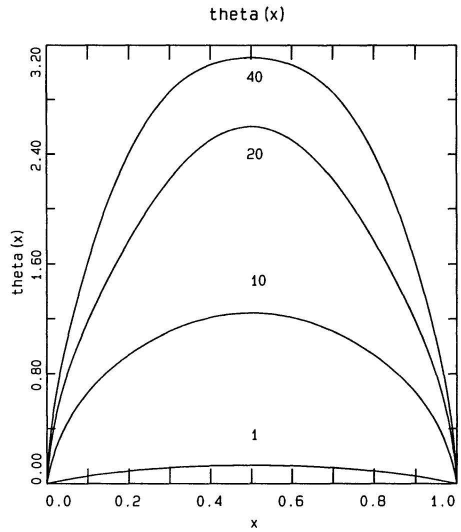

FIG. 1. *The numerical solution to (4.8) for $\phi = .5$ and various values of λ. The steady solution was found by integrating a discretized version of the evolution equation until a steady state was reached.*

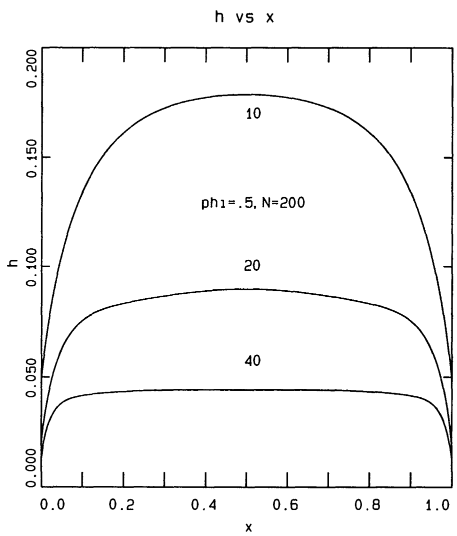

FIG. 2. *The function $\eta(\lambda, x)$ for various values of λ corresponding to the parameters used in Fig.* 1.

Although this is only an approximate solution, it has many of the properties seen in the numerically computed solution (see Fig. 1). The derivative of θ is maximal at $x = 0, 1$. This derivative increases with ϕ and λ increasing. Indeed, as $\phi \to \pi/2$, the solution is not defined as could be guessed, since the implicit function theorem no longer can be applied. In Fig. 1, we show the behavior of the solution to (4.8) on a numerical grid of 200 points for $\phi = .5$ and various values of λ. Clearly, the phases are parabolic, and, as λ increases, the derivative at $x = 0, 1$ becomes increasingly sharp.

In Fig. 2, we show the behavior of $\eta(\lambda, x)$

$$\eta(\lambda, x) = \int_0^1 \exp(-\lambda|x-y|)\cos(\theta(y,t) - \theta(x,t) + \phi)\, dy.$$

Recall that, to apply the Rabinowitz theorem, we require that $\eta(\lambda, x) > 0$ for all

x. It is clear from Fig. 2 that η is decreasing in magnitude as λ increases. We find that, for $\lambda \geq 60$, no locked solutions exist and the oscillators behave independently, slowly drifting apart in phase. We also note that, for $\lambda = 40$, the lag between the middle oscillators and the end oscillators is much greater than $\pi/2 - \phi$, which is the value of the turning point of the periodic function $\sin(z + \phi)$. Thus we have obtained solutions well beyond where we could use the implicit function theorem. As λ increases, the coupling strength between oscillators decreases. Although there are no intrinsic inhomogeneities in the medium (i.e., the frequency $\omega(x) \equiv 0$), the boundary effects play an important role. Oscillators at the ends receive inputs from half as many oscillators as are received by the middle oscillators. The result of an input is to increases the effective local frequency, since $\phi > 0$. Thus, even though this effect becomes increasingly weaker as λ increases, it is sufficient to overcome the weakened coupling, and so locking is lost. If $\phi = 0$, then the synchronous solution is always a stable solution for any value of $\lambda \geq 0$. The loss of locking is a consequence of coupling that does not vanish when the oscillators are in identical states (called *synaptic coupling*) and the intrinsic inhomogeneity due to boundary effects.

4.3. Morris–Lecar model. The results we described in this paper relate to the behavior of systems of "phase" equations that arise from the weak coupling of "real" models. In particular, the behavior of the phase-lags varies in space in a "parabolic" fashion and depends on the space constant of the coupling. We consider the numerical solution to the Morris–Lecar equations (described in reduced form in [RE]), which represent a typical membrane model, below:

$$\begin{aligned}\frac{\partial V}{\partial t} =& I_{\text{pert}}(x) + g_K w(V_K - V(x)) + g_L(V_L - V(x)) \\ &+ [g_{Ca} m_\infty(V(x)) + \int_0^1 c(x,y) m_\infty(V(y)) dy](V_{Ca} - V(x)),\end{aligned}$$

$$\frac{\partial w}{\partial t} = (n_\infty(V(x) - w(x)))/\tau(V(x)),$$

where $c(x, y) = \alpha \exp(-\lambda|x - y|)$ and $I_{\text{pert}} = I_0 + \gamma x$. The functions $m_\infty(V), n_\infty(V)$, and $\tau(V)$ are given in the legend of Fig. 3. We will study the phase-locked solutions of this model as a function of λ, the space constant for coupling, and γ, the current gradient. To make the comparison to our above numerical results, we define the phase in the following manner. We consider the time $t(x)$ at which the voltage $V(x, t)$ crosses a fixed value $\bar{V}$. This time is subtracted from $t(0)$, divided by a period, and multiplied by 2π to obtain a relative phase of firing. Thus $t_R(x) = 2\pi(t(x) - t(0))/T$. If $t_R(x) > \pi$, then 2π is subtracted, indicating that the cell at x precedes that at 0. In Fig. 3, we depict the relative firing times for three values of λ. Note that the cells closest to the edge fire the slowest, as they receive the smallest amount of excitatory synaptic input, which has the effect (in this particular case) of increasing the frequency. In other parameter regimes, excitatory input *slows* the oscillators, and we would expect the parabolas to be inverted. For example, the model in Fig. 1 has the property that excitatory input slows it, and so the parabola is concave down. In Fig. 4, the space constant λ is fixed, and there is a gradient in the current. Higher currents result in faster oscillation, so that the oscillators near $x = 1$ lead those near $x = 0$.

It is not surprising that the firing times and phases are similar for $\alpha = .25$, for then averaging may be valid. Indeed, $\alpha = .25$ means that the total synaptic volley is only a quarter of the local conductance strength $g_{Ca} = 1.0$. The next numerical

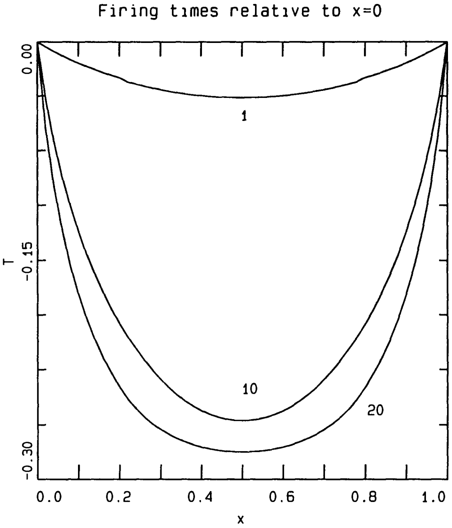

FIG. 3. *The relative firing times in the Morris-Lecar model on the interval* $(0,1)$. $m_\infty(V) = .5(1+\tanh((V-V_1)/V_2))$, $n_\infty(V) = .5(1+\tanh((V-V_2)/V_3))$, *and* $1/\tau(V) = \phi\cosh((V-V_3)/V_4)$. *For the figure, the spatial grid is* 50 *points and an explicit Euler method is used to solve the dynamic equations. Parameters are* $\alpha = .25, I_0 = .2, \gamma = 0, g_{Ca} = 1, g_K = 2, g_L = .5, V_K = -.7, V_{Ca} = 1, V_L = -.5, \phi = .25, v_1 = -.01, v_2 = .15, v_3 = 0.0, v_4 = .08$. *The values for* λ *are shown with each curve.*

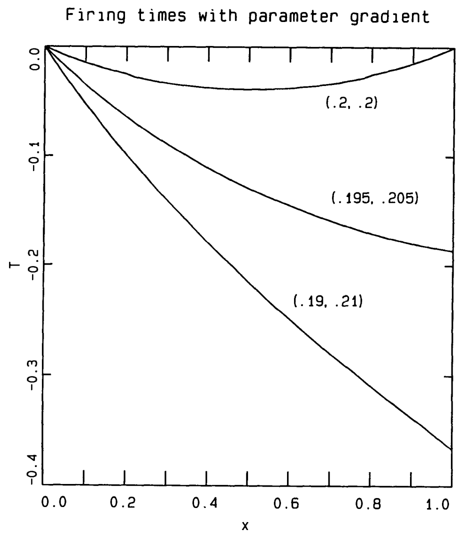

FIG. 4. *Relative firing times with a linear gradient of inhomogeneities. All parameters are the same as in Fig.* 3, *with* $\lambda = 1.0$. *The current gradient is linear with maxima and minima given in parentheses. For larger parameter gradients, locking is lost and phase-drift or frequency plateaus occur.*

experiment shows that, as α increases, the behavior is very similar to the case in which averaging might apply. In Fig. 5, we show the firing times for three different coupling strengths. When $\alpha = 1$, the conductance is of the same order of magnitude as the local conductance g_{Ca}. The increase in coupling strength appears to lead the cells toward greater synchrony, and the relative firing times are compressed. If the coupling strength is increased too much, then it is possible to completely destroy any oscillations, and the phenomenon of phase-death occurs [EK2].

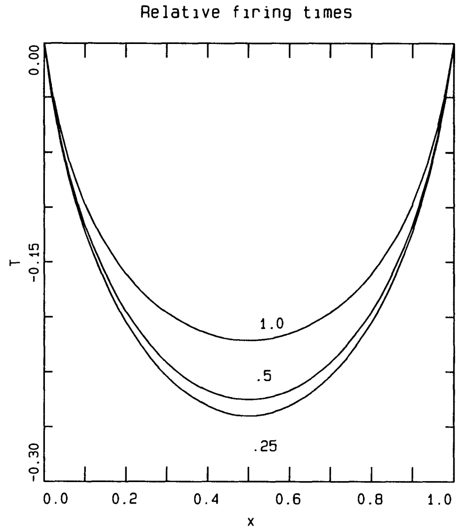

FIG. 5 *Relative firing times as a function of coupling strength, α for fixed current, $I_0 = .2$ and space constant $\lambda = 10$. Values of α appear next to each curve. All other parameters as in Fig.* 3.

Appendix. Direct derivation of the model equations. In this appendix, we will consider two types of neural networks: one is based on *synaptic* coupling of ionic models, and the other is based on coupling Wilson–Cowan-type two-layer neural networks.

A. Ionic models. Let $(V, \vec{w})$ denote the membrane potential V and the vector of recovery variables $\vec{w}$ for a membrane oscillator. For example, in the Hodgkin–Huxley equations, $\vec{w}$ is three-dimensional and consists of m, n, and h. We assume that each "cell" in our network is identical to all other cells up to perturbations of size ϵ, where ϵ is a small parameter related to the strength of coupling between oscillators. In the absence of coupling, the neural oscillators obey the following differential equations:

$$C\frac{dV}{dt} + I_{\text{ionic}}(V, \vec{w}) = I_0, \tag{A1}$$

$$\frac{d\vec{w}}{dt} = \vec{m}(V, \vec{w}). \tag{A2}$$

Here, $I_{\text{ionic}}(V, \vec{w})$ is the nonlinear function that contains all of the gating and ionic currents for the membrane, C is the membrane capacitance, and I_0 is a constant biasing current applied so that (A1), (A2) spontaneously oscillate. For models of this type, external synaptic and input currents are added to the biasing current to couple the neurons. The lth component of the vector function $\vec{w}$ is generally dependent only on the membrane potential and the component itself; typically, we have

$$\frac{dw_l}{dt} = (w_{l\infty}(V) - w_l)/\tau_l(V).$$

We will assume that (A1), (A2) have as a solution an orbitally stable periodic solution

$$(V_0(t+T), \vec{w}_0(t+T)) = (V_0(t), \vec{w}_0(t)) \tag{A3}$$

with period T. Before continuing with the formal analysis, we need some additional definitions and notation. Let $\mathcal{L}(t)$ denote the linear operator obtained from (A1), (A2) by linearizing about the solution (A3). This is a differential operator with a one-dimensional nullspace spanned by the derivative $(V_0'(t), \vec{w}_0'(t))$. The adjoint operator $\mathcal{L}^*(t)$ (obtained by transposing and changing the sign of the Jacobian matrix of (A1), (A2)) also has a one-dimensional nullspace spanned by $(V^*(t), \vec{w}^*(t))$ This adjoint eigenfunction can be be normalized so that

$$\text{(A4)} \qquad \frac{1}{T}\int_0^T \big(V_0'(t)V^*(t) + \vec{w}_0'(t)\cdot\vec{w}^*(t)\big)dt = 1.$$

We now suppose that the membrane oscillators are distributed in a one-dimensional layer in a spatial domain denoted by Σ. Let x parametrize the spatial position of each point. Without loss of generality, we can assume that Σ is the interval $[0,1]$. Thus (A1), (A2) will become integral equations once the summed inputs from all other cells are added. We add a space-dependent term $I[V,x]$ to (A1), which is itself composed of the sum of two components

$$\text{(A5)} \qquad I[V,x] = \epsilon\big(I_{\text{syn}}[V(x),V(y),x] + I_{\text{pert}}(V(x),\vec{w}(x),x)\big).$$

Here, I_{pert} depends only on the local environment, I_{syn} depends on the local potential as well as interactions from all other cells in the layer, and ϵ is a small parameter. The effect of I_{pert} is to induce local differences in the intrinsic frequency of the membrane oscillations, while the role of I_{syn} is to coupled these oscillators together. We need not be specific about the definition of I_{syn}, but we will derive the forthcoming equations with a specific form in mind, namely,

$$\text{(A6)} \qquad I_{\text{syn}}[V(x),V(y),x] = \int_0^1 c(x,y)g(V(y))\big(V_{\text{syn}} - V(x)\big)\,dy.$$

Here $c(x,y)$ is the strength of coupling from a cell at y to that at x, V_{syn} is the reversal potential of the synapse, and $g(V)$ is a nonlinear positive monotone conductance function that depends on the presynaptic membrane potential. We suppose ϵ be small and perform a formal perturbation analysis on (A1), (A2), (A5), and (A6). To lowest order in ϵ, the solution to (A1), (A2), (A5), and (A6) is

$$\text{(A7)} \qquad (V(x,t),\vec{w}(x,t)) = (V_0(t+\theta(x,\tau)), \vec{w}_0(t+\theta(x,\tau))),$$

where $\theta(x,\tau)$ is a phase-shift that depends on x and the slow time $\tau \equiv \epsilon t$. The next term in the perturbation has the following form:

$$\text{(A8)} \qquad \mathcal{L}(t)\mathbf{z}(t) = f(t),$$

where $\mathbf{z}(t)$ is the deviation from the periodic solution and $f(t)$ contains all of the coupling and inhomogeneities. Since $\mathcal{L}(t)$ has a one-dimensional nullspace in the space of T-periodic functions, (A8) will not have a T-periodic solution unless $f(t)$ is orthogonal to the nullspace of the adjoint $L^*(t)$. Formal application of this solvability requirement yields an equation for the phases $\theta(x,\tau)$. They must satisfy

$$\text{(A9)} \qquad \frac{\partial\theta}{\partial\tau} = \omega(x) + \int_0^1 c(x,y)h(\theta(y,\tau)-\theta(x,\tau))\,dy,$$

where

$$\text{(A10)} \qquad \omega(x) = \frac{1}{T}\int_0^T V^*(t)I_{\text{pert}}(V_0(t),\vec{w}_0(t),x)\,dt$$

and

$$h(\phi) = \frac{1}{T}\int_0^T V^*(t)(V_{\rm syn} - V_0(t))g(V_0(t+\phi))\,dt. \tag{A11}$$

Note that the coupling coefficients $c(x, y)$ remain unchanged by this perturbation because the interactions between the individual cells only involve the membrane potentials. If there are other interactions that are spatially distributed, (A9) is more complicated.

Remark on local interactions. In membrane models such as (A1), (A2), (A5), and (A6), there are often local environmental effects as well as gap junctional coupling between cells (see, for example, Rinzel, Sherman, and Stokes [RSS]). In discrete models, gap junctions are modeled by the addition of discrete diffusion terms to the synaptic currents. For continuum models in a homogeneous medium, local interactions appear as continuous diffusion. Thus a term such as

$$\epsilon D \frac{\partial^2 V}{\partial x^2}$$

must be added to (A5). Here, D is the strength of the gap junctions. The natural boundary conditions are Neumann. For equations of the form (A1), (A2), without long-distance interactions, Neu [Ne] has shown that we can formally derive phase models. The terms due to the continuous diffusion are added to (A9) and have the form

$$\alpha \partial^2\theta/\partial x^2 + \beta(\partial\theta/\partial x)^2, \tag{A12}$$

where

$$\alpha = \frac{1}{T}\int_0^T V^*(t)V'(t)\,dt \tag{A13}$$

and

$$\beta = \frac{1}{T}\int_0^T V^*(t)V''(t)\,dt. \tag{A14}$$

The boundary conditions are

$$\partial\theta/\partial x|_{x=0,1} = 0. \tag{A15}$$

The sign of α is crucial and can sometimes be negative [RSS]. For stability of the synchronized solution with no long-distance coupling and no local frequency differences, $\alpha > 0$ is required. A discussion of the consequences of $\alpha < 0$ appears in [Ku].

B. Wilson–Cowan models. Consider a two-layer neural network model with weak excitatory connections and a small imposed spatial pattern on the population of excitatory cells. (This is not unreasonable if we assume that the inhibition is due solely to interneurons, for then the inhibition will be strictly local and no ascending inputs impinge on the cells.) The simplest equations (see, e.g., [EC]) are

$$\begin{aligned}\frac{\partial E(x,t)}{\partial t} &= - E(x,t)\\ &\quad + \mathcal{S}_e\left(\alpha_{ee}E(x,t) - \alpha_{ie}I(x,t) + \epsilon\left(\int_0^1 c(x,y)E(y,t)\,dy + \xi(x)\right)\right),\\ \frac{\partial I(x,t)}{\partial t} &= - I(x,t) + \mathcal{S}_i\big(\alpha_{ei}E(x,t) - \alpha_{ii}I(x,t)\big).\end{aligned} \tag{B1}$$

Here, $E(x,t)$ and $I(x,t)$ are the activities of the excitatory and inhibitory layers, $\mathcal{S}_e$ and $\mathcal{S}_i$ are saturating nonlinearities, and the α's are the local synaptic weights and are nonnegative. As before, ϵ is a small parameter, $c(x,y)$ are connection strengths between excitatory cells in different spatial locations, and $\xi(x)$ is a spatial pattern of inputs. We again assume that when ϵ is zero, (B1) has a stable T-periodic solution $(E_0(t), I_0(t))$ and that the analogous linearized problem has a normalized periodic adjoint solution $(E^*(t), I^*(t))$. Applying the formal perturbation analysis to (A16), we obtain (A9) with the following definitions for $\omega(x)$ and $h(\phi)$:

$$\text{(B2)} \qquad \omega(x) = \left(\frac{1}{T}\int_0^T E^*(t)\mathcal{S}_e'(\alpha_{ee}E_0(t) - \alpha_{ie}I_0(t))\,dt\right)\xi(x)$$

and

$$\text{(B3)} \qquad h(\phi) = \frac{1}{T}\int_0^T V^*(t)(V_{syn} - V_0(t))g(V_0(t+\phi))\,dt.$$

Remark. There are no biophysically meaningful analogues of the local diffusional coupling for the Wilson–Cowan model.

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REFERENCES

[Am] C. Amick, *A problem in neural networks*, Proc. Roy. Soc. A, 118 (1991), pp. 225–236.

[CHR] A. H.Cohen, P. J. Holmes, and R. H. Rand, *The nature of coupling between segmental oscillators of the lamprey spinal generator for locomotion: A mathematical model,* J. Math. Biol., 13 (1982), pp. 345–369.

[E1] G. B. Ermentrout, *Synchronization in a pool of mutually coupled oscillators with random frequencies,* J. Math. Biol., 22 (1985), pp. 1–9.

[E2] ———, *The behavior of rings of coupled oscillators,* J. Math. Biol., 23 (1986), pp. 55–74.

[EC] G. B. Ermentrout and J. D. Cowan, *Large scale spatially organized activity in neural nets,* SIAM J. Appl. Math., 38 (1980), pp. 1–21.

[EK1] G. B. Ermentrout and N. Kopell, *Frequency plateaus in a chain of weakly coupled oscillators* I, SIAM J. Math. Anal., 15 (1984), pp. 215–237.

[EK2] ———, *Oscillator death in systems of coupled neural oscillators,* SIAM J. Appl. Math., 50 (1990), pp. 125–146.

[EK3] ———, *Multiple pulse interactions and averaging in systems of coupled neural oscillators,* J. Math. Biol., 29 (1991), pp. 195–217.

[EK4] ———, *Inhibition produced patterning in chains of coupled nonlinear oscillators*, submitted.

[EP] G. B. Ermentrout and J. Paulett, *Spiral waves in arrays of coupled oscillators,* in preparation.

[ET] G. B. Ermentrout and W. C. Troy, *Phaselocking in a reaction-diffusion system with a linear frequency gradient,* SIAM J. Appl. Math., 39 (1986), pp. 623–660.

[GS] C. M. Grey and W. Singer, *Stimulus-specific neuronal oscillations in orientation columns of the cat visual cortex,* Proc. Nat. Acad. Sci., 86 (1989), pp. 1698–1702.

[Ki] T. Kiemel, *Three problems on coupled nonlinear oscillators,* Ph.D. thesis, Dept. of Applied Math., Cornell Univ., Ithaca, NY, 1989.

[KE] N. Kopell and G. B. Ermentrout, *Symmetry and phaselocking in chains of weakly coupled oscillators*, Comm. Pure Appl. Math., 39 (1986), pp. 623–660.

[KZE] N. Kopell, W. Zhang, and G. B. Ermentrout, *Multiple coupling in chains of oscillators,* SIAM J. Math. Anal., 21 (1990), pp. 935–953.

[Ku] Y. Kuramoto, *Chemical Oscillations, Waves, and Turbulence*, Springer-Verlag, New York, 1984.

[Ne] J. C. Neu, *Coupled chemical oscillators,* SIAM J. Appl. Math., 37 (1979), pp. 307–315.

[Ra] P. Rabinowitz, *Some global results for nonlinear eigenvalue problems,* J. Funct. Anal., 7 (1971), pp. 487–513.

[RE] J. M. Rinzel and G. B. Ermentrout, *Analysis of neural excitability and oscillations*, in Methods in Neuronal Modelling, I. Segev and C. Koch, eds., MIT Press, Cambridge, MA, 1989.

[RSS] J. M. Rinzel, A. Sherman, and C. Stokes, *Channels, coupling, and synchronized rhythmic bursting activity,* in Analysis and Modelling of Neural Systems, F. H. Eeckman, ed., Kluwer Academic Publishers, Boston, MA, 1992, pp. 29–46.

[Sm] J. Smoller, *Shock Waves and Reaction-Diffusion Equations*, Springer-Verlag, New York, 1983.

[SGK] H. Sompolinski, D. Golomb, and D. Kleinfeld, *Global processing of visual stimuli in a neural network of coupled oscillators*, Proc. Nat. Acad. Sci., 87 (1990), pp. 7200–7204.

[SM] S. Strogatz and R. Mirollo, *Stability of incoherence in a population of coupled oscillators*, J. Statist. Phys., 63 (1991), pp. 613–635.

[TM] R. Traub and R. Miles, *Neuronal Networks of the Hippocampus*, Cambridge University Press, Cambridge, UK, 1991.