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PHASELOCKING IN A REACTION-DIFFUSION SYSTEM WITH A LINEAR FREQUENCY GRADIENT*

G. B. ERMENTROUT† AND W. C. TROY‡

Abstract. A simple spatially inhomogeneous oscillatory reaction-diffusion equation is studied. Existence of phaselocked waves is proven with a shooting argument. Stability is determined numerically. Applications to intestinal motility and a chemical experiment are described.

Key words. oscillations, chemical waves, phaselocking

AMS(MOS) subject classifications. 92A09, 35B10, 34B10

1. Introduction. There has been recent interest in the behavior of coupled oscillators and their role in understanding various physiological systems. Ermentrout and Kopell [1], [2] consider discrete chains of weakly coupled oscillators with a gradient of natural frequencies. This mechanism has been used to understand the behavior of the mammalian small intestine and swimming in fish [3], [4], [5]. Other authors have applied the idea of coupled discrete chains of oscillators to swimming in the lamprey [6] and various other phenomena [7], [8]. The works cited above have been primarily concerned with conditions under which phaselocking occurs, that is, conditions on coupling and the form of the gradient for which all the oscillations are synchronized. The methods used in these papers require weak coupling so that the oscillations are not perturbed too much from their uncoupled state.

In this paper, we consider phaselocking in a particular reaction-diffusion system with a *continuous* linear gradient of frequencies. In contrast to the above models, ours is continuous rather than discrete and we do not require "weak-coupling." Winfree [8] has experimentally studied this mechanism. A copper bar is mounted between hot and cold water baths to establish a temperature gradient. A strip of paper soaked in malonic acid reagent (the active component in the Belousov-Zhabotinskii reaction) is laid across the bar. The warmer end oscillates faster than the colder end so that the system represents a continuous array of oscillators diffusively coupled with a gradient of "uncoupled" frequencies.

In this paper, we study a simple prototype for this phenomena and show that phaselocking always occurs. As the gradient increases, we find that the amplitude of the oscillators decreases and ultimately, the uniform rest state appears to become stable. In § 2, we describe the behavior of a simple " λ - ω " system with a gradient of frequencies. We state the main result in this section and depict some numerical results. The main theorem is proven in § 3. We end with a discussion and some suggestions for further work.

2. The simple model. In the neighborhood of a Hopf bifurcation, the dynamics of an oscillation can be described by a simple nonlinear oscillator of the form:

$$(2.1) \quad z' = z(a + bz\bar{z}), \quad a, b, z \in C.$$

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This type of dynamics is often called a “ λ - ω ” oscillator and has been used by numerous authors as a prototype for nonlinear waves and other oscillatory phenomenon [9]. We will consider such a system with diffusion and a linear gradient of natural frequencies:

$$(2.2) \quad \begin{aligned} \frac{\partial z}{\partial t} &= z(1 + i\omega(x) - z\bar{z}) + d \frac{\partial^2 z}{\partial x^2}, & 0 < x < 1, \\ d \frac{\partial z}{\partial x} &= 0, & x = 0, 1 \end{aligned}$$

where $\omega(x) = \Omega_0 - \sigma x$, Ω_0 is the uncoupled frequency at $x=0$ and σ the gradient. If we write this in terms of the real variables $z(x, t) = w(x, t) + iv(x, t)$, we obtain:

$$(2.3) \quad \begin{aligned} \frac{\partial}{\partial t} \begin{pmatrix} w \\ v \end{pmatrix} &= \begin{pmatrix} 1 - w^2 - v^2 & -(\Omega_0 - \sigma x) \\ \Omega_0 - \sigma x & 1 - w^2 - v^2 \end{pmatrix} \begin{pmatrix} w \\ v \end{pmatrix} + d \begin{pmatrix} w_{xx} \\ v_{xx} \end{pmatrix}, & 0 < x < 1, \\ dw_x(0, t) &= dv_x(0, t) = 0, \\ dw_x(1, t) &= dv_x(1, t) = 0. \end{aligned}$$

In absence of diffusion (i.e. $d=0$), the solution to (2.3) is

$$(2.4) \quad \begin{pmatrix} w(x, t) \\ v(x, t) \end{pmatrix} = \begin{pmatrix} \cos [(\Omega_0 - \sigma x)t] \\ \sin [(\Omega_0 - \sigma x)t] \end{pmatrix}.$$

At each point in the medium, there is a stable oscillation with frequency $\Omega_0 - \sigma x$. For $\sigma > 0$ the frequency is highest at $x=0$ and lowest at $x=1$. We ask what happens if there is diffusion added and whether synchronization is possible. We prove that there is a range of values of σ ($0 \leq \sigma \leq \sigma_c$) for which (2.3) phaselocks. That is, each point in the medium undergoes an oscillation of the same frequency, $\Omega_0 - \sigma/2$ and the phase and amplitude of the oscillators vary with x . We let $w(x, t) = r(x, t) \cos(\theta(x, t))$ and $v(x, t) = r(x, t) \sin(\theta(x, t))$. Then (2.3) becomes:

$$(2.5) \quad \begin{aligned} \frac{\partial r}{\partial t} &= r(1 - r^2) + d(r_{xx} - r\theta_x^2), \\ \frac{\partial \theta}{\partial t} &= \Omega_0 - \sigma x + d \left(\frac{2r_x \theta_x}{r} + \theta_{xx} \right), \\ r_x(0, t) &= r_x(1, t) = \theta_x(0, t) = \theta_x(1, t) = 0. \end{aligned}$$

Phaselocked solutions to (2.5) will be of the form:

$$(2.6) \quad \begin{aligned} r(x, t) &= r(x), \\ \theta(x, t) &= \bar{\omega}t + \int_0^x \phi(s) ds. \end{aligned}$$

We substitute (2.6) into (2.5) and obtain:

$$(2.7) \quad \begin{aligned} 0 &= r(1 - r^2) + d(r'' - r\phi^2), \\ 0 &= -\bar{\omega} + \Omega_0 - \sigma x + d \left(\frac{2r'}{r} \phi + \phi' \right), \\ \phi(0) &= 0, & \phi(1) &= 0, \\ r'(0) &= 0, & r'(1) &= 0. \end{aligned}$$

If we set $u = r'/r$ and $\alpha = 1/d$, (2.7) becomes a third order nonautonomous system, namely

$$\begin{aligned}
 (2.8) \quad & \text{(a) } r' = ru, \\
 & \text{(b) } u' = \alpha(r^2 - 1) + \phi^2 - u^2, \quad 0 < x < 1, \\
 & \text{(c) } \phi' = \alpha(\bar{\omega} - \Omega_0 + \sigma x) - 2u\phi, \\
 & \phi(0) = \phi(1) = 0, \\
 & u(0) = u(1) = 0.
 \end{aligned}$$

The boundary conditions at 0 and 1 are the same and the equations are autonomous so that there exists a solution with even symmetry about the midpoint $x = \frac{1}{2}$ with properties:

$$(2.9) \quad r(1-x) = r(x), \quad u(1-x) = -u(x), \quad \phi(1-x) = \phi(x).$$

Therefore, since $\phi'(0) = \alpha(\bar{\omega} - \Omega_0)$ and $\phi'(1) = \alpha(\bar{\omega} - \Omega_0 + \sigma)$, we conclude that

$$(2.10) \quad \bar{\omega} = \Omega_0 - \sigma/2$$

is the phaselocked frequency. We substitute (2.10) into (2.8) and use (2.9) to obtain the problem on $0 < x < \frac{1}{2}$:

$$\begin{aligned}
 (2.11) \quad & \text{(a) } r' = ru, \\
 & \text{(b) } u' = \alpha(r^2 - 1) + \phi^2 - u^2, \\
 & \text{(c) } \phi' = \alpha\sigma(x - \frac{1}{2}) - 2u\phi, \\
 & \text{(d) } \phi(0) = 0, \quad u(0) = 0, \quad u(\frac{1}{2}) = 0.
 \end{aligned}$$

Conditions (d) follow from symmetry and the observation that if (2.11) holds, then a full solution to (2.8) is found by using (2.9). All boundary conditions in (2.8) will automatically hold. We now state our main result:

THEOREM 2.12. *For each $\alpha \leq 1$, if $0 \leq r(0) \leq 1$, there exists a $\sigma > 0$ such that (2.11) has a solution.*

The proof of the theorem is delayed until § 3. However, we find it useful at this point to make some pertinent observations. We first note that when $\sigma = 0$, (no gradient), the solution to (2.11) is $(r(x), u(x), \phi(s)) \equiv (1, 0, 0)$. Thus, when no frequency gradient is present, all solutions have the same amplitude, phase and frequency. For $\sigma > 0$, the solution we find satisfies $u < 0$, $\phi < 0$, $\phi' < 0$ and $r' < 0$ on $0 < x < \frac{1}{2}$ and $u(\frac{1}{2}) = \phi'(\frac{1}{2}) = r'(\frac{1}{2}) = 0$. The solutions to (2.11) obtained using a numerical shooting technique are illustrated in Fig. 2.1 when $\sigma = 5$. In Fig. 2.2 we depict the relationship between $r(0)$ and σ as found numerically. While, we did not prove it, numerical simulations indicate that the $(r(0), \sigma)$ relationship is unique and that there is a largest σ , $\sigma_c \approx 10.47$ above which there are no nonzero solutions. Numerical simulations of (2.3) using the solver PDECOL, indicate that for $0 < \sigma < \sigma_c$ the constructed solutions in the theorem are stable. For $\sigma > \sigma_c$ the rest state $u = v = 0$ becomes stable!

Thus it appears that for $d \geq 1$ (i.e., $\alpha \leq 1$) in this simple model, phaselocking is never lost; rather the amplitude of the oscillations decreases until the origin is restabilized. Before turning to the proof of the theorem, we discuss some qualitative properties of the solutions and the graphs in Figs. 2.1-2.2. For $\alpha = 1$, our numerical results indicate that r is almost constant and $u \approx 0$ along the entire domain $(0, 1)$. Thus, we see that $\phi(x) \sim (\sigma/2)(x^2 - x)$. This function is plotted along with the true solution for $\sigma = 5$ and $\sigma = 10$ in Fig. 2.3. Even when σ is quite large, the agreement between the solution

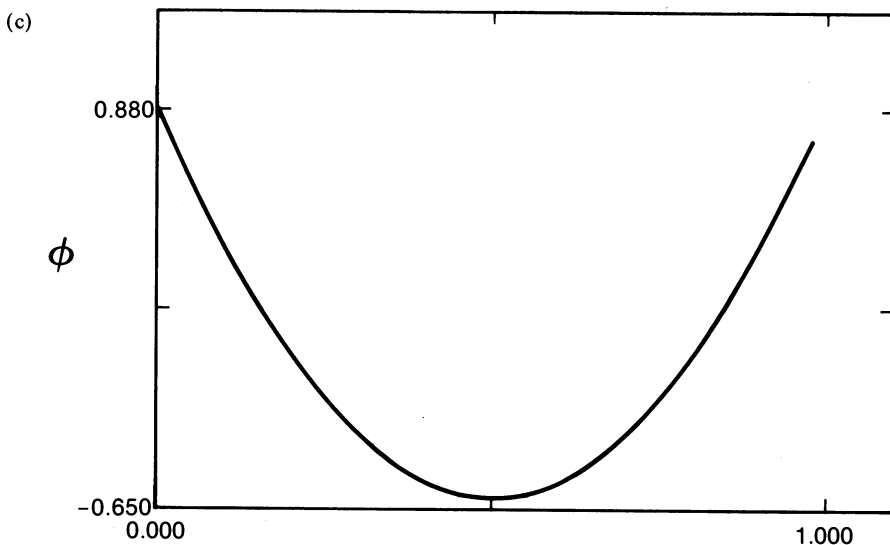
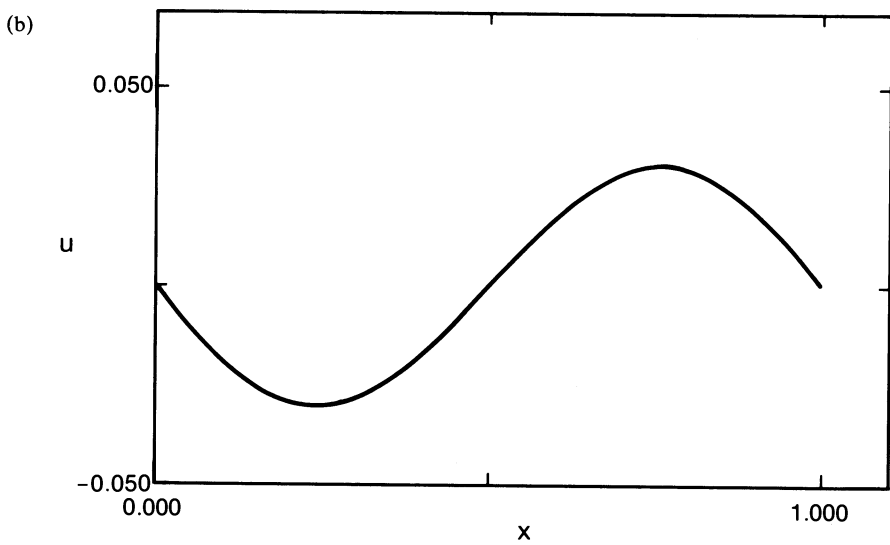
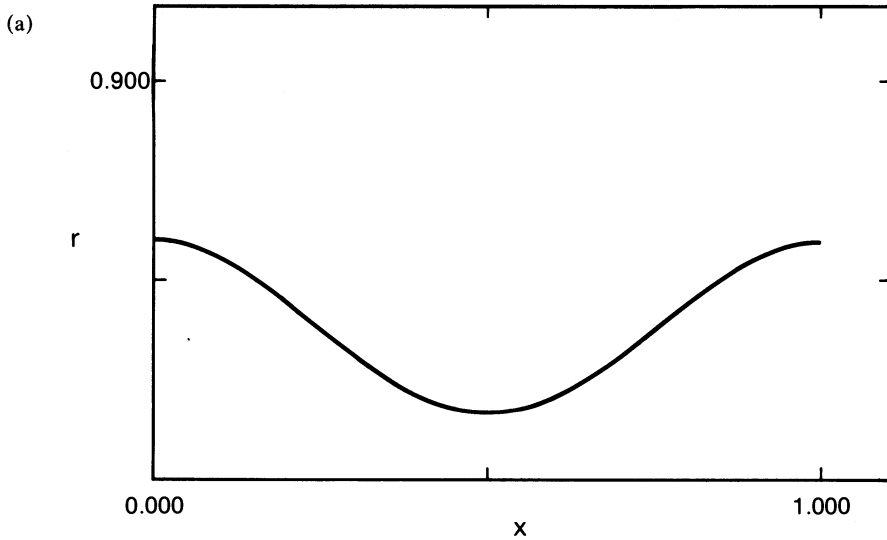


FIG. 2.1. Numerical solution to (2.11) when $\sigma = 5$. (a) $r(x)$, (b) $u(x)$, (c) $\phi(x)$.

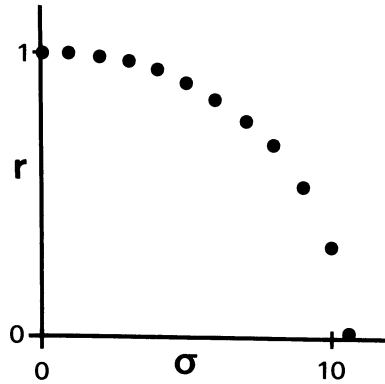


FIG. 2.2. Numerically derived relation between $r(0)$ and σ .

and the approximation is striking. Another observation is that the $(r(0), \sigma)$ graph is almost the semicircle:

$$r(0)^2 + \left(\frac{\sigma}{10.47}\right)^2 = 1.$$

This approximation is very good when σ is small and even at $\sigma = 10$, there is only an error of 7%. We can explain this phenomenon by noting that $u'(x) = 0$ when $x \sim 0.25$ and that $u(x) \sim 0$. If we evaluate our approximation for $\phi(x)$ at $x = 0.25$ and substitute this into (2.11b), we find

$$r(.25)^2 + \left(\frac{\sigma}{10.66}\right)^2 = 1.$$

Since $r(.25) \sim r(0)$ because r is nearly constant, we can empirically obtain the circle we described above. This simple approximation yields $\sigma_c = 10.66$ an error of only 2%.

3. Proof of theorem. In this section we show that the problem

- (3.1) $r' = ru,$
- (3.2) $u' = \alpha(r^2 - 1) + \phi^2 - u^2,$
- (3.3) $\phi' = \alpha\sigma(x - 1/2) - 2u\phi,$
- (3.4) $u(0) = \phi(0) = 0, \quad 0 \leq r(0) \leq 1,$
- (3.5) $u(\frac{1}{2}) = 0$

has a solution for some $\sigma \geq 0$. As noted in § 1, if $r(0) = 1$ and $\sigma = 0$ then $(r(x), u(x), \phi(x)) \equiv (1, 0, 0)$ satisfies (3.1)-(3.5). Thus we assume that $0 \leq r(0) < 1$. The main tool used in the rest of the proof is a shooting method: We define the set

$$A = \{\hat{\sigma} > 0 \mid \text{if } 0 \leq \sigma < \hat{\sigma} \text{ then } u < 0 \forall x \in (0, \frac{1}{2})\}.$$

In Lemma 2.1 below we show that the set A is nonempty, open and bounded above. Next, we define $\sigma^* = \sup A$, set $\sigma = \sigma^*$ in (3.3), and consider the solution of (3.1)-(3.4). The remainder of the proof is devoted to proving that $u(1/2) = 0$.

LEMMA 2.1. *A is nonempty, open and bounded above.*

Proof. We first consider the case $\sigma = 0$. It then follows from (3.3) and (3.4) that $\phi(x) \equiv 0$, and Eqs. (3.1)-(3.2) reduce to

- (3.6) $r' = ru,$
- (3.7) $u' = \alpha(r^2 - 1) - u^2.$

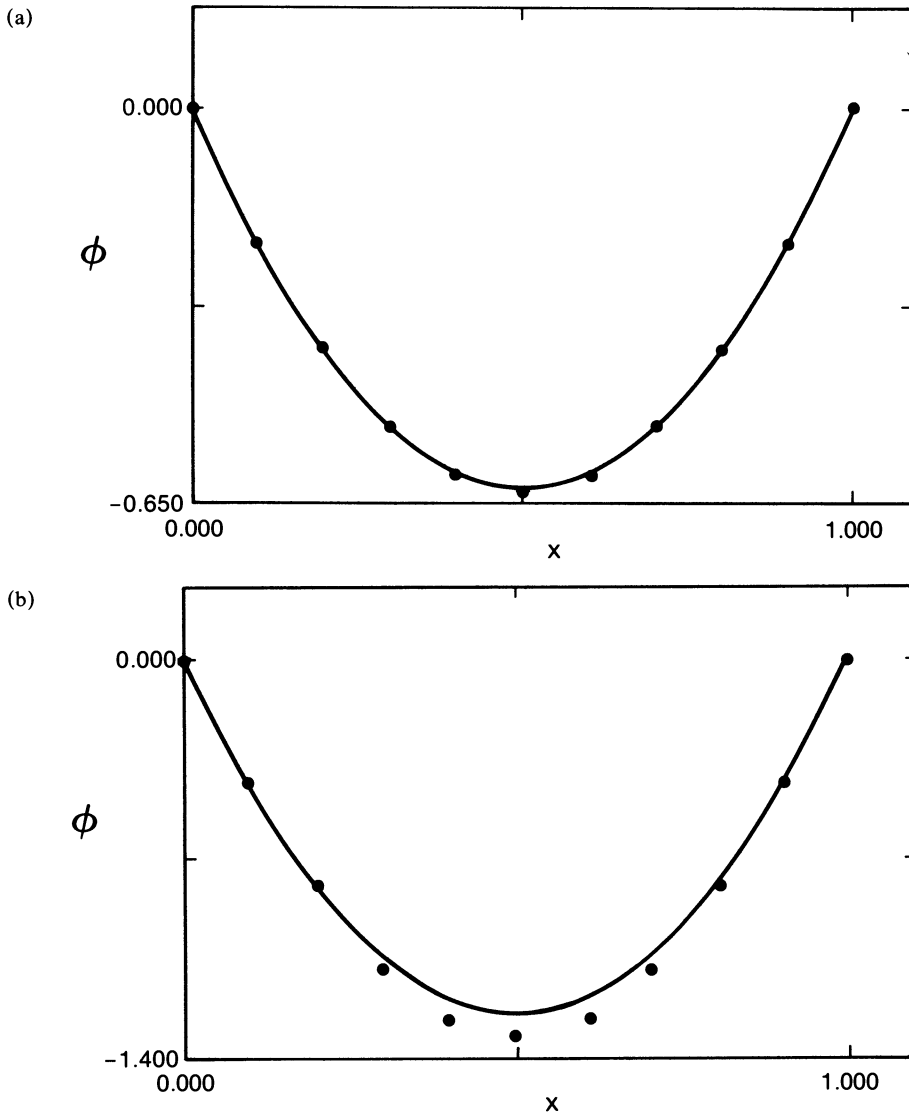


FIG. 2.3. Comparison of approximate solution to $\phi(x)$ with numerical solution (circles). (a) $\sigma=5$, (b) $\sigma=10$.

Equations (3.6) and (3.7) imply that $-(u^2 + \alpha) < u' < -u^2 < 0$ for $x > 0$ as long as a solution exists. Integrating the first inequality, we find $u > \sqrt{\alpha} \tan(-\sqrt{\alpha}x)$ as long as the solution exists. Thus $u' < 0$ for all $x \in (0, \frac{1}{2}]$ and $u(\frac{1}{2}) < 0$ since $\alpha \leq 1$. Further we note that $u'(0) = \alpha(r(0)^2 - 1) < 0$ is independent of $\sigma \geq 0$. From this observation and the continuity of solutions with respect to σ it follows that A is open, and that $\sigma \in A$ for sufficiently small $\sigma > 0$. It remains for us to show that A is bounded above. We observe that (3.3) that $\phi' < \alpha\sigma(x - \frac{1}{2})$ for $x > 0$ as long as $\phi < 0$ and $u < 0$. Integrating this and using (3.2), we obtain

$$\phi < \frac{\alpha\sigma}{2}(x^2 - x), \quad \phi^2 > \frac{\alpha^2\sigma^2}{4}(x^4 - 2x^3 + x^2), \quad u' > \frac{\alpha^2\sigma^2}{4}(x^4 - 2x^3 + x^2) - 2\alpha$$

for $0 < x < \frac{1}{2}$ as long as $\phi < 0$ and $-\sqrt{\alpha} < u < 0$. A further integration of the last inequality

leads to $u(x) > xg(x)$ where

$$g(x) \equiv \frac{\alpha^2 \sigma^2}{4} \left(\frac{x^4}{5} - \frac{x^3}{2} + \frac{x^2}{3} \right) - 2\alpha.$$

It is easily verified that $g(0) = -2\alpha$ and $g'(x) > 0$ for $0 < x \leq \frac{1}{2}$. Since $g'(x) > 0$ for $x \in (0, \frac{1}{2}]$ we conclude that $u > xg(x) > xg(0) = -2\alpha x > -\alpha \geq -\sqrt{\alpha}$ when $\alpha < 1$. Thus $u > -\sqrt{\alpha}$ over $(0, \frac{1}{2})$ as long as $u < 0$, for all $\sigma > 0$. Next, we show that for sufficiently large σ there is an $\bar{x} \in (0, \frac{1}{2})$ such that $g(\bar{x}) = 0$. For this we observe that

$$g\left(\frac{5}{\sqrt{\alpha}\sigma}\right) = \frac{125}{4\sigma^2} - \frac{125\sqrt{\alpha}}{8\sigma} + \frac{\alpha}{12} > 0 \quad \text{for large } \sigma.$$

It follows that for sufficiently large $\sigma > 0$ there is an $\bar{x} \in (0, 5/\sqrt{\alpha}\sigma)$ such that $u(\bar{x}) = 0$, hence $\sigma \notin A$. This completes the proof of the lemma.

We proceed by defining $\sigma^* = \sup A$, and setting $\sigma = \sigma^*$ in (3.3). We show that $u < 0 \forall x \in (0, \frac{1}{2})$, and $u(\frac{1}{2}) = 0$. From (3.2) and (3.4) we see that $u'(0) < 0$. If $u < 0 \forall x \in (0, \frac{1}{2}]$ continuity of solutions with respect to σ implies that $u < 0 \forall x \in (0, \frac{1}{2}]$ if $\sigma - \sigma^* > 0$ is sufficiently small, contradicting the definition of σ . Thus we conclude that there is a first $x \in (0, \frac{1}{2}]$ such that $u(x) = 0$. Suppose that $0 < x < \frac{1}{2}$. Then $u'(x) > 0$. If $u(x) > 0$ then again, continuity implies that $u = 0$ before $x = \frac{1}{2}$ for sufficiently small $\sigma^* - \sigma > 0$, contradicting the definition of σ^* . It remains to eliminate the possibility that $u'(x) = 0$. If this were the case we find that $u''(x) = 2\phi(x)\phi'(x)$. It follows from (3.3) and (3.4) that $\phi' < 0$ and $\phi < 0 \forall x \in (0, x]$. Thus $u''(x) > 0$ and hence $u' < 0$ and $u > 0$ on a small interval to the left of x , contradicting the definition of x . Thus $x = \frac{1}{2}$ and the proof of our theorem is complete.

4. Discussion. We have described the behavior of a simple model for a continuum of diffusively coupled oscillators with a frequency gradient. We found that if the gradient was less than a specific value σ_c , the oscillation is synchronous and each point in the medium oscillates at the average frequency. For gradients steeper than σ_c , no oscillation exists, rather the resting state $u = v = 0$ is stabilized. Our solutions are constructed using a shooting method and their stability analyzed by solving the full partial differential equation.

One generalization which would destroy the symmetry of our problem is to include a term of the form $q(1 - r^2)$ in the equation for the phase, θ . Such terms arise generically in a Hopf bifurcation analysis. Numerical solutions of the full system, (2.3), with the additional term do not differ substantially from the behavior we have already described. Furthermore, there is a new value $\sigma_c(q)$ above which the rest state is stable.

We have only considered the case, $d \geq 1$, that is, the diffusion strength is of the same order of magnitude as the attraction to the limit cycle, $(\lambda'(1))$. We have numerically solved (2.3) for small diffusion ($d = 0.05$) and find that the behavior of the system as the frequency gradient, σ , increases is completely different. We find that for $d = 0.05$ and $\sigma < \sigma_p \sim 1.125$, there is a phase-locked solution and, (r, ϕ) look similar to those for $d \geq 1$. In Fig. 4.1a, we illustrate the phase-locked solutions, showing the regions where $w(x, t) > 0$. If the frequency gradient exceeds σ_p , we have found that phase-locking no longer exists, rather, frequency plateaus occur. That is, we find that the upper part of the medium ($x \sim 0$) synchronizes at a high frequency and the lower part ($x \sim 1$) synchronizes at a low frequency. In the middle, the oscillations are not regular and appear to have components for several frequencies. We have illustrated $w(x, t)$ in Fig. 4.1b for $\sigma = 2$. Compare this figure with the figure in Winfree [8, p. 328]. Winfree claims that the mechanism for plateau formation is related to the length of refractoriness

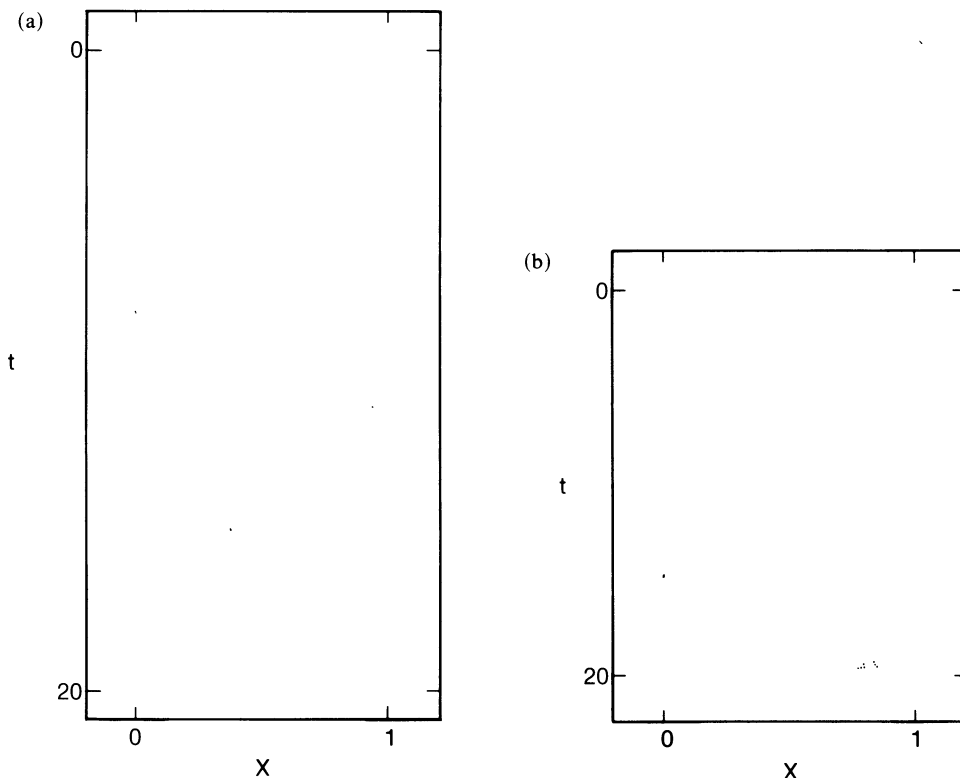


FIG. 4.1. Numerically derived solution to (2.3) showing regions where $w(x, t) > 0$. (a) phaselocked, $d = 0.05$, $\sigma = 1$; (b) plateaus, $d = 0.05$, $\sigma = 2$.

in the medium. While this may be true for the Belousov-Zhabotinskii reagent, there is no analogue to refractoriness in our model. The transition from locking to plateaus remains obscure. Because there are regions where the amplitude goes to zero in the medium, the mechanism for plateaus in (2.3) is not the same as that in [1].

We mention that Ermentrout et al. [10] consider a pair of diffusively coupled " λ - ω " systems and find a similar phenomena. If $d \geq 1$, phaselocking occurs for all frequency differences; beyond a certain critical difference, the rest state 0, becomes stable. For $d < 1$, phaselocking is lost and invariant manifolds closely related to frequency plateaus are formed. Again, the problem with (2.3) is that the amplitude r must go to zero at some point in order for the phase to remain continuous.

This work should be contrasted with that of Hagan [11] in which he considers an oscillatory system with inhomogeneities and weak diffusion. A formal perturbation reduces his system to a single Burgers equation for slow phase. Phaselocking is always found in this model. The reason is that the inhomogeneities and the diffusion are of the same order of magnitude. The phase description is no longer valid if inhomogeneities are large.

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