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FREQUENCY PLATEAUS IN A CHAIN OF WEAKLY COUPLED OSCILLATORS, I.*

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Abstract. A chain of $n+1$ weakly coupled oscillators with a linear gradient in natural frequencies is shown to exhibit "frequency plateaus," or sequences of oscillators having the same frequency, with a jump in frequency from one plateau to another. We first show that the equations for the coupled oscillators admit an invariant $(n+1)$-torus on which the equations have a special form, one in which an n-dimensional subsystem is approximately invariant. We then show that when the linear gradient becomes too steep to allow phaselocking, there emerges a large-scale invariant circle in this n-dimensional system which corresponds to the existence of a pair of plateaus, and whose homotopy class within the n-torus corresponds to the position of the frequency jump. Also discussed are the effects of anisotropic and nonuniform coupling.

1. Introduction. We shall study a chain of $n+1$ weakly coupled oscillators which are uniformly close. For much of the paper, we shall assume that the coupling is nearest neighbor, isotropic (symmetric), homogeneous in k and linear. Thus, the kth oscillator satisfies an equation of the form

$$X_k' = F(X_k) + \varepsilon R_k(X_k, \varepsilon) \equiv F_k(X_k, \varepsilon) \tag{1.1$_k$}$$

where $X_k \in R^m$, F: $R^m \to R^m$ and (1.1), with $\varepsilon = 0$, has a stable limit cycle solution of period $2\pi/\omega_0$. The full equations are

$$X_k' = F_k(X_k) + \varepsilon D(X_{k+1} - 2\gamma X_k + X_{k-1}), \qquad X_0 = 0 = X_{n+2}, \tag{1.2}$$

where D is an $m \times m$-matrix, $\varepsilon \ll 1$ and $\gamma = 0$ or 1. If $\gamma = 1$, the coupling is of the kind associated with diffusion; if $\gamma = 0$, the coupling is of "direct" type used to describe some electrical interactions.

Let ω_k be the frequency of the limit cycle of $(1.1)_k$. By hypothesis, $\omega_k = \omega_0 + O(\varepsilon)$. We first show, in §2, that there is an $(n+1)$-dimensional submanifold of $R^{m(n+1)}$ which is attracting and invariant under (1.2). This manifold is an $(n+1)$-dimensional torus T^{n+1}; we prove that variables $\theta_1, \theta_2, \cdots, \theta_{n+1}$ may be chosen on the torus so that, if $\phi_k \equiv \theta_{k+1} - \theta_k$, then the equations for θ_1 and the $\{\phi_k\}$ take the form

$$\theta_1' = \omega_1 + \varepsilon H(\phi_1) + O(\varepsilon^2), \tag{1.3}$$

$$\begin{aligned} &\phi_k' = \varepsilon[\Delta_k + H(\phi_{k+1}) + H(-\phi_k) - H(\phi_k) - H(-\phi_{k-1})] + O(\varepsilon^2), \\ &H(-\phi_0) = 0 = H(\phi_{n+1}). \end{aligned} \tag{1.4}$$

Here H is 2π-periodic and $\varepsilon\Delta_k = \omega_{k+1} - \omega_k$. The $O(\varepsilon^2)$ terms may depend on all the variables θ_1, $\phi_1, \cdots, \phi_n$. H depends on D, on the form of the coupling and on the dynamics of (1.1) in the neighborhood of the limit cycles. Note that the equations for the $\{\phi_k\}$ are, to lowest order, independent of θ_1. Thus, through $O(\varepsilon)$, we may treat the phase space as T^n, with variables $\phi_1, \cdots, \phi_n$.

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The results of §2 are rigorous generalizations of calculations made by Neu [1], [2], Holmes [3], and Holmes and Rand [4]. Neu's calculations [1] were for a general pair of oscillators with diffusive coupling; Holmes and Rand [4] computed ϕ' for a pair of Van der Pol oscillators, also with diffusive coupling. Holmes [3] worked out examples in which $H(\phi)=\sin\phi$. Now $\sin\phi$ is an odd function of its argument. Also, for two coupled oscillators, H may just as well be odd, since from (1.5) we have that $\phi'=\varepsilon[\Delta-2H_0(\phi)]+O(\varepsilon^2)$, where H_0 is the odd part of H. However, H need not in general be odd. In §2 we give examples to illustrate which features of the dynamics or coupling lead to a function H which is odd. We compute H for $\lambda-\omega$ oscillations and Van der Pol oscillations (in the nearly sinusoidal regime) with various kinds of coupling.

The symmetry, or lack thereof, of H turns out to play an important role in the behavior of (1.4). In this paper, we shall study only the case H odd; later papers will take up the effects of lack of symmetry. If H is assumed to be odd, the governing equations immediately become simpler: letting $\tau=\varepsilon t$ and $\dot{\phi}\equiv d\phi/d\tau=(1/\varepsilon)(d\phi/dt)\equiv(1/\varepsilon)\phi'$, to lowest order, (1.4b) becomes

$$\dot{\boldsymbol{\phi}}=\beta\boldsymbol{\Delta}+K\mathbf{H}(\boldsymbol{\phi}) \tag{1.5}$$

where $\boldsymbol{\phi}=(\phi_1,\cdots,\phi_n)^t$, $\beta\boldsymbol{\Delta}=(\Delta_1,\cdots,\Delta_n)^t$, $\mathbf{H}(\boldsymbol{\phi})=(H(\phi_1),\cdots,H(\phi_n))^t$ and K is a tridiagonal matrix with $K_{ii}=-2$, $K_{i+i,i}=K_{i,i+1}=1$. The parameter $\beta\in R^1$ has been introduced, so we may consider (1.5) as a one-parameter family of equations with $\boldsymbol{\Delta}$ fixed and β measuring the strength of the "detuning."

We prove in §3 that for β sufficiently small, there is a unique stable equilibrium point for the n-dimensional system (1.5) which corresponds to "phase-locked" behavior, i.e., all the oscillators move at the same frequency, with fixed (in time) phase differences between any pair. (For the full $(n+1)$-dimensional equations (1.3), (1.4), the critical point of (1.4) or (1.5) corresponds to a stable limit cycle whose period is the shared period of the coupled oscillators.) The main result, proved in §§3 and 4, concerns "frequency plateaus" which emerge for (1.3), (1.4) when the stable critical point of (1.5) disappears. By a frequency plateau we mean a sequence of oscillators whose frequency is the same; this does not mean that the phase differences within the plateau are constant in time. It is shown that when the stable critical point coalesces with another critical point and disappears (as β is increased), a *large* amplitude stable limit cycle for (1.5) emerges (*not* by a Hopf bifurcation); this can be interpreted to correspond to the existence of a pair of frequency plateaus with different frequencies. The homotopy class of this cycle (as a point set within T^n) indicates the position of the discontinuity in frequency. For this we need more assumptions on H (it must be qualitatively similar to $\sin\phi$) and $\boldsymbol{\Delta}$ which we detail in §3. The methods used involve the construction of a large invariant region for (1.5) on which a set of inequalities hold. These inequalities are reminiscent of those used by Hirsch [5] in his study of cooperative systems. The proof also requires algebraic results about matrices of the form KA where A is diagonal; these are given in the Appendix.

The existence of the large amplitude limit cycle for (1.5) is done in §3; the relation of this to frequency plateaus is discussed in §4. Also done in §4 are a calculation of the size of the frequency jump as a function of the amount of detuning, and numerical computations showing the existence of further plateaus as the spread of natural frequencies increases. Section 5 contains calculations concerning related models: we consider the effect of anisotropy in the coupling, and a gradient in the strength of coupling. For these cases, we consider only phase-locked solutions.

Other papers treating phase-locking in coupled nonlinear oscillators are [6]–[11]. References [2], [3], [8], [9] deal with more than two oscillators. Of these, the approach of Holmes et al. [3], [4], [8] and Hoppensteadt and Keener [9] are closest to ours, using equations governing phase differences. Hoppensteadt and Keener derive their equations under the assumptions that each oscillator is a perturbation of a harmonic oscillator. Their analysis then requires them to make further assumptions about the algebraic relationship of the frequencies; these assumptions are unnecessary in our formulation. References [1], [2], [3] noted that if the natural frequencies of a pair of coupled oscillators are too far apart, the oscillators may lose synchrony. To the best of our knowledge, there has not yet been a mathematical analysis of the fact that, when there are many oscillators, the loss of synchrony can be local, i.e., the frequency may be constant over many oscillators.

This paper was partially motivated by certain phenomena observed in mammalian small intestine, which consists of layers of smooth muscle fiber. It is known that the muscle fibers support travelling waves of electrical activity which run from the oral to the aboral end [12]–[15]. These, in turn, trigger waves of muscular contractions [12], [13] via high frequency electrical spikes. The spikes, which have much higher frequency, are considered to be consequences of the slow waves, so we are concerned only with the slow electrical waves.

The connection with the above mathematics is as follows: If a section of the intestine is sliced into pieces of length 1–3 cms., each piece is capable of supporting spontaneous oscillations at a constant frequency, with a wave form that is close to sinusoidal [15]. (The origin of these oscillations is controversial [13].) Furthermore, over a substantial section of the intestine there is a linear gradient in the frequency of these oscillations, higher in the oral end than in the aboral. In vivo, the measured electrical activity along the (intact) intestine displays the frequency plateaus discussed in this paper. (There are usually more than two plateaus.)

In [16]–[20], this system was modelled by a chain of loosely coupled Van der Pol or related oscillators in the sinusoidal (nonrelaxation) regime, and simulated either digitally or electronically. These papers showed that, with a variety of different couplings (usually anisotropic), and with gradients in frequencies and couplings, frequency plateaus can be produced. Such plateaus share with the physiological data the property that the plateaus lie above the curve of natural (uncoupled) frequencies. (See Fig. 1.1.)

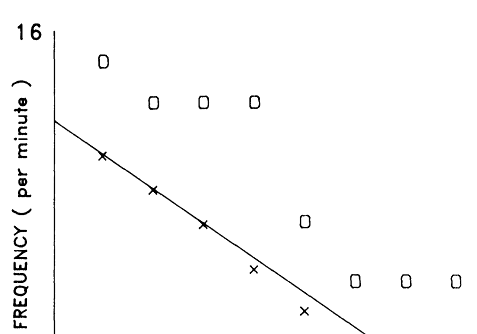

FIG. 1.1. *A schematic representation of frequency measurements in an intact mammalian intestine (top, piecewise constant), and after cutting a* 30*-cm. segment into* 8 *slices. Diagram after Diamont and Bortoff* [15]. *The positions of the plateaus do not remain constant in time* [15].

This paper is the beginning of an attempt to understand in a more general context the underlying reasons for the existence and properties of frequency plateaus. For example, we wish to show that the observations of [16]–[20] can be accounted for by phase models, with all the relevant information about the oscillators encoded in a set of 2π-periodic functions H (which may depend on k). This first paper is aimed primarily at the existence of plateaus. There are other aspects of the physiological data and simulations that cannot be accounted for if H is assumed to be odd and the coupling is isotropic. In particular, if H is odd, the coupling is uniform and isotropic, the natural frequency gradient is linear, and β is small enough that phase-locking occurs, then the phase-locked frequency is the average of the natural frequencies; if β is large enough so there are plateaus, these plateaus must be arranged symmetrically with respect to the average frequency (not above the curve of natural frequencies). Even if nonisotropic or nonuniform coupling is allowed, it is shown in §5 that the phase-locked frequency lies strictly between the highest and the lowest of the natural frequencies. We show in a later paper [21] that plateaus lying above the curve of natural frequencies can be derived from a phase model, provided that H is allowed to have a nonodd component, and n is large. Ultimately, this physiological system should be understood in terms of a continuum model.

2. Equations on an invariant torus. In this section we show that, for ε sufficiently small, there is an $(n+1)$-dimensional invariant submanifold $T^{n+1}(\varepsilon)$ of $R^{m(n+1)}$ which is an $(n+1)$-dimensional torus. On $T^{n+1}(\varepsilon)$, the motion is parametrized by phases θ_k associated to each oscillator. We also show that, to lowest order in ε, the equations have a special form which will enable us to analyze their behavior as the amount of detuning is increased.

It is easy to show that there is an invariant torus $T^{n+1}(\varepsilon)$ if ε is sufficiently small. For if $\varepsilon=0$, the cross products of the limit cycles of (1.1) for each X_k forms such a torus T^{n+1}. Furthermore, since each limit cycle is exponentially stable, this invariant manifold is "normally hyperbolic," i.e., in a neighborhood of T^{n+1}, trajectories approach the invariant manifold at an exponential rate. (See [22],[23] for more precise and general definitions.) It follows that there is an ε_0 such that, for $\varepsilon\le\varepsilon_0$, the invariant manifold persists [22], [23], i.e., there is an invariant $T^{n+1}(\varepsilon)$ close to T^{n+1}.

We now show that coordinates $\theta_1, \phi_1, \cdots, \phi_n$ may be chosen on $T^{n+1}(\varepsilon)$ so that the equations for $\{\phi_k\}$ have the form (1.4). We first make a preliminary change of variables:

LEMMA 2.1. *Suppose that*

$$X'=F(X) \tag{2.1}$$

has a stable limit cycle with period $2\pi/\omega_0$, *where* $X\in R^m$ *and* F: $R^m\to R^m$ *is* C^∞. *Then there exist smooth coordinates* $\theta\in S^1$, $Y\in R^{m-1}$ *in a neighborhood of the limit cycle of* (2.1) *such that* (2.1) *becomes*

$$\theta'=\omega_0, \qquad Y'=L(\theta)Y+O(|Y|^2) \tag{2.2}$$

where the $O(|Y|^2)$ *term may depend on* θ.

Proof. The basic idea is to use coordinates in a neighborhood H of the limit cycle that are adapted to certain codimension-1 submanifolds which are known in the context of oscillations as "isochrons" [24], [25] and more generally as "leaves" of a "foliation" [23]. These leaves are transverse to the limit cycle and have the properties that each leaf gets sent onto another leaf under the action of the differential equation, and that any two points on the same leaf approach each other exponentially as $t \to \infty$. It can be shown that there are such manifolds, and that they vary smoothly with points on the limit cycle [23]. $\theta(X)$ is defined by requiring that the motion of (2.1) be uniform on the limit cycle, and θ be constant on each leaf of the foliation. ($\theta=0$ is chosen arbitrarily.) Since the flow takes each leaf into another leaf at each fixed time, (2.2) holds not only on the limit cycle, but in the entire neighborhood. Also, since the foliation is smooth, $\theta(X)$ is smooth. The Y coordinate may be defined more arbitrarily on each leaf, provided only that $Y=0$ on the limit cycle and $Y(X)$ is smooth. □

Lemma 2.1 shows that there is a smooth transformation $X=G(\theta, Y)$ which takes (1.1), with $\varepsilon=0$, into (2.2). Denote the Jacobian matrix by $J(\theta, Y)$. In a neighborhood of the limit cycles, J is invertible, so (1.2), $k \neq 1, n+1$ may be written as

$$\begin{pmatrix} \theta_k' \\ Y_k' \end{pmatrix} = J^{-1}(\theta_k, Y_k)\{F_k(G(\theta_k, Y_k)) \\ + \varepsilon D[G(\theta_{k+1}, Y_{k+1}) - 2\gamma G(\theta_k, Y_k) + G(\theta_{k-1}, Y_{k-1})]\}.$$

There are similar equations for $k=1, n+1$. By hypothesis,

$$J^{-1}(\theta_k, Y_k)F_k(G(\theta_k, Y_k)) = \begin{pmatrix} \omega_0 + O(\varepsilon) \\ L(\theta_k)Y_k + O(|Y_k|^2, \varepsilon) \end{pmatrix}. \qquad \begin{matrix} (2.3a) \\ (2.3b) \end{matrix}$$

The right-hand side of (2.3a) may be written as

$$\omega_k + \varepsilon \bar{R}_k(\theta_k, Y_k, \varepsilon)$$

where

$$\int_0^{2\pi} \bar{R}_k(\theta_k, 0, \varepsilon)\, d\theta_k = O(\varepsilon)$$

and ω_k, as stated before, is the frequency of the limit cycle of $(1.1)_k$. Let $h(\theta_i, \theta_k)$ denote the θ component of $J^{-1}(\theta_k, Y_k)DG(\theta_i, Y_i)$ at $Y_i=0=Y_k$. h is 2π-periodic in each of its arguments. Also let $\phi_k \equiv \theta_{k+1} - \theta_k$ and $S_k = Y_k/\varepsilon$. (The latter change of variables "blows up" an ε-neighborhood of $T^{n+1}(\varepsilon)$.) Then (2.3) becomes

$$\theta_1' = \omega_1 + \varepsilon h(\theta_2, \theta_1) + O(\varepsilon^2), \tag{2.4a}$$

$$\phi_k' = \varepsilon[\Delta_k + h(\theta_{k+2}, \theta_{k+1}) - 2\gamma h(\theta_{k+1}, \theta_{k+1}) + h(\theta_k, \theta_{k+1}) \\ - h(\theta_{k+1}, \theta_k) + 2\gamma h(\theta_k, \theta_k) - h(\theta_{k-1}, \theta_k)] + O(\varepsilon^2), \tag{2.4b}$$

$$S_k' = O(1)$$

where $\varepsilon\Delta_k \equiv \omega_{k+1} - \omega_k$ and the $O(\varepsilon^2)$ terms may depend on all the variables θ_1, $\{\phi_k\}$ and $\{S_k\}$. (Equation (2.4b) is true for $k=2,\cdots,n-1$. To get the equations for $k=1$ and $k=n$, set $h(\theta_0, \theta_1)=0=h(\theta_{n+1}, \theta_n)$.) Note that, to lowest order, the right-hand side of (2.4a, b) is independent of the $\{S_k\}$. Thus (2.4) may be thought of as the dynamical system on $T^{n+1}(\varepsilon)$. (There is a dependence on $\{S_k\}$ in the $O(\varepsilon^2)$ term. However, on the invariant manifold, $S_k = \bar{S}_k(\theta_1, \cdots, \theta_{n+1})$, and so the $\{S_k\}$ may be eliminated.)

Note also that there are two time scales in (2.4a, b): $\theta_1' = O(1)$ in ε and $\phi_k' = O(\varepsilon)$ for all k. Thus, the $\{\phi_k\}$ form an n-dimensional "slow system" within $T^{n+1}(\varepsilon)$. However, there is not necessarily an n-dimensional submanifold of $T^{n+1}(\varepsilon)$ invariant under

(2.4). Nevertheless, using averaging theory, the difference in time scales can be exploited to write equations for the $\{\phi_k\}$ which, to lowest order, are independent of θ_1. Denote by (2.5) equation (2.4) with the expressions θ_{k+1}, θ_{k+2} and θ_{k-1} replaced by $\theta_k+\phi_k$, $\theta_k+\phi_k+\phi_{k+1}$ and $\theta_k-\phi_{k-1}$ respectively. Using the fact that $\theta_k=\omega_0 t+O(\varepsilon)$ and $\phi_k'=O(\varepsilon)$ for all k, we may now use the averaging theorem [26]. This theorem asserts that there is a near-identity change of coordinates such that, in the new coordinates the right-hand side of (2.5) may be replaced, to lowest order in ε, by its average with respect to t over one period. But, by the periodicity of h and the fact that $\phi_k'=O(\varepsilon)$,

$$(2.6)\quad \begin{aligned}\frac{\omega_0}{2\pi}\int_0^{2\pi/\omega_0} h(\theta_k+\phi_k+\phi_{k+1},\theta_k+\phi_k)\,dt&=\frac{\omega_0}{2\pi}\int_0^{2\pi/\omega_0} h(\theta_k+\phi_{k+1},\theta_k)\,dt+O(\varepsilon)\\ &=\frac{1}{2\pi}\int_0^{2\pi} h(\theta_k+\phi_{k+1},\theta_k)\,d\theta_k+O(\varepsilon).\end{aligned}$$

A similar computation holds for the other terms of (2.5). Define

$$(2.7)\qquad H(\phi)\equiv\frac{1}{2\pi}\int_0^{2\pi}[h(\theta+\phi,\theta)-\gamma h(\theta,\theta)]\,d\theta.$$

We have shown the following:

THEOREM 2.1. *There is an* $(n+1)$*-dimensional submanifold* $T^{n+1}(\varepsilon)$ *invariant under* (1.2). *Variables* θ_1, $\phi_1,\cdots,\phi_n$ *may be chosen on* $T^{n+1}(\varepsilon)$ *so that, on the invariant manifold*, (1.2) *has the form* (1.3), (1.4), *with* H 2π*-periodic.*

We now explicitly calculate the function H for several classes of examples. The first has a natural polar coordinate system representation. However, as we shall see, the natural representation is not the one used in the proof of Theorem 2.1. Consider $m=2$ and

$$(2.8)\qquad F_k\begin{pmatrix}x\\y\end{pmatrix}=\begin{pmatrix}\lambda & -\omega\\ \omega & \lambda\end{pmatrix}\begin{pmatrix}x\\y\end{pmatrix},\qquad D=\begin{pmatrix}d_1 & d_2\\ d_3 & d_4\end{pmatrix}$$

where $\lambda=1-(x^2+y^2)$, $\omega=\omega_k+\hat\omega(x^2+y^2)$, $\hat\omega$: $R^1\to R^1$, $\hat\omega(1)=0$, and $\omega_k=\omega_0+O(\varepsilon)$ for all k. In the usual polar coordinates $(x=r\cos\theta, y=r\sin\theta)$, $X'=F(X)$ is

$$r'=r\lambda(r^2),\qquad \theta'=\omega(r^2).$$

Thus $\omega(r)$ is an amplitude dependent angular frequency. The representation used in Theorem 2.1 has the form $\theta'=\omega_k$, where ω_k is a constant (independent of amplitude). To achieve this, we make the coordinate change $(\theta,r)\to(\bar\theta,r)$, where $\bar\theta=\theta+\mu(r)$ and

$$\mu(r)=\int_1^r\frac{\hat\omega(\bar r)}{\bar r(1-\bar r^2)}\,d\bar r.$$

Again we let S_k be a "blown up" normal coordinate, i.e., $r_k=1+\varepsilon S_k$. Using trigonometric identities, it can be checked that, in S_k, θ_k coordinates, (1.2) is

$$(2.9)\qquad \theta_k'=\omega_k+\varepsilon[\hat\omega'(1)S_k+H_1(\theta_{k-1},\theta_k)+H_1(\theta_{k+1},\theta_k)]+O(\varepsilon^2),\qquad k=2,\cdots,n,$$

$$(2.10)\qquad S_k'=-2S_k+H_2(\theta_{k-1},\theta_k)+H_2(\theta_{k+1},\theta_k),\qquad k=2,\cdots,n,$$

where

$$
\begin{aligned}
H_1(\theta_{k\pm1},\theta_k)=\,&d_1\sin(\theta_{k\pm1}-\theta_k)+(d_4-d_1)\sin\theta_{k\pm1}\cos\theta_k\\
&+(d_1-d_4)\sin\theta_k\cos\theta_k+d_2-(d_2+d_3)\cos^2\theta_k\\
&-d_2\cos(\theta_{k\pm1}-\theta_k)+(d_3+d_2)\cos\theta_{k\pm1}\cos\theta_k,\\
H_2(\theta_{k\pm1},\theta_k)=\,&d_1\cos(\theta_{k\pm1}-\theta_k)+(d_4-d_1)\sin\theta_k\sin\theta_{k\pm1}\\
&-d_1-(d_4-d_1)\sin^2\theta_k\\
&+d_2\sin(\theta_{k\pm1}+\theta_k)+(d_3-d_2)\sin\theta_k\cos\theta_{k\pm1}\\
&-(d_2+d_3)\cos\theta_k\sin\theta_k.
\end{aligned}
$$

Now $\bar\theta_k'=\theta_k'+\mu'(r_k)r_k'=\theta_k'+\varepsilon\mu'(1)S_k'+O(\varepsilon^2)=\theta_k'-\frac{1}{2}\varepsilon\hat\omega'(1)S_k'+O(\varepsilon^2)$ and $\bar\phi_k\equiv\bar\theta_{k+1}-\bar\theta_k$. Using (2.9), (2.10) and averaging as before the equations for ϕ_k', we get

PROPOSITION 2.1. *For example* (2.8),

$$
\begin{aligned}
(2.11)\qquad H(\bar\phi_k)=&\left[(d_1+d_4)\frac{\hat\omega'(1)}{4}+\frac{(d_3-d_2)}{2}\right][\cos(\bar\phi_k)-\gamma]\\
&+\left[(d_2-d_3)\frac{\hat\omega'(1)}{4}+\frac{(d_1+d_4)}{2}\right]\sin\bar\phi_k.
\end{aligned}
$$

Remark. $H(\phi)$ is an odd function only when the coefficient of $\cos(\phi_k)-\gamma$ vanishes. This can happen, for example, if $\hat\omega'(1)=0$ and $d_2=d_3$. $\hat\omega'(1)=0$ implies that (infinitesimally) there is no frequency dependence on amplitude, while $d_2=d_3$ if the "diffusion" matrix D is symmetric. It is interesting to note that the frequency dependence on amplitude and the nonsymmetry of D may cancel each other to produce a function H which is odd.

We now consider a chain of coupled Van der Pol oscillators in the almost-sinusoidal regime, i.e.,

$$(2.12)\qquad \ddot X+\delta(X^2-1)\dot X+X=0$$

with $\delta\ll 1$. Using polar coordinates $X=r\cos\theta$, $\dot X=-r\sin\theta$, (2.12) is

$$
\begin{aligned}
(2.13)\qquad r_t&=\delta(1-r^2\cos^2\theta)(r\sin^2\theta),\\
\theta_t&=1+\frac{\delta}{r}(1-r^2\cos^2\theta)(r\sin\theta\cos\theta).
\end{aligned}
$$

By averaging techniques [26], it can be seen that (2.13) is equivalent to

$$r_t=\delta r\left[\frac{1}{2}-\frac{r^2}{8}\right]+O(\delta^2),\qquad \theta_t=1+O(\delta^2).$$

Thus, for fixed δ small, (2.12) is equivalent (up to $O(\delta^2)$) to a system of the form (2.8) with the special property that $\hat\omega=0$. Allowing detuning and coupling, the full equations have the form:

(2.14)

$$
\begin{aligned}
\ddot X_k+\delta(X_k^2-1)\dot X_k+(1+\delta\omega_k)X_k=\,&\varepsilon\big[b(\dot X_{k+1}-2\dot X_k+\dot X_{k-1})\big]\\
&+c(X_{k+1}-2X_k+X_{k-1})+d(\ddot X_{k+1}-2\ddot X_k+\ddot X_{k-1}).
\end{aligned}
$$

The terms involving the b, c, d represent, respectively, resistive, inductive and capacitive coupling. As before, $\omega_{k+1}-\omega_k=O(\varepsilon)$. Then $H(\phi)$ can be computed as above, and we get

$$H(\phi)=b\sin\phi+(c-d)[\cos\phi-1]. \tag{2.15}$$

Note that, since $\hat{\omega}=0$, all the terms of $H(\phi)$ come from the coupling, and not from the frequency dependence on amplitude.

Remark. In [4], Rand and Holmes compute H for a pair of coupled Van der Pol oscillators, for δ fixed and small. Their formulation is somewhat different, but in terms of our notation, they allow εb and $\varepsilon(c-d)$ to go to zero at different rates as $\varepsilon\to 0$. If the coupling involves substantial resistance, i.e., if $\varepsilon(c-d)\to 0$ at least as fast as εb (as $\varepsilon\to 0$), then for small ε, their result agrees with ours; i.e., to lowest order, H is a multiple of $\sin\phi$. (When $n=2$, the even part of $H(\phi)$ disappears from (1.4), so (2.15) is effectively $b\sin\phi$.) However, if the resistive coupling is significantly smaller than the combined effect of inductive and capacitive coupling, then a more complicated expression may be obtained which is equivalent to the result of carrying out the computation of $H(\phi)$ to order ε^2, with $(c-d)=O(1)$ and $b=O(\varepsilon)$. We note that the same expression is obtained if one works with oscillators of the form (2.8), since (2.12) has been approximated by such an oscillator.

3. Existence of a large amplitude invariant circle. We now restrict ourselves to functions $H(\phi)$ which are odd, i.e. $H(-\phi)=-H(\phi)$, and consider (1.5). Since H is 2π-periodic as well as odd, we have $H(0)=H(\pi)=0$. We shall assume about H that it is qualitatively like $H=\sin\phi$, i.e., that $H>0$ for $0<\phi<\pi$, $H<0$ for $-\pi<\phi<0$, that H has a single maximum M and a single minimum m at ϕ_M and ϕ_m respectively, that H' is monotone increasing from ϕ_m to 0, and that H' is convex on $(\phi_m, 0)$, i.e. that $H'''(\phi)\neq 0$ for $\phi\in(\phi_m, 0)$.

LEMMA 3.1. *For fixed $\mathbf{\Delta}$, there exists β_0 such that, for $\beta<\beta_0$, (1.5) has 2^n critical points. Of these critical points, one is a sink and n are saddle points having one positive eigenvalue and $n-1$ eigenvalues with negative real part.*

Proof. The critical points of (1.5) are solutions to

$$H(\phi)=K^{-1}(-\beta\mathbf{\Delta}). \tag{3.1}$$

Equation (3.1) has a solution if every component of $K^{-1}(-\beta\mathbf{\Delta})$ lies between m and M. Let

$$\beta_0=\max\{\beta | m\le K^{-1}(-\beta\mathbf{\Delta})_i\le M\ \forall i\}.$$

If $\beta<\beta_0$, then for each i there are two distinct solutions $\phi_i^{\pm}(\beta)$ to $H(\phi)=K^{-1}(-\beta\mathbf{\Delta})_i$ with $|\phi_i^{\pm}|<\pi$; ϕ_i^- denotes the solution with smaller absolute value. (Note that $H'(\phi_i^-)>0$ and $H'(\phi_i^+)<0$. See Fig. 3.1.) Thus there are 2^n critical points. Let $\boldsymbol{\xi}_i=\boldsymbol{\xi}_i(\beta)$, $i=1,\cdots,n$, denote the critical point whose kth component $\xi_{ik}(\beta)$ is ϕ_k^-, $k\neq i$ and $\xi_{ii}=\phi_i^+$; $\boldsymbol{\xi}_0(\beta)$ is the critical point with kth component $\xi_{0k}(\beta)=\phi_k^-$ for all k. We will show that $\boldsymbol{\xi}_0$ is a sink, and $\boldsymbol{\xi}_i$ is a saddle having exactly one eigenvalue with positive real part.

The linearization of (1.5) around one of the critical points $\boldsymbol{\xi}$ has matrix $K\mathbf{H}'(\boldsymbol{\xi})$ where $\mathbf{H}'(\boldsymbol{\xi}_i)$ denotes the $n\times n$ diagonal matrix whose kth entry is $H'(\xi_{ik})$. Now if $\boldsymbol{\xi}=\boldsymbol{\xi}_0$, then the kth entry is $H'(\xi_{0k})=H'(\phi_k^-)>0$ for all k. By Proposition A.1 (see Appendix), the eigenvalues of $K\mathbf{H}'(\boldsymbol{\xi}_0)$ all have negative real parts, so $\boldsymbol{\xi}_0$ is a sink. If $\boldsymbol{\xi}=\boldsymbol{\xi}_i$ for some i, then $H'(\xi_{ii})<0$, but $H'(\xi_{ik})>0$ for $k\neq i$. Thus, by Proposition A.3 $\boldsymbol{\xi}_i$

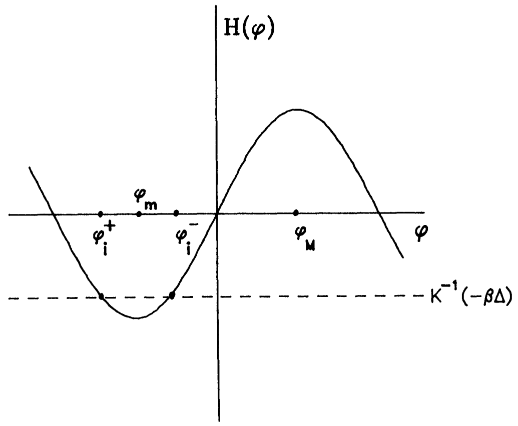

FIG. 3.1. *The two possible choices* $\phi_i^{\pm}$ *for the ith component of a critical point of* (1.5).

is a saddle having exactly one eigenvalue with positive real part. (Note that these stability properties of the critical points cannot change as β increases unless $H'(\xi_{ik}(\beta))$ changes sign for some i; this does not happen for $\beta<\beta_0$.) □

We now further restrict our attention to a linear gradient in frequency; such a gradient is equivalent to a constant vector $\mathbf{\Delta}$ for (1.5). The vector $-\beta(1,1,\cdots,1)^t$ corresponds to a linear *decrease* in frequency for increasing k, as in the measurements on mammalian intestine. For simplicity, we assume n is odd, so there is a unique "middle" phase difference ϕ_j. The main result is as follows. We shall later show that the theorem implies the existence of a pair of frequency plateaus, with a jump in frequency between the j and $(j+1)$st oscillators.

THEOREM 3.1. *Suppose that* $\mathbf{\Delta}=-(1,1,\cdots,1)^t$ *and that* $n=2j-1$ *in* (1.5). *Then for* $\beta\le\beta_0$, $\beta_0-\beta$ *sufficiently small, the closure of the two branches of the unstable manifold of* ξ_j *forms a smooth attracting invariant circle which is homotopic to the circle* $\phi_k=0$, $k\ne j$, $0\le\phi_j\le2\pi$. *This invariant manifold persists for* $\beta>\beta_0$, $\beta-\beta_0$ *sufficiently small.* (*See Fig.* 3.2.)

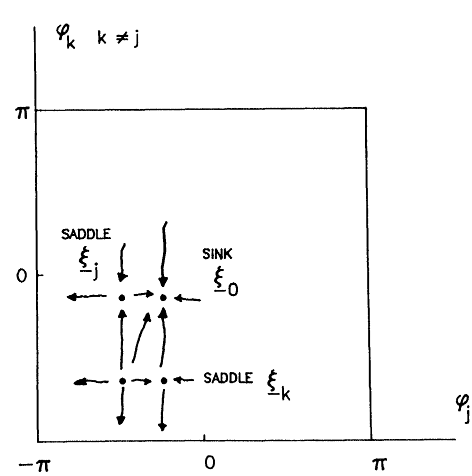

FIG. 3.2. *Schematic representation of the dynamics of* (1.5), *with a unique sink* ξ_0 *and a saddle* ξ_j *which coalesces with* ξ_0 *as* $\beta\to\beta_0$. *The two* (*one-dimensional*) *branches of the unstable manifold of* ξ_j *form a smooth invariant circle.*

Proof. We require several lemmas:

LEMMA 3.2. *Assume the hypotheses of Theorem* 3.1. *Then*

(i) $\phi_k^{\pm}(\beta)<0\ \forall k$ *and all* $\beta\le\beta_0$.

(ii) $m<K^{-1}(-\beta\Delta)_k<0\ \forall k\ne j,\ \beta\le\beta_0$. *For* $k=j,\ m=K^{-1}(-\beta_0\Delta)_j$.

(iii) *The eigenvector* $\mathbf{v}_j$ *of the unique positive eigenvalue of* $\boldsymbol{\xi}_j$ *satisfies* $\operatorname{sgn} v_{jk}=-\operatorname{sgn} v_{jj}\ \forall k\ne j$ *and all* $\beta\le\beta_0$.

Proof. (i) The critical points are solutions to (3.1) and $K^{-1}(\Delta)$ has kth component $k(n+1-k)/2$. Thus all the components of $K^{-1}(-\beta\Delta)$ are negative. Since $H(\phi)>0$ for $0<\phi<\pi$ and $H(\phi)<0$ for $-\pi<\phi<0$, the solutions to $H(\phi)=-\beta k(n+1-k)/2$, with $|\phi|<\pi$, are negative.

(ii) If $n=2j-1$, then $k(n+1-k)/2$ takes its largest value for $k=j$. (β_0 is then defined by $m=-\beta_0 j(j+1)/2$.)

(iii) This follows from Proposition A.5 (see Appendix), as soon as we establish that $\mathbf{H}'(\boldsymbol{\xi}_j)$ has the form $\operatorname{diag}(a_1,a_2,\cdots,a_{j-1},a_j,a_{j-1},\cdots,a_1)$, where $a_k>0$ for $k\ne j$, $a_j<0$, $a_1>a_2>\cdots>a_{j-1}$, and $a_{k-1}+a_{k+1}<2a_k$ for $k=2,\cdots,j-1$. Now $\mathbf{H}'(\boldsymbol{\xi}_j)$ is a diagonal matrix whose kth entry is $H'(\xi_{jk})$, where ξ_{jk}, the kth component of $\boldsymbol{\xi}_j$, is $\phi_k^-(\beta)$ for $k\ne j$ and $\phi_k^+(\beta)$ for $k=j$. ($\phi_k^{\pm}(\beta)$ are defined by $H(\phi_k^{\pm})=K^{-1}(-\beta\Delta)_k=-\beta k(n+1-k)/2$.) Thus $a_k=a_{n+1-k}$. The signs of the a_k follow from the definition of $\boldsymbol{\xi}_j$. Furthermore, $k(n+1-k)/2$ is an increasing function of k for $k<j$, so $|\phi_k^-(\beta)|$ increases with k (i.e, $\phi_k^-=-|\phi_k^-|$ decreases with k). Since H' is monotone increasing on $[\phi_m,0]$, this implies that $a_1>a_2>\cdots>a_{j-1}$. Also, the convexity condition for H' (i.e., $H'''\ne0$ on $(\phi_m,0)$) implies that $(a_{k-1}+a_{k+1})/2<a_k$. □

From Lemma 3.2(ii), we see that $|\phi_j^+-\phi_1^-|\to0$ as $\beta\to\beta_0$. Thus, as $\beta\to\beta_0$, all critical points coalesce in pairs, and for $\beta>\beta_0$ there are no solutions to (3.1). (Recall that each of the 2^n critical points has as its kth component either ϕ_k^+ or ϕ_k^-; thus each point is matched with another point with which it agrees except at the jth component.) The critical point $\boldsymbol{\xi}_j$ has the distinction of being the one that coalesces with the sink $\boldsymbol{\xi}_0$; its components agree with those of $\boldsymbol{\xi}_0$ except for the jth, with $\xi_{0j}=\phi_j^-$ and $\xi_{jj}=\phi_j^+$.

We shall focus separately on the two branches of the unstable manifold of $\boldsymbol{\xi}_j$, which we shall refer to as the left or right branch, depending on whether the jth component v_{jj} of the tangent vector $\mathbf{v}_j$ is negative or positive. We shall show, for $\beta_0-\beta$ sufficiently small, that both of these have the sink in their closure, and hence form an invariant circle. The next lemma deals with the right branch. This is the easier part, since for $\beta_0-\beta$ small, $\boldsymbol{\xi}_j$ and $\boldsymbol{\xi}_0$ are close, with $\boldsymbol{\xi}_0$ to the right of $\boldsymbol{\xi}_j$.

LEMMA 3.3. *For* $\beta_0-\beta$ *sufficiently small, the right branch of the unstable manifold of* $\boldsymbol{\xi}_j$ *contains* $\boldsymbol{\xi}_0$ *in its closure. Furthermore, at* $\boldsymbol{\xi}_0$ *this manifold is tangent to the eigenspace of the least negative eigenvalue of* $K\mathbf{H}'(\boldsymbol{\xi}_0)$.

Proof. $\boldsymbol{\xi}_0$ and $\boldsymbol{\xi}_j$ coalesce as $\beta\to\beta_0$. The techniques of [27] show that, under certain hypotheses, this implies that for $\beta_0-\beta$ sufficiently small, there is a trajectory joining $\boldsymbol{\xi}_0$ and $\boldsymbol{\xi}_j$. The unstable manifold of $\boldsymbol{\xi}_j$ is one-dimensional, so that trajectory must be the unstable manifold of $\boldsymbol{\xi}_j$. It follows from the construction of this trajectory that its tangent at $\boldsymbol{\xi}_0(\beta)$ is the eigenvector of the unique eigenvalue of $K\mathbf{H}'(\boldsymbol{\xi}_0)$ which tends to 0 as $\beta\to\beta_0$.

The hypotheses on (1.6) needed to apply the technique of [27] are those of [27, Thm. 2.2]: we write (1.5) as

$$\dot{\phi}=K\mathbf{H}'(\boldsymbol{\xi}_{\beta_0})(\phi-\boldsymbol{\xi}_{\beta_0})+(\beta-\beta_0)\Delta+Q(\phi-\boldsymbol{\xi}_{\beta_0},\phi-\boldsymbol{\xi}_{\beta_0})+\rho \tag{3.2}$$

where $\boldsymbol{\xi}_{\beta_0}=\boldsymbol{\xi}_0(\beta_0)=\boldsymbol{\xi}_j(\beta_0)$ is the saddle-sink at the critical value of β, Q is a vector-valued quadratic form containing the terms quadratic in $\phi-\boldsymbol{\xi}_{\beta_0}$ and independent of β, and $\rho=o(\beta-\beta_0,|\phi-\boldsymbol{\xi}_{\beta_0}|^2)$. Then we must have

(i) $K\mathbf{H}'(\xi_{\beta_0})$ has rank $n-1$.

(ii) $[K\mathbf{H}'(\xi_{\beta_0}),\boldsymbol{\Delta}]$ has rank n, where $[P,Z]$ denotes the $n\times(n+1)$-matrix formed by adjoining the n-vector Z to the $n\times n$-matrix P as the last column.

(iii) $[K\mathbf{H}'(\xi_{\beta_0}),\ Q(V,V)]$ has rank n, where V is an eigenvector of the zero eigenvalue of $K\mathbf{H}'(\xi_{\beta_0})$ and $Q(V,V)$ is the n-vector obtained by evaluating the quadratic form Q on the vector V.

Now (i) and (ii) follow from (i) and (ii) of Proposition A.2. To establish (iii), we note that $V=(v_1,\cdots,v_n)^t$ with $v_k=0$, $k\neq j$, and $v_j=1$. Hence $Q(V,V)$ contains exactly those terms depending only on ϕ_j (and not $\phi_k, k\neq j$). In particular, there are no such terms in the kth equation of (3.2) with $k\neq j$, $j\pm1$. For $k=j\pm1$, the kth coordinate $Q(V,V)_k$ of $Q(V,V)$ is $\frac{1}{2}H''(\phi_j^-(\beta_0))(\phi_j-\phi_j^-(\beta_0))^2$;

$$Q(V,V)_j=-H''\big(\phi_j^-(\beta_0)\big)\big(\phi_j-\phi_j^-(\beta_0)\big)^2.$$

Thus $Q(V,V)$ is a multiple of $Z=(z_1,\cdots,z_n)^t$ with $z_j=-2$, $z_{j-1}=z_{j+1}=1$, $z_k=0$, $k\neq j, j\pm1$. Then (iii) also follows from (ii) of Proposition A.2. □

We now turn to the left branch of the unstable manifold of ξ_j. For β near β_0, the ϕ_j component must change by nearly 2π before entering the sink ξ_0. Thus we shall need estimates on this branch that are not local. These estimates are contained in the following: Let $\sigma_k=H(\phi_k^\pm)-H(\phi_{k+1}^\pm)$.

LEMMA 3.4. *Let* $R=\{(\phi_1,\cdots,\phi_n)|\phi_{n+1-k}=\phi_k\ \forall k;\ \phi_k^-\leq\phi_k<\phi_M,\ k\neq j,\ H(\phi_j)>H(\phi_j^-),\ \dot\phi_j<0,\ H(\phi_k)\leq H(\phi_{k+1})+\sigma_k,\ k\leq j-1\}$. *Then the left branch is contained in* R. *All trajectories which start in* R *tend to the critical point* ξ_0 *as* $t\to\infty$.

Proof. We shall show that (i) the above statement is true for a neighborhood of ξ_j (i.e., $\xi_j\in\bar R$, the closure of R, and the left branch points into R), and (ii) R is invariant under (1.5) for $t>0$, with all trajectories tending toward ξ_0. We note that if $\boldsymbol{\Delta}=-(1,1,\cdots,1)^t$ the invariance of (1.5) under $\phi_k\leftrightarrow\phi_{n+1-k}$ implies that the points on the one-dimensional unstable manifold of ξ_j satisfy $\phi_{n+1-k}=\phi_k$ for all k. Furthermore, on the (initial piece of the) left branch, $\dot\phi_j<0$ by hypothesis, and $\dot\phi_k>0$ $k\neq j$ by Lemma 3.2. Since $\phi_k=\phi_k^-(k\neq j)$ at the critical point, we have $\phi_k^-<\phi_k<\phi_M$ $(k\neq j)$; also $\dot\phi_j<0$ implies $H(\phi_j)>H(\phi_j^-)=H(\phi_j^+)$. (See Fig. 3.3.)

To finish (i), we have left to show that

$$H(\phi_k)\leq H(\phi_{k+1})+\sigma_k,\qquad k=1,\cdots,j-1,\tag{3.3}$$

along the left branch of the unstable manifold, and in a neighborhood of ξ_j. By definition, $H(\phi_k)=H(\phi_{k+1})+\sigma_k$ at the critical point. Thus, it suffices to show that

$$H'(\phi_k)\dot\phi_k\leq H'(\phi_{k+1})\dot\phi_{k+1},\qquad k=1,\cdots,j-1,$$

along this part of the unstable manifold. Equivalently, we may show that

$$a_kv_{jk}\leq a_{k+1}v_{j,k+1},\qquad k=1,\cdots,j-1,\tag{3.4}$$

where $a_k=H'(\phi_k^-)$, $k\neq j$, $a_j=H'(\phi_j^+)$, and $(v_{j,1},\cdots,v_{j,n})=\mathbf{v}_j$ is the eigenvector of the eigenvalue $\lambda>0$ of $K\mathbf{H}'(\xi_j)$. But the $\{a_k\}$ and $\{v_{jk}\}$ then satisfy the hypotheses of Proposition A.5, so (3.4) holds.

We now go to (ii). The relationship $\phi_{n+1-k}=\phi_k$ for all k is invariant under (1.5) if $\boldsymbol{\Delta}=-(1,1,\cdots,1)^t$, so we shall assume it. We first show that a trajectory cannot leave R through the boundaries $\phi_k=\phi_k^-$ or $\phi_k=\phi_M$, $k\neq j$. The vector field (1.5) does not cross $\phi_k=\phi_M$ for any k. For at $\phi_k=\phi_M$,

$$\dot\phi_k=-\beta+H(\phi_{k-1})-2M+H(\phi_{k+1});$$

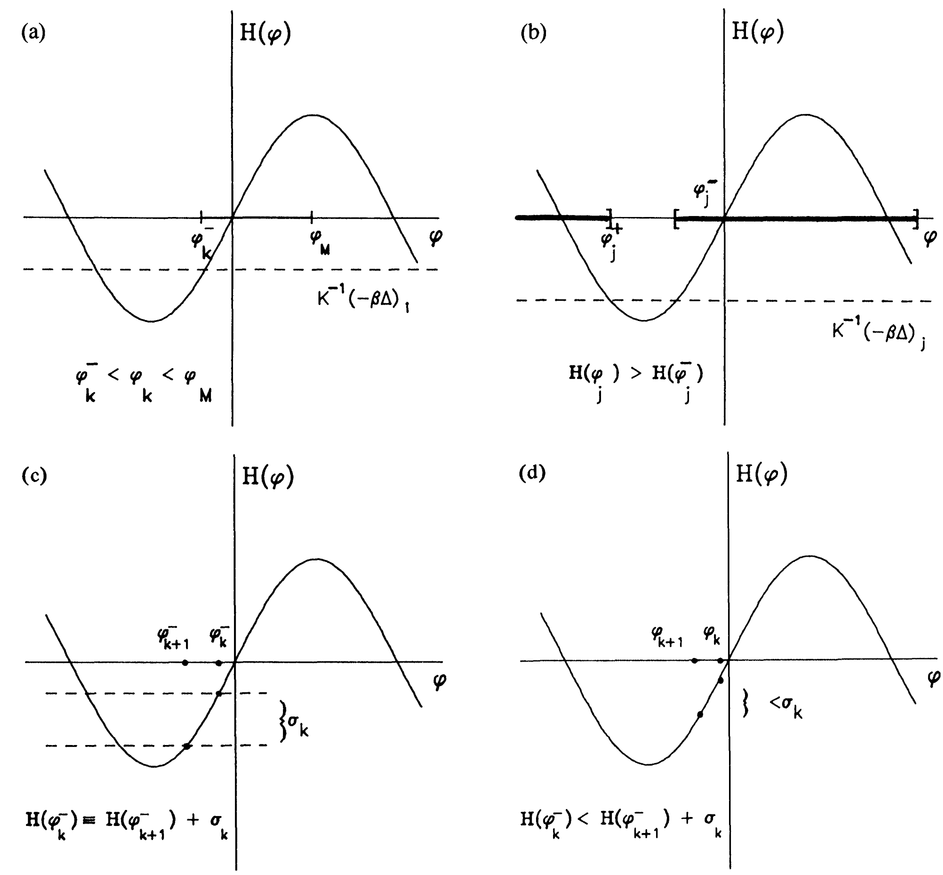

FIG. 3.3. *Some of the constraints on the* $\{\phi_k\}$ *in order that* $\phi\in R$: (a) $\phi_k^-<\phi_k<\phi_M$; (b) $H(\phi_j)>H(\phi_j^-)$; (d) $H(\phi_k)<H(\phi_{k+1})+\sigma_k$, *where* σ_k *is defined as in* (c).

since $H(\phi_{k\pm1})\le M$, $\dot\phi_k<0$. The surface $\phi_k=\phi_k^-$ *can* be crossed by the vector field, but not inside R. For

$$\dot\phi_k=-\beta+H(\phi_{k-1})-2H(\phi_k)+H(\phi_{k+1}). \tag{3.5}$$

The right-hand side of (3.5) vanishes at all critical points. If $\phi_{k\pm1}^-<\phi_{k\pm1}<\phi_M$, we have $H(\phi_{k\pm1})>H(\phi_{k\pm1}^-)$; so if we also have $\phi_k=\phi_k^-$, then $\dot\phi_k>0$ and the vector field points into R. Note that this argument works even if $k=j\pm1$, because all that is needed is that $H(\phi_{k\pm1})\ge H(\phi_{k\pm1}^{\pm})$. Now on the surface $\phi_k=\phi_k^-$, we may have $\dot\phi_k=0$ at some time t_0, i.e., if $\phi_{k\pm1}=\phi_{k\pm1}^-$ (ϕ_j^+ if $k\pm1=j$). But

$$\dot\phi_{k+1}=-\beta+H(\phi_k)-2H(\phi_{k+1})+H(\phi_{k+2}) \tag{3.6}$$

and $H(\phi_{k+2})\ge H(\phi_{k+2}^-)$. Hence, if $\phi_k=\phi_k^-$ and $\phi_{k+1}=\phi_{k+1}^-$ (ϕ_j^+ if $k+1=j$), we have $\dot\phi_{k+1}>0$ (so $H(\phi_{k+1})>H(\phi_{k+1}^-)$ for $t>t_0, t-t_0$ sufficiently small) unless $H(\phi_{k+2})=H(\phi_{k+2}^-)$. Following this argument, we conclude that unless $\phi_k=\phi_k^-$ for all $k\ne j$ and $\phi_j=\phi_j^+$, even if $\dot\phi_k=0$ for some time t, we will have $\phi_k^-\le\phi_k$ for succeeding times.

We next show that trajectories may not exit through surfaces of the form

$$H(\phi_k)=H(\phi_{k+1})+\sigma_k,\qquad k=1,\cdots,j-1. \tag{3.7}$$

For suppose that (3.7) holds for some k at some t_0. Then (3.5), (3.6) become

$$\dot{\phi}_k = -\beta + H(\phi_{k-1}) - H(\phi_k) - \sigma_k, \tag{3.8a}$$

$$\dot{\phi}_{k+1} = -\beta + \sigma_k - H(\phi_{k+1}) + H(\phi_{k+2}). \tag{3.8b}$$

We now use the inequalities (3.3) for $k \pm 1$. These imply that

$$\dot{\phi}_k \leq -\beta - \sigma_k + \sigma_{k-1}, \qquad k = 1, \cdots, j-1, \tag{3.9a}$$

$$\dot{\phi}_{k+1} \geq -\beta + \sigma_k - \sigma_{k+1}, \qquad k = 1, \cdots, j-2. \tag{3.9b}$$

But (3.7) and hence (3.8) hold at the critical point $\boldsymbol{\xi}_j$, where $\dot{\phi}_k = \dot{\phi}_{k+1} = 0$. Inserting the components of $\boldsymbol{\xi}_j$ into (3.8), we get that

$$-\beta - \sigma_k + \sigma_{k-1} = 0 = -\beta + \sigma_k - \sigma_{k+1}.$$

Thus (3.9)

$$\dot{\phi}_k \leq 0, \; \dot{\phi}_{k+1} \geq 0, \qquad k = 1, \cdots, j-2.$$

This implies that, even if (3.7) holds for some t, the trajectory does not exit R through the surface (3.7) with $k = 1, \cdots, j-2$. For $k = j-1$, the deductions from (3.8a), (3.9a) are still valid. We replace (3.8b), (3.9b) by

$$\begin{aligned} \dot{\phi}_j &= -\beta + H(\phi_{j-1}) - 2H(\phi_j) + H(\phi_{j-1}) \\ &= -\beta + 2\sigma_{k-1}. \end{aligned} \tag{3.10}$$

As before, by inserting $\boldsymbol{\phi} = \boldsymbol{\xi}_j$ into (3.10) we see that the right-hand side of (3.10) is zero, i.e., $\dot{\phi}_j = 0$. Since $\dot{\phi}_{j-1} \leq 0$, we have that the trajectory does not exit R through the surface (3.7) with $k = j-1$.

Trajectories may also not exit through the surface

$$0 = -\beta + H(\phi_{j-1}) - 2H(\phi_j) + H(\phi_{j+1}) \tag{3.11}$$

along which $\dot{\phi}_j = 0$. For we have just seen that (3.11) is equivalent to (3.7) for $k = j-1$, and that a trajectory may not exit through this surface.

Finally, trajectories may not exit through the surface $\phi_j = \phi_j^+$ or $\phi_j = \phi_j^-$, the boundaries of $H(\phi_j) > H(\phi_j^{\pm})$. At $\boldsymbol{\xi}_j$, $\phi_j = \phi_j^+$; since $\dot{\phi}_j < 0$, ϕ_j must decrease monotonely, and so cannot pass through $\phi = \phi_j^+$. Also, ϕ_j cannot decrease past $\phi_j = \phi_j^- - 2\pi$. For at $\phi_j = \phi_j^- \pmod{2\pi}$,

$$\dot{\phi}_j = -\beta + 2H(\phi_{j-1}) - 2H(\phi_j^-). \tag{3.12}$$

Since the right-hand side of (3.12) vanishes at the critical point, and $H(\phi_{j-1}) \geq H(\phi_{j-1}^-)$, the right-hand side of (3.12) is ≥ 0 at $\phi_j = \phi_j^- \pmod{2\pi}$. But $\dot{\phi}_j \leq 0$, so trajectories cannot reach $\phi_j = \phi_j^- \pmod{2\pi}$ unless $\phi_{j-1} = \phi_{j-1}^-$. Furthermore, by (3.5) with $k = j-1$, $\phi_j = \phi_j^- \pmod{2\pi}$, and $\phi_{j-1} = \phi_{j-1}^-$, we have $\dot{\phi}_{j-1} > 0$ unless $\phi_{j-2} = \phi_{j-2}^-$; for later times, this implies that $\dot{\phi}_j > 0$, and so contradicts $\dot{\phi}_j \leq 0$. Hence $\phi_{j-2} = \phi_{j-2}^-$. A similar argument shows that if $\phi_j = \phi_j^-$, then $\phi_k = \phi_k^-$ for all k. Thus trajectories of R do not pass through $\phi_j = \phi_j^- - 2\pi$, but rather tend to $\boldsymbol{\xi}_0$ as $t \to \infty$. □

Lemmas 3.3 and 3.4 together show that the two branches of the unstable manifold of $\boldsymbol{\xi}_j$ form an invariant circle. We next show that the circle is smooth. Since (1.5) is C^∞, so is the unstable manifold [23]; thus, smoothness need only be proved at $\boldsymbol{\xi}_0$ where the branches join. We know from Lemma 3.3. that the right branch approaches $\boldsymbol{\xi}_0$ tangent to the (left branch of the) eigenspace of the eigenvalue λ_0 which is closest to zero. In such a circumstance, the degree of contact of the trajectory with the eigenspace is bounded below by the ratio λ_1/λ_0, where λ_1 is the next smallest (in absolute value) eigenvalue of (1.5) at ξ_0; this ratio goes to ∞ as $\beta \to \beta_0$. Thus, to prove that the invariant circle is smooth at ξ_0 (with arbitrary smoothness for $\beta_0 - \beta$ sufficiently small), it suffices to prove

LEMMA 3.5. *The left branch of the unstable manifold of ξ_j enters ξ_0 tangent to the* (*right branch of the*) *eigenspace of the eigenvalue* λ_0.

Proof. Generically, trajectories approaching a sink do approach tangent to the eigenvector of the least negative eigenvalue. The exceptional trajectories approach tangent to the span of the remaining eigenspaces. We shall show that trajectories of R are not exceptional.

By Lemma 3.4, trajectories in R satisfy $\phi_k > \phi_k^-$ $(k \neq j)$, where ϕ_k^- is the kth coordinate of ξ_0; hence, as a trajectory in R approaches ξ_0, we have $\dot{\phi}_k < 0$ for all k. Now ξ_0 is a hyperbolic critical point, so trajectories near it behave like those of the linearization of (1.5) around ξ_0. Since trajectories in the eigenspace of a pair of complex eigenvalues oscillate around the critical point, and we have $\dot{\phi}_k < 0$ for all k, the trajectories in question must in fact approach ξ_0 tangent to the span of the eigenspaces of the remaining (real) eigenvalues. Because the real eigenvalues are ordered, trajectories of the linear system approach tangent to exactly one eigenspace, and, furthermore, to an eigenvector within that eigenspace. Thus, to rule out that trajectories of R are exceptional, it suffices to show, for any real eigenvalue $\lambda \neq \lambda_0$ and associated eigenvector $Z = (z_1, \cdots, z_n)$, that the z_i's cannot all have the same sign. ($\operatorname{Sgn} z_k \equiv \operatorname{sgn} z_1$ for all k is necessary if we are to have $\dot{\phi}_k < 0$ for all k.) But the linearization of (1.5) around ξ_0 has the form KA where $A = \operatorname{diag}(a_1, a_2, \cdots, a_n)$ with $a_k > 0$ $(k \neq j)$, $a_{n+1-k} = a_k$. For $\beta = \beta_0$, $a_j \equiv H'(\phi_j(\beta_0)) = 0$, so the result follows from Proposition A.6. For $\beta - \beta_0$ sufficiently small, it follows by continuity. □

To finish Theorem 3.1, it remains to show that the smooth attracting invariant manifold persists for $\beta > \beta_0$, $\beta - \beta_0$ sufficiently small, and that the circle is homotopic to $\phi_k = 0$ for all $k \neq j$. To prove the first assertion, we perturb (1.5) around $\beta = \beta_0$. For the invariant manifold to persist and be C^r, a certain "Lyapunov-type number" must be $< 1/r$ [22]; this number measures the ratio of the asymptotic (exponential) rate of contraction on the manifold to that of the asymptotic rate of approach to the manifold. This number is determined only by the ω-limit set on the invariant manifold, which, for (1.5) $\beta = \beta_0$, is the unique sink-saddle. For this case, the tangential contraction rate tends to zero as $\beta \to \beta_0$ from below, but the normal contraction rate stays bounded away from zero. (Equivalently, only one eigenvalue of the linearization at ξ_0 tends to zero as the sink and saddle coalesce.) Thus, the invariant manifold persists for $\beta > \beta_0$ and can be made arbitrarily smooth by taking $\beta - \beta_0$ small.

To see that the invariant circle is homotopic to the circle $\phi_k = 0$ for all $k \neq j$, we recall that, along the left branch of the unstable manifold of ξ_j, we have $\phi_k^- < \phi_k < \phi_M$, $k \neq j$. Also, the right branch is arbitrarily small for $\beta_0 - \beta$ small. Thus, as ϕ_j changes by 2π along the closure of the two branches, ϕ_k stays in a neighborhood of $\phi_k = 0$ having length less than 2π. It follows that the closure of the trajectories can be deformed into a circle for which $\phi_k = 0$, for all $k \neq j$. □

Remark. The attracting invariant circle of (1.5) (or equivalently (1.4b)) corresponds to an attracting 2-dimensional torus for (1.4), with variables θ_1 and ϕ_j. The dynamics on this torus is an $O(\varepsilon^2)$ perturbation of an uncoupled flow, with $\theta_1(t)$ satisfying $\theta_1' = \omega_1 + \varepsilon H(\phi_1)$ and $\phi_1(t)$, $\phi_j(t)$ the values along the (slow) limit cycle of (1.5), written in the original time variable t.

4. Frequency plateaus. In §3, we proved the existence of an attracting invariant circle for (1.5) on T^n. We now show why this circle corresponds to a pair of frequency plateaus with a break between the j th and $(j+1)$st oscillators. (Recall that $n+1=2j$.)

The "frequency" of an oscillator coupled to others requires a definition; one reasonable definition is

$$\lim_{T\to\infty}\frac{1}{T}\int_0^T \theta_k'\,dt \tag{4.1}$$

over some trajectory of (1.3), (1.4), provided that (4.1) converges. Note that this definition yields θ' if θ' is constant, and is, a priori, dependent on the trajectory. To compute (4.1) requires going to the full equations (1.3), (1.4). However, to lowest order, the frequency difference

$$\lim_{T\to\infty}\frac{1}{T}\int_0^T \phi_k'\,dt \tag{4.2}$$

can be computed from trajectories of (1.5). For any trajectory in the basin of attraction of the limit cycle of (1.5), (4.2) reduces to

$$\frac{\varepsilon}{T_0}\int_0^{T_0}\dot{\phi}_k\,d\tau$$

where $T_0=T_0(\beta)$ is the period of the limit cycle, and the integration of $\dot{\phi}_k$ is done along the limit cycle. By the fundamental theorem of calculus, (4.2) may be written as

$$\frac{\varepsilon}{T_0}\left[\hat{\phi}_k(T_0)-\hat{\phi}_k(0)\right]$$

where $\hat{\phi}_k(\tau)$ is the covering map of $\phi_k(\tau)$ (i.e., values of $\hat{\phi}_k(\tau)$ are not identified mod 2π). It was shown in §3 that the invariant circle is homotopic to the circle $\phi_k=0$, $k\neq j$, $0\leq\phi_j\leq 2\pi$. Thus $\hat{\phi}_k(T_0)=\phi_k(T_0)$, $k\neq j$. (We may assume that $\hat{\phi}_k(0)=\phi_k(0)$ by choice of covering map.) But $\phi_k(T_0)=\phi_k(0)$ by the periodicity of ϕ along this solution. Thus (4.1) vanishes for $k\neq j$, i.e., for $1\leq k\leq j$, the frequency of the kth oscillator is independent of k; similarly, this is true for $j+1\leq k\leq n$. However, for $k=j$, we have $\hat{\phi}_j(T_0)=\hat{\phi}_j(0)+2\pi$. This implies that the jump in frequency between the $(j+1)$st $+j$th oscillators is $2\pi\varepsilon/T_0$ (in ordinary time).

On each of the two plateaus, the phase differences ϕ_k are periodic in time rather than constant in time. That is, the oscillators remain phase-locked "on the average" rather than at every instant; some authors refer to this phenomenon as "phase-trapping" [28]. Furthermore, the frequency on each of the "plateaus" is not exactly constant, for (1.5) are valid only up to $O(\varepsilon)$ (in the scaled time, or $O(\varepsilon^2)$ in the original time scale). For $H=\sin\phi$, plateaus emerge when $\beta\geq\beta_0=2/j^2=8/(n+1)^2$. This implies that the total change in frequency from oscillators 1 to $n+1$, for $\beta\approx\beta_0$, is $n\varepsilon\beta_0=8\varepsilon n/(n+1)^2=O(\varepsilon,\frac{1}{n})$. Thus, for a fixed total change in frequency, the larger the n, the harder it is to phase-lock. This contrasts with a nonodd function H, e.g. $H=\sin\phi+\delta[\cos\phi-1]$ for which the total change in frequency just prior to loss of phase-locking is $O(\varepsilon)$, but does not go to zero as $n\to\infty$ [21].

To understand how the size of the frequency jump varies as β increases, we first note that $T_0\to\infty$ as $\beta\to\beta_0$. Furthermore, we claim that T_0 varies like $1/\sqrt{\beta-\beta_0}$. For consider the phase-locked solution $\phi(\tau)$ to (1.5), $\beta=\beta_0$, and choose a small interval I around the unique critical point. For $\beta-\beta_0$ sufficiently small, the large interval S^1-I is traversed in a finite amount of time (bounded above independent of β). Within I, a

β-dependent coordinate ψ may be chosen so that the equation takes the form $\dot{\psi}=\psi^2+\nu(\beta)$ where $\nu(\beta_0)=0$, $\nu'(\beta_0)>0$. If $a,b>0$, the time it takes ψ to go from $-a$ to $+b$ is

$$\frac{1}{\nu}\left[\tan^{-1}\left(\frac{\psi}{\nu}\right)\right]_{\psi=-a}^{\psi=b}=O\left(\frac{1}{\sqrt{\beta-\beta_0}}\right).$$

Since the time it takes to traverse I dominates the finite time to cross S^1-I, we see that $T_0=O(1/\sqrt{\beta-\beta_0})$ as $\beta\to\beta_0^+$.

The above computation shows that, as $\beta\to\beta_0^+$, the period T_0 passes continuously to $+\infty$ from a finite number. Thus the jump $2\pi/T_0$ in frequency between the two plateaus changes continuously as β is varied and tends to zero as $\beta\to\beta_0^+$. In particular, there need be no rational relationship between the frequencies of the two plateaus. The calculation also suggests at first glance that the frequency jump is never piecewise constant as β is changed (for $\beta-\beta_0$ small). However, this last conclusion is suspect: as mentioned above, the calculations are accurate only up to $O(\varepsilon^2)$ (in the original time scale). For fixed ε small and $\beta\to\beta_0^+$, the effects of the nonzero ε could lead to piecewise constancy of the frequencies over some (small) intervals in β.

In Fig. 4.1 we show numerical calculations of equations (1.5) for β near β_0 and a larger value of β, i.e., a steeper gradient in natural frequency. Note that more plateaus emerge. We conjecture that when there are $k+1$ plateaus, there is a k-dimensional subtorus T^k of T^n corresponding to k degrees of freedom at the jumps. It is less clear how to analytically define the frequencies on these plateaus.

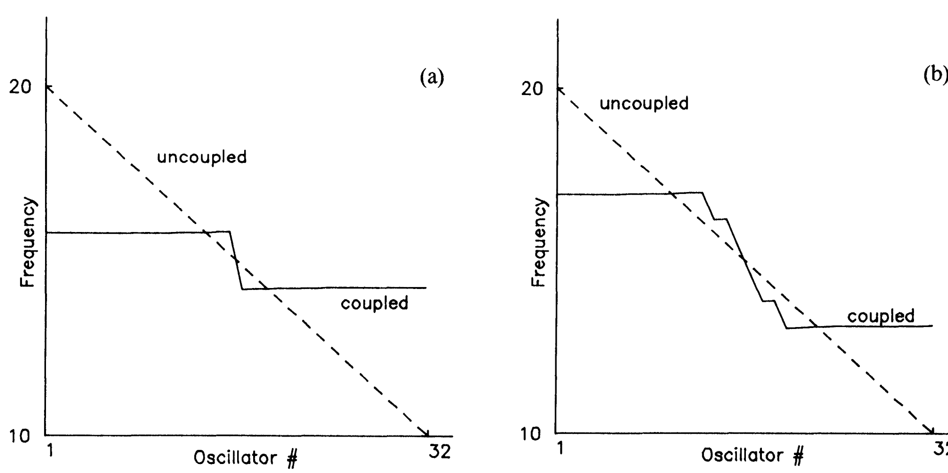

FIG. 4.1. *Frequency vs. k for* $\dot{\phi}_k=-10/31+\delta[\sin\phi_{k+1}-2\sin\phi_k+\sin\phi_{k-1}]$ *for* (a) $\delta=32$, (b) $\delta=18$. *Note that decreasing* δ *and leaving the frequency difference* 10/31 *the same is equivalent* (*under a change of time scale*) *to increasing the frequency difference.*

5. Nonuniform or nonisotropic coupling. In this section we consider some of the effects of relaxing the hypotheses that the coupling be isotropic and uniform; we still assume that only nearest neighbors are coupled, and that the coupling is weak.

5.1. Nonisotropic coupling. In the previous sections, we assumed that adjacent oscillators have symmetric influences on one another. Suppose instead that the forward coupling has a constant (independent of k) ratio α to the backward coupling (see Fig. 5.1.a). The equations for the ϕ_k (with H odd as before) then have the form

$$(5.1)\qquad \begin{aligned} \dot{\phi}_1 &= -\beta + H(\phi_2) - (\alpha+1)H(\phi_1), \\ \dot{\phi}_k &= -\beta + H(\phi_{k+1}) - (\alpha+1)H(\phi_k) + \alpha H(\phi_{k-1}), \qquad k=2,\cdots,n-1, \\ \dot{\phi}_n &= -\beta - (\alpha+1)H(\phi_n) + \alpha H(\phi_{n-1}). \end{aligned}$$

These equations reduce to (1.5) when $\alpha=1$. Note that $\alpha>1$ implies that forward coupling is stronger and $\alpha<1$ means backward coupling is stronger.

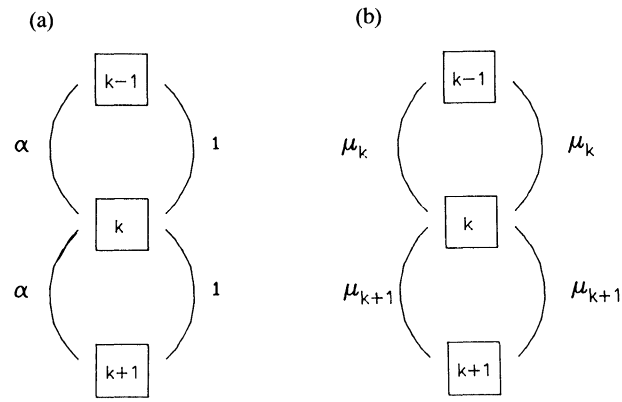

FIG. 5.1. (a) *Nonisotropic coupling. The forward coupling has a constant ratio* α *to the backward coupling.* (b) *Nonuniform coupling. There is a gradient in coupling strength, e.g. the diffusion coefficient associated with pair of cells varies with* k.

PROPOSITION 5.1. *Let* $y_k = H(\phi_k)$. *Then the critical point of* (5.1) *satisfies*

$$(5.2)\qquad y_k = -\frac{\{n+1-k+k\alpha^{n+1}-(n+1)\alpha^k\}}{(1-\alpha)(1-\alpha^{n+1})}\beta.$$

Proof. Insert (5.2) in (5.1) and check. □

Once we know the phase-locked solution of (5.1), we may compute the frequency of entrainment from the first equation of (1.4): when there is phase-locking, the frequency is $\dot{\theta}_k$ for any k, and

$$(5.3)\qquad \begin{aligned} \dot{\theta}_1 &= \omega_1 + \varepsilon H(\phi_1) + O(\varepsilon^2) \\ &= \omega_1 + \varepsilon \frac{[n(\alpha-1)+\alpha(1-\alpha^n)]}{(1-\alpha)(1-\alpha^{n+1})}\beta + O(\varepsilon^2). \end{aligned}$$

(For $\alpha=1$, (5.3) reduces to $\dot{\theta}_1 = \omega_1 - \varepsilon n\beta/2$, the average of the frequencies. (5.2) reduces to $y_k = -\beta k(n+1-k)/2$.)

Figures 5.2 and 5.3 graph y_k vs. k for several α, and $\dot{\theta}_1$ vs. α when $n=9$ and $n=29$. We see from the formulas and the pictures that one effect of e.g. increasing α is to skew the peak of the graph of y_k vs. k toward the higher k (lower frequency) end. thus, when β is large enough that phase-locking is no longer possible, we would expect a break in frequency to occur at the lower frequency end. Changing α also changes the frequency of the phase-locked solution. For example, if $\alpha>1$, then for n large the frequency is close to, but less than, ω_1. Figure 5.4 shows a pair of graphs of frequency vs. k for frequency gradients sufficient to form plateaus. Note that the plateaus are not symmetric with respect to average frequency.

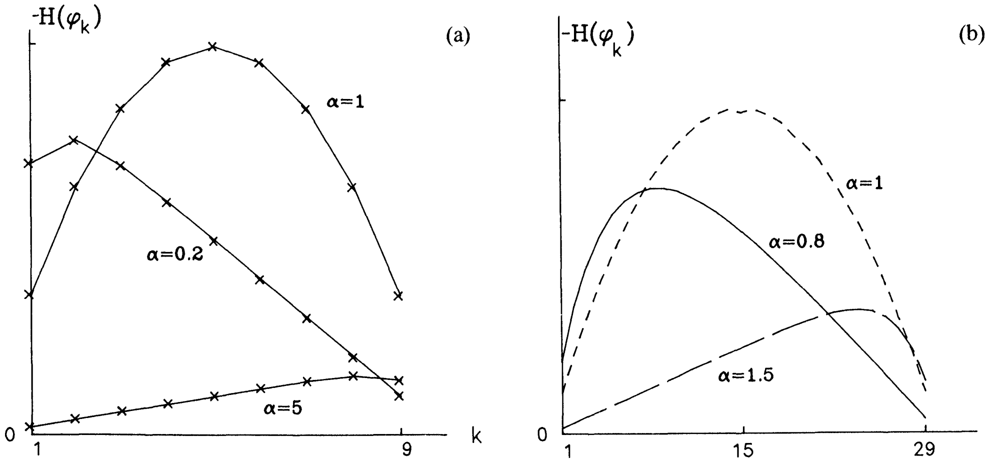

FIG. 5.2. *The graphs of* $-H(\phi_k)$ *vs.* k *for various* α. (a) $n=9$, (b) $n=29$.

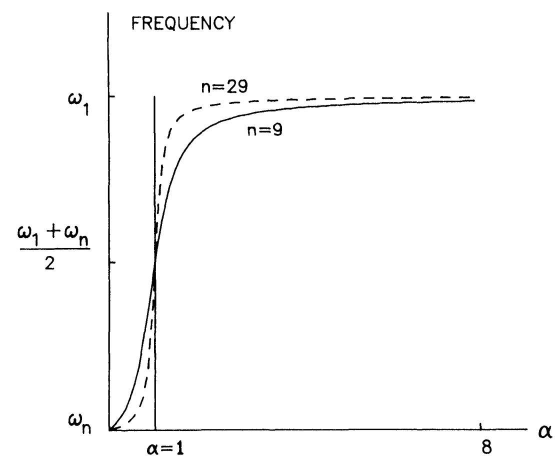

FIG. 5.3. *The frequency of the phase-locked solution as a function of the amount of anisotropy,* $n=9$ *and* $n=29$.

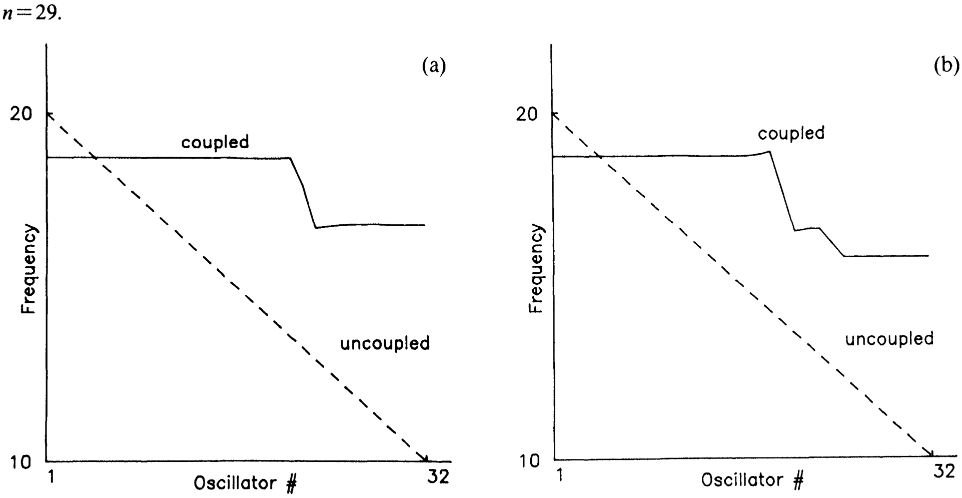

FIG. 5.4. *Frequency vs.* k *for anisotropic coupling, equation* $\dot{\phi}_k=-10/31+\delta[.8\sin\phi_{k+1}-1.8\sin\phi_k+\sin\phi_{k-1}]$, *with* a) $\delta=24$ *and* b) $\delta=10$. *The forward coupling is stronger, and the plateaus are shifted upward.*

5.2. Nonuniform coupling. We now assume that the coupling is isotropic, but varies with k. That is, we suppose that the coupling is diffusive, but that a different diffusion coefficient is associated with each pair of oscillators. (See Fig. 5.1.b.) The phase difference equations now take the form

$$\begin{aligned}\dot{\phi}_k &= -\beta+\mu_{k+1}H(\phi_{k+1})-2\mu_k H(\phi_k)+\mu_{k-1}H(\phi_{k-1}),\\ H(-\phi_0)&=0=H(\phi_{n+1}).\end{aligned} \tag{5.4}$$

The critical point of (5.4) may easily be found: If we let $w_k=\mu_k H(\phi_k)$, then, at phaselocking, the w_k satisfy

$$O=\beta\mathbf{\Delta}+K\mathbf{W}$$

where $\mathbf{\Delta}=-(1,1,\cdots,1)^t$, $\mathbf{W}=(w_1,\cdots,w_n)^t$ and K is as in §3. Hence, as before, $w_k=-\beta k(n+1-k)/2$, so the critical point is given by

$$H(\phi_k)=\frac{-\beta k(n+1-k)}{2\mu_k}. \tag{5.5}$$

It can be seen from (5.5) that a gradient in coupling changes the value k_0 of k at which $\max_k H(\phi_k)$ occurs. (If $\mu(x)$ is monotone increasing (resp. decreasing), k_0 decreases (resp. increases).) This suggests that if β is increased sufficiently to prevent phaselocking, and a pair of plateaus results, then the break will be in the high frequency range for $\mu(x)$ increasing, and low frequency range for $\mu(x)$ decreasing.

The frequency of the phase-locked solution is computed from

$$\dot{\theta}_1=\omega_1+\varepsilon\mu_1 H(\phi_1).$$

From (5.5), we see that $\mu_1 H(\phi_1)$ is independent of the coupling coeffients $\{\mu_k\}$, so that the frequency is the same as for uniform isotropic coupling, i.e. $\dot{\theta}_1=\omega_1-\varepsilon n\beta/2$.

5.3. Nonsymmetric coupling function H. Finally, we give a few simulations (Fig. 5.5) to show an effect of allowing $H(\phi)$ to be nonodd. Note that if $H(\phi)=\sin(\phi+\Phi_0)$ for $\Phi_0>0$, the plateaus may lie entirely above the line of natural frequencies.

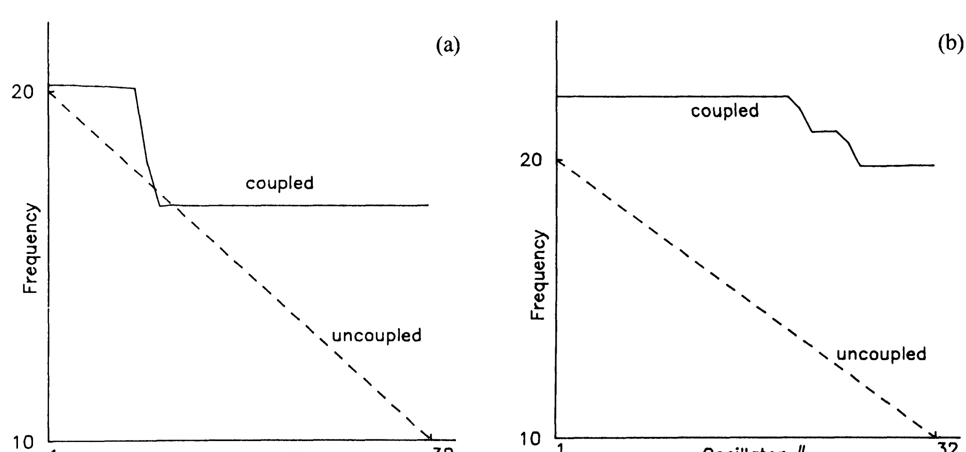

FIG. 5.5. *Frequency vs. k for* $H(\phi)=\sin(\phi+\Phi_0)$, $\Phi_0>0$. (a) $\dot{\phi}_k=-10/31+14[\sin(\phi_{k+1}+.2)-2\sin(\phi_k+.2)+\sin(\phi_{k-1}+.2)]$. (b) $\dot{\phi}_k=-10/31+11[.2\sin(\phi_{k+1}+.4)-1.2\sin(\phi_k+.4)+\sin(\phi_{k-1}+.4)]$.

Appendix. We wish to prove some results about eigenvalues and eigenvectors of matrices of the form KA, where K is the $n\times n$ tridiagonal matrix with $K_{ii}=-2$, $K_{i,i+1}=K_{i+1,i}=1$ and A is a diagonal matrix $A=\operatorname{diag}(a_1,a_2,\cdots,a_n)$.

PROPOSITION A.1. *No eigenvalue of KA is pure imaginary. If $a_k>0$ for all k, then all eigenvalues of KA have negative real parts.*

Proof. KA is a tridiagonal matrix with $(KA)_{ii}=-2a_i$, $(KA)_{i,i+1}=a_{i+1}$, $(KA_{i+1,i})=a_i$. By the Gershgorin theorem [A1], any eigenvalue λ of KA must satisfy

$$|\lambda+2a_k|\le 2|a_k| \tag{A.1}$$

for some k. Since the a_k are real, (A.1) rules out pure imaginary eigenvalues. If $a_k>0$ for all k, then (A.1) implies that $\operatorname{Re}\lambda\le 0$. Now $\operatorname{Re}\lambda=0$ can happen only if λ is pure imaginary, or if $\lambda=0$. But $\det(KA)=\det A\cdot\det K\ne 0$, so $\lambda\ne 0$ and $\operatorname{Re}\lambda<0$. □

PROPOSITION A.2. (i) *Suppose that $a_j=0$ for some j, $a_k\ne 0$ for $k\ne j$. Then there exists a unique zero eigenvalue of KA.*

(ii) *Let $[KA,Z]$ denote the $n\times(n+1)$-matrix obtained from KA by adding the n-vector Z as the last column. If $\{a_k\}$ is as above, then $[KA,Z]$ has rank n for $Z=(1,1,\cdots,1)^t$ and $Z=(z_1,\cdots,z_n)^t$ with $z_j=-2$, $z_{j+1}=z_{j-1}=1$ and $z_k=0$, $k\ne j, j\pm 1$.*

Proof. (i) $\operatorname{Det}(KA)=\det K\cdot\det A=0$, so KA has a zero eigenvalue. It can be checked by direct computation that KA has a unique null-vector $V=(v_1,\cdots,v_n)$, with $v_j=1$, $v_k=0$, $k\ne j$. (The equations for the $\{v_k\}$ split into two systems for $v_1,\cdots,v_{j-1}$ and v_{j-1}, v_{j+1}, $v_{j+2},\cdots,v_n$ respectively. The first has $v_1=\cdots=v_{j-1}=0$ as its only solution; using $v_{j-1}=0$, the other system has $v_{j+1}=\cdots=v_n=0$ as its only solution.) Furthermore, if W is the unique null-vector of $(KA)^t$, it is easy to show that $W_j\ne 0$, and hence $V\cdot W\ne 0$. This implies that KA has a simple zero eigenvalue.

(ii) The rank of $[KA,Z]$ is the dimension of the span of its columns. Since the kth column of KA is a_k times the kth column of K, the rank of $[KA,Z]$ is the same as that of $[KI_j,Z]$, where I_j is the identity matrix except for the jth column, which is zero. To show that $[KI_j,Z]$ has rank n, it suffices to show that $W\cdot Z\ne 0$, where $W=(w_1,\cdots,w_n)$ now denotes the null-vector of $(KI_j)^t$. Thus $w_1,\cdots,w_n$ satisfy the equations

$$\begin{aligned} &-2w_1+w_2=0,\\ &w_{k-1}-2w_k+w_{k+1}=0, \qquad k\ne 1,n,\\ &w_{n-1}-2w_n=0 \end{aligned} \tag{A.2}$$

with the jth equation omitted. From (A.2), we see that w_1 determines $w_2,\cdots,w_j$; indeed, (A.2) implies that $w_k=kw_1$ for $k\le j$. Similarly, w_n determines $w_j,\cdots,w_{n-1}$. It follows that the $\{w_k\}$ all have the same sign, and so $W\cdot(1,1,\cdots,1)\ne 0$.

To see that $W\cdot Z\ne 0$ for $z_j=-2$, $z_{j-1}=z_{j+1}=1$, $z_k=0$, $k\ne j$, $j\pm 1$, we note that $W\cdot Z=0$ implies that (A.2) is supplemented by the jth equation $w_{j-1}-2w_j+w_{j+1}=0$. But the full set of equations $k=1,\cdots,n$ of (A.2) is the system $KW=0$. Since K is nonsingular, and W is nontrivial, this is impossible. □

PROPOSITION A.3. *Suppose that $a_j<0$ for some j and $a_k>0$ for all $k\ne j$. Then there exists a unique eigenvalue of KA with a positive real part.*

Proof. We define a path K_ζ between KA and $K\bar{A}$, where $\bar{A}=\operatorname{diag}(a_1,a_2,\cdots,|a_j|,\cdots,a_n)$ as follows: $K_\zeta=KA$ except for the jth column, and $(K_\zeta)_{ij}=\zeta(KA)_{ij}$. Thus $K_{-1}=K\bar{A}$ and $K_1=KA$. The only value of ζ for which $\det K_\zeta=0$ is $\zeta=0$. By Proposition A.2, K_ζ has a simple zero eigenvalue at $\zeta=0$. Since, by Proposition A.1, all eigenvalues of K_ζ, $\zeta<0$ have negative real part, then for $\zeta>0$, K_ζ must have a unique positive eigenvalue. Since K_ζ has no pure imaginary eigenvalues for any ζ, this is the only eigenvalue with positive real part. □

The comments of Charles Johnson were helpful in proving the following:

PROPOSITION A.4. *Assume that* $A=\operatorname{diag}(a_1,\cdots,a_{j-1},-a_j,a_{j+1},\cdots,a_n)$, *with* $n+1=2j$, $a_k>0$ *for all* k. *Then the unique positive eigenvalue* λ *of* KA *satisfies* $\lambda\le 2a_j$.

Proof. Instead of KA, we shall consider $B=D^{-1}KA\bar{D}$, where $\bar{D}=\operatorname{diag}(d_1,d_2,\cdots,d_{j-1},1,d_{j+1},\cdots,d_n)$, with $d_i=\sqrt{a_j/a_i}$. B is a tridiagonal matrix with $B_{ii}=-2a_i$, $B_{i,i+1}=B_{i+1,i}=\sqrt{a_ia_{i+1}}$, $i=1,\cdots,j-2$ and $i=j+2,\cdots,n$. The 3×3-matrix $B_{ik}, j-1<i, k<j+1$, is

$$\begin{pmatrix} -2a_{j-1} & -\sqrt{a_{j-1}a_j} & 0 \\ \sqrt{a_{j-1}a_j} & 2a_j & \sqrt{a_ja_{j+1}} \\ 0 & -\sqrt{a_ja_{j+1}} & -2a_{j+1} \end{pmatrix}. \tag{A.3}$$

To get the estimate $\lambda\le 2a_j$, we shall estimate the spectrum of $C=\frac{1}{2}(B+B^t)$, and then relate this to the spectrum of B. Since B is symmetric except in the 3×3-block (A.3), $B=C$ outside of that block. $C_{ik}, j-1<i, k<j+1$, is given by the 3×3 diagonal matrix $\operatorname{diag}(-2a_{j-1},2a_j,-2a_{j+1})$. Thus C splits into the direct sum of two $(j-1)\times(j-1)$-matrices C_1, C_2 and the 1×1-matrix with entry $2a_j$. Thus the spectrum of C consists of $2a_j$ plus the spectrum of the C_i. We now show that the spectrum $\sigma(C_1)$ of C_1 is entirely negative. Let $U=(u_1,\cdots,u_{j-1})$. Then

$$\begin{aligned}\langle C_1U,U\rangle &= -2\sum_{i=1}^{j-1} a_iu_i^2+2\sum_{i=1}^{j-2}\sqrt{a_ia_{i+1}}\,u_iu_{i+1}\\ &= -\sum_{i=1}^{j-2}\left(\sqrt{a_i}\,u_i-\sqrt{a_{i+1}}\,u_{i+1}\right)^2-a_1u_1^2-a_{j-1}u_{j-1}^2<0,\end{aligned}$$

so C_1 is negative definite. Similarly, so is C_2. Thus $\max\sigma(C)=2a_j$.

Let $(\cdot,\cdot)$ denote the usual complex inner product and $\mathcal{F}(C)=\{(Cz,z)|z\in\mathbb{C},\|z\|=1\}$. Since C is a real symmetric (hence Hermitian) matrix, $\mathcal{F}(C)$ is the convex hull of $\sigma(C)$ [A2]. In particular, $\max\mathcal{F}(C)=\max\sigma(C)$. But C is the symmetrization of B, so $(Cz,z)=\operatorname{Re}(Bz,z)$. Thus $\max\mathcal{F}(C)=\max\operatorname{Re}\mathcal{F}(B)$. But for any matrix B, $\sigma(B)=\mathcal{F}(B)$. Hence $\max\operatorname{Re}\sigma(B)\le\max\operatorname{Re}\mathcal{F}(B)$. Since B is known to have a unique real positive eigenvalue λ, it follows that $\lambda\le\max\sigma(C)=2a_j$. □

PROPOSITION A.5. *Let* $A=\operatorname{diag}(a_1,\cdots,a_{j-1},a_j,a_{j-1},\cdots,a_1)$, *with* $a_k>0$, $k\ne j$ *and* $a_j<0$. *Assume that* $a_1\ge a_2\ge\cdots\ge a_{j-1}$ *and that* $a_{k-1}+a_{k+1}<2a_k$ *for all* $k=2,\cdots,j-2$. *Let* $V=(v_1,\cdots,v_n)$ *be the eigenvector of the unique positive eigenvalue* λ *of* KA. *Then* $\operatorname{sgn}v_j=-\operatorname{sgn}v_k$ *for all* $k\ne j$. *Also*, $a_kv_k\le a_{k+1}v_{k+1}$ *for* $k\le j-1$.

Proof. The eigenvector V is a nontrivial solution to

$$\begin{aligned} &-(2a_1+\lambda)v_1+a_2v_2=0,\\ &a_{k-1}v_{k-1}-(2a_k+\lambda)v_k+a_{k+1}v_{k+1}=0,\\ &a_{n-1}v_{n-1}-(2a_n+\lambda)v_n=0.\end{aligned} \tag{A.4}$$

If $v_1>0$, then $v_2>0$ by the first equation of (A.4). Also

$$v_2=\frac{2a_1+\lambda}{a_2}v_1>\frac{2a_2+\lambda}{a_2}v_1>2v_1. \tag{A.5}$$

Furthermore,

$$v_{k+1}-v_k=\frac{(2a_k+\lambda)v_k-a_{k-1}v_{k-1}}{a_{k+1}}-v_k \tag{A.6}$$
$$=\frac{2a_k+\lambda-a_{k+1}}{a_{k+1}}\left[v_k-\left(\frac{a_{k-1}}{2a_k+\lambda-a_{k+1}}\right)v_{k-1}\right].$$

Now $\lambda>0$, $a_k>a_{k+1}$ implies that $(2a_k+\lambda-a_{k+1})/a_{k+1}>1$, $k=2,\cdots,j-2$. Also, $a_{k-1}/(2a_k+\lambda-a_{k+1})<a_{k-1}/(2a_k-a_{k+1})<1$. (The last inequality is equivalent to $a_{k-1}+a_{k+1}<2a_k$ which holds by hypothesis.) Hence, from (A.6) we have

$$v_{k+1}-v_k>v_k-v_{k+1}$$

which implies that $\operatorname{sgn} v_k=\operatorname{sgn} v_1$, $k=1,\cdots,j-1$. By symmetry, $v_{n+1-k}=v_k$. Finally, for $k=j$ we see that

$$a_{j-1}v_{j-1}+a_{j+1}v_{j+1}=(2a_j+\lambda)v_j. \tag{A.7}$$

The left-hand side of (A.6) is positive, since $v_{j\pm1}$, $a_{j\pm1}>0$. By Proposition A.4, $\lambda\leq|2a_j|$. Since $a_j<0$, this implies that $v_j<0$.

To show that

$$a_kv_k\leq a_{k+1}v_{k+1}, \qquad k=1,\cdots,j-1, \tag{A.8}$$

we first consider $k=j-1$. By (A.7) and symmetry, $2a_{j-1}v_{j-1}=(2a_j+\lambda)v_j\leq 2a_jv_j$ (since $\lambda>0, v_j<0$). For $k=1$, (A.8) follows from (A.5). Also

$$a_{k+1}v_{k+1}=(2a_k+\lambda)v_k-a_{k-1}v_{k-1}\geq a_kv_k+(a_kv_k-a_{k-1}v_{k-1}).$$

Thus, by induction, we have (A.8) for $k=2,\cdots,j-2$. □

PROPOSITION A.6. *Let* $A=\operatorname{diag}(a_1,\cdots,a_j,a_{j-1},\cdots,a_1)$ *with* $a_j=0$, $a_k>0$, $k\neq j$. *Let* $Z=(z_1,\cdots,z_n)$ *be an eigenvector of any real eigenvalue* $\lambda<0$ *of* KA. *Then for some* k_1, k_2, $\operatorname{sgn} z_{k_1}\neq\operatorname{sgn} z_{k_2}$.

Proof. If for some $k\neq j$ we have $\operatorname{sgn} z_k\neq\operatorname{sgn} z_1$, we are done. Otherwise consider (A.4) with $k=j$:

$$a_{j-1}z_{j-1}+a_{j+1}z_{j+1}=\lambda z_j.$$

Since $a_{j\pm1}>0$, $\lambda<0$, we have $\operatorname{sgn} z_j\neq\operatorname{sgn} z_{j\pm1}$. □

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REFERENCES

[1] J. NEU, *Coupled chemical oscillators*, SIAM J. Applied Math., 37 (1979), pp. 307–315.
[2] ———, *Large populations of coupled chemical oscillators*, SIAM J. Appl. Math., 38 (1980), pp. 305–316.
[3] P. J. HOLMES, *Phase locking and chaos in coupled limit cycle oscillators*, preprint.
[4] R. H. RAND AND P. J. HOLMES, *Bifurcation of periodic motions in two weakly coupled Van der Pol oscillators*, Internat. J. Nonlinear Mech. 15 (1980), pp. 387–399.
[5] M. HIRSCH, *Systems of differential equations which are competitive or cooperative*, I. *Limit sets*, this Journal, 13 (1982), pp. 167–179.
[6] M. KAWATO, M. SOKABE AND R. SUZUKI, *Synergism and antagonism of neurons caused by an electrical synapse*, Biol. Cybernet., 34 (1979), pp. 81–89.

[7] M. KAWATO AND R. SUZUKI, *Two coupled neural oscillators as a model of the circadian pacemaker*, J. Theoret. Biol., 86 (1980), pp. 547–575.

[8] A. H. COHEN, P. J. HOLMES AND R. H. RAND, *The nature of the coupling between segmental oscillators of the lamprey spinal generator*, J. Math. Biol., 13 (1982), pp. 345–369.

[9] F. C. HOPPENSTEADT AND J. P. KEENER, *Phase locking of biological clocks*, J. Math. Biol., 15 (1982), pp. 339–349.

[10] M. ASHKENAJI AND H. G. OTHMER, *Spatial patterns in coupled biochemical oscillators*, J. Math. Biol., 5 (1978), pp. 305–350.

[11] O. E. ROSSLER, *Chemical turbulence: Chaos in a simple reaction-diffusion system*, Z. Naturforsch., 31 (1976), p. 1168.

[12] J. CONNOR, *On exploring the basis for slow potential oscillations in the mammalian stomach and intestine*, J. Experiment. Biol., 81 (1979), pp. 153–173.

[13] E. DANIEL AND S. SARNA, *The generation and conduction of activity in smooth muscle*, Ann. Rev. Pharmacol. Toxicol., 18 (1978), pp. 145–66.

[14] J. CONNOR, A. MANGEL AND B. NELSON, *Propagation and entrainment of slow waves in cat small intestine*, Amer. J. Physiol., 237 (1979), pp. C237–C246.

[15] N. DIAMANT AND A. BORTOFF, Amer. J. Physiol., 216 (1969), pp. 301–307.

[16] N. E. DIAMANT, P. K. ROSE AND E. J. DAVIDSON, *Computer simulation of intestinal slow-wave frequency gradient*, Amer. J. Physiol., 219 (1970), pp. 1684–1690.

[17] S. K. SARNA, E. E. DANIEL AND Y. J. KINGMA, *Simulation of slow-wave electrical activity of small intestine*, Amer. J. Physiol., 221 (1971), pp. 166–175.

[18] B. ROBERTSON-DUNN AND D. A. LINKENS, *A mathematical model of the slow-wave electrical activity of the human small intestine*, Med. Biol. Engrg., 12 (1974), pp. 750–757.

[19] B. H. BROWN, H. L. DUTHIE, A. R. HORN, AND R. H. SMALLWOOD, *A linked oscillator model of electrical activity of human small intestine*, Amer. J. Physiol., 229 (1975), pp. 384–388.

[20] R. J. PATTON AND D. A. LINKENS, *Hodgkin–Huxley type electronic modelling of gastrointestinal electrical activity*, Med. Biol. Engrg. Computing, 16 (1978), pp. 195–202.

[21] G. B. ERMENTROUT AND N. KOPELL, *Frequency plateaus in a chain of coupled oscillators*, II, to appear.

[22] N. FENICHEL, *Persistence and smoothness of invariant manifolds for flows*, Indiana Univ. Math. J., 21 (1971), pp. 193–226.

[23] M. W. HIRSCH, C. C. PUGH AND M. SHUB, *Invariant Manifolds*, Lecture Notes in Mathematics, 583, Springer-Verlag, New York, 1977.

[24] J. GUCKENHEIMER, *Isochrons and phaseless sets*, J. Math. Biol., 1 (1975), pp. 259–273.

[25] A. WINFREE, *The Geometry of Biological Time*, Springer-Verlag, New York, 1980.

[26] J. HALE, *Ordinary Differential Equations*, John Wiley, New York, 1969.

[27] N. KOPELL AND L. N. HOWARD, *Bifurcations and trajectories joining critical points*, Adv. in Math., 18 (1975), pp. 306–358.

[28] R. KRONAUER, C. CZEISLER, S. PILATO, M. MOORE-EDE AND E. WEITZMAN, *Mathematical model of the human circadian system with 2 interacting oscillators*, Am. J. Phys. 242 (1982), pp. R3–R17.

[A1] M. MARCUS, *Basic Theorems in Matrix Theory*, National Bureau of Standards Applied Math Series, 57. U.S. Government Printing Office, Washington, DC, 1964.

[A2] P. R. HALMOS, *Finite Dimensional Vector Spaces*, Van Nostrand, New York, 1958.