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ON CHAINS OF OSCILLATORS FORCED AT ONE END*

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Abstract. Chains of oscillators periodically forced at one end may be entrained to a range of forcing frequencies. That range depends on the nature of the coupling, the size of the chain, and the end that is being forced, and gives clues to the properties of the connections along the chain. For long chains of equal oscillators with coupling in both directions, the unforced chain generically has a pattern of phase lags that depends mainly on the coupling in only one of the two directions. For a large class of coupling functions, entrainment is possible at each end over a range of frequencies that contains an open interval independent of the number of oscillators. For this class, the dominant direction can be deduced from the relationship between the ensemble frequency of the unforced chain and the boundaries of the ranges of entrainment when a long chain is forced at each end. This theory is applied to data from the central pattern generator for undulatory locomotion in a primitive vertebrate. The mathematical technique includes the use of a one-dimensional, locally defined, discrete dynamical system to analyze how the phase relationships among the oscillators change with the forcing frequency and the end being forced. This dynamical system makes possible the analysis of the behavior for long chains. The stability of the solutions is verified using techniques related to monotone methods of partial differential equations. For another class of coupling functions, the techniques show that, even if the coupling in the two directions are of roughly comparable amplitude, the range of entrainment for forcing at one of the ends may shrink to a point as the number of oscillators grows, while the range for forcing at the other end remains bounded away from zero in size.

Key words. oscillators, entrainment, central pattern generator, discrete dynamical system, monotone methods

AMS(MOS) subject classifications. 34, 58

1. Introduction. The purpose of this paper is to work out a theory of chains of oscillators forced at one end. The theory is motivated by an ongoing effort to understand neural networks known as central pattern generators (CPGs) [1] and, in particular, the CPG of undulating locomotion in fishlike animals [2]. The assumptions on the oscillators and the coupling will correspond to those made about neural oscillators in previous papers in this series [3]-[7], and the aim of the theory is to show how data from forced chains can yield information about the structure of the coupling in the unforced chain.

The theory describes how the phase relationships among the oscillators in the chain change as the forcing frequency is varied. It also describes how locking is lost as the frequency goes outside some range of parameters, and how that range depends on the nature of the coupling and the length of the chain. In addition, we show that the range of entrainment and pattern of phases among the oscillators may depend strongly on which end of the chain is forced, even if the chain is made up of identical oscillators. Finally, we will relate these ideas to some data on the central pattern generator for swimming in the lamprey [8].

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In the absence of forcing, chains of identical oscillators coupled to their nearest neighbors can be described by the equations

$$\dot{\theta}_1 = \omega + H^+(\theta_2 - \theta_1), \tag{1.1}$$

$$\dot{\theta}_k = \omega + H^+(\theta_{k+1} - \theta_k) + H^-(\theta_{k-1} - \theta_k), \qquad 1 < k < n, \tag{1.2}$$

$$\dot{\theta}_n = \omega + H^-(\theta_{n-1} - \theta_n). \tag{1.3}$$

Here θ_k is the phase of the oscillator at the kth position on the chain and ω is the natural (uncoupled) frequency of each oscillator. The functions H^+ and H^- are scalar 2π-periodic functions that represent the coupling in the directions of decreasing and increasing k, respectively. Equations such as these can be generalized to nonidentical oscillators [3], [5], nonnearest neighbor coupling [4], and coupling whose strength varies along the chain [5], but we will not do so here.

Equations (1.1)–(1.3) can be derived from much more general equations describing oscillators coupled to their nearest neighbors in a chain ([3], [9], appendices to [6], [7]). The oscillators may be given by any set of differential equations having stable limit cycle solutions. The crucial hypothesis on the coupling is that the method of averaging be applicable to the equations. This hypothesis is valid in the case that the coupling is weak [10]. Even for moderately strong coupling, this method can sometimes be used, and we develop such a theory for neural oscillators in [6]. The effect of the averaging is to replace terms that depend separately on θ_k and θ_{k+1} by ones that depend only on the difference between them.

When the chain is forced, the first or last equation is replaced by

$$\dot{\theta}_1 = \omega + H^+(\theta_2 - \theta_1) + H_F(\Omega t, \theta_1) \tag{1.4}$$

or

$$\dot{\theta}_n = \omega + H^-(\theta_{n-1} - \theta_n) + H_F(\Omega t, \theta_n), \tag{1.5}$$

where Ω is the frequency of the forcing and H_F is 2π-periodic in each of its variables. We will assume that $H_F(\theta, \tilde{\theta})$ has the form

$$H_F = H_F(\theta - \tilde{\theta}). \tag{1.6}$$

Remark 1.1. The form (1.6) was chosen for ease of analysis. As a control, we have done numerical simulations with forcing functions of pulse type. We have not detected qualitative differences from the theory we will present, which concerns only (1.6).

Phase-locked solutions to (1.2) must satisfy

$$\Omega = \omega + H^+(\phi_k) + H^-(-\phi_{k-1}) \tag{1.7}$$

for $k \neq 1, n$, where $\phi_k \equiv \theta_{k+1} - \theta_k$. We will show that (1.7) may be considered a discrete dynamical system for $k \in Z$ and some range of ϕ; a phase-locked solution of (1.1), (1.2), (1.5) or (1.4), (1.2), (1.3) corresponds to a particular trajectory of (1.7). (For other work on locally defined dynamical systems, see [11].) If the chain is forced at θ_n (respectively, θ_1), the initial condition is defined by (1.1) (respectively, (1.3)). We will explore how the assumptions on H^+ and H^- and the value of n affect the qualitative behavior of the trajectories and the range of Ω for which there are solutions.

The organization of the paper is as follows. In § 2, we give the hypotheses on the coupling functions that we will use throughout the paper. In § 3, we review some of the relevant conclusions from earlier work on unforced chains of oscillators. We develop the notion of "dominance" of forward coupling versus backward coupling, a concept that generalizes the usual idea of "stronger." In particular, for long unforced chains, the phase lags depend almost entirely on the coupling in only one direction (the "dominant" one).

In § 4, we investigate one aspect of entrainment, which we will refer to as "internal entrainment." We will say that a chain forced at θ_n can "entrain internally" to a frequency Ω if there is a locked solution to (1.7), (1.5), (1.1) with $\dot{\theta}_k = \Omega$, $k = 1, \cdots, n$, for any H_F sufficiently large. This can be done if there is a solution to (1.1), (1.7) with $\dot{\theta}_k = \Omega$. The internal phase relationships among the oscillators of the chain are then independent of the forcing function, as long as H_F is large enough. Such phase relationships are possible only for a limited range of Ω, independent of H_F. As Ω moves outside this range, the loss of locking is due to internal relationships, not the lack of strength of the forcing. (See the beginning of § 4 for a simple example.) We show (Theorem 4.1) that under the hypotheses of § 2 there is a nonempty interval of such Ω for which internal entrainment is possible for all n, and we give bounds for this set. We also produce examples, satisfying slightly weaker hypotheses, for which the range of entrainment shrinks to a point as $N \to \infty$ for forcing at one end, but stays finite for forcing at the other end.

Equation (1.5) is a further condition for locking that specifies what is meant by H_F "sufficiently large." We show in § 5 that, for forcing that is not "too large," (1.5) provides the essential constraint that alone determines the range of entrainment (Theorem 5.1). Locking then fails when $\Omega t - \theta_n$ exceeds a certain value that is independent of n, H^+, or H^-; furthermore, the range of entrainment decreases as n increases.

The solutions to (1.1), (1.2), (1.5) and (1.4), (1.2), (1.3) are constructed within an interval in which $H^+(\phi)$ is monotone increasing and $H^-(-\phi)$ is monotone decreasing. We show in § 6 that these solutions are asymptotically stable. Furthermore, we show that the solutions can be unstable if the $\{\phi_k\}$ lie outside this region.

Section 7 is devoted to the consequences of dominance for the range of frequencies at which the chain can entrain. We say that one *end* is dominant if the coupling from that end to its neighbor is in the direction of the dominant coupling. We show that for forcing at the dominant end, the unforced (ensemble) frequency is in the interior of the range of entrainment, while forcing at the other end has a range of entrainment with the ensemble frequency very near to a boundary. (This follows from the definition of dominance given in § 3 and the lower bounds for entrainment established in Theorem 4.1.). It provides a way to determine dominance experimentally, as discussed in § 8.

Finally, in § 8 we give a further discussion of mathematical issues and relate the work to some current experiments on a central pattern generator.

2. Hypotheses and notation. Let $f(\phi)$ and $g(\phi)$ be defined by

$$H^+(\phi) = f(\phi) + g(\phi), \tag{2.1}$$

$$H^-(-\phi) = f(\phi) - g(\phi). \tag{2.2}$$

(Note that, if $H^+ = H^-$, then f and g are the even and odd parts, respectively, of $H^+ = H^-$.) Let ϕ_L and ϕ_R be defined by

$$H^-(-\phi_L) = 0, \tag{2.3}$$

$$H^+(\phi_R) = 0 \tag{2.4}$$

(see Fig. 2.1). Note that ϕ_L and ϕ_R can be thought of as boundary conditions for (1.1)-(1.3). That is, (1.1) and (1.3) can be replaced by (1.2) with $k = 1$ or $k = n$, providing that we define ϕ_0 and ϕ_n by $\phi_0 = \phi_L$ and $\phi_n = \phi_R$.

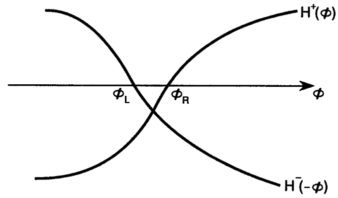

FIG. 2.1. *Coupling functions $H^+(\phi)$ and $H^-(-\phi)$. Note that H^+ is monotone increasing near ϕ_R and $H^-(-\phi)$ is monotone decreasing near ϕ_L.*

Using (2.1) and (2.2), (1.7) may be rewritten as

$$\Omega = \omega + f(\phi_k) + g(\phi_k) + f(\phi_{k-1}) - g(\phi_{k-1}). \tag{2.5}$$

We assume that there is an interval J in S^1 such that

(1) Equations (2.3) and (2.4) may be solved uniquely for ϕ_L and ϕ_R in J.

(2) $H^+(\phi)$ is monotone increasing and $H^-(-\phi)$ is monotone decreasing in J, i.e., $(f+g)' > 0$, $(g-f)' > 0$.

(3) Equations $f(\phi) = f(\phi_L)$ and $f(\phi) = f(\phi_R)$ each have two roots in J. This implies that there is a $\phi_T \in J$ such that $f'(\phi_T) = 0$.

(4) $f'' \neq 0$ in J.

(5) At least one of the following holds: $f'(\phi_L) < 0$ or $f'(\phi_R) > 0$.

In previous papers [2]–[7], we required that $\phi_L \neq 0 \neq \phi_R$. Such a requirement guarantees that, even for a homogeneous chain of oscillators, the unforced chain does not synchronize (i.e., $\phi_k \equiv 0$ is not a solution). For the theory to be presented here, that hypothesis is not necessary. Hypothesis 2 is used in the paper to show that certain steady states that figure in the theory are stable or unstable, but not marginally stable. In other papers in this series, it is needed to show that, for large n, the unforced chain of identical oscillators has phase lags that converge to a constant ϕ away from $k = 0, n$. This hypothesis is also used to establish the stability of the above solution. Hypothesis 3 is needed to get entrainment intervals that do not shrink to zero as $n \to \infty$. Hypothesis 4 is a genuine nonlinearity condition that is satisfied for a large collection of examples. (As we will see, the behavior changes depending on the sign of f''; more complicated behavior can occur if f'' is allowed to vanish.) Hypothesis 5 is also satisfied for a large set of coupling functions. It rules out the existence of solutions that converge (away from $k = 0, n$) to $\phi_k \equiv \phi_T$. A simple example of functions H^+, H^- satisfying the above hypotheses is $H^+(\phi) = H^-(\phi) = A \cos \phi + B \sin \phi$, with $B > 0$, A not too large. (See [9] for the computation of this $H^+ = H^-$ from much more general equations.)

We also need a hypothesis on the forcing function H_F. We assume that H_F is smooth, 2π-periodic, and takes both signs, i.e., the forcing is capable of speeding up or slowing down the cycle, depending on the relationship of the phases of the forced and forcing oscillators.

Note that (2.5) is invariant under the transformations

$$f \to -f, \quad k \to n-k, \quad \omega \to -\omega, \quad \Omega \to -\Omega. \tag{2.6}$$

Hence, we may assume without loss of generality that $f'' > 0$.

3. Unforced chains and dominance. We now briefly review the theory of phaselocking in unforced chains of oscillators. This theory is somewhat more difficult, mostly because the frequency at which the ensemble locks is not known a priori. (The locked frequency is not in general equal to ω [3], [5].) It is shown in [3] that, for n sufficiently large and under the above hypotheses, there is generically a unique phase-locked solution (i.e., a time-independent solution to (1.1), (1.2), (1.3) with $\dot{\theta}_k = \Omega$ for all k).

When the oscillators are identical, for large n this solution approaches a constant with a possible boundary layer near either $k = 0$ or $k = n$. This constant is either ϕ_L or ϕ_R. (If condition (5) of § 2 fails, this constant is ϕ_T instead.) We will say that the ascending coupling H^+ (respectively, descending coupling H^-) *dominates* if the solution approaches ϕ_R (respectively, ϕ_L) as $n \to \infty$.

If H^+ (respectively, H^-) dominates, the ensemble frequency Ω of the chain is given (in the limit as $n \to \infty$) by Ω_R (respectively, Ω_L), where

$$\Omega_R = \omega + 2f(\phi_R) = \omega + H^-(-\phi_R),$$
$$\Omega_L = \omega + 2f(\phi_L) = \omega + H^+(\phi_L). \tag{3.1}$$

Thus the ensemble frequency differs from the uncoupled frequency ω by a term that measures the effect of the *non*dominant coupling at the phase lag determined by the dominant one. Formulas (3.1) follow from (1.7).

It remains to give conditions that determine which coupling function dominates. This is summarized by the following:

$$H^+ \text{ (respectively, } H^-\text{) dominates iff } |H^-(-\phi_R)| < |H^+(\phi_L)| \quad \text{(respectively, } |H^-(-\phi_R)| > |H^+(\phi_L)|\text{)}. \tag{3.2}$$

Condition (3.2) says that the dominant coupling is the one for which the ensemble frequency Ω is closest to the uncoupled frequency ω. (See Fig. 3.1.)

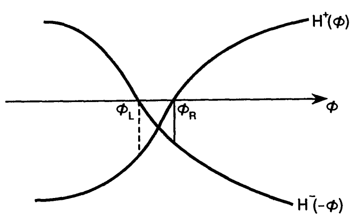

FIG. 3.1. *A geometric interpretation of* (3.2). *In this picture, H^+ is dominant, since the quantity $|H^-(-\phi_R)|$, which is represented by the solid line, is less than $|H^+(\phi_L)|$, represented by the dashed line.*

It is natural (and correct) to guess that if H^+ and H^- are the same except for amplitude, then the larger of the two determines the ensemble frequency. That is, we have the following proposition.

PROPOSITION 3.1. *Suppose that $H^+ = \gamma H^-$ with $\gamma > 0$. If $\gamma > 1$ (respectively, $\gamma < 1$), then $\Omega = \Omega_R$ (respectively, $\Omega = \Omega_L$).*

Proof. Since $H^+ = \gamma H^-$ with $\gamma > 0$, the definitions of ϕ_L and ϕ_R imply that $\phi_R = -\phi_L$. Hence, $H^+(-\phi_R) = H^+(\phi_L) = \gamma H^-(\phi_L)$. This implies $\gamma > 1$ if and only if $|H^-(-\phi_R)| < |H^+(\phi_L)|$. □

The proof that there is a unique solution approaching ϕ_L or ϕ_R with dominance determined by (3.2) is found in [5]. The formulation in [5] is considerably more general; in particular, the uncoupled frequency is allowed to vary with k, as is the strength of coupling. In that case, the solution does not approach a constant as $n \to \infty$, but it does approach something that may be easily calculated. The ensemble frequency is given by a generalization of (3.1). There is still a characterization of dominance, which reduces to (3.2) when the uncoupled frequencies are independent of k. Since this characterization is considerably more complicated than (3.2), and the reduction is not instantly apparent, we do the reduction in the Appendix.

Remark. For the proof of the existence and uniqueness of phase-locked solutions to the equations for the unforced chain, and formula (3.2), only hypotheses (1), (2), and (5) of § 2 are needed. In particular, H^+, H^- (and therefore f) could be linear, and so hypotheses (3) and (4) would fail. Hypotheses (3) and (4) are important to the behavior of the forced chain.

4. Internal entrainment. It is useful to contrast a forced "chain" having only one oscillator with a forced chain of length two. Consider the single forced oscillator

$$\dot{\theta}_1 = \omega + \alpha H_F(\Omega t - \theta_1).$$

Let $\hat{\theta} = \Omega t - \theta_1$. Locking occurs if $\Omega - \omega = \alpha H_F(\hat{\theta})$ can be solved for $\hat{\theta}$. Assuming that the forcing function takes both positive and negative values, then for α large enough we can always solve the equation.

Now consider the chain of two oscillators forced at one end. When the forcing is at oscillator #2, the equations are $\Omega = \omega + H^-(-\phi_1) + \alpha H_F(\hat{\theta})$ and

$$\Omega = \omega + H^+(\phi_1). \tag{4.1}$$

When the forcing is at oscillator #1, they are $\Omega = \omega + H^+(\phi_1) + \alpha H_F(\hat{\theta})$ and

$$\Omega = \omega + H^-(-\phi_1). \tag{4.2}$$

The main difference from the case of one forced oscillator is that an additional equation (4.1) or (4.2) must be solved. Note that (4.1) and (4.2) are independent of the forcing. If (4.1) is not solvable, the system cannot be entrained by forcing at #2 with frequency Ω, no matter how large α is. Similarly, if (4.2) cannot be solved, the chain cannot be entrained by forcing at #1 with frequency Ω.

This can lead to differences in entrainment range for forcing at the two ends, even with the same forcing function H_F. As a simple example, consider $H^+ = \gamma H^-$, $\gamma \ll 1$. Then (4.2) is solvable for a much larger range of frequencies than is (4.1). Hence, for large α, we can entrain at some frequencies by forcing at #1 but not at #2.

In general, as in a chain of two oscillators, entrainment may be lost in one of two ways. (1) The forcing strength may not be strong enough to satisfy the end condition. (2) One of the remaining equations may not be solvable. For strong enough forcing, (2) becomes the limiting constraint, and the limits on the entrainment range of forcing frequencies are independent of the forcing function H_F.

In this section, we show how the properties of H^+ and H^- determine those limits, at least for long chains ($N \gg 1$). Unlike the simple example above for two oscillators, the limits do not depend merely on the amplitudes of H^+ and H^-, but also on more subtle properties. These are uncovered by considering (1.7) as a locally defined dynamical system and studying the behavior of that dynamical system.

Equation (1.7) may be regarded as a first-order difference equation for ϕ_k, provided that the trajectory remains in a region in which H^+, H^- are invertible, e.g., $\phi_k \in J$ for all k. For definiteness, asume that the chain is forced at θ_n, at frequency Ω. We will find the range of Ω for which (1.1) may be solved along with (1.7), $k = 1, \cdots, n-1$. This requires only that H^+ be invertible. (For forcing at θ_1, only H^- need be invertible.) Let $J^+ = \{\phi \mid (H^+)'(\phi) > 0\}$.

The underlying idea is that the large k behavior of a trajectory of a dynamical system is determined by the critical points of the system. (For a locally defined dynamical system, the critical points must be in the range of definition of the system.) The "trajectory" of phase lags $\phi_1, \phi_2, \phi_3, \cdots$, has behavior that is determined by whether there are critical points in J^+ and the relationship of the "initial value" ϕ_1 to those critical points. All of these factors change with Ω. For Ω inside some range, the trajectory tends to a stable critical point inside J^+, and hence (1.7) is solvable for all k. For such Ω, we have internal entrainment. For other Ω, the trajectory moves outside J^+ in a finite number of steps, and the equations are not solvable for larger k. We will use this to produce a range of entrainment that is sharp at the lower end (if $f''>0$), but not sharp at the upper end. In § 7, we relate the characterization of the lower end to dominance.

The first proposition locates the relevant critical points and establishes stability or instability as solutions to (1.7). We pay particular attention to $\Omega=\Omega_L$, which turns out to be near one boundary of the range of entrainment for N large. Define Ω_T in analogy to Ω_L and Ω_R by $\Omega_T=\omega+2f(\phi_T)$.

PROPOSITION 4.1. *For some neighborhood N of Ω_L with lower endpoint Ω_T there exist critical points ϕ_Ω^-, $\phi_\Omega^+\in J$ for* (1.7) *with $\phi_\Omega^-<\phi_\Omega^+$. ϕ_Ω^- is an unstable critical point of* (1.7) *and ϕ_Ω^+ is a stable critical point.* (*See Fig.* 4.1.) *At $\Omega=\Omega_L$, $\phi_L=\phi_\Omega^-$ if $\phi_L<\phi_T$ and $\phi_L=\phi_\Omega^+$ if $\phi_L>\phi_T$.*

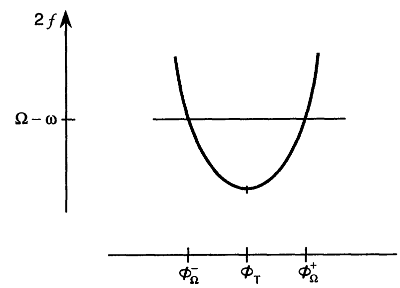

FIG. 4.1. *The critical points ϕ_Ω^+ and ϕ_Ω^- satisfy $\Omega=\omega+2f(\phi)$.*

Proof. Let $\Delta=\Omega-\omega$. Critical points of (1.7) satisfy

$$\Delta=H^+(\phi)+H^-(-\phi)=2f(\phi). \tag{4.3}$$

Since $f''>0$, with a minimum at $\phi_T\in J$, for some range of $\Delta\geqq 2f(\phi_T)$ there are two solutions ϕ_Ω^- and ϕ_Ω^+ to (4.3) with $\phi_\Omega^-<\phi_\Omega^+$. Because the minimum value of $\Delta\equiv\Omega-\omega$ is $2f(\phi_T)$, we see that the minimum value of Ω is $\Omega_T=\omega+2f(\phi_T)$. From the fact that $f''>0$, we have $f'(\phi_\Omega^-)<0$, $f'(\phi_\Omega^+)>0$. From this, we can deduce the stability of the steady states: linearizing (2.5) around a fixed point ϕ_Ω, we have

$$0=(f+g)'(\phi_\Omega)\rho_{k+1}+(f-g)'(\phi_\Omega)\rho_k, \tag{4.4}$$

where $\rho_k=\phi_k-\phi_\Omega$. Equation (4.4) may be rewritten as

$$\rho_{k+1}=\{[g'(\phi_\Omega)-f'(\phi_\Omega)]/[g'(\phi_\Omega)+f'(\phi_\Omega)]\}\rho_k.$$

The equilibrium point is stable if the coefficient of ρ_k is less than 1. Since $g'>|f'|$ in J, we see that ϕ_Ω is stable if and only if $f'(\phi_\Omega)>0$. Thus, ϕ_Ω^+ is stable and ϕ_Ω^- is unstable.

It follows immediately from the definitions of Ω_L and ϕ_L that ϕ_L is a critical point of (1.7) when $\Omega=\Omega_L$. Its stability as a solution to (1.7) depends on its position with respect to ϕ_T, i.e., whether $\phi_L=\phi^-$ or $\phi_L=\phi^+$. □

Remark 4.1. The stable critical point ϕ_Ω^+ increases with Ω. Although $\phi_\Omega^+\in J$ for $\Omega=\Omega_L$, for Ω sufficiently large ϕ_Ω^+ leaves J^+, and then locking is lost for n sufficiently large. Indeeed, there may be no entrained solution even for somewhat lower Ω. The solution can be lost if the upper critical point ϕ_Ω^+ loses its stability as a solution to

(1.7). This happens if $g'<0$. (At $g'=0$, the eigenvalue is -1.) For larger Ω, the trajectory may then oscillate around ϕ_Ω^+ with increasing amplitude and eventually leave J^+, so the trajectory is no longer defined. Even if the trajectory remains well defined for some Ω for which $g'(\phi_\Omega^+)<0$, there is reason to suspect that the resulting solutions will be temporally unstable. (See § 6 for more discussion.) We will work with the interval of Ω for which $\phi_\Omega^+ \in J$. Within this interval of Ω, ϕ_Ω^+ is stable as a solution to (1.7) and trajectories stay in J (and hence in J^+). The upper bound of this range is not a sharp limit on the range of entrainment, and is probably not sharp even on the range of temporally stable entrainment. (See § 6.) The lower bound is sharp because, for Ω below the lower limit, trajectories do leave J^+ and hence cease to be defined.

Remark 4.2. By hypothesis (3) of § 2, *both* ϕ_Ω^- and ϕ_Ω^+ belong to J for $\Omega=\Omega_L$ (and so $g'>|f'|>0$). If we omit this hypothesis, it is easy to construct examples in which $\phi_\Omega^- \in J$, but ϕ_Ω^+ is not even in J^+. (See Remark 4.4.) In that case, as shown in Theorem 4.1, the range of entrainment tends to a single point as $n\to\infty$.

We now discuss how the relationship of the "initial condition" $\phi_1(\Omega)$ to the critical points ϕ_Ω^-, ϕ_Ω^+ changes as Ω is varied. This initial condition is defined by

$$\Omega=\omega+H^+(\phi_1). \tag{4.5}$$

As shown by Proposition 4.2 below, this relationship is crucial to the existence of internal stability. The proposition will show the direction taken by trajectories $\{\phi_k\}$ for Ω in a neighborhood of Ω_L, for the cases $\phi_L<\phi_T$ and $\phi_L>\phi_T$. This result will be used in Theorem 4.1 to show that, for large n, Ω_L provides a lower limit to the entrainment frequency range if $\phi_L<\phi_T$, whereas Ω_T provides the limit if $\phi_L>\phi_T$.

In Figs. 4.2(a), and 4.2(b), the critical points ϕ_Ω^- and ϕ_Ω^+ are plotted against Ω. (See Fig. 4.1.) Proposition 4.2 justifies the plots of $\phi_1(\Omega)$ relative to those of ϕ^+ and ϕ^- for $\phi_L<\phi_T$ (Fig. 4.2(a)) and $\phi_L>\phi_T$ (Fig. 4.2(b)). The stability of ϕ_Ω^+ and ϕ_Ω^- lead to the phase diagrams of Fig. 4.3.

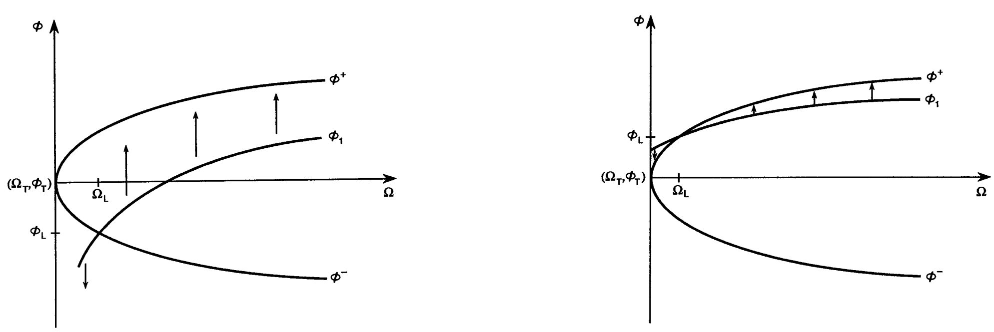

FIG. 4.2. *Plots of* ϕ_1, ϕ^+, *and* ϕ^- *as functions of* Ω. *The origin is chosen to be* $\phi=\phi_T$, $\Omega=\Omega_T$. *Note that* $\phi_1(\Omega)=\phi_L$ *for* $\Omega=\Omega_L$. *The arrows denote the direction of the trajectory, which goes from* ϕ_1 *toward* ϕ^+ *if* ϕ_1 *is in the basin of attraction of* ϕ^+. (*Also see Fig.* 4.3.) (a) $\phi_L<\phi_T$. *Note that* $\phi_1=\phi^-$ *at* $\Omega=\Omega_L$. (b) $\phi_L>\phi_T$. *Note that* $\phi_1=\phi^+$ *at* $\Omega=\Omega_L$.

PROPOSITION 4.2. *Assume that* Ω *is such that* ϕ_Ω^+, $\phi_\Omega^- \in J$, *and* (4.5) *can be solved for* $\phi_1 \in J$. *Then*:

(i) *If* $\Omega=\Omega_L$, *then* $\phi_1=\phi_L$, *a critical point in J. Hence* $\phi_k=\phi_L$ *for all k.*

(ii) *Suppose that* $\phi_L<\phi_T$. *For* $\Omega<\Omega_L$, *the solution* $\phi_1(\Omega)$ *to* (4.5) *satisfies* $\phi_1(\Omega)<\phi_\Omega^-$; *for* $\Omega>\Omega_L$, *we have* $\phi_1(\Omega)>\phi_\Omega^-$. *Since* ϕ_Ω^- *is an unstable critical point, trajectories*

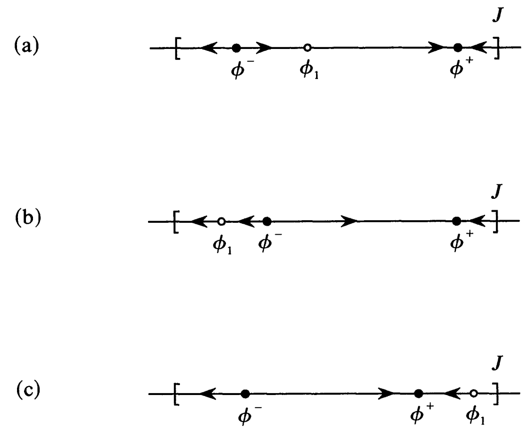

FIG. 4.3. *Phase diagram for* (1.7) *with critical points* ϕ_Ω^- *and* ϕ_Ω^+. ϕ_Ω^- *is repelling and* ϕ_Ω^+ *is attracting.* (a) $\Omega>\Omega_L$. *In this case,* $\phi^-<\phi_1<\phi^+$ *and the trajectory tends toward* ϕ^+. (b) $\Omega<\Omega_L$, $\phi_L<\phi_T$. *In this case,* $\phi_1<\phi^-$ *and hence the trajectory leaves J.* (c) $\Omega<\Omega_L$, $\phi_L>\phi_T$. *In this case,* $\phi_1>\phi^+$, *and the trajectory approaches* ϕ^+ *from above.*

tend toward ϕ_Ω^+ *for* $\Omega>\Omega_L$. (*See Figs* 4.2(a) *and* 4.3(a).) *For* $\Omega<\Omega_L$, *trajectories eventually leave* J^+ (*see Figs.* 4.2(a) *and* 4.3(b)).

(iii) *Suppose that* $\phi_L>\phi_T$, *and* $\Omega>\Omega_T$ (*so* $\phi^\pm$ *exist*). *Then* ϕ_1 *is in the domain of attraction of* ϕ^+. *Furthermore,* $\Omega>\Omega_L$ *implies that* $\phi_1<\phi_\Omega^+$ *and* $\Omega<\Omega_L$ *implies that* $\phi_1>\phi_\Omega^+$. (*See Figs.* 4.2(b), 4.3(a), *and* 4.3(c).)

Proof. (i) It is immediate from (4.5) and the definition of Ω_L that $H^+(\phi_1)=H^+(\phi_L)$ when $\Omega=\Omega_L$. Since H^+ is monotone in J, we have $\phi_1=\phi_L$.

(ii) Suppose that $\phi_L<\phi_T$. Since $f''>0$, $\phi_\Omega^-<\phi_L$ if and only if $\Delta=\Omega-\omega=2f(\phi_\Omega^-)\geqq 2f(\phi_L)=\Omega_L-\omega$ if and only if $\Omega>\Omega_L$. (See Fig. 4.1.) We claim that $\phi_\Omega^-<\phi_L$ if and only if $\phi_1(\Omega)>\phi_\Omega^-$. (See Fig. 4.2a.) We first note that

$$\Delta=H^+(\phi_1)=(f+g)(\phi_1), \tag{4.6}$$

so from (4.3)

$$2g(\phi_\Omega^-)=(f+g)(\phi_1(\Omega)). \tag{4.7}$$

Since $f+g$ is monotone increasing, we have that $\phi_\Omega^-<\phi_1(\Omega)$ if and only if $(f+g)(\phi_\Omega^-)<(f+g)(\phi_1(\Omega))$. Using (4.7), this is true if and only if $(f+g)(\phi_\Omega^-)<2f(\phi_\Omega^-)$. Hence $(f-g)(\phi_\Omega^-)>0$. But $(f-g)$ is monotone *decreasing* and vanishes at ϕ_L, so $\phi_1(\Omega)>\phi_\Omega^-$ if and only if $\phi_\Omega^-<\phi_L$. Similarly, $\Omega<\Omega_L$ if and only if $\phi_1(\Omega)<\phi_\Omega^-$. The assertion about the trajectories is clear. (See Figs. 4.3(a) and 4.3(b).)

(iii) Suppose that $\phi_T\leqq\phi_L$. (See Fig. 4.2(b).) To show that ϕ_1 is in the domain of attraction of ϕ^+, it suffices to show that $\phi_1(\Omega)>\phi_\Omega^-$. Actually, we show that $\phi_1\geqq\phi_T\geqq\phi^-$. This is true if and only if $H^+(\phi_1)>H^+(\phi_T)$ if and only if $\Delta>(f+g)(\phi_T)$ if and only if $\Delta-2f(\phi_T)>(g-f)(\phi_T)$. Now $(g-f)(\phi_L)=0$ and $\phi_L>\phi_T$, so $(g-f)(\phi_T)<0$. Finally, $\Omega>\Omega_T$, so $\Delta-2f(\phi_T)=\Omega-\omega-2f(\phi_T)>0$. Thus, we have $\phi_1>\phi_T$. The trajectory is as in Figs. 4.3(a) or 4.3(c).

Since $\phi_L>\phi_T$, $f'(\phi^+)$, $f'(\phi_1)>0$. Using (4.1) and (4.3), we have $(f+g)(\phi_1)=2f(\phi^+)$. Hence $\phi^+>\phi_1$ (as in Fig. 4.3(a)) if and only if $(f+g)(\phi_1)>2f(\phi_1)$ or $(f-g)(\phi_1)<0$. Since $(f-g)(\phi_L)=0$ and $(f-g)$ is monotone decreasing, $(f-g)(\phi_1)<0$ if and only $\phi_1>\phi_L$. Using (4.1) and (2.3), $\phi_1>\phi_L$ if and only if $\Omega-\Omega_L=(f+g)(\phi_1)-2f(\phi_L)>(f+g)(\phi_L)-2f(\phi_L)=(g-f)(\phi_L)=0$. Hence we are done. □

Remark 4.3. Proposition 4.2(i) shows that for $\Omega=\Omega_L$, $\phi_k=\phi_L$ for all k. However, for $\phi_L<\phi_T$, ϕ_L is an unstable critical point. Hence, if there is any noise in the system to move some ϕ_k away from ϕ_L, the trajectory will behave as in Proposition 4.2(ii) or (iii).

In the following theorem, we investigate the upper and lower bounds for the interval of Ω over which internal entrainment is possible. This interval varies with n. Let I_n denote the range of Ω for which there is a solution in J to (1.7), $2\leqq k\leqq n-1$. Let Ω_n^- and Ω_n^+ denote the endpoints of the interval I_n. Ω_n^- and Ω_n^+ satisfy

$$\phi_{n-1}(\Omega_n^+)=\partial^+J,\qquad \phi_{n-1}(\Omega_n^-)=\partial^-J, \tag{4.8}$$

where ∂^+J and ∂^-J are the upper and lower boundaries of J. The following theorem shows that if ϕ_Ω^+, $\phi_\Omega^-\in J$ for $\Omega=\Omega_L$ there is an interval $[\Omega_L,\Omega^+]$ of frequencies permitting internal entrainment for all n. Furthermore, the lower boundary is sharp in the limit $n\to\infty$ if $\phi_L<\phi_T$. Part (iii) weakens the hypothesis of § 2 to permit $\phi_\Omega^+\notin J^+$ for $\Omega=\Omega_L$.

THEOREM 4.1.

(i) *Suppose that* $\phi_L<\phi_T$. *Then*

(*a*) $\Omega_n^+>\Omega^+$ *for all n and* $\lim_{n\to\infty}\Omega_n^+=\Omega^+$, *where* Ω^+ *is the value of* Ω *at which* ϕ_Ω^+ *is the upper boundary of* J^+.

(b) $\Omega_n^-<\Omega_L$ *for all n and* $\lim_{n\to\infty}\Omega_n^-=\Omega_L$.

(ii) *If* $\phi_L\geqq\phi_T$, *then* (a) *holds and* $\Omega_n^-<\Omega_T$, $\lim_{n\to\infty}\Omega_n^-=\Omega_T$.

(iii) *Suppose that* $\phi_L<\phi_T$. *Assume that* $\phi_\Omega^+\notin J^+$ *for* $\Omega=\Omega_L$, *but* $\phi_\Omega^-\in J$ *and hypotheses* (1), (2), (4), *and* (5) *of* § 2 *hold. Then for any* $\Omega\neq\Omega_L$, $\phi_n\notin J^+$ *for some n sufficiently large, depending on* Ω. *Thus, as* $n\to\infty$, *the range of frequencies permitting internal entrainment shrinks to* $\{\Omega_L\}$.

Proof. (i). First suppose that $\phi_L<\phi_T$. (a) As we have seen in the proof of Proposition 4.2, $\phi_1(\Omega)$ increases and ϕ_Ω^- decreases as Ω increases from Ω_L; the latter implies that ϕ_Ω^+ increases. By Proposition 4.2, for $\Omega>\Omega_L$, $\phi_1(\Omega)<\phi_k<\phi_\Omega^+$. Thus if $\phi_\Omega^+\in J^+$, i.e., $\Omega<\Omega^+$, the entire trajectory $\{\phi_k\}$ of (1.7) lies in J^+. It follows that $\Omega_n^+>\Omega^+$. Since $\phi_n\to\phi_\Omega^+$ as $n\to\infty$, we have that $\Omega_n^+\to\Omega^+$.

(b) For $\Omega<\Omega_L$, $\phi_1(\Omega)<\phi_\Omega^-$ by Proposition 4.2. For such trajectories of (1.7), ϕ_k moves away from the unstable critical point ϕ_Ω^- toward the lower boundary of J^+. It suffices to show that for any $\Omega<\Omega_L$, $\{\phi_k\}$ exits from J^+ for k sufficiently large. We will show that there is a lower bound on $|\phi_k-\phi_{k-1}|$, so the trajectory must exit in a finite number of steps. The lower bound is dependent on Ω and the number of steps goes to ∞ as $\Omega\to\Omega_L$. From (1.7),

$$\begin{aligned}(f+g)(\phi_k)-(f+g)(\phi_{k-1})&=\Delta-(f-g)(\phi_{k-1})-(f+g)(\phi_{k-1})\\&=\Delta-2f(\phi_{k-1})\\&=2f(\phi_\Omega^-)-2f(\phi_{k-1})\end{aligned} \tag{4.9}$$

by (4.3). For $\phi_k<\phi_L<\phi_T$, $f'\neq0$. More precisely, there is a constant $K>0$ such that $|\phi_\Omega^- -\phi_{k-1}|>\delta$ implies $|f(\phi_\Omega^-)-f(\phi_{k-1})|>K\delta$. From (4.9) and an upper bound on $(f+g)'$ on the compact set $\mathrm{Cl}(J^+)$ we get a lower bound for $|\phi_k-\phi_{k-1}|$.

(ii) Now consider the case $\phi_L\geqq\phi_T$. If $\Omega\geqq\Omega_T$, $\phi_1\geqq\phi_T$ by Proposition 4.2, and the entire trajectory beginning with ϕ_1 lies between ϕ_1 and ϕ^+. Thus, Ω_T is in I_k for all k. For $\Omega<\Omega_T$, there are no critical points, and, as above, the trajectory must exit from J^+ in a finite number of steps. This shows that $\lim_{k\to\infty}\Omega_k^-=\Omega_T$. The proof that part (a) holds is as above.

(iii) If $\phi_\Omega^+ \notin J^+$ for $\Omega = \Omega_L$, there is no stable critical point for (1.7). Trajectories leave J^+ and so cease to be defined, rather than tending toward a stable limit point. For Ω close to Ω_L, this may take a large number of steps; if Ω is further from Ω_L, so $\phi_1 - \phi_\Omega^-$ is not infinitesimally small, this happens for a low value of k. □

Remark 4.4. All the cases that occur in Theorem 4.1 can easily be obtained using simple coupling functions H^+ and H^-. Case (i) is satisfied by any small perturbations of $H^+ = H^- = A \cos \phi + B \sin \phi$, $A < 0$, $|A|$ sufficiently small, as in Fig. 2.1. If $H^+ = H^-$ as above, then $\phi_L = -\phi_R$. For $\Omega = \Omega_L$, we then have $\phi_\Omega^- = \phi_L \in J^-$. By symmetry, $\phi_\Omega^+ = -\phi_L = \phi_R \in J^+$.

Examples satisfying (ii) can be constructed using a large anisotropy in strength. That is, $H^+(\phi) = H(\phi)$, $H^-(\phi) = \gamma H(\phi)$, $0 < \gamma < 1$ sufficiently close to zero. See Fig. 4.4.

Examples of case (iii) can be constructed using networks that are "tuned." By this we mean that phase lags that would be created by H^+ alone or H^- alone are equal, i.e., $\phi_L = \phi_R$. For example, let $H^+(\phi) = \sin(\phi - \hat{\phi})$, $H^-(\phi) = \gamma \sin(\phi + \hat{\phi})$, so $\phi_R = \phi_L = \hat{\phi}$. (See Fig. 4.5.) It is easy to check that $2f(\phi) = (1-\gamma)H^+(\phi)$. Therefore, for $\gamma > 1$, $2f(\phi) = \Omega_L - \omega$ has only one solution in the region where $(H^+)'(\phi) > 0$; furthermore, at this solution $f'(\phi) = (1-\gamma)(H^+)'(\phi) < 0$, so the critical point is unstable. Thus, the system can be entrained for large n, by forcing at θ_n, only for a very small range of frequencies tending to $\{\Omega_L\}$ as $n \to \infty$. If $\gamma < 1$, there is such a tiny entrainment range if the forcing is done at θ_1. We conclude that for long chains, some tuned systems can be entrained over a substantial range of frequencies only at one end *or* the other, not both. This remark is of interest because such tuned systems have been used to investigate other aspects of lamprey central pattern generator data [12].

Remark 4.5. If the forcing is done at $\theta = \theta_1$ instead of $\theta = \theta_n$, there are similar results. If $\phi_R > \phi_T$, the range of frequencies permitting internal entrainment contains $[\Omega_R, \Omega^+]$ for some Ω^+. If $\phi_R \leqq \phi_T$, the range contains $[\Omega_T, \Omega^+]$.

5. Entrainment range and loss of locking. We now go from the study of internal entrainment to entrainment possible with a given forcing function H_F. If we assume

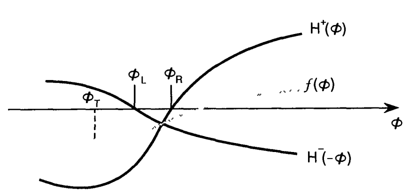

FIG. 4.4. *The functions* $H^+ = A\cos\phi + B\sin\phi$, $H^-(-\phi) = \gamma H^+(-\phi)$, γ *small, and* $f(\phi) = \frac{1}{2}(H^+(\phi) + H^-(-\phi))$. *For* $\gamma \approx 0$, ϕ_T *is close to the lower boundary of* J^+, *i.e., where* $(H^+)' = 0$.

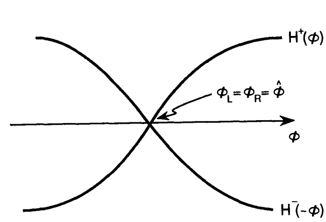

FIG. 4.5. *A coupling system tuned so that the two components each alone would yield the same phase lag. Here* $H^+(\phi) = \sin(\phi - \hat{\phi})$, $H^-(\phi) = \gamma \sin(\phi + \hat{\phi})$, *so* $\phi_L = \phi_R = \hat{\phi}$.

that internal entrainment is possible ($\Omega \in I_n$) then the final condition for locking is

$$\Omega = \omega + H^-(-\phi_{n-1}) + H_F(\Omega t - \theta_n). \tag{5.1}$$

Denote the range of values of the forcing function H_F by $[\delta^-, \delta^+]$. Then (5.1) is satisfied if $\Omega \in I_n$ and

$$P_n(\Omega) \equiv \Omega - \omega - H^-(-\phi_{n-1}(\Omega)) \quad \in \quad [\delta^-, \delta^+], \tag{5.2}$$

where $\phi_{n-1}(\Omega)$ is the $(n-1)$th point of the trajectory of (4.2) with initial condition $\phi_1(\Omega)$ given by (4.1). To summarize, we have the following proposition.

PROPOSITION 5.1. *A necessary and sufficient condition for locking with phase lags in J is that $\Omega \in I_n$ and $\delta^- < P_n(\Omega) < \delta^+$.*

We wish to investigate how locking is lost as Ω and n are varied for a fixed forcing function H_F. To do this, we must first establish some qualitative properties of P_n. For n large, P_n has a limit, and this helps to investigate entrainment in that limit. P_n also changes in a predictable way with Ω and n.

PROPOSITION 5.2. (a) *For $\Omega > \Omega_L$ and n sufficiently large (depending on Ω), $P_n(\Omega) \to H^+(\phi_\Omega^+)$.*

(b) *$P_n(\Omega)$ is an increasing function of Ω. For $\Omega > \Omega_L$ it is also an increasing function of n. See Fig.* 5.1.

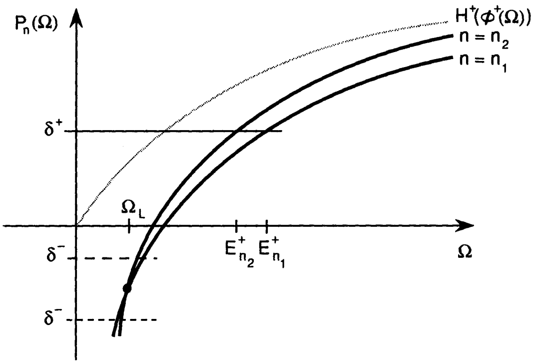

FIG. 5.1. *$P_n(\Omega)$ as a function of Ω for two values of n, with $n_2 > n_1$. As $n \to \infty$, $P_n(\Omega) \to H^+(\phi_\Omega^+)$ for $\Omega > \Omega_L$. The Ω value of the intersection of the graph with the horizontal lines at height δ^+, δ^- define E^+ and E^-. E^+ decreases with increasing n and increases with increasing δ^+. E^- decreases as δ^- decreases. The behavior of E^- with respect to n depends on whether $\delta^- < P_n(\Omega_L)$, as in the line with small dashes, or $\delta^- > P_n(\Omega_L)$, as in the line with the large dashes.*

Proof. (a) For $\Omega > \Omega_L$, $\phi_1(\Omega) > \phi_\Omega^-$ by Proposition 4.2, so $\lim_{k\to\infty} \phi_k(\Omega) = \phi_\Omega^+$. Thus $P_n(\Omega) \to \Omega - \omega - H^-(-\phi_\Omega^+) = \Delta - (f-g)(\phi_\Omega^+) = \Delta - 2f(\phi_\Omega^+) + (f+g)(\phi_\Omega^+) = H^+(\phi_\Omega^+)$, since $2f(\phi_\Omega^+) = \Delta$.

(b) To show that P_n is monotone in Ω, first note that by (4.1), ϕ_1 is an increasing function of Ω. Using (4.2), $(g-f)' > 0$ and induction on k, we see that for each fixed k, ϕ_k is an increasing function of Ω. From this it follows easily that P_n is monotone increasing in Ω.

Now suppose that $\Omega > \Omega_L$. Then $\phi^- < \phi_1 < \phi^+$, and so ϕ_k increases with k. Thus $-H^-(-\phi_n)$ is an increasing function of n, and hence so is $P_n(\Omega)$. □

We can now see how locking is lost when Ω is extended beyond the range of entrainment. There are two possibilities. One is that locking is lost by loss of internal entrainment as discussed in the previous section. The other is that the external constraint cannot be satisfied.

Let $\hat{\theta}(\Omega)$ denote the phase lag between the forcing oscillator and the nearest oscillator in the chain, i.e., $\Omega t-\theta_n$. The next theorem describes how $\hat{\theta}(\Omega)$ depends on Ω, n, H^+, and H^-. When internal entrainment is preserved but locking is lost by not satisfying the external constraint, $\hat{\theta}(\Omega)$ is independent of n, H^+, and H^-. This is *not* true if locking is lost by loss of internal entrainment. Thus, this provides a test to determine which is the limiting constraint.

THEOREM 5.1. *Assume that P_n is defined.*

(i) *Suppose that locking is lost by not satisfying the external constraint. Then*

(a) *$\hat{\theta}$ is a monotonically increasing function of Ω.*

(b) *At $\Omega=E_n^+\equiv P_n^{-1}(\delta^+)$ or $E_n^-\equiv P_n^{-1}(\delta^-)$, $\hat{\theta}(\Omega)$ is independent of n, H^-, or H^+; it depends only on the forcing function H_F.*

(c) *E_n^+ decreases as n increases and increases as δ^+ increases; E_n^- decreases as $|\delta^-|$ increases. The behavior of E_n^- with respect to n depends on the position of δ^-: if $P_n^{-1}(\delta^-)<\Omega_L$ then E_n^- increases with n. If $P_n^{-1}(\delta^-)>\Omega_L$, then E_n^- decreases as n increases. See Fig.* 5.1.

(ii) *Suppose that the internal entrainment fails first. Then the value of $\hat{\theta}$ at loss of locking is not independent of n.*

Proof. (i) (a) This follows from the monotonicity of P_n with respect to Ω and the assumption that $H'_F>0$ on $[\delta^-, \delta^+]$.

(b) By Proposition 5.2, P_n is an increasing function of Ω. Locking is lost as $P_n(\Omega)$ exceeds δ^+ (respectively, is less than δ^-), since we have assumed that internal locking persists past that point. At $\Omega=E_n^+$ (respectively, E_n^-), $H_F(\Omega t-\theta_n)=\delta^+$ (respectively, δ^-), which is independent of n, H^-, and H^+. This critical phase lag is the upper (respectively, lower) limit of an interval in which H_F is monotone increasing. See Fig. 5.2.

(c) From Proposition 5.2, for $\Omega>\Omega_L$, P_n is an increasing function of n as well as of Ω. It follows that if $n_1<n_2$, then $P_{n_1}=\delta^+$ (respectively, δ^-) at a value of Ω that is larger (respectively, smaller) than the value at which $P_{n_2}=\delta^+$. See Fig. 5.1. The monotonicity with respect to δ^+ and $|\delta^-|$ follows from the monotonicity of P_n with respect to Ω.

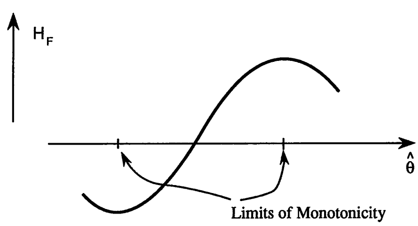

FIG. 5.2. *If the external constraint is the essential constraint on locking, then at loss of locking, the phase lag $\hat{\theta}$ between the forcing oscillator and the oscillator* directly *forced is independent of H^+, H^-, and n; it occurs at one of the points at which H_F ceases to be monotone increasing.*

(ii) Locking is lost at Ω_n^+ when H^+ loses monotonicity, i.e., when $\phi_{n-1}(\Omega)=\partial^+J^+$, the upper boundary of J^+. At this value of Ω, $\hat{\theta}$ satisfies

$$H_F(\hat{\theta})=\Omega_n^+-\omega-H^-(-\partial^+J^+). \tag{5.3}$$

Ω_n^+ is a decreasing function of n. Thus the value of $\hat{\theta}$ at loss of locking decreases with n. That is, if internal entrainment fails first, the value of $\hat{\theta}$ at loss of locking is not independent of n. From (5.5), it is clear that it depends on H^- as well. □

Remark 5.1. Suppose that (i) holds. Then at loss of locking, $\hat{\theta}$ depends only on H_F and is easy to find. By contrast, the limits E_n^- and E_n^+ of entrainment frequencies, at which $\hat{\theta}$ reaches $H'_F(\hat{\theta})=0$, are difficult to calculate; this requires understanding the whole trajectory $\{\phi_k\}$, $k=1,\cdots,n$.

Remark 5.2. There is a curious consequence to result (i)(c) of Theorem 5.1 for the lower bound of the range of entrainment. The result implies that examples may be constructed in which it is possible at some frequencies to entrain a long chain, but not a short one. If $P_n^{-1}(\delta^-)>\Omega_L$ (i.e., if the horizontal line at height δ^- in Fig. 5.1 lies above the intersection of the graphs of all of the curves P_n) then the lower boundary of external entrainment is a decreasing function of n, i.e., a longer chain has a lower limit. For example, suppose that for some $\Omega>\Omega_L$, $P_2(\Omega)<\delta^-<P_\infty(\Omega)\equiv\Omega-\omega-H^-(-\phi_\Omega^+)<\delta^+$ (See Fig. 5.1). Then the external constraint would fail for $n=2$, but not for sufficiently high n.

Remark 5.3. Similar results hold if the chain is forced at $\theta=\theta_1$ instead of $\theta=\theta_n$. To get the correct statements, replace ϕ_L by ϕ_R, Ω_L by Ω_R, the sequence $\{\phi_1,\phi_2,\cdots\}$ by $\{\phi_{n-1},\phi_{n-2},\cdots\}$, and interchange H^+ with H^- and "greater than" with "less than."

6. Temporal stability of entrained solutions. We now investigate the stability of an entrained solution to (1.1), (1.2), (1.5). (This does not follow from the stability criteria on the critical points ϕ_Ω^-, ϕ_Ω^+ as solutions to (1.7).) Similar arguments work if the forcing is done at $\theta=\theta_1$. We first assume that the phase lags ϕ_k lie in the interval J in which $H^+(\phi)$ is monotonically increasing and $H^-(-\phi)$ is monotonically decreasing. We also assume that the value of $\hat{\theta}$ lies in a region in which H_F is monotonically increasing. We show that the solution is then asymptotically stable. The techniques follow closely those of "monotone methods" of partial differential equations, but work for chains of any length, not just in the limit of long chains. The techniques were used in [3] to show asymptotic stability of some phaselocked solutions to unforced chains.

At the end of this section we show that if the solutions do not lie in J, stability is not guaranteed. This is part of the motivation for not considering entrained solutions that lie outside of J.

We first rewrite (1.1), (1.2), (1.5) in terms of the variables $\{\phi_k\}$ and $\hat{\theta}\equiv\Omega t-\theta_n$. For ease of notation, we will relable $\hat{\theta}$ as ϕ_n. The equations are

$$\begin{aligned}\dot{\phi}_1&=H^+(\phi_2)+H^-(-\phi_1)-H^+(\phi_1),\\ \dot{\phi}_k&=H^+(\phi_{k+1})+H^-(-\phi_k)-H^+(\phi_k)-H^-(-\phi_{k-1}),\\ \dot{\phi}_{n-1}&=H^-(-\phi_{n-1})-H^+(\phi_{n-1})-H^-(-\phi_{n-2})+H_F(\phi_n),\\ \dot{\phi}_n&=(\Omega-\omega)-H^-(-\phi_{n-1})-H_F(\phi_n).\end{aligned}\tag{6.1}$$

Asymptotic stability is established by constructing "upper and lower solutions" for the given solution, which we will define below. As we will show, upper solutions have the property that an actual solution having an upper solution as initial data ($t=0$) decreases as time increases, while one having a lower solution for initial data increases as time increases. Thus, if the upper and lower solutions bracket the given solution, with the upper solution above and the lower solution below, the region between these sets of initial conditions tends to some time-independent solution. We show, more strongly, that there are families of upper solutions and lower solutions converging to the given solution, and that this implies that the *given solution* is asymptotically stable.

DEFINITION 6.1. An upper (respectively, lower) solution to (6.1) is a solution $\{\phi_k(t)\}$, such that for all $1\leqq k\leqq n$, $d\phi_k/dt<0$ (respectively, >0) at $t=0$.

LEMMA 6.1. *Let $\{\bar{\phi}_k\}$ be a time-independent solution to* (6.1), *with $\bar{\phi}_k\in J$ for all k. Then there is a family of upper solutions $\{\phi_k^\delta(t)\}$ to* (6.1) *parameterized by $\delta>0$ such* *that* $\phi_k^\delta(0) > \bar{\phi}_k$ *and* $\phi_k^\delta(0) \to \bar{\phi}_k$ *as* $\delta \to 0$. *Similarly, there is a family of lower solutions* $\{\phi_k^\delta(t)\}$, $\delta < 0$, *whose initial conditions bound* $\{\bar{\phi}_k\}$ *from below and which converge to* $\{\bar{\phi}_k\}$ *as* $\delta \to 0$.

Proof. Let $(6.1)_{\delta,\rho}$ denote (1.1), (1.2), (1.5) with ω replaced by $\omega - \rho$ and $(k-1)\delta$ added to the right-hand side of the equation for $\dot{\theta}_k$, $1 \leqq k \leqq n$. (Thus, the value of ϕ_1 is affected by ρ but not δ.) For δ and ρ sufficiently small, it follows from the previous work that there is still a time-independent solution to $(6.1)_{\delta,\rho}$ with phase lags that lie in J. We denote those phase lags by $\{\bar{\phi}_k^{\delta,\rho}\}$. These lags are also time-independent solutions to equations obtained from $(6.1)_{\delta,\rho}$ by pairwise differences, with $\bar{\phi}_n^{\delta,\rho} \equiv \Omega t - \theta_n$ as before. These equations are

$$(6.2)_{\delta,\rho} \qquad \begin{aligned} \dot{\phi}_1 &= \delta + H^+(\phi_2) + H^-(-\phi_1) - H^+(\phi_1), \\ \dot{\phi}_k &= \delta + H^+(\phi_{k+1}) + H^-(-\phi_k) - H^+(\phi_k) - H^-(-\phi_{k-1}), \\ \dot{\phi}_{n-1} &= \delta + H^-(-\phi_{n-1}) - H^+(\phi_{n-1}) - H^-(\phi_{n-2}) + H_F(\phi_n), \\ \dot{\phi}_n &= (\Omega - \omega + \rho + \delta) - H^-(-\phi_{n-1}) - H_F(\phi_n). \end{aligned}$$

Let $\{\phi_k^{\delta,\rho}(t)\}$ be the solution to (6.1) with $\phi_k^{\delta,\rho}(0) = \{\bar{\phi}_k^{\delta,\rho}\}$. It is immediate from Definition 6.1 and $(6.2)_{\delta,\rho}$ that $\{\phi_k^{\delta,\rho}(t)\}$ is an upper solution for (6.1) for all $\delta, \rho > 0$ and sufficiently small.

For $\rho = 0$, the above solution does not lie above $\{\bar{\phi}_k\}$. We now show that δ and ρ may be chosen so that $\phi_k^{\delta,\rho}(0) \equiv \bar{\phi}_k^{\delta,\rho} > \bar{\phi}_k$ for all $1 \leqq k \leqq n$. First note that if $\rho > 0$, we have $\bar{\phi}_1^{\delta,\rho} > \bar{\phi}_1$, using the fact that H^+ is monotone increasing. Also, all but the last equation of $(6.2)_{\delta,\rho}$ are independent of ρ. It follows that for $\delta = 0$, $\rho > 0$, we have $\bar{\phi}_k^{\delta,\rho} > \bar{\phi}_k$, $k < n$; by continuity this is also true for δ sufficiently small (depending on ρ). Using the increased monotonicity of H_F, the last equation of $(6.2)_{\delta,\rho}$ implies that we also have $\bar{\phi}_n^{\delta,\rho} > \bar{\phi}_n$. Lower solutions lying below $\{\bar{\phi}_k\}$ are constructed in an analogous manner. □

Having demonstrated the existence of families of upper solutions and lower solutions that bracket the given solution, we now sketch the arguments why lower solutions increase and upper solutions decrease as time increases. These arguments are very similar to those in [3].

LEMMA 6.2. *Suppose that* $\{\phi_k^1(t)\}$ *and* $\{\phi_k^2(t)\}$ *are two solutions to* (1.1), (1.2), (1.5) *such that* $\phi_k^1(0) < \phi_k^2(0)$. *Then* $\phi_k^1(t) \leqq \phi_k^2(t)$ *for all* $t \geqq 0$.

Proof. For $1 < k < n-1$ we have

$$(6.3) \qquad \begin{aligned} (d/dt)(\phi_k^2 - \phi_k^1) = {} & [(f+g)(\phi_{k+1}^2) - (f+g)(\phi_{k+1}^1)] \\ & + [(g-f)(\phi_{k-1}^2) - (g-f)(\phi_{k-1}^1)] + 2[-g(\phi_k^2) + g(\phi_k^1)]. \end{aligned}$$

For $k = 1$, the second bracket on the right-hand side is missing. For $k = n-1$ and $k = n$, the equations are

$$(6.3)_{n-1} \qquad \begin{aligned} (d/dt)(\phi_{n-1}^2 - \phi_{n-1}^1) = {} & [(g-f)(\phi_{n-2}^2) - (g-f)(\phi_{n-2}^1)] \\ & + 2[-g(\phi_{n-1}^2) + g(\phi_{n-1}^1)] + [H_F(\phi_n^2) - H_F(\phi_n^1)], \end{aligned}$$

$$(6.3)_n \quad (d/dt)(\phi_n^2 - \phi_n^1) = [(g-f)(\phi_{n-1}^2) - (g-f)(\phi_{n-1}^1)] + [-H_F(\phi_n^2) + H_F(\phi_n^1)].$$

By hypothesis, at $t = 0$, $(\phi_k^2 - \phi_k^1) > 0$ for all $1 \leqq k \leqq n$. Suppose for some k_1 and t_1 that $\phi_{k_1}^2(t_1) = \phi_{k_1}^1(t_1)$. Then the bracket in the k_1 equation having terms in the ϕ_{k_1} vanishes. The other brackets are nonnegative due to the increasing monotonicity of $(f+g)$, $(g-f)$ and H_F. Thus $\phi_k^2(t)$ cannot cross $\phi_k^1(t)$ at any point k_1 and time t_1. □

COROLLARY 6.1. *If* $\{\phi_k^u(t)\}$ *is an upper solution to* (1.1), (1.2), (1.5), *then* $(d/dt)\phi_k^u \leqq 0$ *for all* $t \geqq 0$. *If* $\{\phi_k^l\}$ *is a lower solution to* (1.1), (1.2), (1.5), *then* $(d/dt)\phi_k^l \geqq 0$ *for all* $t \geqq 0$.

Proof. Apply Lemma 6.1 to $\{\phi_k^u(t)\}$ and $\{\phi_k^u(t+h)\}$, where $\{\phi_k^u(t)\}$ is an upper solution and h is small and positive. □

LEMMA 6.3. *Let* $\{\phi_k^u(t)\}$ *and* $\{\phi_k^l(t)\}$ *be any upper and lower solutions constructed as in Lemma* 6.1. *Then* $\lim_{t\to\infty}\phi_k^u(t)=\bar{\phi}_k=\lim_{t\to\infty}\phi_k^l(t)$.

Proof. The proof is the same as for Lemma 7.3 of [3]. (The proof uses the existence of the family of upper and lower solutions, not just an individual upper and lower solution.)

Together, the above lemmas prove the following theorem.

THEOREM 6.1. *Suppose that* $\{\bar{\phi}_k, \hat{\theta}\}$ *is a time-independent solution to* (1.1), (1.2), (1.5) *such that* $\bar{\phi}_k \in J$ *for all* k *and* $H'_F(\hat{\theta})>0$. *Then the solution is asymptotically stable as a solution to* (1.1), (1.2), (1.5).

We now discuss the issue of stability if the phase lags are not in J or $H'_F(\hat{\theta})<0$. It is easiest to see that potential instability in the case of the shortest relevant chains, i.e., $n=2$. In that case, the equations for $\phi\equiv\theta_2-\theta_1$ and $\hat{\theta}$ are

$$\begin{aligned}\dot{\phi}&=H^-(-\phi)-H^+(\phi)+H_F(\hat{\theta}),\\ \dot{\hat{\theta}}&=(\Omega-\omega)-H^-(-\phi)-H_F(\hat{\theta}).\end{aligned}\tag{6.4}$$

Assume a time-independent solution $(\bar{\phi}, \bar{\theta})$. The matrix of the linearization of (6.4) around this solution is

$$\begin{pmatrix}-(H^-)'(-\bar{\phi})-(H^+)'(\bar{\phi}) & H'_F(\bar{\theta})\\ (H^-)'(-\bar{\phi}) & -H'_F(\bar{\theta})\end{pmatrix}.$$

If $\bar{\phi}\in J$ and $H'_F(\bar{\theta})>0$, then the determinant of the matrix is positive and the trace is negative. Thus the eigenvalues have negative real part, so the solution is stable. From the form of the determinant and the trace, we see that the sign of the determinant depends only on H^+ and H_F, but the trace depends on H^- as well. Using the formulas for the determinant and trace, we see that stability is lost immediately as soon as $\bar{\phi}$ exits from J^+. The eigenvalues do not change in sign immediately when $\bar{\phi}$ exits J^-; we see from the formula for the trace that $(-H^-)'(-\bar{\phi})$ must be sufficiently positive to accomplish this.

For long chains, it is not so easy to calculate the eigenvalues. However, from formal continuum limits and rigorous arguments [3] relating these to unforced equations, we suspect that if $g'<0$ along the phase lags, the equations behave like backward heat equations. Hence we believe that $g'(\bar{\phi}_k)>0$ along the trajectory is a necessary condition for stability. The still stronger condition $\{\bar{\phi}_k\}\in J$ is necessary in order that monotonicity arguments as used above be relevant. For unforced chains it was shown in [3] that the condition $\{\bar{\phi}_k\}\in J$ is related to the convergence of the solution to that of a similar continuum equation; in the absence of that condition, there may still be a time-independent, temporally stable solution, but this solution has oscillations in k not seen in the solution to the continuum equation. This suggests that there may be solutions to (1.1), (1.2), (1.5) not lying in J that are temporally stable but not governed by monotonicity arguments.

Remark. We can linearize (6.1) about the equilibrium $\{\bar{\phi}_k\}$ and use the Gershgorin circle theorem to show that if $\bar{\phi}_k\in J$, then asymptotic stability holds. Furthermore, an elementary calculation shows that the determinant of the linearized solution vanishes if the derivative of H^+ or H_F vanishes at any of the $\bar{\phi}_k$. As any $\bar{\phi}_k$ exits J^+, the determinant changes sign, so there is a change of stability. Choosing a root of H_F for which $H'_F<0$ also yields an unstable equilibrium solution. A similar result holds for forcing at θ_1, with $H^+(\phi)$ replaced by $H^-(-\phi)$ and J^+ replaced by J^-.

The advantage of using monotone methods over eigenvalue calculations is that they can be used to provide estimates on the size of the domains of attraction. (The above Gershgorin argument does not even bound the eigenvalues away from zero.) These estimates come from the region between the upper solution and the lower solution for any choices of δ, ρ for which time-independent solutions to $(6.1)_{\delta,\rho}$ exist. Consider, for example, $\delta=0$. Then, from $(6.2)_{0,\delta}$ and the fact that ρ affects ϕ_1, there exists an $0(1)$ neighborhood of $\rho=0$ in which $(6.1)_{0,\delta}$ has a time-independent solution uniformly in n. For δ sufficiently small (e.g., $\delta=0(1/n^2)$), there continue to exist such solutions, and they are upper solutions for (6.1). For any initial data between such time-independent solutions to $(6.1)_{\delta,\rho}$ and the time-independent solution to (6.1), the initial data decay downward to the latter. Similarly, data above the lower solution also tend to the solution to (6.1).

7. Dominance and ensemble frequency. Recall the review of the behavior of unforced chains given in § 3. We address here the question of how the ensemble frequency is connected to the range of Ω over which the chain can be entrained when it is forced at one end or the other. As in the previous part of the paper, we assume that $f''>0$; as we summarize in § 8, there are similar results if $f''<0$, but some inequalities are reversed.

We have seen from Theorem 4.1 that if forcing is done at $\theta=\theta_n$ (respectively, $\theta=\theta_1$) internal entrainment occurs for a range that includes Ω_L (respectively, Ω_R) and some interval above it, independent of n. (If $\phi_L>\phi_T$ (respectively, $\phi_R<\phi_T$) the range for internal entrainment goes lower to Ω_T). None of these results depend on the analysis of the unforced chain. However, the comparison of these ranges to the ensemble frequency does so depend, and in particular on which coupling H^+ or H^- is dominant.

Suppose that H^+ dominates H^-. As shown in the Appendix, this implies that $\phi_R>\phi_T$. If the chain is forced at $\theta=\theta_n$, the ensemble frequency, which is close to Ω_R, lies above the lower boundary Ω_L or Ω_T for internal entrainment. That is, internal entrainment is possible both above and below the ensemble frequency. By contrast, if the chain is forced at θ_1, this ensemble frequency is approximately equal to the lower boundary of frequencies for internal entrainment, so internal entrainment can happen (for long chains) only above the ensemble frequency. The situation is reversed if H^- dominates H^+; then the chain forced at θ_n can entrain internally only to frequencies larger than the ensemble frequency Ω_R, while the chain forced at θ_1 can entrain to frequencies on both sides.

The need to satisfy the external constraint (5.1) changes the boundaries of entrainment. However, because of the hypothesis that $\delta^-<0<\delta^+$, (5.1) can always be satisfied at the value $\Omega=\Omega_R$ for which $P_n(\Omega)=0$. Thus, it is still true that the ensemble frequency is in the interior of the entrainment range. Similar statements are true for forcing at θ_1.

8. Discussion.

8.1. Further mathematical comments. (1) In the previous sections, we discussed the case $f''>0$. Using the symmetry (2.6) we can infer the results for $f''<0$. We focus here on what results are independent of hypotheses such as $f''>0$ or H^+ dominates H^-, and which are dependent. The latter enables us to infer from observations about a forced chain of oscillators some of the properties of the coupling in the chain.

We first discuss the analogous results for $f''<0$. The notion of dominance given in § 3 is independent of the sign of f''. Thus, the dominant coupling is that for which the difference between the natural frequency ω and the ensemble frequency Ω is the smallest. The results for internal entrainment (analogous to Theorem 4.1) are as follows:

Suppose that the chain is forced at $\theta=\theta_n$ and that $\phi_L>\phi_T$ (respectively, $\phi_L\leqq\phi_T$). Then the range of frequencies permitting internal entrainment tends, as $n\to\infty$ to

$[\Omega^-, \Omega_L]$ (respectively, $[\Omega^-, \Omega_T]$). Here Ω^- is defined as the value of Ω such that $\phi_\Omega^- = \partial^- J^+$, the lower boundary of J^+. If the chain is forced at $\theta = \theta_1$ there are similar results with Ω_L replaced by Ω_R.

The major difference between the two cases is that, if $f'' < 0$ (and, e.g., ϕ_L and ϕ_R lie on opposite sides of ϕ_T so that the upper boundary of the range of entrainment is Ω_L or Ω_R, not Ω_T) then a chain forced at the nondominant end can be entrained only *below* the ensemble frequency, instead of only above as in the case $f'' > 0$. The analogue of Theorem 4.1, about external constraints, has the same conclusions for $f'' > 0$ and $f'' < 0$.

Some of the conclusions of the theory are independent of which coupling is dominant, and we review those here:

(a) If loss of locking is due to inability to satisfy the external constraints, then it occurs at a phase lag $\hat{\theta}$ (between the forcing oscillator and the forced one) that is independent of n. If the locking is lost due to lack of internal entrainment, $\hat{\theta}$ is not independent of n.

(b) $\hat{\theta}$ increases monotonically with Ω.

(c) As long as the forcing function provides the essential constraint, the size of entrainment interval increases with the size of the forcing.

(2) Since many of the conclusions of the theory are independent of the sign of f'', we might ask how the chain would behave if $f'' = 0$, e.g., if H^+ and H^- were linear in some ranges. (Since H^+ and H^- are periodic functions, they cannot be globally linear.) Assume hypotheses 1 and 2 of § 2. If H^+ and H^- are linear, then (1.7) has only one critical point ϕ_c instead of two. This critical point is stable if $f' > 0$ and unstable if $f' < 0$. The question of dominance is decided totally by the sign of f': if $f' > 0$ (respectively, $f' < 0$) then H^+ is dominant (respectively, H^-) is dominant.

Assume for definiteness that $f' > 0$. If the chain is forced at the dominant end ($\theta = \theta_n$), the stability of the critical point implies that internal entrainment cannot fail. (Of course, the initial point θ_1 of the trajectory must be in the region in which H^+ and H^- are linear for this to be true.) If the chain is forced at the nondominant end, however, the range of entrainment for a given n collapses as $n \to \infty$ to a single frequency $\Omega = \Omega_c \equiv \omega + 2f(\phi_c)$. That is, in contrast to the nonlinear case, there is not a range of entrainment independent of n for forcing at both ends. It can easily be checked that these conclusions are still true if $f' < 0$; then the critical point is stable for backward "time" k, and unstable for increasing k, so again the forcing at the nondominant end has a range of entrainment that collapses to a point as $n \to \infty$. Thus, "tuned" chains behave under forcing like linear ones. (See Remark 4.4.)

8.2. Forcing and the structure of a central pattern generator. Central pattern generators are networks of neurons that are involved in the production and regulation of rhythmic motor output. One of the most studied CPGs for vertebrates is the pattern generator for undulatory locomotion, and one very useful preparation for studying this CPG has been the primitive vertebrate lamprey, for which it is possible to isolate the spinal cord [13] and elicit behavior in vitro that is essentially equivalent to that of an intact behaving animal [14]. It has been generally accepted that this CPG can be described roughly as a chain of oscillators [15].

Experiments by Grillner, McClellan, Perret, and Sigvardt [16], [17] have established that the isolated cord contains mechanoreceptors that transduce bending into neural activity, and that such activity can entrain the centrally generated rhythm. This feedback is thought to be important in controlling the relative timing of muscle activation and local curvature [18]. Further experiments have established that the mechanoreceptors act directly mainly on cells very close to the position of bending [19]. However, since the cells of the CPG are interconnected, the bending has indirect effects throughout the cord. In particular, a rhythmic bending of one end of the cord, with most of the cord pinned down to prevent motion, can entrain the activity of the entire cord.

One motivation of this paper is to investigate what can be deduced about the coupling system from experiments in which isolated cords are forced mechanically. Further experiments were done as the theory was developed [8]. Cords of different lengths were used, and each piece was forced at each end at a variety of frequencies, to determine entrainment range and patterns of phase lags. The experiments were designed to control for potential differences in mechanoreceptors at different parts of the cord.

Not all of this data has yet been analyzed. However, the data concerning regions of entrainment have been analyzed. It was found that for both long and short cords, entrainment could occur at frequencies on each side of the unforced ensemble frequency if the forcing was done at the caudal (tailward) end of the piece. However, if the forcing was done at the rostral (headward) end, entrainment took place only for an interval above the rest frequency. This is exactly what is predicted in the theory described above for forced chains with nearest neighbor coupling, provided that $f''>0$ and the caudal end is the dominant end. Thus the theory suggests that the ascending (caudal to rostral) coupling dominates the descending (rostral to caudal) coupling. It further suggests that $f''>0$; for almost all classes of models that we have investigated; this is associated with coupling that has the property that the coupled chain has an ensemble frequency lower than the uncoupled natural frequencies. It remains to understand the behavior of forced chains when the coupling includes the long-range fibers that are known to exist.

The number of possible choices for long-distance coupling is very large, and, in the absence of a theory, it is not possible to be certain that simulations have adequately covered the possibilities, even qualitatively. However, we have done some simulations to check the effects of long-distance and multiple coupling. The first set of simulations starts with nearest neighbor coupling $n=20$, $H^+(\phi)=\sin(\phi-.5)$, and $H^-(\phi)=\gamma H^+(\phi)$, with $\gamma<1$, so ascending coupling is dominant. Hence, we can entrain with caudal forcing at frequencies above and below the ensemble frequency, but only above the ensemble frequency with forcing at the rostral end. We now add halflength "inhibition" of the form $H^+_{\text{in}}(\phi)=-\sin\phi$, $H^-_{\text{in}}(\phi)=-\beta\sin\phi$. (This coupling produces a wave with wavelength equal to the length of the chain.) If $\beta<1$, so the long ascending coupling dominates the long descending coupling, the above conclusion continues to hold. In another set of experiments, the long-range coupling is replaced by multiple local coupling of the form $\sum_{i=n_{\text{up}}}^{n_{\text{down}}} H(\theta_{k+i}-\theta_k)$, where $H(\phi)=\sin(\phi-.5)$. If $n_{\text{up}}>n_{\text{down}}$, the above conclusions again hold.

Appendix. In [5], existence and uniqueness are proved, and the ensemble frequency is shown to be one of five quantities, including Ω_L and Ω_R. If ω and the coupling strengths are independent of k as in this paper, only the three quantities Ω_L, Ω_R, and $\Omega_0=\omega+2f(\phi_T)$ are relevant. As in [5], we are making the generic assumption that Ω_L, Ω_R, and Ω_0 are distinct. For definiteness, we continue to assume that $f''>0$. It is then shown in [5] that the ensemble frequency Ω satisfies

(i) $\Omega=\Omega_L$, if $\phi_L<\phi_T$ and

$$\Omega_L>\Omega_R, \quad \text{or}$$

$$\Omega_R>\Omega_L \quad \text{and} \quad \phi_R<\phi_T.$$

(ii) $\Omega = \Omega_R$, if $\phi_R > \phi_T$ and

$$\Omega_R > \Omega_L, \quad \text{or}$$

$$\Omega_L > \Omega_R \quad \text{and} \quad \phi_L > \phi_T.$$

(iii) $\Omega = \Omega_0$, if $\phi_R < \phi_T < \phi_L$.

These correspond to cases (a), (b), and (f) of Theorem 3.1 of [5]; the other cases do not occur if the frequencies and coupling strengths are independent of k as in this paper. Case (iii) is also ruled out by hypothesis (5) of § 2, since it implies that $f'(\phi_R) < 0 < f'(\phi_L)$. We now show that (3.2) holds in case (i); a similar argument shows that it also holds in case (ii).

First assume that $\phi_L < \phi_T$, $\Omega_L > \Omega_R$. Then $H^+(\phi_L) > H^-(-\phi_R)$. This implies (3.2) provided that $H^+(\phi_L)$, $H^-(-\phi_R) < 0$. To see this, recall that by definition $H^+(\phi_R) = 0 = H^-(-\phi_L)$. Hence, to know that $H^+(\phi_L) < 0$, it suffices by the monotonicity of H^+ to show that $\phi_L < \phi_R$. Similarly, since $H^-(-\phi)$ is monotone decreasing in ϕ, the inequality $H^-(-\phi_R) < 0$ also follows if $\phi_L < \phi_R$. The latter is a consequence of $\phi_L < \phi_T$ and $\Omega_L > \Omega_R$, since $\phi_L < \phi_T$ and $\phi_R \leqq \phi_L$ implies $\Omega_L \leqq \Omega_R$.

Now assume that $\phi_L < \phi_T$, $\Omega_R > \Omega_L$, and $\phi_R < \phi_T$. Then $H^+(\phi_L) < H^-(-\phi_R)$. This implies (3.2) provided that $H^+(\phi_L)$, $H^-(-\phi_R) > 0$. Since $\phi_L < \phi_T$, the hypotheses $f'' > 0$, $\Omega_R > \Omega_L$, and $\phi_R < \phi_T$ imply that $\phi_R < \phi_L$. By monotonicity, as above, we then have $H^+(\phi_L) > 0$, $H^-(-\phi_R) > 0$.

Remark. In [5], $f'' \neq 0$ is a crucial hypothesis for some of the results, and hence all the arguments of [5] are done by cases using the sign of f''. However, if the chain is made up of equal oscillators, the sign of f'' is not relevant to the notion of dominance. In particular, a similar argument shows that (3.2) is also valid if $f'' < 0$. Furthermore, (3.2) can easily be checked if $f'' \equiv 0$.

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