An adaptive model for synchrony in the firefly *Pteroptyx malaccae*

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Abstract. We describe a new model for synchronization of neuronal oscillators that is based on the observation that certain species of fireflies are able to alter their free-running period. We show that by adding adaptation to standard oscillator models it is possible to observe the frequency alteration. One consequence of this is the perfect synchrony between coupled oscillators. Stability and some analytic results are included along with numerical simulations.

Key words: Fireflies – Synchronization – Nonlinear oscillations

1. Introduction

Synchronization of large groups of fireflies has been recognized for the last four hundred years. Buck and coworkers have quantified this phenomenon for several species of insects [1, 2, 5, 6] by studying the responses of an isolated insect to single and periodically varying flashes of light. There appear to be several different mechanisms for synchrony and entrainment among the different species. These include phase advance synchrony, phase delay synchrony, and perfect synchrony. In phase advance synchrony, the insect is able to advance its phase to a pulse of light, but cannot delay it under any circumstances. This model appears to apply to the American species, *Photinus pyralis* which does not congregate and flash synchronously in large groups, although transient synchronization is sometimes seen. One can make a simple mathematical model of this by using an "integrate and fire" oscillator which responds to a pulse of light by always advancing the phase (see e.g. Peskin [11]). Mirollo and Strogatz [13] have recently shown that *N* such oscillators, each coupled to all of the others, will always tend to the perfectly synchronized state except for a set of initial conditions that has measure zero. One could probably generalize their theorem to the case in which the oscillators were of slightly different frequency. In [1], Buck suggests the linear analogue of an integrate and fire model to explain this type of entrainment.

Phase delay synchrony is a mechanism by which the oscillator is inhibited by the pulse of light and which allows it to either advance or delay its phase depending on where the pulse arises. This appears to be the method utilized by *P. cribellata* which has the ability to entrain over a broad range of frequencies. This particular species will lock to differing frequencies but has a distinct phase shift that increases as the forcing frequency diverges from the intrinsic frequency of the pacemaker. In fact, the shift is exactly the difference between the free-running period and the forcing period. Buck et al. [2] studied the free-running rhythm of this insect and found that the flashing was controlled by an endogenous neural pacemaker. The timing of the flashes does not depend on the insect seeing his own flash nor even that he flash. The pacemaker is extraordinarily robust with a variation in interflash intervals of less that 3%. The firefly entrains to a range of periodic stimuli within one or two impulses, but attains zero phase lag only when driven at his intrinsic frequency. Large swarms of *P. cribellata* congregate in trees and flash rhythmically.

By perfect synchrony, we mean that the insect can entrain with zero phase lag even when the stimulating frequency is not the same as the intrinsic frequency. Three tropical Asian species, *P. malaccae*, *Pteroptyx tener*, and *Luciola pupilla* appear to be able to achieve this perfect synchronization with the stimulus. Hanson [6] describes the difference between these species and *P. cribellata*:

> ... synchrony is attained much differently by the Malaysian firefly *Pteroptyx malaccae*. Entrainment does not result in a constant phase angle equal to the difference between pacing frequency and free-running period as it does in *P. cribellata*; instead, *P. malaccae* nulls all phase angle differences during pacing. ... The mechanism of attaining synchrony by *P. malaccae* can be summarized. When the pacer changes, this firefly requires several cycles to reach a steady state. Once this steady state is achieved, the phase angle difference is near zero irrespective of the pacer period. This result can be explained only by the animal adjusting the period of its oscillator to equal that of the driving oscillator.

The range of frequencies at which the animals can be entrained is very small and once the stimulus leaves that range, the oscillator drifts with respect to the stimulus. Zero phase shift synchrony is rarely seen; Buck notes that humans and certain species of crickets [1] are the only other organisms that appear to be able to attain null phase lags with respect to the stimulus. *P. malaccae* is unusual in that it can actually alter its period as much as 15% in both directions.

In a previous paper [12], we suggested a mechanism to explain the patterns of drift observed in *P. malaccae* when the stimulating frequency was beyond the range of entrainment of the firefly. The qualitative behavior is identical to that of the experimental system after locking is lost, but the model fails to account for the fact that the phase difference at the point at which locking is lost is nearly zero. In fact, there appear to be no models which will give a zero phase difference for a range of frequencies away from the intrinsic frequency of the oscillator. Related to the insects' ability to synchronize to a periodic stimulation is the formation of "firefly trees". Thousands of individual insects will settle on a tree and proceed to flash in perfect synchrony. As described by Buck this is a striking and beautiful display [1]. In [6], Hanson shows a three channel recording from a firefly tree in which the recording sites were 4 meters apart; each peak in light is perfectly synchronized. A model for phase-locking of many coupled oscillators which are coupled "all to all" and in which the frequencies were allowed to vary randomly in some interval was described and analyzed in [3]. This model has the same deficiencies as [12], the phase-locked patterns are perfectly synchronous

only if the frequencies are identical. Similar results hold for coupling in other geometries, e.g., nearest neighbor coupling.

Here we propose a mechanism explaining the ability of the insect to synchronize at a nearly zero phase difference. This model has a PRC that is the same as that measured for *P. malaccae* but differs from typical models (e.g. [4], see below) in that the frequency of the oscillator is allowed to slowly adapt. Eventually, the phase shift between the stimulus and the oscillator becomes $O(\varepsilon)$, where ε is a small relaxation parameter that could be experimentally measured. The size of this phase shift remains small as the limits of entrainment are reached. This contrasts with the models of pacemakers that depend only on the phase response curve. The most interesting mathematical feature of this model is that the phase response curve is identical to one studied by numerous investigators [4, 7, 8], but the behavior under sustained periodic stimulus is quite different due to the adaptive nature of the model. The phase shift to the stimulus remains $O(\varepsilon)$ in the entire entrainment range except for an $O(\varepsilon)$ region around the boundary of the range. In Sect. 2, we summarize previous models of synchrony for the periodically driven and the coupled systems. We show that as the limits of entrainment are reached, the phase shift tends to some nonzero value that is away from zero. In Sect. 3, we propose a model that has the additional property of the ability to modify the intrinsic frequency in order to attain a zero phase shift. We analyze the stability and range of entrainment for this model. Section 4 discusses the collective effect of two or more fireflies coupled together. We simulate a pair of insects and then a random collection of insects that can "see" all insects a certain distance from each other. We study the onset of synchrony and the slow adaptation to the same collective frequency. These results are compared to the same interactions without frequency adaptation. We analyze the coupled model in the case of all to all coupling with some range of natural frequencies when we can average interactions. Finally, we discuss some more general questions about synchronization and possible applications of the present techniques to circadian modelling.

2. Simple first order models

Consider a single periodically forced oscillator of the form:

$$d\theta/dt = \omega + P(t/\tau)\, \Delta(\theta) \bmod(1). \qquad (2.1)$$

Here, ω is the intrinsic frequency of the unforced oscillator, $P(\phi)$ is the periodic forcing stimulus, and $\Delta(\theta)$ is the phase response curve (PRC). All functions are periodic with period 1. When $P(\phi)$ is a periodic Dirac δ-function, (2.1) becomes a map:

$$\theta_{n+1} = \theta_n + \omega\tau + \Delta(\theta_n + \omega\tau). \qquad (2.2)$$

θ_n is the phase of the oscillator after the nth stimulus. Alternatively, if $P(\phi)$ is smoother and the forcing is not large in magnitude or the PRC, $\Delta(\phi)$, is shallow one can average (2.1) to obtain the following:

$$d\theta/dt = \omega + H(t/\tau - \theta), \qquad (2.3)$$

where

$$H(\phi) = \int_0^1 P(s)\, \Delta(s - \phi)\, ds. \qquad (2.4)$$

We proceed to look for $1:1$ phase-locked solutions of (2.2) or (2.3). The phase-locked solution of (2.2) is:

$$\theta_n \to \tilde{\theta}, \qquad \Delta(\tilde{\theta} + \omega\tau) = 1 - \omega\tau. \tag{2.5}$$

Thus as long as the term $1 - \omega\tau$ does not exceed the maximum of Δ or fall below the minimum of Δ, we can solve (2.5):

$$\tilde{\theta} = 1 - \omega\tau + \Delta^{-1}(1 - \omega\tau). \tag{2.6}$$

If we suppose that $\Delta(0) = 0$, then synchrony occurs only if $\omega\tau \equiv 1$, that is, the forcing frequency is the same as the intrinsic frequency. As the forcing frequency diverges from the intrinsic frequency, the phase shift between the oscillation and the stimulation increases in magnitude. In Fig. 1 (next section), we sketch $\tilde{\theta}$ as a function of τ for $\Delta(\phi) = -(\beta/2\pi)\sin(2\pi\phi)$. The critical frequency at which locking is lost occurs when $1 - \omega\tau$ exceeds the maximum or minimum of $\Delta(\theta)$. For this Δ, we find that the critical phase at which locking is lost is:

$$\phi^* = \frac{\beta}{2\pi} \pm \frac{1}{4}.$$

In particular, for β small (which is the case for *P. malaccae*), the critical phase is close to a quarter cycle. The PRC for this species is qualitatively similar to a small amplitude sine curve, thus, if one applies the simple PRC model, one must conclude that there is a critical phase at which locking is lost and this is close to a quarter cycle. For frequencies within the critical range, the phase varies from zero to the critical values, zero occurring only when $1 - \omega\tau \equiv 0$. We also note that for the PRC model, as long as $-1 < \Delta'(\tilde{\theta} + \omega\tau) < 0$, this solution is stable.

For the continuous model, the phase shift between the periodic forcing and the firing of the oscillator is given by:

$$\tilde{\theta} = -H^{-1}\left(\frac{1 - \omega\tau}{\tau}\right). \tag{2.7}$$

As above, if $H(0) = 0$, the phase shift vanishes only if $\omega\tau - 1 \equiv 0$; otherwise it increases in magnitude as $|1 - \omega\tau|$ increases. We note that a good model for *Pteroptyx cribelatta* is Eq. (2.3) with H the piecewise linear map with slope 1. For, then, the phase shift is matched by the difference in periods.

Both the map and the continuous model exhibit similar behaviors for frequencies outside of the range of entrainment although the map has, in addition, very complex behaviors (see e.g. Glass et al. [4, 8]). Both predict that the phase shift between the forcing stimulus and the forced oscillator should increase as the forcing frequency deviates from the intrinsic frequency of the oscillator.

Similar considerations hold for coupled oscillators. The analogue of (2.1) for N oscillators coupled together with differing frequencies is:

$$d\theta_j/dt = \omega_j + \sum_{k=1}^{N} P_{kj}(\theta_k)\,\Delta(\theta_j). \tag{2.8}$$

Here, $P_{kj}(\phi)$ depends on the relative influence of oscillator k on oscillator j. If P_{kj} is small, then one can apply the method of averaging to (2.8) by making the change of variables $\theta_j = \omega t + \tilde{\theta}_j$, where ω is close to the mean frequency. Averaging (2.8) and, dropping the hats and rescaling time results in the analogue of (2.3):

$$d\theta_j/dt = \omega_j + \sum_{k=1}^{N} H_{kj}(\theta_k - \theta_j). \tag{2.9}$$

This was analyzed in [3] (and by numerous authors, see [13] and [3] for other references) for $H_{kj}(\phi) \equiv H(\phi) = (\beta/N) \sin(2\pi(\phi + \xi))$. One of the main results is that there can be phase-locking, but the phase differences between two oscillators can be as large as half a cycle before locking is lost. This type of model is therefore inadequate for explaining firefly trees which synchronize with almost no phase shifts between oscillators.

The model of Strogatz and Mirollo [14] can synchronize with no phase lag even in the presence of frequency inhomogeneities. But, the model is probably not a good analogue to the behavior of *P. malaccae* for several reasons. First, the integrate and fire model that Strogatz et al. use can only be forced at frequencies higher than its intrinsic frequency. *P. malaccae* has a range of frequencies above and below the natural frequency at which it can entrain. The ability to entrain with no lags requires that the stimulus be very strong and when entrainment occurs, it occurs within a few cycles. In contrast, the PRC of *P. malaccae* is quite small and entrainment requires many cycles [1].

3. An adaptive frequency model

We now suppose that the insect has a preferred frequency of firing, which we call ω_{nat}, and a maximum (ω_{max}) and minimum (ω_{min}) frequency to which it can adapt. We replace (2.1) by:

$$d\theta/dt = \omega, \tag{3.1}$$

where ω is a time-dependent variable frequency. We will assume a slow damping of ω to the natural frequency in absence of any stimulation. We furthermore require that if the stimulus comes early in the cycle then ω will be pushed toward a maximal frequency and if the stimulus comes late, it will be pushed toward the minimal frequency. Thus, ω satisfies the differential equation:

$$d\omega/dt = \varepsilon(\omega_{nat} - \omega) + P(t/\tau)G(\omega, \theta). \tag{3.2}$$

The parameter ε measures the rate at which the oscillator returns to its natural frequency. The form of G must conform to the requirements that the system (3.2) have a PRC like that of the firefly and that it push the frequency high or low depending on where the stimulus occurs. Before continuing the analysis, we show that in some limiting cases, (3.1–3.2) tends to (2.1). Suppose that $G(\omega, \theta)$ is $O(\varepsilon)$ and independent of ω, e.g., $G(\omega, \theta) = \varepsilon \Delta(\theta)$. Differentiation of (3.1) leads to:

$$d^2\theta/dt^2 = \varepsilon(\omega_{nat} - d\theta/dt) + \varepsilon P(t/\tau) \Delta(\theta). \tag{3.3}$$

Divide by ε and let $\varepsilon \to \infty$. Clearly, (3.3) tends to (2.1). Since we wish to avoid the behavior of (2.1), we must assume that adaptation is slow or that the formation $G(\omega, \theta)$ is not independent of ω.

Consider the response of (3.1–3.2) to an instantaneous pulse. In absence of any forcing, $\omega \equiv \omega_{nat}$. Thus, the response will be an instantaneous shift in the frequency by an amount $G(\omega_{nat}, \theta_{old})$ where θ_{old} is the phase at which the brief pulse is given. Thus, $\omega = \omega_{nat} + G(\omega_{nat}, \theta_{old})$. After $t \sim O(1/\omega_{nat})$, the phase of the oscillator is $\theta_{old} + G(\omega_{nat}, \theta_{old})/\omega_{nat}$. This little calculation shows that the

function G must behave proportionally to the PRC. In much of what follows, we will suppose that $G(\omega, \theta)$ has the specific form:

$$g^+(\theta)(\omega_{min} - \omega) + g^-(\theta)(\omega_{max} - \omega), \qquad (3.4)$$

where $g^\pm(\theta)$ are periodic functions satisfying:

$$g^+(0) = 0; \quad g^+(\phi) > 0, \quad 0 < \phi < \tfrac{1}{2}; \qquad g^+(\phi) \equiv 0, \quad \tfrac{1}{2} < \phi < 1 \qquad (3.5)$$

$$g^-(0) = 0; \quad g^-(\phi) > 0, \quad \tfrac{1}{2} < \phi < 1; \qquad g^-(\phi) \equiv 0, \quad 0 < \phi < \tfrac{1}{2}. \qquad (3.6)$$

One can crudely interpret these in a physiological manner. Each $g^\pm$ is non-negative and thus behaves as a gate or channel which forces ω upwards or downwards. This could be due to ionic effects. Recent results of Kepler et al. [9] show that attaching a hyper- or depolarizing source to an oscillator can alter its intrinsic frequency.

Let τ denote the forcing period and ω_n denote the frequency between the nth and $(n + 1)$st impulses. Let θ_n denote the phase after the nth stimulus. Then:

$$\theta_{n+1} = \theta_n + \omega_n \tau. \qquad (3.7)$$

We need an equation for ω_n. We assume that if the $(n + 1)$st impulse is ahead of the stimulus (i.e. in the interval $0 < \theta < \tfrac{1}{2}$) then we will slow down the frequency and if it is behind the stimulus, we will speed it up. Thus, ω_n will satisfy:

$$\omega_{n+1} = \omega_n + \varepsilon(\omega_{nat} - \omega_n) + g^+(\theta_n + \tau\omega_n)(\omega_{min} - \omega_n)$$
$$+ g^-(\theta_n + \tau\omega_n)(\omega_{max} - \omega_n). \qquad (3.8)$$

This model implies that without forcing (i.e., $g^\pm \equiv 0$), the frequency will relax to its natural frequency, ω_{nat}. Suppose, ε is very small. Then if the oscillator is consistently ahead of the forcing stimulus, g^+ is positive and g^- is zero so that ω_n will tend toward ω_{min}. Equations (3.4–3.6) suggest a PRC for this model. Suppose that the oscillator is unforced so that $\omega_n \to \omega_{nat}$. A single stimulus comes at a phase ϕ in the cycle. This will alter the timing of the next spike by an amount:

$$\varepsilon(\omega_{nat} - \omega_{nat}) + g^+(\phi)(\omega_{min} - \omega_{nat}) + g^-(\phi)(\omega_{max} - \omega_{nat}).$$

Thus, then new phase is the old phase plus the above amount; hence the PRC is given by:

$$\Delta(\phi) = g^+(\phi)(\omega_{min} - \omega_{nat}) + g^-(\phi)(\omega_{max} - \omega_{nat}). \qquad (3.9)$$

The experiments on *P. malaccae* do not indicate whether the actual frequency change of the insect is the same size as the PRC. Unpublished data provided by Frank Hanson shows that, for a driven insect, a single change in the period of one of the stimulating flashes is enough to alter the period and several cycles are required before it returns to the driving period. If we choose

$$g^+(\phi) = \max\!\left(\frac{1}{2\pi}\sin(2\pi\phi), 0\right) \quad \text{and} \quad g^-(\phi) = -\min\!\left(\frac{1}{2\pi}\sin(2\pi\phi), 0\right)$$

then, the general shape of the PRC is the same as that in Sect. 2 and of the firefly *P. malaccae*.

There can be $1:1$ locking if and only if $\omega_n\tau = 1$ since this requires that $\theta_n = \theta_{n+1}$ mod 1. Thus, we must have $\omega_n \to 1/\tau$, and $\theta_n \to \phi$, where ϕ satisfies:

$$\varepsilon(\omega_{nat} - 1/\tau) + g^+(\phi)(\omega_{min} - 1/\tau) + g^-(\phi)(\omega_{max} - 1/\tau) = 0. \qquad (3.10)$$

Suppose that $\omega_{nat} > 1/\tau$. Then, ϕ satisfies:

$$g^+(\phi) = \frac{\varepsilon(\omega_{nat} - 1/\tau)}{(1/\tau - \omega_{min})} . \tag{3.11}$$

As long as $(1/\tau - \omega_{min}) \gg \varepsilon$, this phase difference will be small. Only when the forcing is extremely close to the critical frequency will there be significant phase shift with respect to the stimulus. Similar results hold for $\omega_{nat} < 1/\tau$. Although *P. malaccae* has a narrow range of possible frequencies, this adaptive mechanism can support large differences in frequencies with negligible phase differences by choosing ω_{max} and ω_{min} appropriately. For *P. malaccae* these frequencies are narrowly constrained so that the insect can synchronize only to a narrow range of periodic stimuli. If the insect has a very labile intrinsic frequency, then ε may be very close to zero. (For humans attempting to follow a rhythm such as hand-clapping, the range of frequencies to which perfect synchrony can be attained is almost infinite; for such a task there may be no fixed intrinsic frequency and thus ε may be zero [1].) In Fig. 1, we plot the phase shift ϕ as a function of the frequency within the range of admissible frequencies. It remains close to 0 for all but a region that is $O(\varepsilon)$ around the endpoints. Compare this to the analogous behavior for Eq. (2.1) with Δ as defined by (3.5) (note that $T = 1/\omega_{nat}$). The range of entrainable frequencies is much greater and the phase shift remains small for a large percentage of the entrainment range. In Fig. 2, we show the evolution over many cycles of the frequency and the phase as they approach equilibrium. If, e.g., $g^+(\phi) = \sin \phi$ then the value of ϕ at which locking is lost will be $\pm \pi/2$.

Suppose that $1/\tau < \omega_{min}$ and that we try to get locking. Then, it is clear that (3.10) can never be satisfied since the right hand side is negative and the left is positive. Similarly, no locking can occur if $1/\tau > \omega_{max}$. In Fig. 3, we depict the solution to (3.7–3.8) for τ larger than the maximal entrainable period ($\approx 1/\omega_{min}$). The frequency shows little variation from its natural value and the phase shift from the stimulus drifts over all phases.
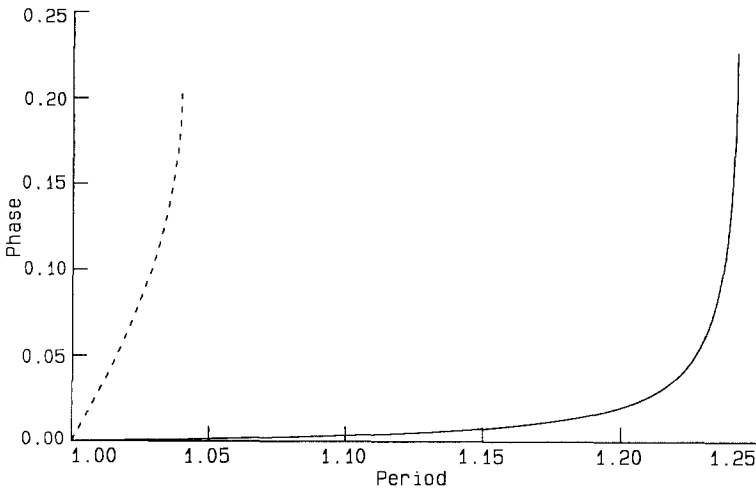

Fig. 1. The phase versus the stimulus period for the adaptive (solid) and the nonadaptive (dashed) models for locking. For the nonadaptive model, $\beta = 0.25$ and for the adaptive model, $\varepsilon = 0.004$, $\omega_{min} = 0.8$, $\omega_{max} = 1.2$, $\omega_{nat} = 1.0$
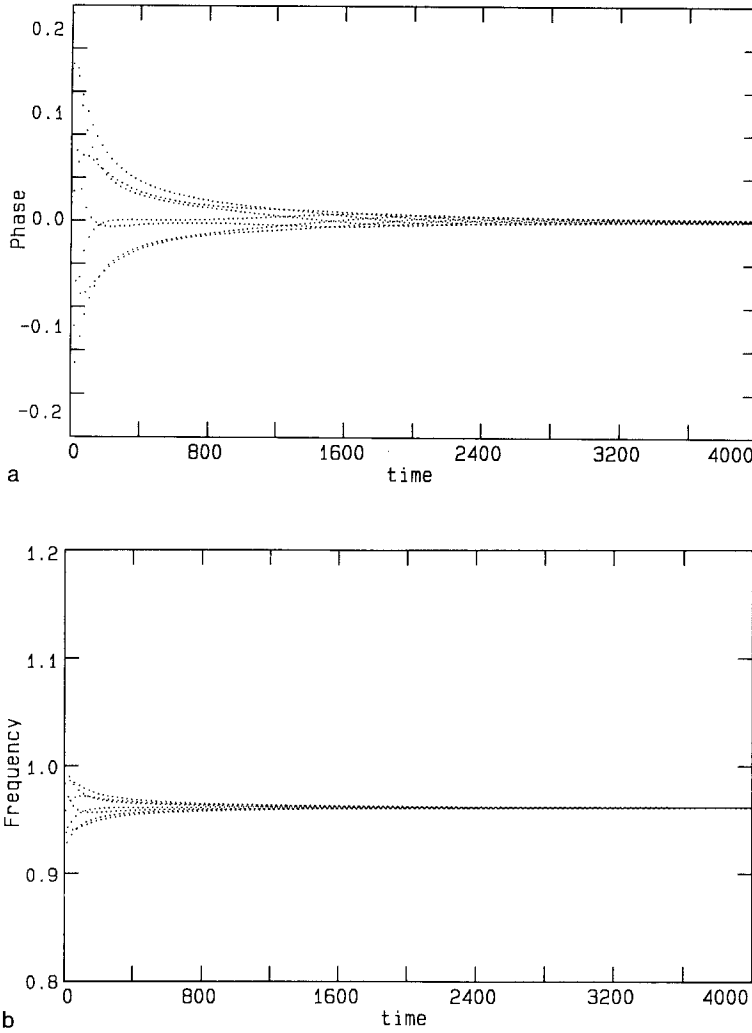
Fig. 2. Phase (a) and frequency (b) as functions of time for the adaptive model. Parameters as in Fig. 1 with $\tau = 1.04$

We briefly address the stability of solutions for $\omega_{min} + O(\varepsilon) < 1/\tau \lessgtr \omega_{nat}$. Similar results will hold for $\omega_{nat} \lessgtr 1/\tau < \omega_{max} - O(\varepsilon)$. Linearization about an equilibrium value of $\omega = 1/\tau$ and $\theta = \phi \approx O(\varepsilon)$ yields a 2×2 matrix with determinant and trace given by:

$$DET = \mathscr{G}(1 - \tau\omega_{min}) - \varepsilon \frac{\tau\omega_{nat} - \tau\omega_{min}}{1 - \tau\omega_{min}},$$

$$TR = 1 - \varepsilon \frac{\tau\omega_{nat} - \tau\omega_{min}}{1 - \tau\omega_{min}}. \tag{3.12}$$

$\mathscr{G}$ is the derivative g^+ evaluated at ϕ. The condition for stability is that $2 > 1 + DET > |TR|$. For ε sufficiently small and $1/\tau$ away from ω_{min}, $TR > 0$, so
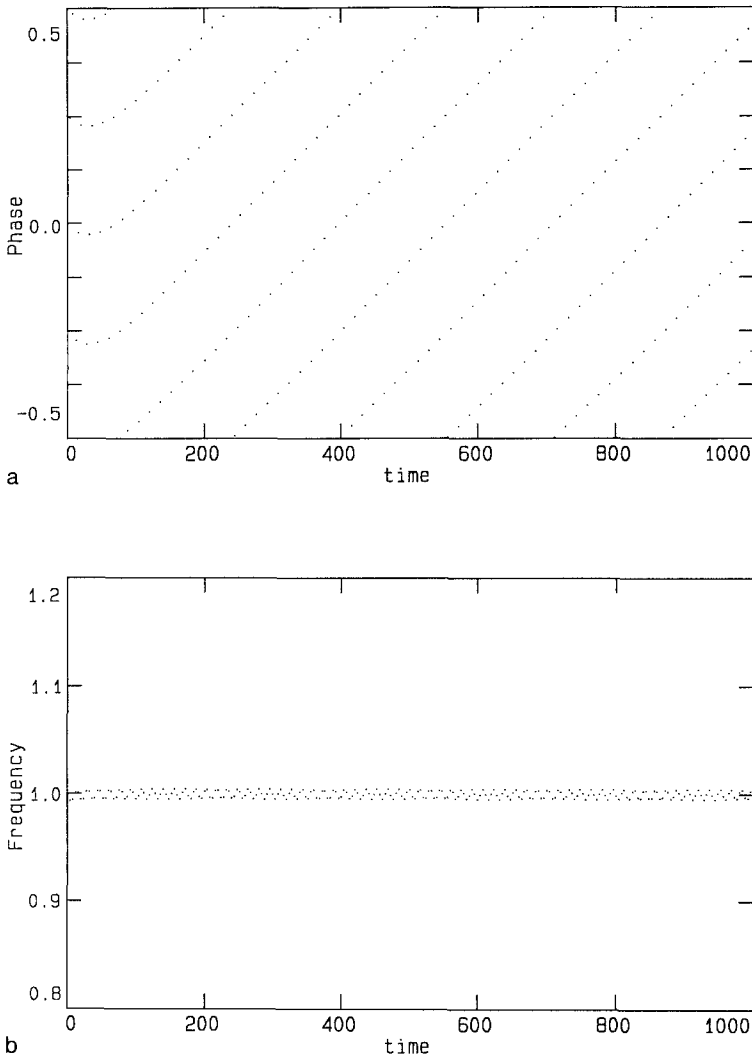
a

b

Fig. 3. Phase (a) and frequency (b) as functions of time for the adaptive model when outside the range of entrainment. Parameters as in Fig. 1 with $\tau = 1.31415$

the stability condition becomes:

$$1 > \mathscr{G}(1 - \tau\omega_{min}) - \varepsilon \frac{\tau\omega_{nat} - \tau\omega_{min}}{1 - \tau\omega_{min}} > -\varepsilon \frac{\tau\omega_{nat} - \tau\omega_{min}}{1 - \tau\omega_{min}}. \qquad (3.13)$$

As long as the term $\mathscr{G}(1 - \tau\omega_{min})$ is not too large, (i.e., the PRC is not too sharp), then stability holds away from the region where $1 - \tau\omega_{min} = O(\varepsilon)$.

4. Collective behavior

Let us now return to Eqs. (3.1–3.2), but instead of periodically forcing the oscillators, we allow coupling between many such oscillators with slightly

different frequencies. Consider:

$$d\theta_j/dt = \omega_j \tag{4.1}$$

$$d\omega_j/dt = \varepsilon(\tilde{\omega}_j - \omega_j) + \sum_k P_{kj}(\theta_k)G_j(\omega_j, \theta_j), \tag{4.2}$$

where $P_{kj}(\theta)$ represents the "strength" of a pulse of the kth oscillator observed by the jth oscillator. $\tilde{\omega}_j$ is the intrinsic frequency of the jth oscillator and G measures the effect of a pulse on the intrinsic frequency. Buck et al. [2] note that the flash of a firefly is somewhat Gaussian in shape so that we have chosen P_{kj} to have the same qualitative form. In Fig. 4 we show how the phase difference between two fireflies that have different intrinsic frequencies slowly tends to zero as the flashing frequencies become equal. The final frequency is not the same as the intrinsic frequency of either; the faster insect slows down and the slower speeds up. This is not a *necessary* consequence of our model, rather, it is due to our choice of functions $g^{\pm}$. The collective frequency can be faster or slower than the intrinsic frequencies depending on these functions.

To mimic a "firefly" tree, we consider the following simple model. We randomly distribute N insects in a two-dimensional grid. According to Hanson (personal communication), the insects will stay no closer than about a foot from each other. Hanson also notes that the insects have nearly a 360° field of vision and respond to other insects as far away as three feet. Thus, we allow the randomly spaced oscillators to interact with all other oscillators that are within a radius of three feet. The oscillators are each endowed with a narrow range of frequencies to which they will entrain. The model that results is (4.1–4.2) with:

$$G_j(\omega_j, \theta_j) = g^+(\theta_j)(\omega_{j\min} - \omega_{j\mathrm{nat}}) + g^-(\theta_j)(\omega_{j\max} - \omega_{j\mathrm{nat}}), \tag{4.3}$$

where $\omega_{j\min}$, $\omega_{j\max}$, $\omega_{j\mathrm{nat}} \equiv \frac{1}{2}(\omega_{j\min} + \omega_{j\max})$
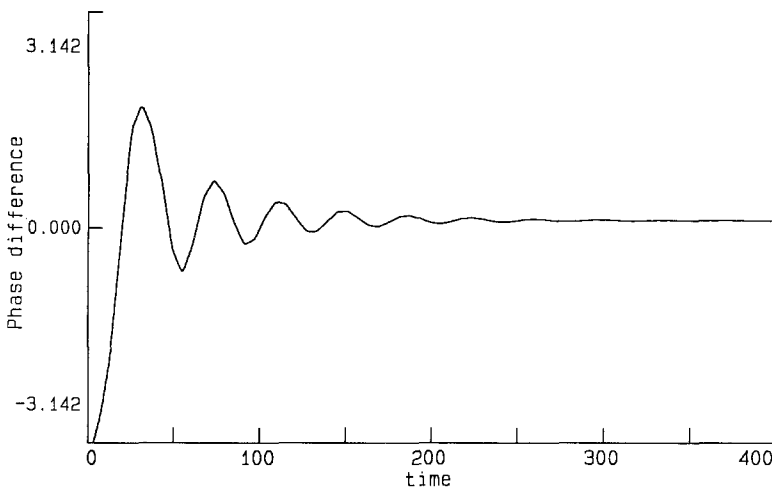

Fig. 4. Phase-difference between two adaptive oscillators as a function of time. The equations are (4.1–4.2) with $P_{12}(\theta) = P_{21}(\theta) = \min(p_{\max}(0.5 + 0.5\cos\theta)^m, \nu)$ and $g^+(\theta) = \max(\sin\theta, 0)$, $g^-(\theta) = -\min(\sin\theta, 0)$, $\nu = 0.7$, $p_{\max} = 0.5$, $\varepsilon = 0.01$, $\omega_{2\min} = 0.9$, $\omega_{2\max} = 1.3$, $\omega_{1\min} = 0.8$, $\omega_{1\max} = 1.2$, $\omega_{2\mathrm{nat}} = 1.1$, $\omega_{1\mathrm{nat}} = 1.0$

are the minimum, maximum, and natural frequencies of the jth insect. The functions $g^\pm$ are as above. In the following figures, we use Eqs. (4.1–4.3) with the term:

$$\sum_k P_{kj}(\theta_j)G_j(\omega_j, \theta_j)$$

replaced by:

$$\max\left(S_{\max}, \sum_{j \text{ sees } k} p_{\max}(0.5 + 0.5 \cos 2\pi\theta_k)^m\right)G_j(\omega_j, \theta_j).$$

This latter form says that the insect responds to all nearby insects in precisely the same way and that the animal does not vary its response once the nearby illumination exceeds the value $S_{\max}$. The contribution of a single insect is $p_{\max}$ and the sharpness of the stimulation is governed by the parameter m. In Fig. 5 we show several frames from a simulation of 120 oscillators distributed on a 65×65 grid. Initially, very few are synchronous but at later times more and more become recruited into the oscillation. Eventually, they all fire at nearly the same time. Finally, we quantitatively depict the synchrony in Fig. 6. This shows the summed output of the oscillators:

$$S(t) \equiv \sum_{j=1}^{N} P(\theta_j(t)),$$

where $P(\theta) = p_{\max}(0.5 + 0.5 \cos 2\pi\theta_k)^m$. If the oscillators are perfectly synchronized, then $S(t)$ has a maximum of $NP(0)$. The figure shows that close to 85% are synchronized. By way of comparison, we have simulated (2.8) with Δ given by (3.9) and plotted $S(t)$. Without adaptation, $S(t)$ is much broader and achieves a maximum of less than 30% of complete synchrony.

One can gain some analytic insight into the collective oscillations by simplifying the problem slightly. Because the response to a flash is weak for *P. malaccae*, we can average Eq (4.2) without losing too much information. This leads to an equation of the form:

$$d\omega_j/dt = \varepsilon(\tilde\omega_j - \omega_j) + \sum_k H_{kj}(\theta_k - \theta_j, \omega_j), \qquad (4.4)$$

where

$$H_{kj}(\phi, \omega) = \frac{1}{T_j} \int_0^{T_j} P_{kj}(s + \phi)G(\omega_j, s)\, ds, \qquad T_j = 1/\tilde\omega_j.$$

For ε sufficiently small, we expect that the phase shift between oscillators will remain $O(\varepsilon)$ and all oscillators will tend to a locked frequency, Ω. We assume that $H_{kj}(0, \omega) = 0$, since no change should be made in the intrinsic frequencies if the oscillators are in phase. Let

$$\theta_j = \Omega t + \varepsilon\psi_j, \qquad \omega_j = \Omega.$$

Then (4.4) becomes to lowest order in ε:

$$0 = \tilde\omega_j - \Omega + \sum_{k=1}^{N} \beta_{kj}(\psi_k - \psi_j), \qquad j = 1, \dots, N, \qquad (4.5)$$

where $\beta_{kj} = H'_{kj}(0, \Omega)$. This is a set of N linear equations in the $N + 1$ unknowns, ψ_j and Ω. But, we have the additional constraint that $\psi_k + C$ is a solution for any constant C, thus, we must set $\psi_0 = 0$, e.g. Eq. (4.5) can be solved in various
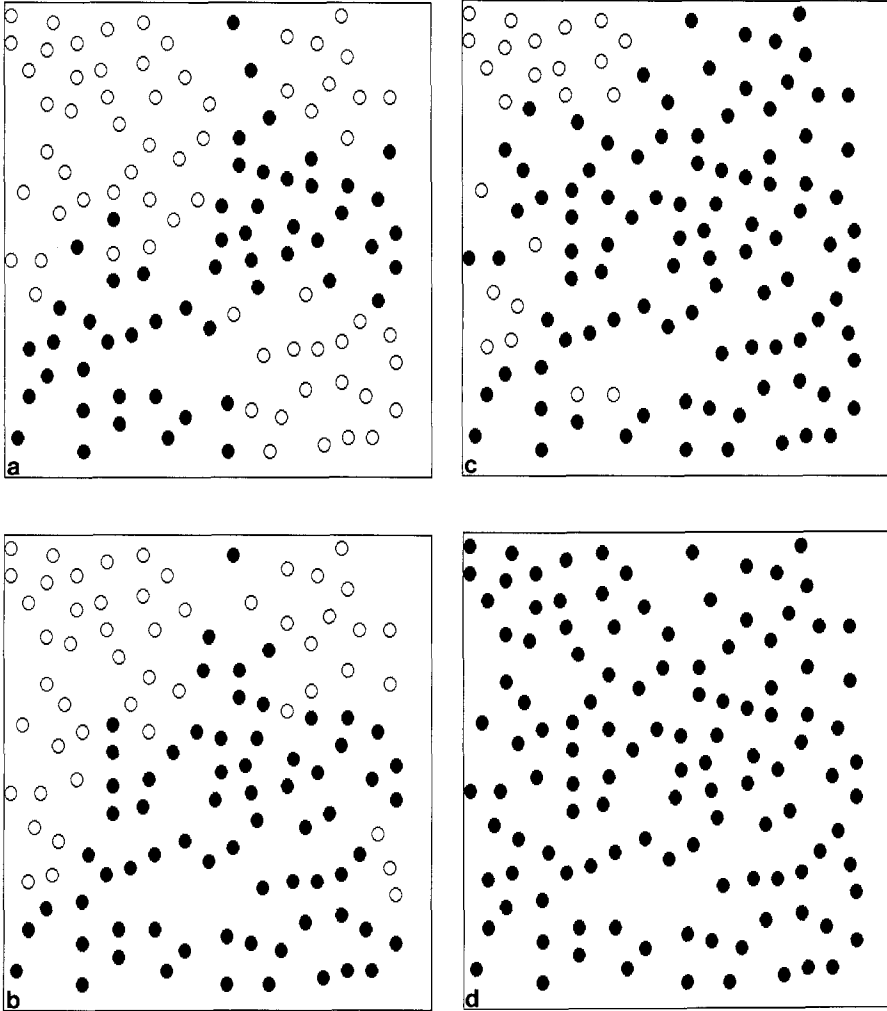
Fig. 5. Frames from a stimulation of (4.1–4.3) for $N = 120$ insects in a 65×65 grid. Blackened circles represent animals in their firing cycle. Times are chosen to maximize the number of firing oscillators for that period. The times are: 45.8, 59.0, 91.0, 122.8. Parameters are $\varepsilon = 0.01$, $p_{max} = 0.5$, $v = 0.8$, $m = 16$. The interactions are as in Fig. 4. The frequencies are randomly chosen from a uniform distribution: $\omega_{max} = 1.2 \pm 0.1$, $\omega_{min} = 0.8 \pm 0.1$, and $\omega_{nat} = \frac{1}{2}(\omega_{max} + \omega_{min})$ for each oscillator

geometries. We will consider only all to all coupling; for small densely packed "firefly trees", this is not a bad approximation. In this case, $\beta_{kj} = \alpha/N$, a constant, and we can thus easily solve (4.5):

$$\Omega = \langle \tilde{\omega}_j \rangle, \qquad \psi_j = (\tilde{\omega}_j - \Omega)/\alpha. \tag{4.6}$$

Recalling the definition of ψ_j, we see that all the oscillators synchronize to a frequency which is the mean of all the individual oscillators and with a phase-difference that is $O(\varepsilon)$.

The present calculation requires that G be differentiable with respect to ϕ. The specific model given by (4.3) is not differentiable at 0. If we assume that the
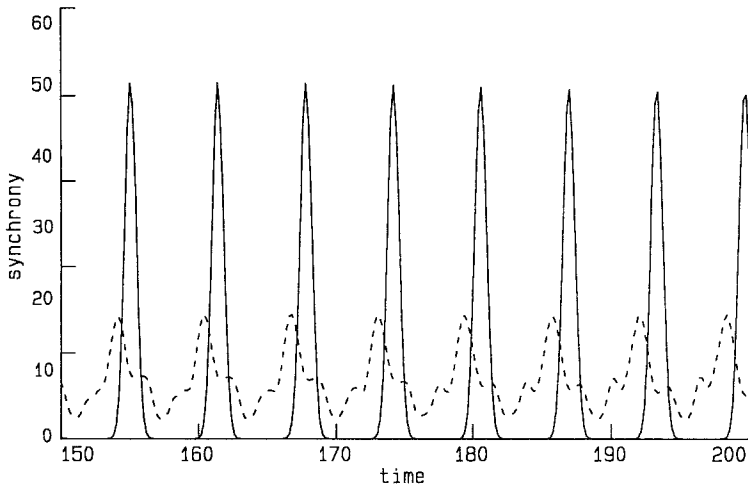
Fig. 6. Measure of synchrony of the 120 insects (see text). Solid line is for the adaptive model and dashed line is for the nonadaptive model

maximum and minimum frequencies are the same for all oscillators with only the free-running frequency variable and assume all to all coupling, then we can solve the synchrony equations. In the Appendix, we show that synchronization occurs within order ε as long as the intrinsic frequencies lie within the range of entrainable frequencies $(\omega_{min}, \omega_{max})$.

5. Discussion

This model provides a number of predictions. The most obvious experiment to try is to plot the interflash interval before the entraining stimulus, during the stimulus, and after the stimulus. There should be a decay in the interflash interval after entrainment as the insect returns to its intrinsic frequency. If it is possible to measure the behavior near criticality, then the model predicts a phase shift that is not close to zero as the limits of entrainment are reached. But, this may be difficult to achieve since the range of entrainment is very small and the time to reach entrainment can be very long. (From a recent conversation with Frank Hanson the first of these predictions appears to be true; the firefly slowly regains his intrinsic interflash interval after the stimulus is removed.) Like *P. malaccae*, large swarms of *P. cribellata* congregate in trees and flash rhythmically, but whether they indeed synchronize and the mechanisms responsible for synchrony (if it exists) are not clear.

Altering of frequencies has been observed in some mammalian circadian systems. Mice which are entrained to a twenty hour cycle maintain a faster cycle for many days after being returned to a completely dark regime (see [10], pp. 46–47). Indeed, it takes more than one hundred days before the periods of animals entrained to a twenty-eight hour cycle and those entrained to a twenty hour cycle merge in a dark environment. These *aftereffects* as they are called in the circadian literature could be due to a mechanism such as the present one.

There are other instances of apparent synchrony in nervous system behavior. Most models of coupled and forced nonlinear oscillators lead to significant

phase shifts as the stimulus is detuned from the intrinsic frequency of the system. Relaxation oscillators are capable of maintaining nearly zero phase shifts over a range of frequencies, but this occurs only when forced below or above the natural frequency and never both (work in progress, L. Abbot, personal communication). The mechanism we describe here could be put into biophysical terms by assuming that some parameter controlling the frequency of the oscillator is allowed to change due to external perturbations of the oscillator. Thus, this type of model represents a form of learning the simple task of synchronization.

In a broader context, the equations we consider in this paper are similar to those describing an interconnected oscillatory neural network. Indeed, each firefly flash is controlled by an endogenous neural oscillation [2]. The interaction between these neural oscillators is also neural as it is mediated through the visual system. The only significant difference between the firefly tree and an oscillatory neural network is in the time scale (milliseconds for the neural network and seconds for the firefly tree) and the space scale (microns for the neural system and meters for the insects). Ultimately, a goal is to couch these abstract adapting oscillators in strict biophysical terms.

The ability to synchronize plays an important role in the mating repetoire of fireflies (see Buck [1] for some of the many theories); hence it is important for a mechanism to evolve that can allow for synchrony to stimuli that are close to the native frequency. We have suggested one possible method by altering the notion of a PRC to include adaptation of the natural frequency.

Appendix

Here, we derive an integral equation in the continuum limit for Eqs. (4.1–4.3). This is then reduced to a differential equation that is easily solved. The existence of the phase-locked solution becomes a question about the solvability of a scalar transcendental equation. Let $\omega_0 = \frac{1}{2}(\omega_{max} + \omega_{min})$, and shift all frequencies by an amount ω_0. Thus, the phaselocked frequency will be shifted by ω_0 as will all other frequencies. (This can be done since the interactions between oscillators depend only on the phase-differences.) Let $\omega_{max} - \omega_0 = \alpha = \omega_0 - \omega_{min}$. Thus, with respect to the new shifted frequency, $\omega_{max} = \alpha$ and $\omega_{min} = -\alpha$. Since coupling is all-to-all, we can order the oscillators in ascending frequency so that $\omega_1 \leqslant \omega_2 \leqslant \cdots \leqslant \omega_N$. We make the reasonable ansatz that oscillators that have faster intrinsic frequencies will be phase-advanced with respect to those that have slower frequencies. With these assumptions and the above ordering of the oscillators, we seek solutions to:

$$0 = \varepsilon(\tilde{\omega}_j - \Omega) + \frac{1}{N} \sum_{k=1}^{j} g^+(\theta_j - \theta_k)(-\alpha - \Omega) + \frac{1}{N} \sum_{k=j}^{N} g^-(\theta_j - \theta_k)(\alpha - \Omega). \tag{A1}$$

(A1) holds because g^+ vanishes if the phase difference is between $\frac{1}{2}$ and 1, thus, only oscillators which are "slower" than θ_j will contribute. Similar considerations hold for the g^- term. We next assume that $\tilde{\omega}_j$ tend to some monotonic function $\omega(x)$ and $N \to \infty$. If $\varepsilon \equiv 0$, then the solution to (A1) is $\theta_j \equiv \theta_k$, so we expect $O(\varepsilon)$ synchrony. As in Sect. 4, we look for solutions of the form:

$$\theta_j = \Omega t + \varepsilon \psi_j.$$

Substituting this into (A1), collecting $O(\varepsilon)$ terms, and passing to the continuum limit yields:

$$0 = \omega(x) - \Omega + \beta^+(-\alpha - \Omega) \int_0^x \psi(x) - \psi(y) \, dy - \beta^-(\alpha - \Omega) \int_x^1 \psi(x) - \psi(y) \, dy.$$

Here, $\beta^+ \equiv g^{+\prime}(0)$, $\beta^- \equiv -g^{-\prime}(0)$ are both positive numbers. This is a linear integral equation. Differentiation with respect to x yields a linear differential equation:

$$\omega'(x) + \beta^+(-\alpha - \Omega)x\psi'(x) - \beta^-(\alpha - \Omega)(1 - x)\psi'(x) = 0. \tag{A3}$$

This is easily solved:

$$\psi(x) = \int_0^x dy \, \omega_r(y)/[y\beta^+(\alpha + \Omega) + (1 - y)\beta^-(\alpha - \Omega)] \equiv q(x, \Omega). \tag{A4}$$

This integral is defined as long as $-\alpha < \Omega < \alpha$. $q(x, \Omega)$ is a monotonically increasing positive function since $\omega' \geqq 0$ and the denominator is positive. To find Ω, we must use (A2). Set $x = 0$ in (A2) to obtain:

$$\Omega = \omega(0) + \beta^-(\alpha - \Omega) \int_0^1 q(x, \Omega) \, dx \equiv \zeta(\Omega). \tag{A5}$$

$\zeta(\Omega)$ decreases monotonically with $\zeta(\alpha) = \omega(0)$ and $\zeta(-\alpha) > \omega(0)$. By rescaling the time-variable, we can assume without loss of generality that $\alpha \equiv 1$. When $\beta^+ = \beta^- = \beta$ (as is the case in our example), and when $\omega(x) = \omega(0) + \kappa x$, then $\zeta(\Omega)$ can be explicitly determined:

$$\zeta(\Omega) = \kappa \frac{1 - \Omega}{2\Omega} \left[(1 + \Omega) \log\left(\frac{1 + \Omega}{1 - \Omega}\right) - 1 \right] + \omega(0). \tag{A6}$$

$\zeta(1) = \omega(0)$ and $\zeta(-1) = \omega(1)$. Thus, as long as $\omega(0) < 1$ and $\omega(1) > -1$, we can find a unique solution to (A5). In the more general case, one would have to explicitly integrate (A4) to check for solutions to (A5).

As long as Ω lies in the range of frequencies to which the insect can entrain, the solution $\psi(x)$ is well defined as is therefore $\theta(x) \equiv \varepsilon\psi(x) + \Omega t$. Despite the insects having a possibly $O(1)$ spread of intrinsic frequencies, the phase-difference between individuals stays extremely small.

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