Dynamics of two van der Pol oscillators coupled via a bath

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Abstract

In this work we study a system of two van der Pol oscillators, x and y, coupled via a "bath" z:

$$\ddot{x} - \epsilon(1 - x^2)\dot{x} + x = k(z - x)$$

$$\ddot{y} - \epsilon(1 - y^2)\dot{y} + y = k(z - y)$$

$$\dot{z} = k(x - z) + k(y - z)$$

We investigate the existence and stability of the in-phase and out-of-phase modes for parameters $\epsilon > 0$ and $k > 0$. To this end we use Floquet theory and numerical integration. Surprisingly, our results show that the out-of-phase mode exists and is stable for a wider range of parameters than the in-phase mode. This behavior is compared to that of two directly coupled van der Pol oscillators, and it is shown that the effect of the bath is to reduce the stability of the in-phase mode. We also investigate the occurrence of other periodic motions by using bifurcation theory and the AUTO bifurcation and continuation software package.

Our motivation for studying this system comes from the presence of circadian rhythms in the chemistry of the eyes. We present a simplified model of a circadian oscillator which shows that it can be modeled as a van der Pol oscillator. In our model although there is no direct connection between the two eyes, they can influence each other by affecting the concentration of melatonin in the bloodstream, which is represented by the bath.
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1. Introduction

The dynamics of coupled van der Pol oscillators has been of interest since the 1920s, when van der Pol used three of them to model the beating of the heart (van der Pol and van der Mark, 1982). More recently,

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the dynamics of two *directly coupled* van der Pol oscillators has been studied in connection with the neurobiology of the lamprey (Rand and Holmes, 1980). An example of such "direct coupling" is given by the equations (Storti and Reinhall, 1997):

$$\ddot{x} - \epsilon(1 - x^2)\dot{x} + x = k(y - x) \tag{1}$$

$$\ddot{y} - \epsilon(1 - y^2)\dot{y} + y = k(x - y) \tag{2}$$

Many other applications of directly coupled van der Pol oscillators exist, for example to laser dynamics (where delay coupling is important, Wirkus and Rand, 2002), and to sleep dynamics (Moore-Ede et al., 1982).

In the present work, we are interested in the dynamics of two van der Pol oscillators which are coupled via a "bath":

$$\ddot{x} - \epsilon(1 - x^2)\dot{x} + x = k(z - x) \tag{3}$$

$$\ddot{y} - \epsilon(1 - y^2)\dot{y} + y = k(z - y) \tag{4}$$

$$\dot{z} = k(x - z) + k(y - z) \tag{5}$$

where ϵ is a nonlinearity coefficient and k is a coupling coefficient (see Fig. 1).

Our motivation for studying this system comes from the chemistry of the eyes. There is experimental evidence that there exist circadian rhythms in each of the two eyes of vertebrates (Bernard et al., 1997; Manglapus et al., 1999). These are periodic motions, limit cycles, with periods of approximately 24 h, e.g. melatonin levels have been observed to vary periodically in this way. It has been conjectured that the visual system, which must operate over some 10 orders of magnitude in the course of night and day, has its sensitivity controlled through these oscillations by anticipating the changes in light intensity which occur at dusk and dawn.

We model each of the circadian rhythms by the limit cycle of a van der Pol oscillator. In the Appendix A we offer a model of the biochemistry of circadian rhythms which takes the form of a van der Pol oscillator. Although there is no direct connection between the two eyes, they can influence each other by affecting the concentration of melatonin in the bloodstream. Alternatively, the eyes may be coupled via neural pathways in the brain. In this work we have chosen to model the former method of coupling between the eyes. x and y represent the concentrations of melatonin in each of the eyes, and z represents the concentration of melatonin in the bloodstream (here referred to as a bath).

Under normal circumstances, production of melatonin in the eyes is periodically forced due to diurnal variations in sunlight. This effect would correspond to the presence of periodic forcing terms such as $A \cos \omega t$ on the right hand sides of Eqs. (3) and (4). Without such terms, the assumed system (3)–(5) corresponds to eyes kept in constant light (or darkness) conditions. In the laboratory of author HH, chicks
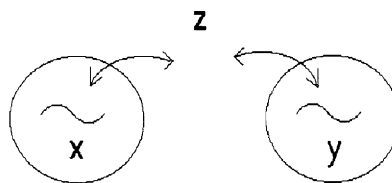

Fig. 1. Two van der Pol oscillators x and y coupled via a bath z.

have been grown under constant light conditions (Li et al., 2000). This permits the conclusions of our mathematical model to be compared with experimental results.

In what follows we shall study the existence and stability of the in-phase and out-of-phase modes of the system (3)–(5). We shall also consider additional motions which turn out to be born in bifurcations occurring due to changes in stability of the in-phase mode.

2. In-phase mode

The in-phase mode is a periodic motion which satisfies $x(t) = y(t)$. Substituting $x(t) = y(t) = f(t)$ and $z(t) = g(t)$ into Eqs. (3)–(5) yields

$$\ddot{f} - \epsilon(1 - f^2)\dot{f} + f = k(g - f) \quad \text{and} \quad \dot{g} = 2k(f - g) \tag{6}$$

The in-phase mode, if it exists, resides in the 3-dimensional space f–$\dot{f}$–g which is itself an invariant manifold in the original 5-dimensional space x–$\dot{x}$–y–$\dot{y}$–z. The in-phase mode turns out to be born in a Hopf bifurcation which occurs as the origin in this 3-dimensional space becomes unstable. The condition for the existence of the in-phase mode is obtained by linearizing Eq. (6) about the origin and requiring a pair of pure imaginary eigenvalues (a Hopf). This gives the condition

$$4\epsilon k^2 - 2k^2 - 2\epsilon^2 k + \epsilon k + \epsilon > 0 \tag{7}$$

If Eq. (7) holds, then the in-phase mode exists and is stable in the 3-dimensional space f–$\dot{f}$–g. Note that this does not imply that the in-phase mode is stable in the containing 5-dimensional phase space since the 3-dimensional subspace may not be attractive. Numerical integration of the system (6) supports this result (see Fig. 2).

Although the origin changes its stability in the 3-dimensional space f–$\dot{f}$–g, it turns out to always be unstable in the containing 5-dimensional phase space for $k > 0$, $\epsilon > 0$. For a proof which uses Routh–Hurwitz criteria (see Camacho, 2002).
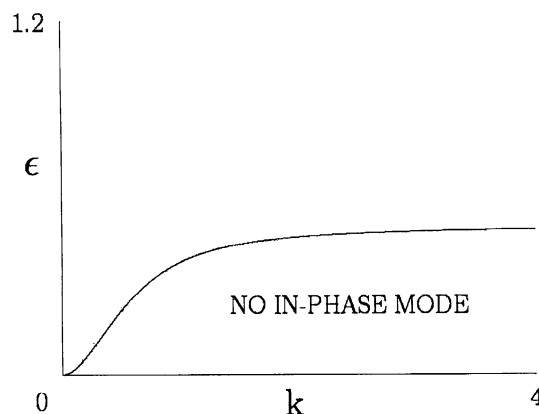

Fig. 2. For a given value of coupling $k > 0$, the nonlinearity coefficient $\epsilon > 0$ must be sufficiently large in order for the in-phase mode to exist. Existence region defined by Eq. (7). See text.

3. Out-of-phase mode

The out-of-phase mode is a periodic motion which satisfies $x(t) = -y(t)$. Substituting $x(t) = -y(t) = f(t)$ into Eqs. (3) and (4) and adding these two equations shows that $z(t)$ must vanish for the out-of-phase mode to exist. $z(t) = 0$ also satisfies Eq. (5), which becomes $\dot{z} = -2kz$. We find that $f(t)$ must satisfy the equation

$$\ddot{f} - \epsilon(1 - f^2)\dot{f} + (1 + k)f = 0 \tag{8}$$

But Eq. (8) is just a van der Pol oscillator with frequency $\sqrt{1 + k}$. Since van der Pol's equation is well known to possess a stable limit cycle for all ϵ, we see that the out-of-phase mode exists for all $\epsilon, k > 0$. Note that the out-of-phase mode resides in a 3-dimensional invariant subspace (the f–$\dot{f}$ phase plane together with the plane $z = 0$) and although it is stable in that space, it may not be stable in the containing 5-dimensional phase space.

4. Stability

In order to determine the stability of a periodic motion such as the in-phase or out-of-phase modes, we study the linearized variational equations, which for the system (3)–(5) become

$$\frac{d^2\xi}{dt^2} - \epsilon(1 - X^2)\frac{d\xi}{dt} + \left(1 + 2\epsilon X\frac{dX}{dt}\right)\xi = k(\zeta - \xi) \tag{9}$$

$$\frac{d^2\eta}{dt^2} - \epsilon(1 - Y^2)\frac{d\eta}{dt} + \left(1 + 2\epsilon Y\frac{dY}{dt}\right)\eta = k(\zeta - \eta) \tag{10}$$

$$\frac{d\zeta}{dt} = k(-2\zeta + \xi + \eta) \tag{11}$$

where $x(t) = X(t)$, $y(t) = Y(t)$ and $z(t) = Z(t)$ is the periodic solution whose stability is to be determined, and where the linearized variations ξ, η and ζ are given by

$$\xi(t) = x(t) - X(t), \qquad \eta(t) = y(t) - Y(t) \qquad \text{and} \qquad \zeta(t) = z(t) - Z(t) \tag{12}$$

Eqs. (9)–(11), while linear, have periodic coefficients, and thus cannot be solved in closed form. Instead we may determine stability by using numerical integration in conjunction with Floquet theory (Rand, 2003). This is a two-step process. The first step involves numerically integrating the equations which define the periodic motion whose stability is to be found. In the case of the in-phase mode, the defining equation are (6), while for the out-of-phase mode the defining equation is (8). The resulting steady state solution is used to define the periodic coefficients in the linear variational equations (9)–(11). Once this has been done, we proceed to the second step (Floquet theory) which requires that we numerically integrate the linear fifth order system (9)–(11) five times for five linearly independent initial conditions, in order to generate a "fundamental solution matrix" $M(t)$. We evaluate this matrix at a time t equal to the period T of the periodic motion whose stability we are investigating. (Note that the period T is a priori unknown and must be computed numerically when the periodic motion is obtained in the first step.) Finally we compute the eigenvalues of the resulting matrix $M(T)$. Floquet theory (Rand, 2003) tells us that the periodic motion will be stable if all five of the eigenvalues have absolute value $\leqslant 1$. If any of the eigenvalues has absolute value >1, the motion is unstable.

Proceeding in this way, we find that the out-of-phase mode is stable for all $\epsilon, \delta > 0$, whereas the in-phase mode is stable only for those parameters which lie in the black region in Fig. 3.
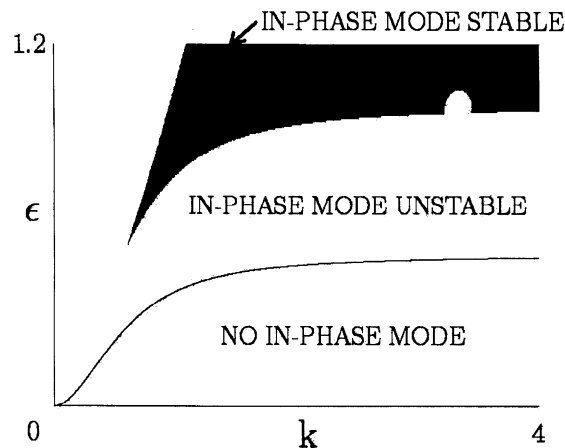
Fig. 3. Stability of the in-phase mode. Black region represents parameters for which the in-phase mode is stable. Results obtained by numerical integration and Floquet theory.

5. Bifurcations

A generic feature of nonlinear systems is that when a change in parameters causes a change in stability, it is accompanied by a change in the qualitative nature of the phase flow, such as a change in the number of equilibria or periodic motions. Here we are talking about the in-phase mode only, since the out-of-phase mode does not change stability for $\epsilon, \delta > 0$. In the case of Floquet theory, the nature of the associated bifurcation can be determined by the behavior of the eigenvalues of the matrix $M(T)$ as stability changes. For example, if a single eigenvalue passes through the unit circle in the complex plane, we may expect a "saddle-node" bifurcation of periodic motions (Guckenheimer and Holmes, 1983), or in the case of a system with symmetry, a "pitchfork" bifurcation of periodic motions. If on the other hand a pair of complex eigenvalues passes through the unit circle, then we may expect a "secondary Hopf" or "Neimark–Sacker" bifurcation in which an invariant torus and associated quasiperiodic motion is born.

Since the matrix $M(T)$ is 5×5, it will possess five eigenvalues. Of these, three will always have absolute value $\leqslant 1$ since the in-phase mode is stable in the 3-dimensional invariant subspace f–$\dot{f}$–g, Eq. (6). One of these three will always be exactly equal to unity since the original motion whose stability is being investigated is periodic (Cesari, 1963, p. 98). That leaves two eigenvalues of $M(T)$ which can cause instability.

We find that along the left edge of the black region in Fig. 3 a single eigenvalue passes through unity corresponding to a pitchfork bifurcation of periodic motions. The same behavior is observed in the "dimple" region. Along the rest of the boundary of the black region we find that a pair of complex eigenvalues pass through the unit circle corresponding to a secondary Hopf bifurcation in which an invariant torus is born enclosing the in-phase mode (see Fig. 4).

The linear eigenanalysis of Floquet theory cannot predict the stability of the newly created structures (periodic motions and invariant tori). For this we used the AUTO bifurcation and continuation software package (Doedel et al., 1997) in conjunction with numerical integration of the nonlinear Eqs. (3)–(5). These numerical inquiries revealed that this system involves numerous other periodic and quasiperiodic motions besides the in-phase and out-of-phase modes. As our purpose in this paper is to investigate the existence and stability of the in-phase and out-of-phase modes, we will not present an exhaustive treatment of these other motions. Instead we offer a sample of the bifurcations which occur in this system by examining in detail what happens along the line $k = 1$ in Fig. 3, as ϵ varies between 1.05 and 1.08. We choose these values
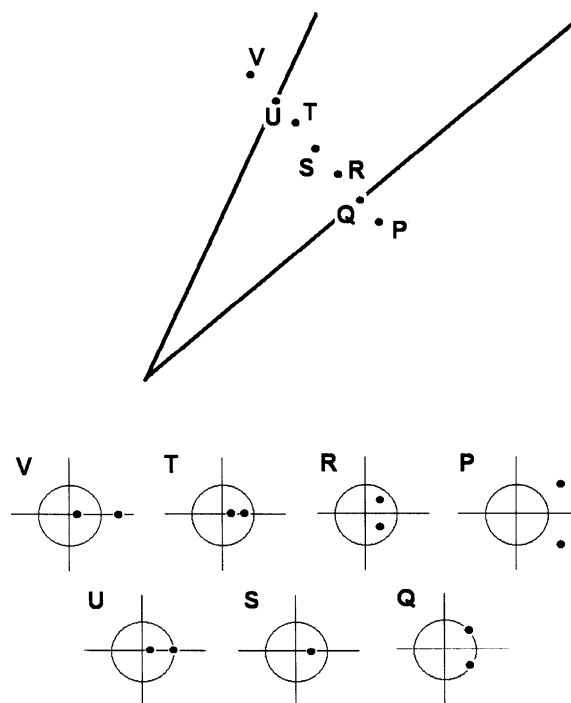
Fig. 4. Schematic diagram showing the behavior of Floquet eigenvalues as we traverse the black region in Fig. 3. At point Q a secondary Hopf bifurcation occurs in which an invariant torus is born, surrounding the in-phase mode. At point U a pitchfork bifurcation occurs in which two new periodic motions are born out of the in-phase mode.

of ϵ because the line $k = 1$ crosses the left edge of the black region in Fig. 3 at $\epsilon = 1.068936$, and so we are examining bifurcations which occur as the in-phase mode changes stability.

At $\epsilon = 1.05$, we are in the stable region of the in-phase mode (IP) (see Fig. 3). In this region the out-of-phases mode (OP), which is stable for all $\epsilon, \delta > 0$, is also stable. Their separatrix is an unstable invariant torus, which we refer to as T1, see the bifurcation diagram in Fig. 5. This torus is born as we enter the black region of Fig. 3 from below via a subcritical secondary Hopf bifurcation.
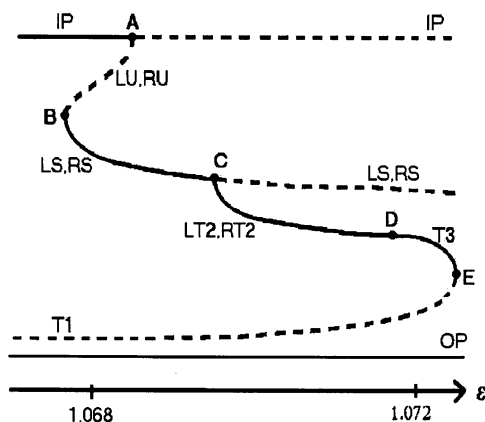

Fig. 5. Bifurcation diagram for $k = 1$ and ϵ varying. Results obtained by use of AUTO software. See text.

As we continue to increase ϵ beyond 1.05, the in-phase mode loses its stability at $\epsilon = 1.068936$ (point A in Fig. 5) through a subcritical pitchfork bifurcation. There is, however, another bifurcation that occurs for a smaller value of ϵ, inside the stable region of the IP. The computer program AUTO confirms that there is a point B, located at $\epsilon = 1.067137$, where two pairs of periodic motions are born in a saddle-node bifurcation of cycles in two separate folds. We shall refer to these pairs as L (left) and R (right) because they are reflections of each other in the invariant plane $x = y$. In each pair, one periodic motion is stable and one is unstable. We will therefore refer to them as LS (left stable), LU (left unstable), RS (right stable), and RU (right unstable). Although both pairs of periodic motions are born close to the IP, they are not born out of the IP. Thus for values of ϵ between points A and B ($\epsilon \in (1.067137, 1.068936)$), there are seven special trajectories: IP (stable), OP (stable), unstable torus T1, LS (stable), LU (unstable), RS (stable), RU (unstable). The unstable motions act as separatrices for the stable motions. The periodic motions LU and RU separate those initial conditions which go to the IP from those initial conditions which go to the periodic motions LS and RS. The torus flow, T1 separates those initial conditions which go to the OP from those initial conditions which go to the periodic motions LS and RS.

As the IP loses its stability at $\epsilon = 1.068936$, each of the unstable periodic motions, RU and LU, merge with the IP in a pitchfork bifurcation of cycles (point A in Fig. 5). This results in the disappearance of RU and LU and a change in stability of the IP. Thus for values of ϵ slightly greater than 1.068936 (point A), we have five special trajectories: IP (unstable), OP (stable), T1 (unstable), LS (stable), RS (stable).

This situation persists until we reach $\epsilon = 1.070172$ (point C in Fig. 5). At this point, the two trajectories LS and RS lose their stability in secondary Hopf bifurcations in which two invariant stable tori are born, one out of LS and one out of RS. We will refer to these tori as LT2 and RT2 respectively. For values of ϵ slightly greater than 1.070172, we again have seven special trajectories: IP (unstable), OP (stable), T1 (unstable), LS (unstable), RS (unstable), LT2 (stable), RT2 (stable).

This situation persists as ϵ increases until we get to point D in Fig. 5 (somewhere between ϵ values of 1.071 and 1.072). For values of ϵ slightly greater than that of point D, we find that the two tori LT2 and RT2 have merged together to form a single, stable torus which is symmetrical with respect to the plane $x = y$. This new torus will be referred to as T3 (see Fig. 5). We thus have six special trajectories: IP (unstable), OP (stable), T1 (unstable), LS (unstable), RS (unstable), T3 (stable). As ϵ is increased further, there is a point E (somewhere between 1.0721 and 1.0722) where the stable torus T3 merges with the unstable torus T1 in another fold. Both tori coalesce, leaving only four special trajectories: IP (unstable), OP (stable), LS (unstable), RS (unstable). This situation persists for values of ϵ beyond that of point E.

In summary, we present this bifurcation sequence in order to give the reader a taste of the kinds of bifurcations and of the various periodic and quasiperiodic motions which occur in Eqs. (3)–(5). See Figs. 6 and 7 which display samples of these motions. In the case of unstable motions, we were able to obtain approximations to them by choosing initial conditions to lie (approximately) on their stable manifolds. Note that all these bifurcations occur in a very small region of parameter space which lies near the boundary of the region of stability of the in-phase mode. Thus although they are interesting from a dynamical point of view, it is unlikely that the observed periodic and quasiperiodic motions will play an important role in applications.

6. Conclusions

In order to assess the effect of the bath on the dynamics of the system (3)–(5), we now offer a comparison with the corresponding results for a system of directly coupled van der Pol oscillators, Eqs. (1) and (2), as summarized in Storti and Reinhall (1997). Both systems (direct and bath coupling) predict that the out-of-phase mode exists and is stable for all values of $\epsilon, k > 0$. But the two systems differ in their predictions of the existence and stability of the in-phase mode (see Fig. 8). As can be seen by comparing Figs. 3 and 8, the
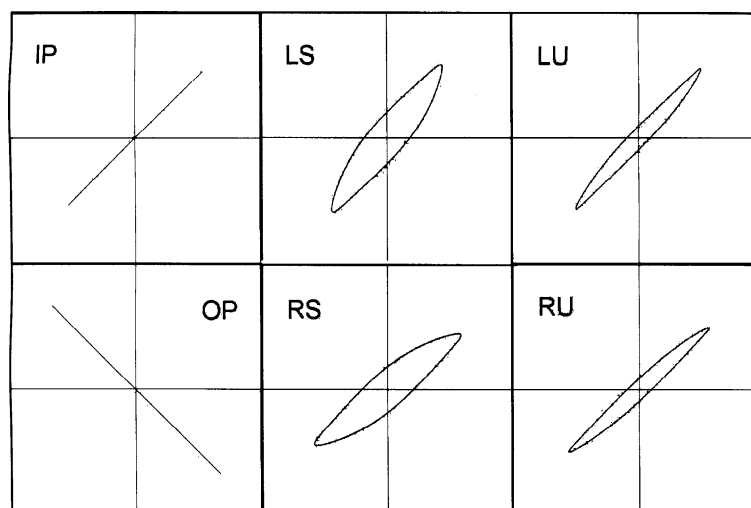
Fig. 6. Periodic motions displayed in the x–y plane, $-3 < x < 3$, $-3 < y < 3$. Parameters are $k = 1$ and $\epsilon = 1.068$. The four motions LS, RS, LU, RU have bifurcated in two folds at point B in Fig. 5. For these parameters, both the in-phase (IP) mode and the out-of-phase (OP) mode are stable. Results obtained by numerical integration. See text.
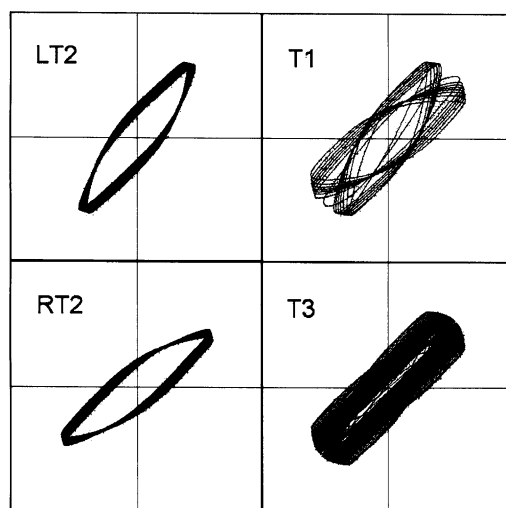

Fig. 7. Quasiperiodic motions displayed in the x–y plane, $-3 < x < 3$, $-3 < y < 3$. All lie on invariant tori. Motion T1 corresponds to parameters $k = 1$ and $\epsilon = 1.068$ and is unstable. Motions LT2 and RT2 correspond to $k = 1$ and $\epsilon = 1.071$ and are stable. These motions arise from LS and RS respectively via secondary Hopf bifurcations at point C in Fig. 5. Motion T3 corresponds to $k = 1$ and $\epsilon = 1.072$ and is stable. It is created out of LT2 and RT2 in a symmetry-breaking bifurcation at point D in Fig. 5. Motions T1 and T3 merge in a fold at point E. See text.

stable region in the bath-coupled case is much smaller. Thus we may conclude that the bath tends to destabilize the in-phase mode.

Returning to the system with bath-coupling, we ask what is the biological significance of our conclusion, that the in-phase mode is stable for a smaller parameter set than the out-of-phase mode? Firstly, we note
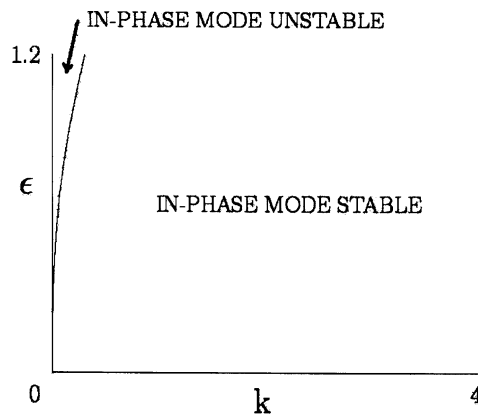
Fig. 8. Stability of the in-phase mode for a system of two directly coupled van der Pol oscillators, after Storti and Reinhall (1997). Comparison with Fig. 3 shows that the bath tends to destabilize the in-phase mode.

that in normal circumstances, the eyes are forced by a 24 h light cycle. This would correspond in our model to the presence of forcing terms such as $A \cos \omega t$ on the right hand sides of Eqs. (3) and (4). Preliminary numerical studies by us have shown that under such loading the in-phase mode becomes stable, even for very small forcing amplitudes A. Thus the model predicts that under normal light loads the eyes operate in a synchronized fashion.

Nevertheless, the autonomous (unforced) system studied in this work can be simulated in the laboratory by growing animals (chicks, for example) in constant light conditions. These experiments are being performed in the laboratory of author HH (Li et al., 2000). If it is found that the in-phase mode is less stable than the out-of-phase mode, in agreement with the prediction of the model studied in this paper, then this points to the biological importance of bath (i.e., serum melatonin) coupling. If, on the other hand, the in-phase mode is found to be more stable than the out-of-phase mode, then we may conclude that coupling via neural pathways in the brain may be biologically essential. We await the experimental results. In either case, this work represents a collaboration between mathematical modeling and the design of laboratory experiments.

Acknowledgements

Appendix A

In this appendix we present a mathematical model of circadian rhythm, based on a biochemical scenario which has been described in the biological literature (Giebultowicz, 2000; Scully and Kay, 2000). The basic idea is that two genes called PER ($= x$) and TIM ($= y$) are transcribed from DNA in the nucleus of a cell. RNA leaves the nucleus and causes a complex, PER–TIM ($= z$) to be formed in the cell, outside the nucleus. Then PER–TIM reenters the nucleus and inhibits the further transcription of PER and TIM. The PER–TIM complex eventually dissipates and transcription begins again, starting the process over. One

cycle takes about 24 h. The presence of light is known to decrease the concentration of TIM, allowing for the entrainment of the biological clock by light.

We imagine a 2-compartment model consisting of 1, the nucleus and 2, the rest of the cell. The model may be described in words as follows: x and y, manufactured in compartment 1, the nucleus, move into compartment 2, where they form z. Then z, produced in compartment 2, moves into compartment 1, where it inhibits the production of x and/or y.

Our model consists of three first order ODE's on the three quantities x, y and z.

$$\frac{\mathrm{d}x}{\mathrm{d}t} = k_4 x - k_5 x^3 - k_2 z \tag{A.1}$$

The term $k_4 x - k_5 x^3$ represents the rate at which x is produced if z is absent. If no z is present, $x \to \sqrt{k_4/k_5} = $ constant. The term $-k_2 z$ says that the presence of z inhibits the production of x.

$$\frac{\mathrm{d}z}{\mathrm{d}t} = k_1 xy - k_6 y \tag{A.2}$$

The term $k_1 xy$ states that the production of z results from an interaction between x and y. Both x and y are needed to produce z. The term $-k_6 y$ says that y inhibits the production of z. We found that we needed this term to prevent x from going negative.

$$\frac{\mathrm{d}y}{\mathrm{d}t} = k_7 - k_8 f(t) - k_3 y \tag{A.3}$$

where $f(t)$ represents light intensity: $f(t) = 1$ means light is ON, while $f(t) = 0$ means light is OFF. In the presence of light, $y \to \frac{k_7 - k_8}{k_3}$, while in the absence of light, $y \to \frac{k_7}{k_3}$. Thus the presence of light decreases y, as in experiments.

Diurnal light changes can be modeled by taking $f(t)$ as a periodic function which varies between 0 and 1.

Note that y is not affected by x or z, but that z (and hence x) are affected by y. Thus the role of y is to allow light to entrain the oscillator.

Algebraic manipulation of these equations reveals that they are equivalent to a van der Pol oscillator, and thus that they exhibit a periodic steady state (a limit cycle), even in constant light. We begin by differentiating the x-equation (A.1) to obtain

$$\frac{\mathrm{d}^2 x}{\mathrm{d}t^2} = k_4 \frac{\mathrm{d}x}{\mathrm{d}t} - 3k_5 x^2 \frac{\mathrm{d}x}{\mathrm{d}t} - k_2 \frac{\mathrm{d}z}{\mathrm{d}t} \tag{A.4}$$

Next we replace $\frac{\mathrm{d}z}{\mathrm{d}t}$ in Eq. (A.4) by using the z-equation (A.2) to obtain:

$$\frac{\mathrm{d}^2 x}{\mathrm{d}t^2} = k_4 \frac{\mathrm{d}x}{\mathrm{d}t} - 3k_5 x^2 \frac{\mathrm{d}x}{\mathrm{d}t} - k_2(k_1 xy - k_6 y) \tag{A.5}$$

At steady state in constant light, $y \to y_\infty$, giving

$$\frac{\mathrm{d}^2 x}{\mathrm{d}t^2} - (k_4 - 3k_5 x^2)\frac{\mathrm{d}x}{\mathrm{d}t} + k_2 k_1 y_\infty x = k_2 k_6 y_\infty \tag{A.6}$$

which is the equation for a version of the van der Pol oscillator.

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