Resonant Phenomena in Coupled Oscillators Arising in the Interaction and Production of Two Enzymes[1]

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Abstract

A class of diffusively coupled oscillators is discussed. The model is governed by reaction-diffusion equations with nonlinear boundary conditions. The two linear uncoupled equations describe the diffusion process, while the nonlinear boundary conditions describe all reaction and interaction. By using the boundary conditions, the system can be translated into two uncoupled oscillators of two dimensions, it is found that the Hopf bifurcations are always degenerate due to the internal resonance of the system.

Keyword: Hopf bifurcations; Coupled oscillators; Diffusion process.

1 Introduction

Many chemical and biological phenomena can be described by systems of coupled limit cycle oscillators and the coupling of oscillators is of considerable general theoretical and practical interest in a number of contexts, especially biological. Coupled oscillators offers much rich dynamic behaviors, some of which may not be observed from single oscillators, such as "phase trapping", multiple stable periodic states, loss of periodicity [7], [1], [9]. Although extensive study has been conducted toward a complete understanding of the free and forced dynamical behavior of a single nonlinear oscillator, however, much less is known for coupled oscillators, such as how different modes of coupling affect the dynamical behavior of coupled oscillators.

In this paper, we study the following system:

$$\left.\begin{aligned} x_t &= x_{\xi\xi} - \gamma^2 x \\ y_t &= y_{\xi\xi} - \gamma^2 y \end{aligned}\right\} \quad \text{in} \quad (0,1)\times\mathbf{R}^+ \tag{1.1}$$

which satisfies boundary conditions:

$$\left.\begin{aligned} x_\xi(0,t) &= -\mu\gamma f(y(0,t)) \\ y_\xi(1,t) &= \mu\gamma(1-f(x(1,t))) \\ x_\xi(1,t) &= y_\xi(0,t) = 0 \end{aligned}\right\} \quad \text{in} \quad \mathbf{R}^+. \tag{1.2}$$

This model has been used for the study of the interaction and production of two enzymes [2], where x and y are normalized concentrations of two products, denoted by U and V, respectively. $\gamma > 0$ is the decay rate, $\mu > 0$ is the parameter, and f is a smooth function with $f' > 0$. This model describes that the enzyme E_1 is bound to the membrane M_1 at $x = 0$ and its product U affects the activity of the enzyme E_2, bound to membrane M_2 at $x = 1$, whose product V affects in turn the activity of E_1. The membranes are open to passage of the substrates of E_1 and E_2, but impermeable to their respective products, U and V. These diffuse between the membranes on the interval $(0, l)$, and experience decay there from processes not involving E_1 and E_2.

2 Stationary Points

First of all, let us determine stationary points of the system (1.1)-(1.2). The stationary solutions satisfy equations:

$$\begin{aligned} \frac{d^2x^s(\xi)}{d\xi^2} - \gamma^2 x^s(\xi) &= 0 \\ \frac{d^2y^s(\xi)}{d\xi^2} - \gamma^2 y^s(\xi) &= 0 \end{aligned} \tag{2.3}$$

with boundary conditions

$$\begin{aligned} x^s_\xi(0) &= -\mu\gamma f(y^s(0)) \\ y^s_\xi(1) &= \mu\gamma(1-f(x^s(1)) \\ x^s_\xi(1) &= y^s_\xi(0) = 0 \end{aligned} \tag{2.4}$$

We can write these stationary solutions as

$$\begin{aligned} x^s(\xi) &= x^s(1)\cosh\gamma(1-\xi) \\ y^s(\xi) &= y^s(0)\cosh\gamma\xi \end{aligned} \tag{2.5}$$

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where $(x^s(1), y^s(0))$ must satisfy

$$\begin{aligned} x^s(1) &= \frac{\mu}{\sinh\gamma} f(y^s(0)) \\ y^s(0) &= \frac{\mu}{\sinh\gamma}(1 - f(x^s(1)). \end{aligned} \tag{2.6}$$

Lemma 1. *For each $\mu > 0$, the system (1.1)-(1.2) has a unique stationary point.*

Let $(a(\mu), b(\mu)) = (x^s(1), y^s(0))$ and $\bar{x} = x - x^s$ and $\bar{y} = y - y^s$, then (1.1) becomes

$$\left.\begin{aligned} \tilde{x}_t &= \tilde{x}_{\xi\xi} - \gamma^2 \tilde{x} \\ \tilde{y}_t &= \tilde{y}_{\xi\xi} - \gamma^2 \tilde{y} \end{aligned}\right\} \quad \text{in} \quad (0,1) \times \mathbf{R}^+ \tag{2.7}$$

with boundary conditions:

$$\begin{aligned} &\tilde{x}_\xi(0,t) = -\mu\gamma f(\tilde{y}(0,t) + b(\mu)) + a(\mu)\gamma \sinh\gamma \\ &\tilde{y}_\xi(1,t) = \mu\gamma(1 - f(\tilde{x}(1,t) + a(\mu)) - b(\mu)\gamma\sinh\gamma \\ &\tilde{x}_\xi(1,t) = \tilde{y}_\xi(0,t) = 0. \end{aligned} \tag{2.8}$$

3 Linearization

We now linearize the system (1.1)-(1.2). Since the non-linearity only appears on the boundary, the linearized system has the form:

$$\left.\begin{aligned} \bar{x}_t &= \bar{x}_{\xi\xi} - \gamma^2 \bar{x} \\ \bar{y}_t &= \bar{y}_{\xi\xi} - \gamma^2 \bar{y} \end{aligned}\right\} \quad \text{in} \quad (0,1) \times \mathbf{R}^+ \tag{3.9}$$

with boundary conditions:

$$\begin{aligned} \bar{x}_\xi(0,t) &= -\mu\gamma f'(b)\bar{y}(0,t) \\ \bar{y}_\xi(1,t) &= -\mu\gamma f'(a)\bar{x}(1,0) \\ \bar{x}_\xi(1,t) &= \bar{y}_\xi(0,t) = 0. \end{aligned} \tag{3.10}$$

The above linearized system admits solutions of a form

$$\begin{aligned} \bar{x}(\xi,t) &= A\cos\lambda(1-\xi)e^{(-\lambda^2-\gamma^2)t} \\ \bar{y}(\xi,t) &= B\cos\lambda\xi e^{(-\lambda^2-\gamma^2)t} \end{aligned}$$

observing the boundary conditions, A and B satisfy:

$$\begin{aligned} A\lambda\sin\lambda + B\mu\gamma f'(b) = 0 \\ A\mu\gamma f'(a) - B\lambda\sin\lambda = 0. \end{aligned} \tag{3.11}$$

The linearized system (3.10) has a nontrivial solution if and only if λ satisfies

$$\lambda^2 \sin^2\lambda + \mu^2\gamma^2 f'(a) f'(b) = 0. \tag{3.12}$$

Let $\lambda = \rho + i\sigma$ and $x(\xi,t) = (\phi_1(t) + i\phi_2(t))\cos\lambda(1-\xi)$.

Lemma 2. *Let $\lambda = \rho + i\sigma$. Then*

$$\begin{aligned} \sigma\cos\rho\sinh\sigma - \rho\sin\rho\cosh\sigma = 0 \\ -\rho\cos\rho\sinh\sigma - \sigma\sin\rho\cosh\sigma = \pm\mu\gamma\sqrt{f'(a)f'(b)}. \end{aligned}$$

Lemma 3. *Let $\lambda = \rho + i\sigma$. There exists $\mu_0 > 0$ such that*

$$\rho_0^2 - \sigma_0^2 + \gamma^2 = 0 \tag{3.13}$$

where $\rho_0 = \rho(\mu_0), \sigma_0 = \sigma(\mu_0)$. In this case system (1.1)-(1.2) undergoes a Hopf bifurcation.

4 Hopf Bifurcation

Let $(x(\xi,t), y(\xi,t))$ be the solution of (1.1) with

$$\begin{aligned} x(\xi,t) &= (\phi_1(t) + i\phi_2(t))\cos\lambda(1-\xi) \\ y(\xi,t) &= (\psi_1(t) + i\psi_2(t))\cos\lambda\xi. \end{aligned} \tag{4.14}$$

Then ϕ_1, ϕ_2 and ψ_1, ψ_2 satisfy

$$\begin{bmatrix} \dot{\phi}_1 \\ \dot{\phi}_2 \end{bmatrix} = \begin{bmatrix} -(\rho^2 - \sigma^2 + \gamma^2) & 2\rho\sigma \\ -2\rho\sigma & -(\rho^2 - \sigma^2 + \gamma^2) \end{bmatrix} \begin{bmatrix} \phi_1 \\ \phi_2 \end{bmatrix}$$

and

$$\begin{bmatrix} \dot{\psi}_1 \\ \dot{\psi}_2 \end{bmatrix} = \begin{bmatrix} -(\rho^2 - \sigma^2 + \gamma^2) & 2\rho\sigma \\ -2\rho\sigma & -(\rho^2 - \sigma^2 + \gamma^2) \end{bmatrix} \begin{bmatrix} \psi_1 \\ \psi_2 \end{bmatrix}$$

and

$$\begin{aligned} (\lambda\sin\lambda)(\phi_1 + i\phi_2) = -\mu\gamma f(\psi_1 + i\psi_2 + b) + a\gamma\sinh\gamma \\ (-\lambda\sin\lambda)(\psi_1 + \psi_2) = \mu\gamma\left(1 - f(\phi_1 + i\phi_2 + a)\right) - b\gamma\sinh\gamma. \end{aligned}$$

Lemma 3. *The real and the imaginary parts of (4.14) are, respectively,*

$$\begin{aligned} Rex(\xi,t) &= \phi_1(t)\cos\rho(1-\xi)\cosh\sigma(1-\xi) \\ &+\phi_2(t)\sin\rho(1-\xi)\sinh\sigma(1-\xi) := x_1(\xi,t) \\ Imx(\xi,t) &= -\phi_1(t)\sin\rho(1-\xi)\sinh\sigma(1-\xi) \\ &+\phi_2(t)\cos\rho(1-\xi)\cosh\sigma(1-\xi) := x_2(\xi,t). \end{aligned}$$

and

$$\begin{aligned} Rey(\xi,t) &= \psi_1(t)\cos(\rho\xi)\cosh(\sigma\xi) \\ &\quad +\psi_2(t)\sin(\rho\xi)\sinh(\sigma\xi) := y_1(\xi,t) \\ Imy(\xi,t) &= -\psi_1(t)\sin(\rho\xi)\sinh(\sigma\xi) \\ &\quad +\psi_2(t)\cos(\rho\xi)\cosh(\sigma\xi) := y_2(\xi,t). \end{aligned}$$

Direct calculation yields

$$\begin{aligned} \frac{\partial}{\partial\xi} x_1(0,t) &= \phi_1(t)\left(\rho\sin\rho\cosh\sigma - \sigma\cos\rho\sinh\sigma\right) \\ &+\phi_2(t)\left(-\rho\cos\rho\sinh\sigma - \sigma\sin\rho\cosh\sigma\right) \end{aligned}$$

and

$$\begin{aligned} \frac{\partial}{\partial\xi} x_2(0,t) &= \phi_1(t)\left(\rho\cos\rho\sinh\sigma + \sigma\sin\rho\cosh\sigma\right) \\ &+\phi_2(t)\left(\rho\sin\rho\cosh\sigma - \sigma\cos\rho\sinh\sigma\right) \end{aligned}$$

and

$$\begin{aligned} y_{1\xi}(t,1) &= \psi_1(t)\left(-\rho\sin\rho\cosh\sigma+\sigma\cos\rho\sinh\sigma\right)\\ &\quad+\psi_2(t)\left(\rho\cos\rho\sinh\sigma+\sigma\sin\rho\cosh\sigma\right) \end{aligned}$$

and

$$\begin{aligned} y_{2\xi}(t,1) &= -\psi_1(t)\left(\rho\cos\rho\sinh\sigma+\sigma\sin\rho\cosh\sigma\right)\\ &\quad+\psi_2(t)\left(-\rho\sin\rho\cosh\sigma+\sigma\cos\rho\sinh\sigma\right). \end{aligned}$$

Lemma 3. *Let*

$$\Delta : = \rho\cos\rho\sinh\sigma+\sigma\sin\rho\cosh\sigma. \tag{4.15}$$

Then we have

$$\begin{aligned} \frac{\partial}{\partial\xi}x_1(0,t) &= -\Delta\phi_2(t)\\ \frac{\partial}{\partial\xi}x_2(0,t) &= \Delta\phi_1(t) \end{aligned}$$

and

$$\begin{aligned} \frac{\partial}{\partial\xi}y_1(1,t) &= \Delta\psi_2(t)\\ \frac{\partial}{\partial\xi}y_2(1,t) &= -\Delta\psi_1(t). \end{aligned}$$

Let

$$\begin{aligned} F_\mu(x) : &= -\mu\gamma f(x+b)+a\gamma\sinh\gamma\\ G_\mu(x) : &= \mu\gamma\left(1-f(x+a)\right)-b\gamma\sinh\gamma. \end{aligned}$$

Observing the boundary conditions,

$$\begin{aligned} x_{1\xi}(0,t) &= -\mu\gamma f(\psi_1(t)+b)+a\gamma\sinh\gamma\\ x_{2\xi}(0,t) &= -\mu\gamma f(\psi_2(t)+b)+a\gamma\sinh\gamma \end{aligned}$$

and

$$\begin{aligned} y_{1\xi}(1,t) &= \mu\gamma\left(1-f(\phi_1(t)+a)\right)-b\gamma\sinh\gamma\\ y_{2\xi}(1,t) &= \mu\gamma\left(1-f(\phi_2(t)+a)\right)-b\gamma\sinh\gamma \end{aligned}$$

and from Lemma 1, we have

$$\begin{aligned} \phi_1(t) &= \frac{1}{\Delta}F_\mu\left(\frac{1}{\Delta}G_\mu(\phi_1)\right)\\ \phi_2(t) &= -\frac{1}{\Delta}F_\mu\left(-\frac{1}{\Delta}G_\mu(\phi_2)\right) \end{aligned}$$

and

$$\begin{aligned} \psi_1(t) &= -\frac{1}{\Delta}G_\mu\left(-\frac{1}{\Delta}F_\mu(\psi_1)\right)\\ \psi_2(t) &= \frac{1}{\Delta}G_\mu\left(\frac{1}{\Delta}F_\mu(\psi_2)\right) \end{aligned}$$

Thun we have

Theorem 5. *System (1.1)-(1.2) can be translated into the following two systems of two dimensions, preserving the nonlinearities of the original system.*

$$\begin{aligned} \dot\phi_1 &= \frac{2\rho_0\sigma_0}{\Delta^2}F'_{\mu_0}\left(\frac{1}{\Delta}G_{\mu_0}(\phi_1)\right)G'_{\mu_0}(\phi_1)\phi_2\\ &:= F_1(\phi_1,\phi_2)\\ \dot\phi_2 &= -\frac{2\rho_0\sigma_0}{\Delta^2}F'_{\mu_0}\left(-\frac{1}{\Delta}G_{\mu_0}(\phi_2)\right)G'_{\mu_0}(\phi_2)\phi_1\\ &:= F_2(\phi_1,\phi_2) \end{aligned}$$

and

$$\begin{aligned} \dot\psi_1 &= -\frac{2\rho_0\sigma_0}{\Delta^2}G'_{\mu_0}\left(-\frac{1}{\Delta}F_{\mu_0}(\psi_1)\right)F'_{\mu_0}(\psi_1)\psi_2\\ &:= G_1(\phi_1,\phi_2)\\ \dot\psi_2 &= \frac{2\rho_0\sigma_0}{\Delta^2}G'_{\mu_0}\left(\frac{1}{\Delta}F_{\mu_0}(\psi_2)\right)F'_{\mu_0}(\psi_2)\psi_1\\ &:= G_2(\phi_1,\phi_2). \end{aligned}$$

Notice that the matrix

$$\begin{bmatrix} -(\rho^2-\sigma^2+\gamma^2) & 2\rho\sigma\\ -2\rho\sigma & -(\rho^2-\sigma^2+\gamma^2) \end{bmatrix}$$

has eigenvalue $-(\rho^2-\sigma^2+\gamma^2)+i2\rho\sigma$ and the corresponding eigenvector is

$$q=\begin{bmatrix}1\\ i\end{bmatrix}$$

Let

$$p=\frac{1}{2}\begin{bmatrix}1\\ i\end{bmatrix}.$$

Clearly, we have $<p,q>=1$, where $<\cdot,\cdot>$ means the standard scalar product in $\mathbf{C^2}$: $<p,q>=\overline{p}_1q_1+\overline{p}_2q_2$.

Let $\phi=zq+\overline{zq}$, where $\phi=(\phi_1,\phi_2)$. Then $\phi_1=z+\overline{z}$ and $\phi_2=i(z-\overline{z})$ and

$$\dot z=<p,\dot\phi>=\frac{1}{2}\left(F_1(z,\overline{z})-iF_2(z,\overline{z})\right). \tag{4.16}$$

Similarly,

$$\dot z=<p,\dot\psi>=\frac{1}{2}\left(G_1(z,\overline{z})-iG_2(z,\overline{z})\right). \tag{4.17}$$

Note

$$\begin{aligned} &\tfrac{\partial}{\partial z}\left(F_1(z,\overline{z})-iF_2(z,\overline{z})\right)\\ &=\tfrac{2\rho_0\sigma_0}{\Delta^2}\Big[\tfrac{1}{\Delta}F''_{\mu_0}\left(\tfrac{1}{\Delta}G_{\mu_0}(z+\overline{z})\right)\left(G'_{\mu_0}(z+\overline{z})\right)^2 i(z-\overline{z})\\ &\qquad+F'_{\mu_0}\left(\tfrac{1}{\Delta}G_{\mu_0}(z+\overline{z})\right)G''_{\mu_0}(z+\overline{z})i(z-\overline{z})\\ &\qquad+F'_{\mu_0}\left(\tfrac{1}{\Delta}G_{\mu_0}(z+\overline{z})\right)G'_{\mu_0}(z+\overline{z})i\\ &+\tfrac{1}{\Delta}F''_{\mu_0}\left(-\tfrac{1}{\Delta}G_{\mu_0}(iz-i\overline{z})\right)\left(G'_{\mu_0}(iz-i\overline{z})\right)^2(z+\overline{z})\\ &-F'_{\mu_0}\left(-\tfrac{1}{\Delta}G_{\mu_0}(iz-i\overline{z})\right)G'_{\mu_0}(iz-i\overline{z})G''_{\mu_0}(iz-i\overline{z})(z+\overline{z})\\ &+iF'_{\mu_0}\left(\tfrac{1}{\Delta}G_{\mu_0}(iz-i\overline{z})\right)G'_{\mu_0}(iz-i\overline{z})\Big] \end{aligned}$$

which implies that

$$\dot z=i2\rho_0\sigma_0 z+h(z,\overline{z}), \tag{4.18}$$

where $h=O(z,\overline{z})^2$.

Lemma 7.

$$\frac{\partial^2 h}{\partial z^2}\Big|_{z=0} = \frac{4\rho_0\sigma_0}{\Delta^2}\Big(\frac{2i}{\Delta}f''(b)[f'(a)]^2 + (-1+i)f'(b)f''(a)\Big)$$

and

$$\frac{\partial^2 h}{\partial \bar{z}\partial z}\Big|_{z=0} = 0, \quad Re\frac{\partial^3 h}{\partial \bar{z}\partial z^2}\Big|_{z=0} = 0.$$

Lemma 8. *The first Lyapunov coefficient of (4.18) at $\mu = 0$ is zero.*

Theorem 9. *The Hopf bifurcations of system (1.1) with boundary condition (1.2) are always degenerate, regardless of the choice of function f.*

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