BIOCONVECTION GENERATED BY EUGLENA GRACILIS UNDER STATIONARY ILLUMINATION FROM THE BOTTOM

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Abstract

Microorganisms are known to form spatiotemporal patterns similar to those formed in the Rayleigh-Bénard model for thermal convection. Among such, Euglena gracilis form distinct patterns induced by phototaxes and sensitivity to the gradient of the light intensity. A model for the convection patterns for Euglena gracilis was proposed by Suematsu et al. [4] and we discuss the dynamics of equilibria of the system in this thesis. The model is a reaction-diffusion equation with a nonlocal term and without the nonlocal term it is possible to analyze the dynamics of equilibria of the system as a pendulum. First, the author analyzes the system without the nonlocal term using the phase portrait analysis. Second, the author considers equilibria of the full system as perturbations and then discuss the physical interpretation of the results.

Contents

Chapter 1

Introduction

Microorganisms are known to form spatiotemporal patterns similar to those formed in the Rayleigh-Bénard model for thermal convection. Among such, Euglena gracilis form distinct patterns induced by phototaxes and sensitivity to the gradient of the light intensity.

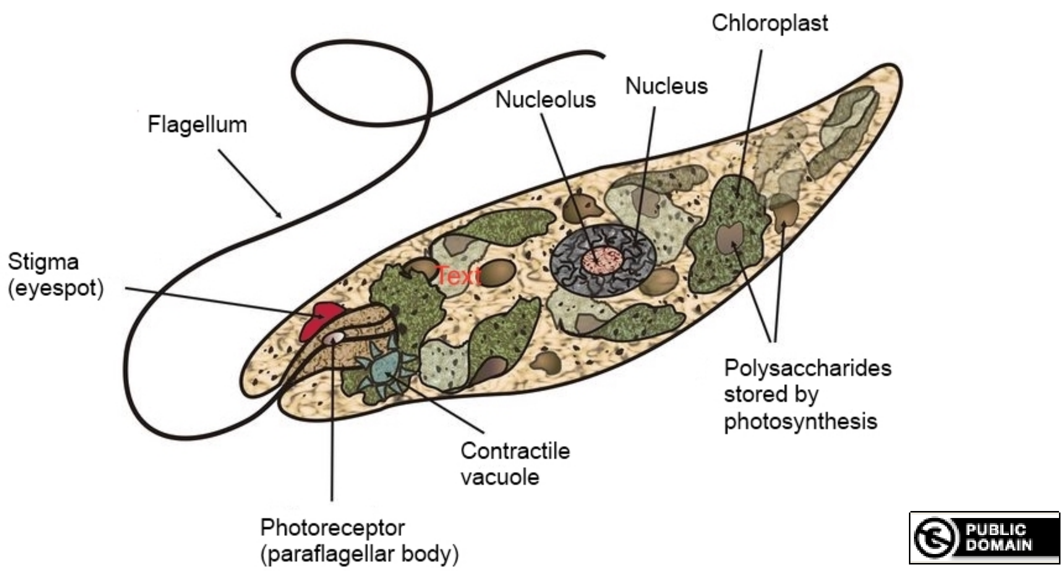

Figure 1.1: Diagram of Euglena gracilis

Euglena gracilis is a microorganism, which is a photosensitive unicellular flagellate, and they swim away from high-intensity-light (called "negative phototaxis") whereas they swim toward low-intensity-light (called "positive phototaxis"). Additionally, they are sensitive to the gradient of the light intensity and in particular, if the light intensity is high enough throughout the domain to activate the negative phototaxis, they seek places where the intensity is locally lower.

Suematsu et al. [4] reported bioconvection patterns generated by Euglena gracilis under stationary illumination from the bottom. Consider a sealed container with cells of Euglena gracilis inside and place it on an LED light plate. Then cells form spatiotemporal patterns and after some time they look like the following:

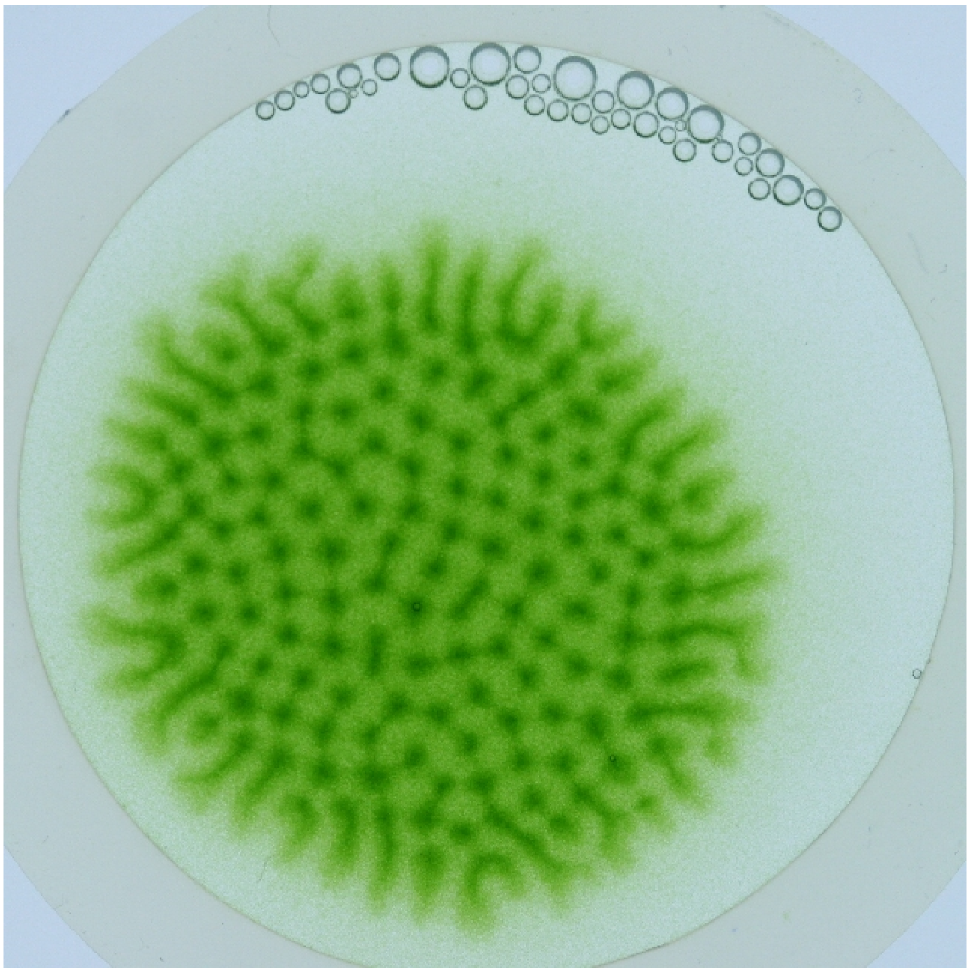

Figure 1.2: Bioconvection of Euglena gracilis ©Nobuhiko J. Suematsu

In this thesis, we will introduce a model proposed by Suematsu et al. [4] and analyze the dynamics of equilibria of the system: In chapter 2, we derive the model based on observations in the experiments. In chapter 3, we analyze equilibria; first, we consider the case where the nonlocal term is absent, in which case we are able to obtain a relation between the two variables, and then find that the resulting system is a pendulum. Here we use the phase portrait analysis. Then we make use of the relation to deal with the case with the nonlocal term as perturbations. In chapter 4, we interpret the results. In the appendix, we briefly refer to a relevant mathematical tool to answer further questions to arise.

Chapter 2

Modeling

We consider density of cells in the quasi-one-dimensional space that has two layers, and regard the transition of density from the lower to the upper layer, and vice versa, as bioconvection generated by Euglena gracilis.

2.1 Assumptions

We consider the cross section of the container along the diameter and assume that the container can be divided into two layers, namely a thin upper layer and a thick lower layer. Let L be the length of the diameter, h be the height of the container, and suppose that the upper layer has height sh and the lower layer has height $(1-s)h$, where $0 < s \ll 1$.

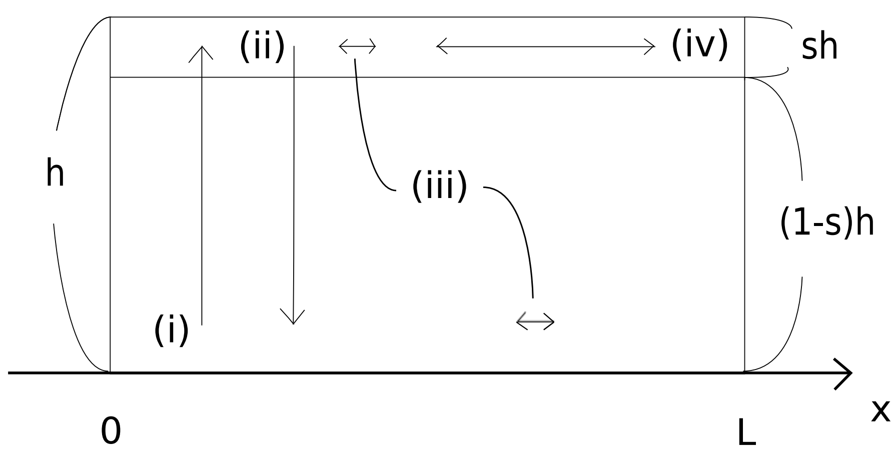

Figure 2.1: Diagram of the cross section of the container

We discretize the height and consider a quasi-one-dimensional space that has two layers, to whose points we assign density of cells. Let $m_u(X,t)$ be the mass of cells at position X and time t in the upper layer. The upper layer has depth sh so the cell density at position X and time t in the upper layer is $\rho_u(X,t) = m_u(X,t)/sh$. Similarly, let $m_\ell(X,t)$ be the mass of cells at position X and time t in the lower layer and consider the cell density at position X and time t in the lower layer $\rho_\ell(X,t) = m_\ell(X,t)/(1-s)h$. The cell density at position X and time t is now $(\rho_u + \rho_\ell)/h$.

We regard the transition of density of cells from the lower to the upper layer, and vice versa, as bioconvection generated by Euglena gracilis due to illunimation from the bottom. We assume that the following four properties cause the transition of density, hence generate the patterns:

(i) Negative phototaxis to drive Euglena gracilis from the lower to the upper layer,

(ii) Sinking of cells by gravity from the upper to the lower layer,

(iii) Diffusion of cells in both layers, and

(iv) Nonlocal interaction of cells based on the "self-shading" effect in the upper layer.

2.1.1 Negative Phototaxis

The upper layer obtains mass from the lower layer while the lower layer loses the same amount of mass as follows:

$$\begin{array}{ll} \text{UPPER} & +\mu G \underbrace{(1-s)h\rho_\ell(X,t)}_{=m_\ell(X,t)} \\ \text{LOWER} & -\mu G(1-s)h\rho_\ell(X,t), \end{array}$$

where μ is the efficiency of negative phototaxis and G is the gradient of the light intensity in the vertical direction. The product μG is the velocity of the upward swimming.

2.1.2 Sinking of Cells

Conversely, the lower layer obtains mass when cells sink, while the upper layer loses the same amount of mass. Sinking occurs at places where density is higher and once the aggregate starts sinking, it is hard for cells to escape from the downward flow.

We assume that the velocity of the downward flow is given by

$$f\left(\frac{m}{\rho_{water}}\frac{\rho_u+\rho_\ell}{h}\right),$$

where the function f depends on the mass density of water ρ_{water}, the mass of a single cell m, and density of cells at that point.

Furthermore, we assume that the sinking rate is a constant v_g and the function f has the form

$$f\left(\frac{m}{\rho_{water}}\frac{\rho_u+\rho_\ell}{h}\right) = \alpha\left(\frac{m}{\rho_{water}}\frac{\rho_u+\rho_\ell}{h}\right)^\gamma,$$

where α and γ are constants.

Thus

$$
\begin{array}{ll}
\text{UPPER} & -\alpha\left(\dfrac{m}{\rho_{water}}\dfrac{\rho_u+\rho_\ell}{h}\right)^{\gamma} v_g \underbrace{sh\rho_u(X,t)}_{=m_u(X,t)} \\
\text{LOWER} & +\alpha\left(\dfrac{m}{\rho_{water}}\dfrac{\rho_u+\rho_\ell}{h}\right)^{\gamma} v_g sh\rho_u(X,t).
\end{array}
$$

Remark. The dynamics depends on the specific value of γ, which comes from "Sinking of Cells" in the modeling. The value $\gamma = 2$ corresponds to the hypothesis that cells sink, from the upper to the lower layer, with speed of order γ, with density as the variable. In terms of resistance, it is reasonable that cells sink with such speed, as the viscous resistance is close to the order of 2, while the inertial resistance to the order of 3. In our settings, cells sink in an aqueous solution, and the case $\gamma = 2$ seems the most stimulating as well as is easy to calculate by hand.

2.1.3 Diffusion

We assume that cells diffuse in both layers, with different diffusion rates. From observations in the experiments, we assume that the diffusion rate in the lower layer is much smaller than that in the upper layer, as vertical movement was seen dominant in the lower layer. Thus

$$
\begin{array}{ll}
\text{UPPER} & +d_1\partial_{XX}\rho_u(X,t) \\
\text{LOWER} & +d_2\partial_{XX}\rho_\ell(X,t),
\end{array}
$$

where $0 < d_2 \ll d_1$.

2.1.4 Nonlocal Interaction

We want to measure the velocity of the flow of cells seeking darker places, induced by the "self-shading" effect as well as their sensitivity to the gradient of the light intensity. The "self-shading" effect is a phenomenon whereby cells themselves contribute to "darkness." Namely, the higher the density, the lower the intensity of light, or the darker the place gets, at that point. Suppose that, without the interaction, it is bright throughout the domain $(0, L)$, with the light intensity C_0. We consider "darkness," which we define by $C(X,t)$, which is the difference in intensity caused by absorption of light by cells and decay of light in the medium. Although the light source is beneath the container, the gradient of light in the horizontal direction, hence the gradient of "darkness," is formed as light is scattered by the medium and the wall of the container.

Moreover, we assume that each point in the upper layer is a source of "darkness," just like each luminous body can be a light source in darkness. Intuitively, cells "eat" light so that the very point where they are gets darker.

Figure 2.2 shows the concept of "darkness."

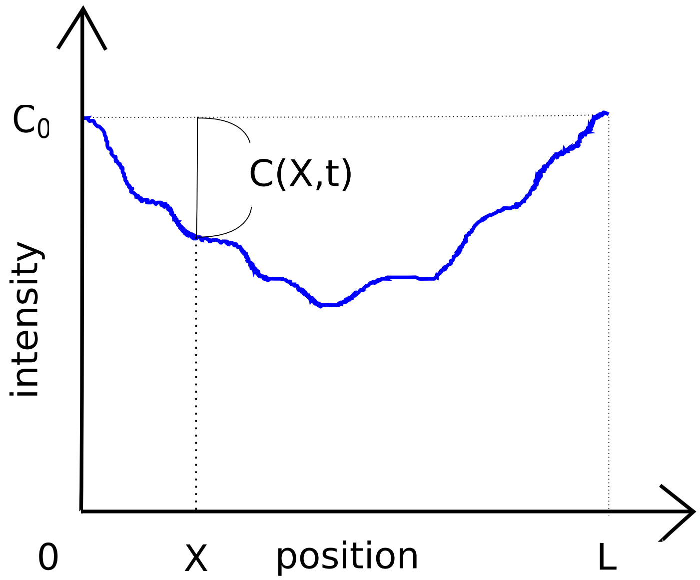

Figure 2.2: Concept of "darkness"

By the Beer-Lambert law, the intensity of light gets attenuated as light travels through the medium, i.e.

$$\frac{I_{out}}{I_{in}} = constant \cdot length,$$

where I_{out} denotes the decayed light intensity and I_{in} denotes the initial light intensity. Hence the decayed light intensity due to travelling a distance of length X is

$$I(X) = I_{in} \exp(|X|/\tilde{\Lambda}),$$

where $\tilde{\Lambda}$ is a constant. Figure 2.3 shows $I(X)$ plotted with values $I_{in} = 1$, $L = 1$, and $\tilde{\Lambda} = 1/10$.

The intensity at a point is determined by a contribution made by cells themselves, i.e. the "self-shading" effect, and decay of light according to the field of "darkness." More precisely, we consider convolution $\frac{\rho_u(X,t)}{sh} * I(X)$ of density and decay of light.

In other words, we consider the product $\frac{\rho_u(Y)}{sh} I(X-Y)$, where Y represents a point, belonging to points, density at which we have to consider to include the "self-shading" effect, and X is the point at which we want to determine the decayed intensity. Taking all the points in the upper layer into account, we integrate over the interval $(0, L)$ to obtain

$$C(X,t) := \frac{\rho_u(X,t)}{sh} * I(X) = \frac{I_{in}}{sh} \int_0^L \rho_u(Y,t) \exp\left(-\frac{|X-Y|}{\tilde{\Lambda}}\right) dY.$$

Euglena gracilis is sensitive to the gradient of "darkness" $C(X,t)$, and we assume further that the velocity of the lateral flow is proportional to the gradient, i.e.

$$velocity = \mu \partial_X C(X,t),$$

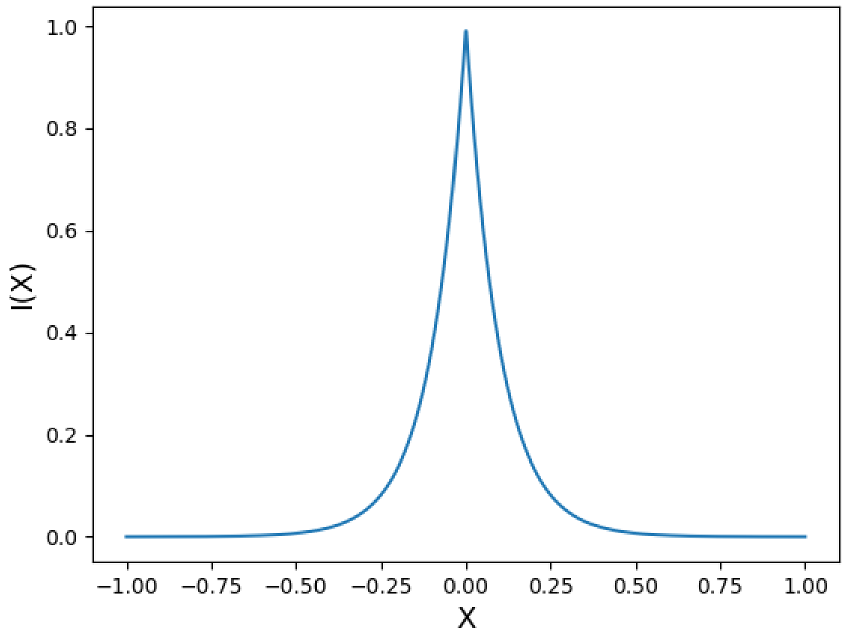

Figure 2.3: Decay of light as it travels through the medium

where μ is the efficiency of negative phototaxis appeared in negative phototaxis.

Here the gradient of the field can be calculated as

$$\begin{aligned}
\partial_X C(X,t) &= \frac{I_{in}}{sh}\int_0^L \rho_u(Y,t)\left\{\partial_X \exp\left(-\frac{|X-Y|}{\tilde{\Lambda}}\right)\right\}dY \\
&= \frac{I_{in}}{sh}\left[\int_X^L \rho_u(Y,t)\left\{\partial_X \exp\left(-\frac{|X-Y|}{\tilde{\Lambda}}\right)\right\}dY \right.\\
&\qquad\qquad \left. + \int_0^X \rho_u(Y,t)\left\{\partial_X \exp\left(-\frac{|X-Y|}{\tilde{\Lambda}}\right)\right\}dY\right] \\
&= \frac{I_{in}}{sh}\left[\int_X^L \rho_u(Y,t)\left\{\frac{1}{\tilde{\Lambda}} \exp\left(-\frac{|X-Y|}{\tilde{\Lambda}}\right)\right\}dY \right.\\
&\qquad\qquad \left. + \int_0^X \rho_u(Y,t)\left\{-\frac{1}{\tilde{\Lambda}} \exp\left(-\frac{|X-Y|}{\tilde{\Lambda}}\right)\right\}dY\right] \\
&=: \frac{I_{in}}{sh\tilde{\Lambda}}(\Psi_+ - \Psi_-),
\end{aligned}$$

where

$$\Psi_+ = \int_X^L \rho_u(Y,t) \exp\left(-\frac{|X-Y|}{\tilde{\Lambda}}\right) dY$$
$$\Psi_- = \int_0^X \rho_u(Y,t) \exp\left(-\frac{|X-Y|}{\tilde{\Lambda}}\right) dY.$$

By a continuity equation, i.e.

$$\partial_t[density] + \nabla[velocity \cdot density] = 0,$$

we have

$$\begin{array}{rl} \text{UPPER} & -\mu \dfrac{I_{in}}{sh\tilde{\Lambda}} \partial_x[(\Psi_+ - \Psi_-)\rho_u(X,t)] \\ \text{LOWER} & \text{No change in density due to this interaction.} \end{array}$$

Remark. Alternatively, we may express the nonlocal term as

$$-\mu \frac{I_{in}}{sh\tilde{\Lambda}} \partial_X[(\Psi_+ - \Psi_-)\rho_u(X,t)] = -\tilde{c}\partial_X[(\rho_u * \partial_X I)\rho_u],$$

where $\tilde{c} := \mu I_{in}/sh\tilde{\Lambda}$ and $I(X) = I_{in}\exp(-|X|/\tilde{\Lambda})$ as above.

2.2 System

Organizing constants as $a := \alpha(m/\rho_{water})^\gamma v_g sh$ and $\lambda := \mu G(1-s)h$, we obtain the following system:

$$\partial_t \rho_u = -a\left(\frac{\rho_u + \rho_\ell}{h}\right)^\gamma \rho_u + \lambda\rho_\ell + d_1\partial_{XX}\rho_u - \tilde{c}\partial_X[(\Psi_+ - \Psi_-)\rho_u]$$
$$\partial_t \rho_\ell = a\left(\frac{\rho_u + \rho_\ell}{h}\right)^\gamma \rho_u - \lambda\rho_\ell + d_2\partial_{XX}\rho_\ell,$$

where

$$\Psi_+ := \int_X^L \rho_u(Y,t) \exp\left(-\frac{|X-Y|}{\tilde{\Lambda}}\right) dY$$
$$\Psi_- := \int_0^X \rho_u(Y,t) \exp\left(-\frac{|X-Y|}{\tilde{\Lambda}}\right) dY,$$

with the Neumann boundary conditions $\partial_X \rho_u(X,t)\big|_{X=0,L} = \partial_X \rho_\ell(X,t)\big|_{X=0,L} = 0$ and the no-cell-conditions for the compliment of the domain $(0,L)$, i.e. $\rho_u(X,t) = \rho_\ell(X,t) = 0$ for $X \in (-\infty, 0) \cap (L, \infty)$.

2.3 Rescaled System

First, we change scaling so that h inside exponentiation of γ disappers: Let $u(X,t) := h\rho_u(X,t)$ and $v(X,t) := h\rho_\ell(X,t)$.

Then, we change scaling of the spacial variable X to access the diffusion rates, i.e. $x := c_3 X$, as well as organizing constants as $c := c_3 h\tilde{c}$, $c_3^2 d_2 := 1$, $\epsilon := d_2/d_1 = c_3^2 d_2$, $\ell := c_3 L$, and $\Lambda := c_3\tilde{\Lambda}$ to obtain

$$u_t = -a(u+v)^\gamma u + \lambda v + u_{xx} - c\partial_x[(\psi_+ - \psi_-)u] \tag{2.1}$$

$$v_t = a(u+v)^\gamma u - \lambda v + \epsilon v_{xx}, \tag{2.2}$$

where

$$\psi_+ := \int_x^\ell u(y,t) \exp\left(-\frac{|x-y|}{\Lambda}\right) dy$$

$$\psi_- := \int_0^x u(y,t) \exp\left(-\frac{|x-y|}{\Lambda}\right) dy,$$

with the Neumann boundary conditions $\partial_x u(x,t)|_{x=0,\ell} = \partial_x v(x,t)|_{x=0,\ell} = 0$ and the no-cell-conditions for the compliment of the domain $(0,\ell)$, i.e. $u(x,t) = v(x,t) = 0$ for $x \in (-\infty,0) \cup (\ell,\infty)$. Here, all the constants are positive and ϵ is small, i.e. $a, \lambda, c, \gamma, \ell > 0$, and $0 < \epsilon \ll 1$.

Chapter 3

Equilibria

We observe that the two equations in the system are identical except the signs and presence of the nonlocal term. First, we consider the case where $c = 0$ and then make use of the relation we have obtained as an "Ansatz" to analyze the case where $c \neq 0$.

3.1 Without the Nonlocal Term

Suppose that $c = 0$ in the system (2.1), (2.2); then, for equilibria, we have the following:

$$0 = -a(u+v)^{\gamma}u + \lambda v + u_{xx} \tag{3.1}$$
$$0 = a(u+v)^{\gamma}u - \lambda v + \epsilon v_{xx}. \tag{3.2}$$

Adding the two equations, we obtain

$$0 = u_{xx} + \epsilon v_{xx}.$$

Now, we integrate this with respect to the spacial variable x, use the Neumann boundary conditions to eliminate the constant of integration, and integrate that again with respect to x, to reach

$$\beta = u + \epsilon v, \tag{3.3}$$

where β is a constant.

Now we substitute the relation $u = \beta - \epsilon v$ for u in the equation (3.2) to reach

$$\epsilon v_{xx} = -a[(1-\epsilon)v + \beta]^{\gamma}(\beta - \epsilon v) + \lambda v.$$

To analyze the dynamics of the pendulum, we change variables as $z = \epsilon^{1/2}x$, i.e.

$$v_{zz} = -a[(1-\epsilon)v + \beta]^{\gamma}(\beta - \epsilon v) + \lambda v =: f(v, \epsilon). \tag{3.4}$$

The dynamics of equilibria of the system (3.1), (3.2), is now a pendulum of a slow variable z of the spacial variable x, which is governed by the potential $U = -\int_0^v f(\tilde{v}, \epsilon)\, d\tilde{v}$ of order $\gamma + 1$ where $\gamma > 1$, or of order 2 if $0 < \gamma \leq 1$. See [1] for a general exposition of the pendulum.

3.1.1 The case of $\gamma = 2$

Suppose that $\gamma = 2$. Then the pendulum equation reads

$$\begin{aligned} v_{zz} &= -a[(1-\epsilon)v+\beta]^2(\beta-\epsilon v)+\lambda v \\ &= \epsilon(1-\epsilon)^2 a v^3 + (-1+4\epsilon-3\epsilon^2)a\beta v^2 + (\lambda - 2a\beta^2 + 3\epsilon a\beta^2)v - a\beta^3, \end{aligned}$$

so the potential is

$$\begin{aligned} U(v(z),\epsilon) &= -\int_0^v f(\tilde{v},\epsilon)\, d\tilde{v} \\ &= -\frac{1}{4}[\epsilon(1-\epsilon)^2 a]v^4 - \frac{1}{3}(-1+4\epsilon-3\epsilon^2)a\beta v^3 - \frac{1}{2}(\lambda-2a\beta^2+3\epsilon a\beta^2)v^2 + a\beta^3 v. \end{aligned}$$

Consider the level curve of the Hamiltonian

$$H(v, v_z) = \frac{1}{2}v_z^2 + U(v(z),\epsilon) = H(0,0) = 0,$$

or

$$v_z = \pm\sqrt{-2U(v(z),\epsilon)}.$$

In other words, we have the explicit expression of the orbit in the phase space through the equilibrium $(v, v_z) = (0, 0)$:

$$v_z = \pm\sqrt{\frac{1}{2}[\epsilon(1-\epsilon)^2 a]v^4 + \frac{2}{3}(-1+4\epsilon-3\epsilon^2)a\beta v^3 + (\lambda-2a\beta^2+3\epsilon a\beta^2)v^2 - 2a\beta^3 v}.$$

The Jacobi matrix at the equilibrium $(v, v_z) = (0, 0)$ is

$$J = \begin{pmatrix} 0 & 1 \\ \lambda - 2a\beta^2 + 3\epsilon a\beta^2 & 0 \end{pmatrix},$$

with eigenvalues $\pm\sqrt{\lambda - 2a\beta^2 + 3\epsilon a\beta^2}$. Thus, the equilibrium $(v, v_z) = (0, 0)$ is hyperbolic, provided $\lambda - 2a\beta^2 + 3\epsilon a\beta^2 \neq 0$.

For visualization, below are plots of the potential $U(v,\epsilon)$ in blue and the level 0 of the energy in red, together with the homoclinic orbit emanating from the hyperbolic equilibrium $(v, v_z) = (0, 0)$, with values $\epsilon = 0.01$, $\lambda = 1$, $a = 1$, and $\beta = \frac{1}{4}$:

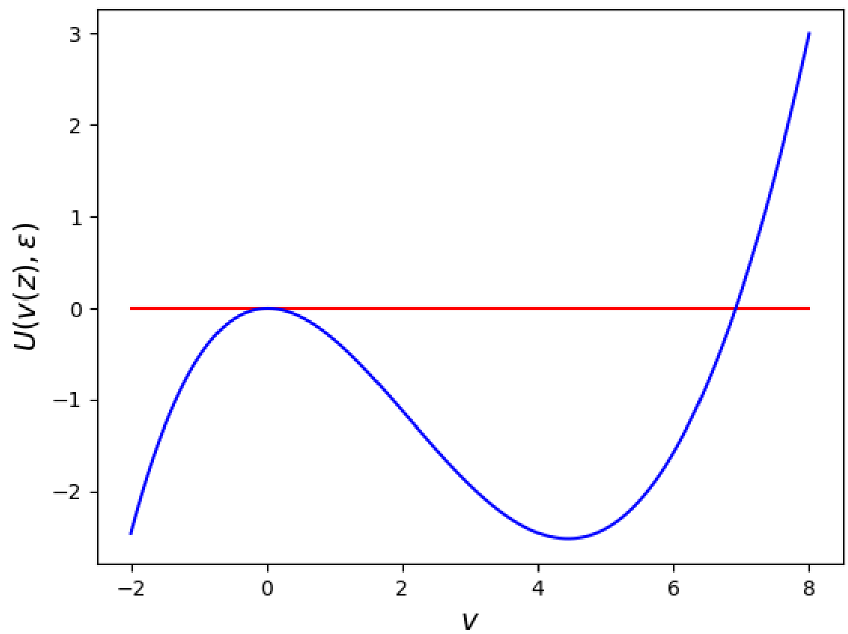

Figure 3.1: $\gamma = 2$. Potential $U(v(z), \epsilon)$ (in blue) with the level 0 of the energy (in red)

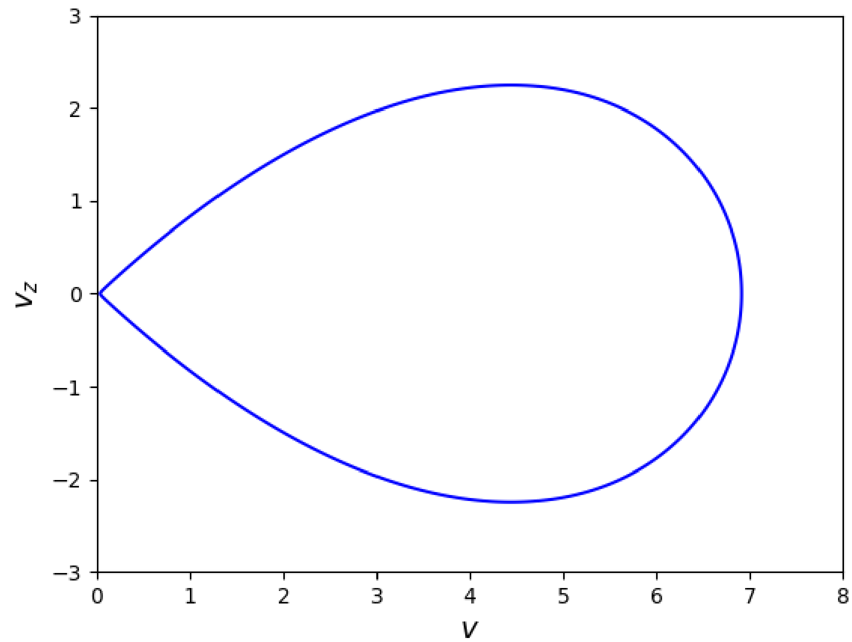

Figure 3.2: $\gamma = 2$. The Homoclinic orbit emanating from $(v, v_z) = (0, 0)$

Inside the homoclinic orbit, there is an equilibrium surrounded by periodic orbits. These periodic orbits can also be explicitly expressed using the Hamiltonian, with different energy levels.

For instance, the periodic orbit through the point $(v, v_z) = (1, 0)$ has the expression

$$H(v, v_z) = H(1, 0) = -\frac{1}{4}[\epsilon(1-\epsilon)^2 a] - \frac{1}{3}(-1+4\epsilon-3\epsilon^2)a\beta - \frac{1}{2}(\lambda - 2a\beta^2 + 3\epsilon a\beta^2) + a\beta^3,$$

which is $H(v, v_z) \approx -0.345$, where $\epsilon = 0.01$, $\lambda = 1$, $a = 1$ and $\beta = \frac{1}{4}$.

The local minimum of the potential $U(v(z), \epsilon)$ corresponds to the level of energy that gives the expression of the equilibrium surrounded by periodic orbits and, with the same values as above, it is approximately $H(v, v_z) \approx H(4.45, 0) \approx -2.522$. Below is the equilibrium surrounded by the periodic orbits, plotted with values $\epsilon = 0.01$, $\lambda = 1$, $a = 1$ and $\beta = \frac{1}{4}$:

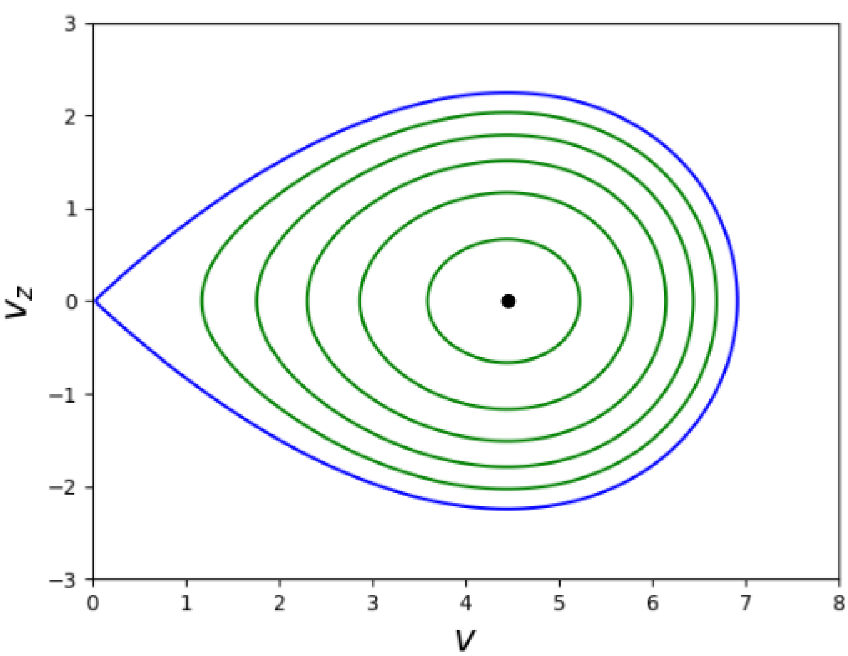

Figure 3.3: $\gamma = 2$. The equilibrium (in black) surrounded by periodic orbits (in green)

Provided $\lambda - 2a\beta^2 + 3\epsilon a\beta^2 = 0$, the structure of the orbits, namely, the existence of a homoclinic orbit emanating from a hyperbolic equilibrium embracing an equilibrium surrounded by periodic orbits, is robust under ϵ-perturbation because the Jacobi matrix has nonzero eigenvalues for any ϵ. The unstable and stable manifolds of the equilibrium $(v, v_z) = (0, 0)$ are exactly the orbit determined by $H(v, v_z) = H(0, 0) = 0$. Inside the homoclinic orbit, for any ϵ small, there is an equilibrium and periodic orbits surrounding it, as well.

Remark. If $\lambda - 2a\beta^2 + 3\epsilon a\beta^2 = 0$, then the equilibrium $(v, v_z) = (0, 0)$ is no longer hyperbolic. Indeed, the derivative at $v = 0$ of the potential becomes 0 and the potential looks as follows, plotted with same values of constants but with critical λ:

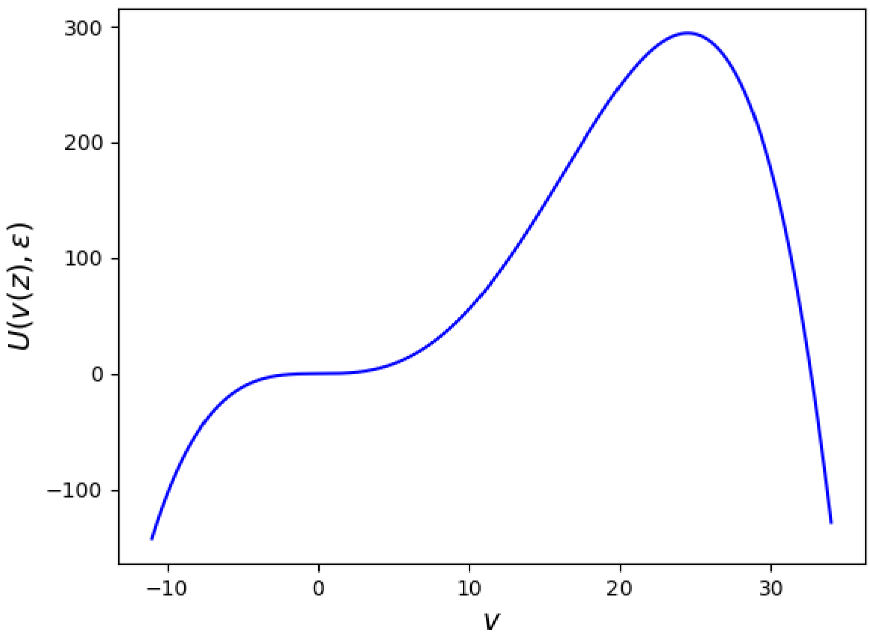

Figure 3.4: $\gamma = 2$. Potential $U(v(z), \epsilon)$ with critical λ

Consider the energy level $H(v, v_z) = H(0, 0) = 0$. We find that there is no orbit corresponding to this level as

$$v_z = \pm\sqrt{\frac{1}{2}[\epsilon(1-\epsilon)^2 a]v^4 + \frac{2}{3}(-1 + 4\epsilon - 3\epsilon^2)a\beta v^3 - 2a\beta^3 v},$$

which becomes imaginary as long as ϵ is small.

Thus, the homoclinic orbit dissappears. Moreover, there is no interesting dynamics as, except an equilibrium corresponding to the peak of the potential, no homoclinic or heteroclinic orbits, no periodic orbits, and no equilibria exist.

3.1.2 The case of $\gamma = 3$

Suppose that $\gamma = 3$. Then the pendulum equation reads

$$\begin{aligned} v_{zz} &= -a[(1-\epsilon)v+\beta]^3(\beta-\epsilon v)+\lambda v \\ &= \epsilon(1-\epsilon)^3 a v^4 + (-1+6\epsilon-9\epsilon^2+4\epsilon^3)a\beta v^3 \\ &\quad + [-3\beta+(2\beta^2+6\beta+1)\epsilon+(-2\beta^2-3\beta-1)\epsilon^2]a\beta v^2 + (\lambda-3a\beta^3+4a\beta^3\epsilon)v - a\beta^4, \end{aligned}$$

so the potential is

$$\begin{aligned} U(v(z),\epsilon) &= -\int_0^v f(\tilde{v},\epsilon)\,d\tilde{v} \\ &= -\frac{1}{5}\epsilon(1-\epsilon)^3 a v^5 + \frac{1}{4}(1-6\epsilon+9\epsilon^2-4\epsilon^3)a\beta v^4 \\ &\quad + \frac{1}{3}(2\beta^2\epsilon^2+3\beta\epsilon^2+\epsilon^2-2\beta^2\epsilon-6\beta\epsilon-\epsilon+3\beta)a\beta v^3 \\ &\quad + \frac{1}{2}(-\lambda+3a\beta^3-4a\beta^3\epsilon)v^2 + a\beta^4 v. \end{aligned}$$

Similarly to the case where $\gamma = 2$, we find a hyperbolic homoclinic orbit emanating from the point $(v, v_z) = (0, 0)$, provided that $\lambda - 3a\beta^3 + 4a\beta^3\epsilon \neq 0$.

We have the explicit expression of the orbit in the phase space through the equilibrium $(v, v_z) = (0, 0)$:

$$H(v, v_z) = \frac{1}{2}v_z^2 + U(v(z),\epsilon) = H(0,0) = 0,$$

or

$$v_z = \pm\sqrt{-2U(v(z),\epsilon)}.$$

Below are plots of the potential $U(v,\epsilon)$ in blue and the level 0 of the energy in red, together with the homoclinic orbit emanating from the hyperbolic equilibrium $(v, v_z) = (0, 0)$, with values $\epsilon = 0.01$, $\lambda = 1$, $a = 1$, and $\beta = \frac{1}{4}$:

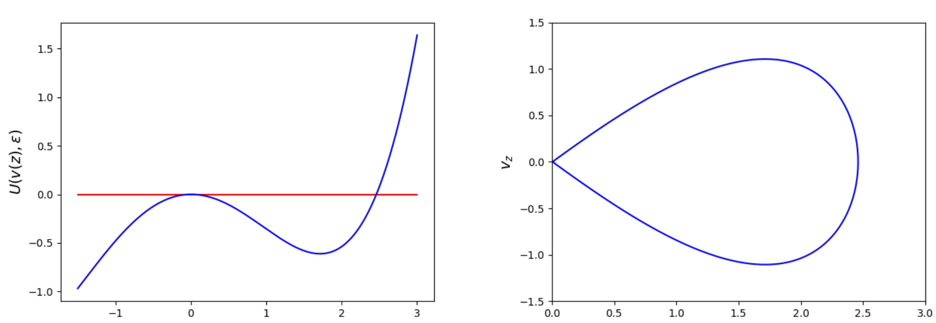

Figure 3.5: $\gamma = 3$. Potential $U(v(z),\epsilon)$ (in blue) with the level 0 of the energy (in red) and the homoclinic orbit emanating from $(v, v_z) = (0, 0)$

Remark. Similarly to the case where $\gamma = 2$; if $\lambda - 3a\beta^3 + 4a\beta^3\epsilon = 0$, then the equilibrium $(v, v_z) = (0, 0)$ is no longer hyperbolic. Indeed, the derivative at $v = 0$ of the potential becomes 0 and the potential looks as follows, plotted with same values of constants but with critical λ:

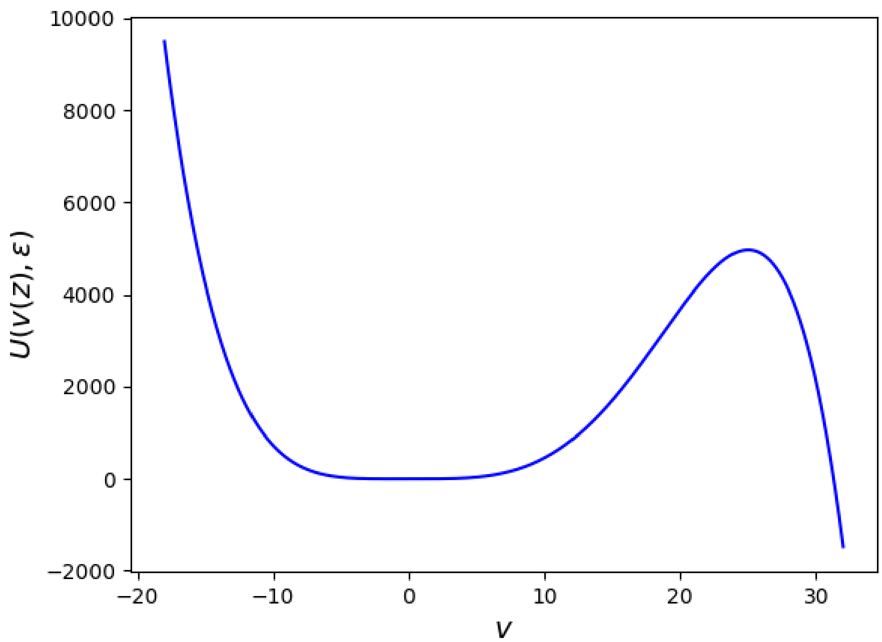

Figure 3.6: $\gamma = 3$. Potential $U(v(z), \epsilon)$ with critical λ

Unlike the case of $\gamma = 2$, the point $(v, v_z) = (0, 0)$ is an equilibrium and there are periodic orbits surrounding it. However, positivity of solutions seems to be destroyed and the conditions which resulted in the above seem to be no longer realistic.

3.2 Perturbations by the Nonlocal Term

We are interested in a close-to-Hamiltonian system, perturbed by the nonlocal term, in the case where the homoclinic orbit exists without the nonlocal term. Suppose that $\gamma = 2$ and $\lambda - 2a\beta^2 + 3\epsilon a\beta^2 \neq 0$; or $\gamma = 3$ and $\lambda - 3a\beta^3 + 4a\beta^3\epsilon \neq 0$.

First, we simplify the form of the nonlocal term where ϵ is small. Assuming that u and v have the relation $u = \beta - \epsilon v$, substituting it for u in the equation (2.1) with $u_t = 0$, and changing variables as $z = \epsilon^{1/2}x$, we obtain

$$\begin{aligned}
v_{zz} &= -a(u+v)^\gamma u + \lambda v - c\partial_x[(\psi_+ - \psi_-)u] \\
&= -a[(1-\epsilon)v + \beta]^\gamma(\beta - \epsilon v) + \lambda v \\
&\quad - \epsilon^{-1} c\partial_z \Bigg\{ \Bigg[\int_z^{\epsilon^{1/2}\ell} (\beta - \epsilon v)\exp\left(-\frac{|\epsilon^{-1/2}||z-\tilde{z}|}{\Lambda}\right) d\tilde{z} \\
&\qquad\qquad - \int_0^z (\beta - \epsilon v)\exp\left(-\frac{|\epsilon^{-1/2}||z-\tilde{z}|}{\Lambda}\right) d\tilde{z} \Bigg] (\beta - \epsilon v) \Bigg\} \\
&= -a[(1-\epsilon)v + \beta]^\gamma(\beta - \epsilon v) + \lambda v \\
&\quad + c\beta\partial_z \Bigg[\int_z^{\epsilon^{1/2}\ell} v\exp\left(-\frac{|\epsilon^{-1/2}||z-\tilde{z}|}{\Lambda}\right) d\tilde{z} - \int_0^z v\exp\left(-\frac{|\epsilon^{-1/2}||z-\tilde{z}|}{\Lambda}\right) d\tilde{z} \Bigg] \\
&\quad - \epsilon c\partial_z \Bigg\{ \Bigg[\int_z^{\epsilon^{1/2}\ell} v\exp\left(-\frac{|\epsilon^{-1/2}||z-\tilde{z}|}{\Lambda}\right) d\tilde{z} - \int_0^z v\exp\left(-\frac{|\epsilon^{-1/2}||z-\tilde{z}|}{\Lambda}\right) d\tilde{z} \Bigg] v \Bigg\} \\
&= -a[(1-\epsilon)v + \beta]^\gamma(\beta - \epsilon v) + \lambda v \\
&\quad + c\beta \Bigg[\int_z^{\epsilon^{1/2}\ell} \left(v_z + \frac{\epsilon^{-1/2}}{\Lambda}v\right)\exp\left(-\frac{|\epsilon^{-1/2}||z-\tilde{z}|}{\Lambda}\right) d\tilde{z} \\
&\qquad\qquad - \int_0^z \left(v_z - \frac{\epsilon^{-1/2}}{\Lambda}v\right)\exp\left(-\frac{|\epsilon^{-1/2}||z-\tilde{z}|}{\Lambda}\right) d\tilde{z} - 2v \Bigg] \\
&\quad - \epsilon c \Bigg[\int_z^{\epsilon^{1/2}\ell} \left(v_z + \frac{\epsilon^{-1/2}}{\Lambda}v\right)\exp\left(-\frac{|\epsilon^{-1/2}||z-\tilde{z}|}{\Lambda}\right) d\tilde{z} \\
&\qquad\qquad - \int_0^z \left(v_z - \frac{\epsilon^{-1/2}}{\Lambda}v\right)\exp\left(-\frac{|\epsilon^{-1/2}||z-\tilde{z}|}{\Lambda}\right) d\tilde{z} - 2v \Bigg] v \\
&\quad - \epsilon c \Bigg[\int_z^{\epsilon^{1/2}\ell} v\exp\left(-\frac{|\epsilon^{-1/2}||z-\tilde{z}|}{\Lambda}\right) d\tilde{z} - \int_0^z v\exp\left(-\frac{|\epsilon^{-1/2}||z-\tilde{z}|}{\Lambda}\right) d\tilde{z} \Bigg] v_z \\
&=: -a[(1-\epsilon)v + \beta]^\gamma(\beta - \epsilon v) + \lambda v + c\beta[\delta_1(\epsilon) - 2v] - \epsilon c[\delta_1(\epsilon) - 2v]v - \epsilon c\delta_2(\epsilon)v_z,
\end{aligned} \tag{3.5}$$

where both $\delta_1(\epsilon) > \delta_2(\epsilon)$ approach 0 as $\epsilon \to 0$.

Thus the perturbation changes the equation even in the limiting case $\epsilon \to 0$. We deal with the limiting system using the potential and the energy levels.

3.2.1 The Case of $\gamma = 2$

We find that, for $\gamma = 2$, the limiting equation reads

$$\begin{aligned} v_{zz} &= -a[(1-\epsilon)v + \beta]^2(\beta - \epsilon v) + \lambda v \\ &= \epsilon(1-\epsilon)^2 a v^3 + (-1 + 4\epsilon - 3\epsilon^2)a\beta v^2 + (\lambda - 2a\beta^2 + 3\epsilon a\beta^2 - 2c\beta)v - a\beta^3, \end{aligned}$$

so the potential is

$$\begin{aligned} &U(v(z), \epsilon) = -\int_0^v f(\tilde{v}, \epsilon)\, d\tilde{v} \\ &= -\frac{1}{4}[\epsilon(1-\epsilon)^2 a]v^4 - \frac{1}{3}(-1 + 4\epsilon - 3\epsilon^2)a\beta v^3 - \frac{1}{2}(\lambda - 2a\beta^2 + 3\epsilon a\beta^2 - 2c\beta)v^2 + a\beta^3 v. \end{aligned}$$

The level 0 of the energy corresponds with

$$v_z = \pm\sqrt{\frac{1}{2}[\epsilon(1-\epsilon)^2 a]v^4 + \frac{2}{3}(-1 + 4\epsilon - 3\epsilon^2)a\beta v^3 + (\lambda - 2a\beta^2 + 3\epsilon a\beta^2 - 2c\beta)v^2 - 2a\beta^3 v}.$$

The behavior of the solutions are not totally different from those of the unperturbed system. Indeed, the limiting system with the nonlocal term is a perturbation of the unperturbed system with respect to c. Moreover, as we can explicitly calculate level sets of the energy, we know that the structure of the solutions remains similar for reasonable values of c. Below are plots of the potential $U(v, \epsilon)$ in blue and the level 0 of the energy in red, together with the homoclinic orbit emanating from the hyperbolic equilibrium $(v, v_z) = (0, 0)$, with values $\epsilon = 0.01$, $\lambda = 1$, $a = 1$, $\beta = \frac{1}{4}$, and $c = 1$:

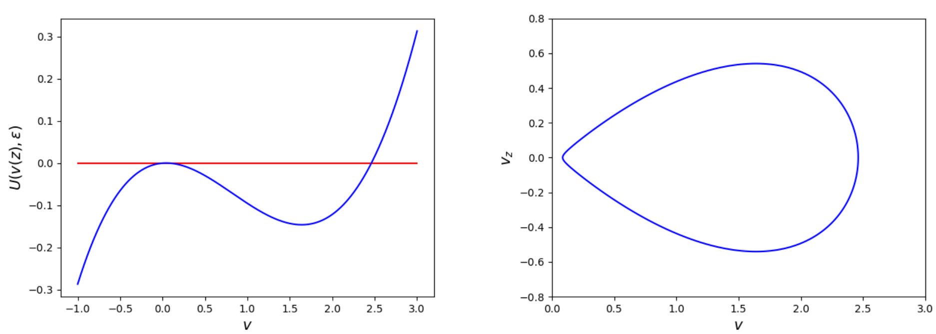

Figure 3.7: $\gamma = 2$. Potential $U(v(z), \epsilon)$ (in blue) with the level 0 of the energy (in red) and the homoclinic orbit emanating from $(v, v_z) = (0, 0)$

3.2.2 The Case of $\gamma = 3$

As is the case of $\gamma = 2$, we can calculate level sets of the energy, we know that the structure of the solutions remains similar for reasonable values of c. Indeed, for $\gamma = 3$, the limiting equation reads

$$\begin{aligned} v_{zz} &= -a[(1-\epsilon)v+\beta]^3(\beta-\epsilon v)+\lambda v \\ &= \epsilon(1-\epsilon)^3 a v^4 + (-1+6\epsilon-9\epsilon^2+4\epsilon^3)a\beta v^3 \\ &\quad + [-3\beta+(2\beta^2+6\beta+1)\epsilon+(-2\beta^2-3\beta-1)\epsilon^2]a\beta v^2 \\ &\quad\quad + (\lambda-3a\beta^3+4a\beta^3\epsilon-2c\beta)v - a\beta^4, \end{aligned}$$

so the potential is

$$\begin{aligned} U(v(z),\epsilon) &= -\int_0^v f(\tilde{v},\epsilon)\,d\tilde{v} \\ &= -\frac{1}{5}\epsilon(1-\epsilon)^3 a v^5 + \frac{1}{4}(1-6\epsilon+9\epsilon^2-4\epsilon^3)a\beta v^4 \\ &\quad + \frac{1}{3}(2\beta^2\epsilon^2+3\beta\epsilon^2+\epsilon^2-2\beta^2\epsilon-6\beta\epsilon-\epsilon+3\beta)a\beta v^3 \\ &\quad\quad + \frac{1}{2}(-\lambda+3a\beta^3-4a\beta^3\epsilon-2c\beta)v^2 + a\beta^4 v. \end{aligned}$$

Again, we have the explicit expression of the orbit in the phase space through the equilibrium $(v, v_z) = (0, 0)$:

$$H(v, v_z) = \frac{1}{2}v_z^2 + U(v(z),\epsilon) = H(0,0) = 0,$$

or

$$v_z = \pm\sqrt{-2U(v(z),\epsilon)}.$$

Below are plots of the potential $U(v,\epsilon)$ in blue and the level 0 of the energy in red, together with the homoclinic orbit emanating from the hyperbolic equilibrium $(v, v_z) = (0, 0)$, with values $\epsilon = 0.01$, $\lambda = 1$, $a = 1$, $\beta = \frac{1}{4}$, and $c = 1$:

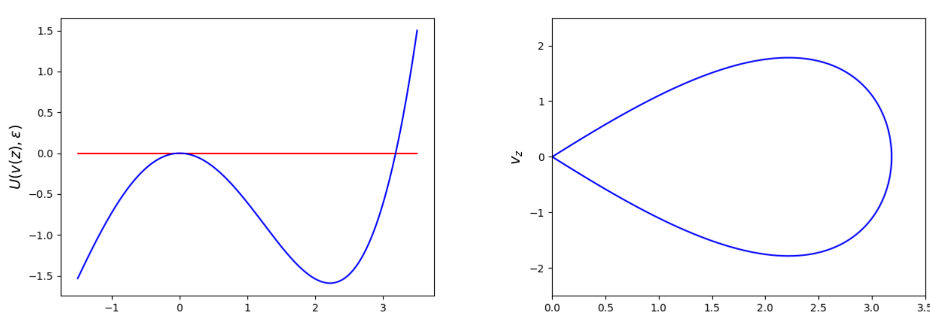

Figure 3.8: $\gamma = 3$. Potential $U(v(z),\epsilon)$ (in blue) with the level 0 of the energy (in red) and the homoclinic orbit emanating from $(v, v_z) = (0, 0)$

3.2.3 Perturbations

Let $\gamma = 2$ or 3. Consider the initial value problems

$$\begin{aligned} v_{zz} &= -a[(1-\epsilon)v+\beta]^\gamma(\beta-\epsilon v)+\lambda v+c\beta[\delta_1(\epsilon)-2v]-\epsilon c[\delta_1(\epsilon)-2v]v-\epsilon c\delta_2(\epsilon)v_z \\ &=: f^0(v,z)+\delta_1(\epsilon)f^{1,1}(v,z,\epsilon)+\delta_2(\epsilon)f^{1,2}(v,z,\epsilon), \\ \mathbf{v}(0) &= \mathbf{a} \end{aligned}$$

and

$$\begin{aligned} w_{zz} &= -a\beta(w+\beta)^\gamma+\lambda w-2c\beta w = f^0(w,z), \\ \mathbf{w}(0) &= \mathbf{a}, \end{aligned}$$

where $\mathbf{a} = (a_1, a_2) = (a_1, 0)$ is a point in the phase space whose v_z-coordinate is 0. We are interested in the behavior of solutions of the perturbed and the limiting systems. We claim that the solutions of the limiting system are asymptotic approximations of those of the perturbed system (3.5). That is, we have

$$\mathbf{v}(z) - \mathbf{w}(z) = \mathcal{O}(\delta(\epsilon))$$

on the time scale 1. We proceed as in [3].

We write the differential equations as integral equations

$$\begin{aligned} \mathbf{v}(z) &= \mathbf{a} + \int_0^z f^0(v(\tilde{z}),\tilde{z})+\delta_1(\epsilon)f^{1,1}(v(\tilde{z}),\tilde{z},\epsilon)+\delta_2(\epsilon)f^{1,2}(v(\tilde{z}),\tilde{z},\epsilon)d\tilde{z}, \\ \mathbf{w}(z) &= \mathbf{a} + \int_0^z f^0(w(\tilde{z}),\tilde{z})d\tilde{z}. \end{aligned}$$

Subtracting the equations and taking the norm of the difference we have

$$\begin{aligned} &\|\mathbf{v}(z)-\mathbf{w}(z)\| \\ &= \left\|\int_0^z f^0(v(\tilde{z}),\tilde{z})-f^0(w(\tilde{z}),\tilde{z})+\delta_1(\epsilon)f^{1,1}(v(\tilde{z}),\tilde{z},\epsilon)+\delta_2(\epsilon)f^{1,2}(v(\tilde{z}),\tilde{z},\epsilon)d\tilde{z}\right\| \\ &\le \int_0^z \|f^0(v(\tilde{z}),\tilde{z})-f^0(w(\tilde{z}),\tilde{z})\|d\tilde{z} \\ &\qquad + \delta_1(\epsilon)\int_0^z \|f^{1,1}(v(\tilde{z}),\tilde{z},\epsilon)\|d\tilde{z}+\delta_2(\epsilon)\int_0^z \|f^{1,2}(v(\tilde{z}),\tilde{z},\epsilon)\|d\tilde{z}. \end{aligned}$$

The Lipschitz continuity implies that

$$\|\mathbf{v}(z)-\mathbf{w}(z)\| \le L\int_0^z \|\mathbf{v}(\tilde{z})-\mathbf{w}(\tilde{z})\|d\tilde{z}+\delta_1(\epsilon)Mz+\delta_2(\epsilon)Nz,$$

where L, M, N are Lipshitz constants. Since $\delta_1(\epsilon) > \delta_2(\epsilon)$, we have

$$\delta_1(\epsilon)Mz+\delta_2(\epsilon)Nz \le \delta_1(\epsilon)(M+N)z.$$

We apply the following form of the Gronwall Lemma.

Lemma 3.2.1 *Suppose that, for* $z_0 \leq z \leq z_0 + T$,

$$\phi(z) \leq \delta_2(z - z_0) + \delta_1 \int_{z_0}^{z} \phi(\tilde{z}) d\tilde{z} + \delta_3,$$

where $\phi(z)$ *is continuous for* $z_0 \leq z \leq z_0 + T$ *and constants satisfy* $\delta_1 > 0, \delta_2 \geq 0, \delta_3 \geq 0$, *then*

$$\phi(z) \leq \left(\frac{\delta_2}{\delta_1} + \delta_3\right) \exp(\delta_1(z - z_0)) - \frac{\delta_2}{\delta_1},$$

for $z_0 \leq z \leq z_0 + T$.

Taking $\delta_1 = L, \delta_2 = (M + N)\delta_1(\epsilon), \delta_3 = 0$ in the Gronwall lemma, we obtain

$$\|\mathbf{v}(z) - \mathbf{w}(z)\| \leq \delta_1(\epsilon)\frac{M + N}{L} \exp(Lz) - \delta_1(\epsilon)\frac{M + N}{L}. \tag{3.6}$$

Therefore, $\mathbf{w}$ is an asymptotic approximation of $\mathbf{v}$ with error $\delta_1(\epsilon)$ if Lz is bounded by a constant independent of ϵ; so the approximation is valid on the time scale 1.

Due to the time scale 1, the homoclinic orbit may get torn off, however, we only need information close to $z = 0$ because we took the change of variables $z = \epsilon^{1/2}x$. The behavior of the solutions of the perturbed system where z is close to 0 deviate only a little from those of the limiting system.

Chapter 4

Conclusion

We derived the model proposed by Suematsu et al. [4] and rescaled the system to obtain (2.1), (2.2). We considered equilibria of the system, first taking $c = 0$ and found the relation (3.3). This is related to the mass of cells and we succeeded in reducing the system to a pendulum. Then we took the slow variable $z = \epsilon^{1/2}x$ to study the dynamics. We found that, with respect to the spacial variable z, the pendulum possesses a homoclinic orbit and an equilibrium surrounded by periodic orbits. Moreover, for practical values of constants, the structure is robust under small change in ϵ, which is the ratio of the diffusion rates.

Due to the Neumann boundary conditions, we are only interested in solutions that lie on the v-axis at the beginning and the end of the spacial variable z.

We considered the effect of the nonlocal term and found that the effect is limited, in the sense that even though the nonlocal term changes the linear part, the resulting system is similar to the unperturbed system, and it only perturbs the orbits to follow and solutions of the perturbed and limiting systems differ only at most some error (3.6). Therefore, the equilibria of the system (2.1), (2.2) are similar to those of the system without the nonlocal term but with some error.

An interpretation of the results is that density of cells at equilibria is governed by a pendulum in terms of the spacial variable z with some deviation. Specifically, some periodic orbits whose periods are relatively short seem to be biologically relevant. In other words, solutions that wind a certain number of times starting and ending on the v-axis seem to be consistent with the phenomenon seen in figure 1.2. Furthermore, the values v and v_z are slow to respond to the original spacial variable x because of the factor $\epsilon^{1/2}$, and the nonlocal term becomes subtle as the integral is over an interval of finite length, which becomes short.

Thus the dynamics of equilibria of the system (2.1), (2.2) is governed by a relatively simple mechanism with some error originated from the nonlocal term whose influence is limited due to compression of the spacial variable.

Appendix A

Melnikov's Method

In this thesis, we have dealt with the dynamics of equilibria of the system (2.1) and (2.2). Biologically, the solutions of the system cannot know whether the underlying perturbed system has the homoclinic orbit because the solutions traverse only the beginning of the orbits of the underlying system. Mathematically, however, it is interesting to investigate what kind of perturbations could destroy the homoclinic orbit of the underlying system. To discuss whether the stable and unstable manifolds get torn off, we may use the Melnikov's method [2]. We consider the case of $\gamma = 2$ and some simplified perturbation terms. We have a pendulum equation

$$\begin{aligned}\begin{pmatrix} v \\ v_z \end{pmatrix}_z &= \begin{pmatrix} v_z \\ \epsilon(1-\epsilon)^2 a v^3 + (-1+4\epsilon-3\epsilon^2)a\beta v^2 + (\lambda - 2a\beta^2 + 3\epsilon a\beta^2 - 2c\beta)v - a\beta^3 \end{pmatrix} \\ &=: \begin{pmatrix} f_1(v) \\ f_2(v) \end{pmatrix}\end{aligned}$$

and consider perturbations by

$$\epsilon \begin{pmatrix} g_1(v, v_z, c) \\ g_2(v, v_z, c) \end{pmatrix}.$$

Since we are primarily interested in a specific perturbation (3.5), we assume that $g_1(v, v_z, c) = 0$. Concerning the unperturbed system, let us denote the homoclinic orbit by $\gamma_0(z)$ and the hyperbolic equilibrium by $\mathbf{v}_0$. The Melnikov function is then defined by

$$M(c) := \int_{-\infty}^{\infty} f(\gamma_0(z)) \wedge g(\gamma_0(z), c)dz = \int_{-\infty}^{\infty} f_1(\gamma_0(z))g_2(\gamma_0(z), c)dz, \tag{A.1}$$

where the wedge product is defined by $f \wedge g := f_1 g_2 - f_2 g_1$.

We simplify our perturbation term, based on the observation of the limiting case as $\epsilon \to 0$. Namely we take

$$g_2(v, v_z, z) = c(\beta + 2\epsilon v^2).$$

Here, in our perturbation term, we replaced $\delta_{1,2}(\epsilon)$ by ϵ and ignored $-\epsilon^2 v$ and $-\epsilon^2 v_z$.

As $f_1(v, v_z, z) = v_z$, we need to multiply the v_z-component of time-parametrization of the homoclinic orbit with $g_2(v(z), v_z(z), c)$ evaluated on the homoclinic orbit; and then integrate with respect to z.

Time-parametrization of the homoclinic orbit can be calculated from the level set of the Hamiltonian $H(v, v_z) = H(0, 0) = 0$ using the relation $v_z = \frac{dv}{dz}$, i.e.

$$v_z = \frac{dv}{dz} = \pm\sqrt{\frac{1}{2}[\epsilon(1-\epsilon)^2 a]v^4 + \frac{2}{3}(-1+4\epsilon-3\epsilon^2)a\beta v^3 + (\lambda - 2a\beta^2 + 3\epsilon a\beta^2)v^2 - 2a\beta^3 v}.$$

Thus we have time-parametrization of $v(z)$ by

$$\int \frac{dv}{\sqrt{\frac{1}{2}[\epsilon(1-\epsilon)^2 a]v^4 + \frac{2}{3}(-1+4\epsilon-3\epsilon^2)a\beta v^3 + (\lambda - 2a\beta^2 + 3\epsilon a\beta^2)v^2 - 2a\beta^3 v}} = \pm\int dz.$$

We have time-parametrization of $v_z(z)$ just by differentiating $v(z)$ with respect to z.

In principle, we are now able to evaluate the Melnikov function directly, even though it is difficult to compute it in our case.

An aperiodic version of the Melnikov's method says the following:

Theorem A.0.1 *Consider the perturbed planar system of the form*

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}) + \epsilon\mathbf{g}(\mathbf{x}, \mathbf{c})$$

with $\mathbf{f} \in C^1(\mathbb{R}^2)$ *and* $\mathbf{g} \in C^1(\mathbb{R}^2 \times \mathbb{R}^m)$. *Assume that* $\mathbf{f}$ *is a Hamiltonian vector field and, for* $\epsilon = 0$, *the system has a homoclinic orbit* γ_0 *through a hyperbolic saddle point* $\mathbf{v}_0$.

If there exists a $\mathbf{c} \in \mathbb{R}^m$ *such that the Melnikov function (A.1) satisfies*

$$M(\mathbf{c}_0) = 0 \quad \text{and} \quad \partial_{\mathbf{c}_1} M(\mathbf{c}_0) \neq 0,$$

then, for all sufficiently small ϵ, *there is a* $\mathbf{c}_\epsilon = \mathbf{c}_0 + \mathcal{O}(\epsilon)$ *such that the system with* $\mathbf{c} = \mathbf{c}_\epsilon$ *has a unique homoclinic orbit in an* $\mathcal{O}(\epsilon)$ *neighborhood of the homoclinic orbit. Furthermore, if* $M(\mathbf{c}_0) \neq 0$ *then for all sufficiently small* $\epsilon \neq 0$ *and* $|\mathbf{c} - \mathbf{c}_0|$ *the system has no separatrix cycle in an* $\mathcal{O}(\epsilon)$ *neighborhood of* $\gamma_0 \cup \{\mathbf{v}_0\}$.

In our case, $M(\mathbf{c}_0) = 0$ is satisfied with $\mathbf{c}_0 = c = 0$. However,

$$\partial_{\mathbf{c}_1} M(\mathbf{c}_0) = \int_{-\infty}^{\infty} v_z[\beta + 2\epsilon v^2]dz = 0,$$

due to symmetry of the homoclinic orbit. In other words, the homoclinic orbit $\gamma_0 = (v(z), v_z(z))$ lies in the right half-plane and line-symmetric with respect to the v-axis.

Thus this theorem does not immediately imply anything; the homoclinic orbit may or may not be destroyed by perturbations. It is interesting to investigate further to clarify which perturbation terms destroy or preserve the homoclinic orbit and this work is on progress.

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Eidesstattliche Erklärung

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Datum Unterschrift

Errata

This thesis was submitted on May 11, 2017. As of May 16, 2017, the author is aware of the following typographical errors:

- **Page 11, line 18:** (original) provided $\lambda - 2a\beta^2 + 3\epsilon a\beta^2 \neq 0$
  (correction) provided $\lambda - 2a\beta^2 + 3\epsilon a\beta^2 > 0$
- **Page 13, line 12:** (original) Provided $\lambda - 2a\beta^2 + 3\epsilon a\beta^2 = 0$
  (correction) Provided $\lambda - 2a\beta^2 + 3\epsilon a\beta^2 > 0$
- **Page 13, line 15:** (original) nonzero eigenvalues
  (correction) eigenvalues with nonzero real part
- **Page 15, line 12:** (original) provided that $\lambda - 3a\beta^3 + 4a\beta^3\epsilon \neq 0$
  (correction) provided that $\lambda - 3a\beta^3 + 4a\beta^3\epsilon > 0$
- **Page 17, line 4:** (original) $\lambda - 2a\beta^2 + 3\epsilon a\beta^2 \neq 0$
  (correction) $\lambda - 2a\beta^2 + 3\epsilon a\beta^2 > 0$
- **Page 17, line 4:** (original) $\lambda - 3a\beta^3 + 4a\beta^3\epsilon \neq 0$
  (correction) $\lambda - 3a\beta^3 + 4a\beta^3\epsilon > 0$