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RESEARCH ARTICLE PHYSICAL SCIENCE

AN ANALYSIS OF MODES IN A CARICATURE OF A MODEL FOR MORPHOGENESIS

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Abstract: In this paper, we have investigated a simple one-dimensional caricature model proposed by Maini *et al*. (1988) for cell pattern formation. In our analysis the model exhibits the similar linear behavior of complex model proposed by Nagorika *et al*. (1987). We also present a nonlinear analysis that gives the possibility of superposition of modes subject to parameter values and initial conditions.

Key words: Landau equation, morphogenesis, stability, unstability

Introduction

Cell pattern formation has been a long history in mathematical biology. Several models have been proposed for cell pattern formation Oster *et al*. (1983, 1984, 1985), Britton (1988). In the early stage of embryo it is considered that spatial pattern forms in cells density. This can occur in several ways. Cell can move in response to gradients in certain chemicals and many researchers showed that such chemical interactions can lead to spatial pattern formation (Segel, 1971; Maini *et al.,* 1988). Cells can also respond to mechanical cases, such as movement in response to adjective forces exerted by cells on a common substratum, or due to movement up gradients in adhesive activity. Oester *et al*. (1983) first proposed a model interpreting these ideas. These models are mathematically complex and their primary analysis got high influenced from linearization and numerical simulation. It is a formidable task if one wish to analysis fully the nonlinear system. However, recently some analysis of simple models has been revealed. It is predicted from linear theory that the same result can be achieved as non-linear cases in particular domain. In this paper we analyzed the caricature model proposed by Maini (1989) for morphogenesis. This is now a common phenomena to set a simple model for studying a more complex model. This simple one-dimensional caricature model gives the similar prediction to the models proposed by Nagorcka *et al*. (1987). We also analyzed the full model for a certain set of initial conditions.

Model and Linear Analysis

In our caricature model we choose the model of the form $Lu = -u^p$

Where,

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$$\left.\begin{aligned} Lu &= \frac{\partial u}{\partial t} + Du - \lambda u \\ Du &= \left(\frac{\partial^2}{\partial x^2} + \alpha^2\right)^2 \left(\frac{\partial^2}{\partial x^2} + \beta^2\right)^2 \end{aligned}\right\} \tag{2.1}$$

Where, x and t are space and time respectively, $u = u(x,t)$, α, β and λ are real numbers and p is an integer greater than 1. For the sake of simplicity of analysis the right hand side of (2.1) has been taken the simplest type of non-linearity.

For steady and uniformity, we have $\frac{\partial u}{\partial t} = 0$ and $\frac{\partial u}{\partial x} = 0$ respectively. On simplifying, (2.1) becomes

$$(\alpha^4 \beta^4 - \lambda)u = -u^p$$

This implies

$$u = 0 \text{ and } u = (\lambda - \alpha^4 \beta^4)^{\frac{1}{p-1}} \tag{2.2}$$

To analyse the stability of zero steady state we consider a little perturbation from zero. In which nonlinear terms are neglected. Let

$$u = \overline{u}(x,t)\,,\ |\overline{u}(x,t)| < \varepsilon$$

Substituting this into (2.1), we have the linearized equation

$$\frac{\partial \overline{u}}{\partial t} + D\overline{u} - \lambda \overline{u} = 0 \tag{2.3}$$

and we are seeking a solution of the form

$$\overline{u} \propto e^{\partial\delta + ikx} \text{ or } \overline{u} = c\, e^{\delta t + ikx}$$

where c is a constant of proportionality. Now differentiating $\overline{u}$ partially with respect to t, putting them into (2.3) and after simplification, we get the relation

$$\sigma(k^2) = \lambda - (k^2 - \alpha^2)^2 (k^2 - \beta^2)^2 \tag{2.4}$$

This is shown in the Fig. 1.

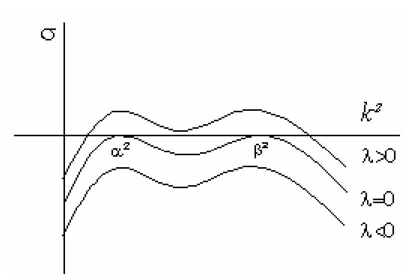

Fig. 1. Sketch of the relation (2.4) for different λ.

It is evident from the figure that λ plays an important role of the bifurcation parameter. The value of the $\lambda = 0$ is the bifurcation value in this case. When $\lambda < 0$, $\sigma(k^2) < 0 \,\forall k^2$. This implies that all perturbations die out exponentially in time and the uniform steady state $u = 0$ is marginally stable. If $\lambda > 0$, then $\sigma(k^2) > 0 \,\forall k^2$ for two sets of wave numbers, one in the neighbourhood of α, the other in the neighbourhood of β. Linear analysis predicts that these wave numbers will grow unboundedly.

The Weakly Nonlinear Case

Now we discuss the nonlinear analysis of the model. For simplicity we restrict ourselves to the case of cubic nonlinearity, that is $p = 3$ in (2.1). Thus we consider the problem

$$Lu = -u^3, \; x \in (0, 1) \tag{3.1}$$

With $\dfrac{\partial^n u}{\partial x^n}(0, t) = \dfrac{\partial^n u}{\partial x^n}(1, t) = 0 \quad \forall t, n = 1,3,5,7$

To analyse the weakly nonlinear case we assume λ to be very close to its bifurcation value of 0 and use a multi-time scale perturbation procedure. We introduce a long time scale T to find the asymptotic solution of (3.1). For that we set

$$\lambda = \varepsilon^2, \quad T = \varepsilon^2 t, \quad u(x,t,T) = \sum_{i=1} \varepsilon^i u_i(x,t,T) \tag{3.2}$$

where $0 < \varepsilon << 1$.

We know that

$$\frac{d}{dt} = \frac{\partial}{\partial T}\frac{\partial T}{\partial t} + \frac{\partial}{\partial t}$$
$$= \varepsilon^2 \frac{\partial}{\partial T} + \frac{\partial}{\partial t}$$

Now (3.1) becomes

$$\left(\varepsilon^2 \frac{\partial}{\partial T} + \frac{\partial}{\partial t}\right)u + Du - \varepsilon^2 = -u^3$$

$$\Rightarrow - \quad \varepsilon^2 \left(1 - \frac{\partial}{\partial T}\right)u + \frac{\partial u}{\partial t} + Du = -u^3$$

$$\Rightarrow L_0 u = \quad \varepsilon^2 \left(1 - \frac{\partial}{\partial T}\right)u - u^3$$

$$\Rightarrow L_0(\varepsilon u_1 + \varepsilon^2 u_2 + \varepsilon^3 u_3 + \dots\dots) = \quad \varepsilon^2 \left(1 - \frac{\partial}{\partial T}\right)(\varepsilon u_1 + \varepsilon^2 u_2 + \varepsilon^3 u_3 + \dots\dots) - (\varepsilon u_1 + \varepsilon^2 u_2 + \varepsilon^3 u_3 + \dots\dots)^3 \tag{3.3}$$

Where $L_0 u = \dfrac{\partial u}{\partial t} + Du$

Equating the coefficients of powers of ε of (3.3), we get

$$L_0 u_1 = 0 \tag{3.4}$$

with the boundary conditions,

$$\frac{\partial^n u_1}{\partial x^n}(0,\ t, T) = \frac{\partial^n u}{\partial x^n}(1,\ t, T) = 0 \qquad n = 1, 3, 5, 7$$

The solution of this equation can be considered as

$$u_1(x, T) = A(T)\cos\alpha x + B(T)\cos\beta x \tag{3.5}$$

where $A(T)$ and $B(T)$ are functions of T to be determined. The $O(\varepsilon^2)$ gives the similar expression for $u_2(x,\ T)$. That is,

$$L_0 u_2 = 0$$

The $O(\varepsilon^3)$ gives following expression,

$$L_0 u_3 = u_1 - u_1^3 - \frac{\partial u_1}{\partial T} \tag{3.6}$$

using (3.5) in (3.6), we get the relation as-

$$\begin{aligned} L_0 u_3 = {} & \left(A - \frac{3}{4}A^3 - \frac{3}{2}AB^2 - \frac{dA}{dT} \right)\cos\alpha x + \left(B - \frac{3}{4}B^3 - \frac{3}{2}A^2 B - \frac{dB}{dT} \right)\cos\beta x + \\ & \frac{1}{4}A^3\cos 3\alpha x - \frac{3}{4}A^2 B\left[\cos(2\alpha+\beta)x + \cos(2\alpha-\beta)x\right] \\ & + \frac{1}{4}B^3\cos 3\beta x - \frac{3}{4}AB^2\left[\cos(\alpha+2\beta)x + \cos(\alpha-2\beta)x\right] \end{aligned} \tag{3.7}$$

In this case the secular term arises when $\beta = 3\alpha$. Thus, we consider two cases $\beta \neq 3\alpha$, $\beta = 3\alpha$

Case I: $\beta \neq 3\alpha$. In this case, the equations are

$$\begin{aligned} \frac{dA}{dT} &= A - \frac{3}{4}A^3 - \frac{3}{2}AB^2 \\ \frac{dB}{dT} &= B - \frac{3}{4}B^3 - \frac{3}{2}A^2 B \end{aligned} \tag{3.8}$$

The above system of equations has the steady states $(0,\ 0)$, $(0,\ \pm 2/\sqrt{3})$, $(\pm\frac{2}{3},\ \mu\,\frac{2}{3})$, $(\pm 2/\sqrt{3},\ 0)$ and $(\pm\frac{2}{3},\ \pm\frac{2}{3})$. The stability of these steady states is easily determined and it is found that $(0,\ 0)$ is an unstable node, $(\pm\frac{2}{3},\ \mu\,\frac{2}{3})$ and $(\pm\frac{2}{3},\ \pm\frac{2}{3})$ are unstable saddle points and $(\pm 2/\sqrt{3},\ 0)$ and $(0,\ \pm 2/\sqrt{3})$ are stable nodes. The solution of $u_1(x)$ when $T \to \infty$ will be one of the forms

$$u_1(x) = \pm\frac{2}{\sqrt{3}}\cos\alpha x \quad or \quad u_1(x) = \pm\frac{2}{\sqrt{3}}\cos\beta x \tag{3.9}$$

Case II: $\beta = 3\alpha$. In this case the equations are

$$\frac{dA}{dT} = A - \frac{3}{4}A^3 - \frac{3}{2}AB^2 - \frac{3}{4}A^2B$$
$$\frac{dB}{dT} = B - \frac{3}{4}B^3 - \frac{3}{2}A^2B - \frac{1}{4}A^3 \tag{3.10}$$

The steady states of the above system are $(0,\ 0)$, $(0,\ \pm 2/\sqrt{3})$, $(\pm 0.572, \mp 0.866)$, $(\pm 0.66,\ \mp 0.524)$ and $(\pm 1.233,\ \mp 0.342)$. Among the steady states (0,0) is an unstable node, $(0,\ \pm 2/\sqrt{3})$ and $(\pm 1.233,\ \mp 0.342)$ are stable nodes and $(\pm 0.572, \mp 0.866)$, $(\pm 0.66,\ \mp 0.524)$ are unstable saddle points. The possible solutions, in this case, for $u_1(x)$ when $T \to \infty$ are

$$u_1(x) = \pm \frac{2}{\sqrt{3}} \cos \alpha x \quad \text{or} \quad u_1(x) = \pm 1.233 \cos \alpha x \pm 0.342 \cos 3\alpha x \tag{3.11}$$

We complete this section by considering $O(\varepsilon^4)$ of (3.3). In this case we have

$$L_0 u_4 = u_2 - \frac{\partial u_2}{\partial T} - 3u_1^2 u_2 \tag{3.12}$$

Proceeding as in (3.6), we have also two cases here, $\beta \neq 3\alpha$, $\beta = 3\alpha$.

Case I: $\beta \neq 3\alpha$. In this case, the equations of (3.12) are

$$\frac{dA}{dT} = A - \frac{3}{4}A^3 - \frac{3}{2}AB^2$$
$$\frac{dB}{dT} = B - \frac{3}{4}B^3 - \frac{3}{2}A^2B \tag{3.13}$$

The steady states of the system are $(0,\ 0)$, $(0,\ \pm \frac{2}{3})$, $(\pm \frac{2}{3},\ 0)$, $(\pm 0.3849,\ \pm 0.3849)$, $(\pm 0.3849,\ \mp 0.3849)$. Among these $(0,\ 0)$ is an unstable node, $(0,\ \pm \frac{2}{3})$, $(\pm \frac{2}{3},\ 0)$ are stable nodes and $(\pm 0.3849,\ \pm 0.3849)$, $(\pm 0.3849,\ \mp 0.3849)$ are unstable saddle points. The phase portrait of (3.13) is given in Fig. 2. The solutions of $u_1(x)$, for this case, when $T \to \infty$ are

$$u_1(x) = \pm \tfrac{2}{3} \cos 3\alpha, \quad \text{and} \quad u_2(x) = \pm \tfrac{2}{3} \cos \alpha$$

Case II: $\beta = 3\alpha$. In this case the equations are

$$\frac{dA}{dT} = A - \frac{9}{4}A^3 - \frac{9}{2}AB^2 - \frac{9}{4}A^2B$$
$$\frac{dB}{dT} = B - \frac{9}{4}B^3 - \frac{9}{2}A^2B - \frac{3}{4}A^3 \tag{3.14}$$

Here the steady states of this system are (0, 0), $(0,\ \pm 0.667)$ and $(\pm 0.712,\ \mp 0.198)$ are stable nodes; and $(\pm 0.382,\ \pm 0.303)$ and $(\pm 0.330,\ \mp 0.500)$ are unstable saddle points.

The phase portrait of (3.14) is shown in Fig. 3. The solutions of $u_1(x)$, for this case, when $T \to \infty$ are

$$u_1(x) = \pm 0.667 \cos 3\alpha, \quad \text{and} \quad u_2(x) = \pm 0.712 \cos \alpha \pm 0.198 \cos 3\alpha$$

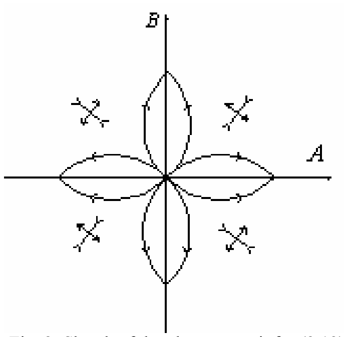

Fig. 2: Sketch of the phase portrait for (3.13)

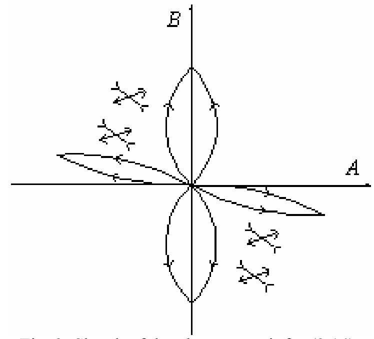

Fig. 3: Sketch of the phase portrait for (3.14).

Discussion

In this paper, we attempted to gain some insight into the expected behavior of the system that there is a special relation between the two unstable wave numbers, which would give rise to extra secular terms. We have also analyzed a simple caricature model, giving rise to similar linear behavior. To simplify our analysis, we restricted our attention to the case of a cubic non-linearity and to periodic spatial disturbance.

From the non-linear analysis of this model we found that it is possible to get superposition of modes, depending on initial conditions and the relationship between the unstable modes. We see that superposition of modes occurs only in the special case that is for special initial conditions. This caricature model does not capture all the behavior of the full system, but enables analysis of certain cases, which are formidable in the full system.

Conclusion

In analysis of this paper we conclude that it is possible to get superposition of modes, depending on initial conditions and the relationship between the unstable modes. This analysis also suggests that superposition of modes occurs only in special cases. Hence, the caricature model does not occupy all the behaviours of full system but enables analysis certain cases only.

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