Nonlinear Analysis: Real World Applications 22 (2015) 155–175

Contents lists available at ScienceDirect

Nonlinear Analysis: Real World Applications

journal homepage: www.elsevier.com/locate/nonrwa

Steady state bifurcations for a glycolysis model in biochemical reaction☆

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ARTICLE INFO

Article history:
Received 29 July 2012
Received in revised form 18 August 2014
Accepted 20 August 2014
Available online 15 September 2014

Keywords:
Glycolysis model
Turing's instability
Steady state solutions
Lyapunov–Schmidt procedure
Normal form

ABSTRACT

In this paper, a two-species glycolysis model is investigated in which one species is substrate and the other is activator. A linear stability analysis shows that there is a critical value for the diffusion rate of the substrate above which the constant steady state solution is of Turing's instability. Next, the steady state bifurcations are analyzed not only from a simple eigenvalue, but more difficultly, from a double one. The theoretical results are confirmed by numerical simulations. Our main methods are based on bifurcation theory, Lyapunov–Schmidt technique and singularity theory.

1. Introduction

In 1952, Alan Turing [1] proposed the famous reaction–diffusion system to model biological pattern formation and suggested that instability is driven by diffusion, i.e. the well-known Turing instability. Since then, a great deal of research has been devoted to the study of Turing instability in chemical and biological contexts. About forty years after Turing's paper, his predictions were observed by chemical experiments [2,3]. So far, diffusion driven instability as a mechanism for pattern formation has been extensively used in studying various specific problems in many fields. More information of Turing's instability can be found in [4–6]. Here we consider a glycolysis model in biochemical reaction in which bifurcation can occur after the Turing's instability, with the goal of revealing the existence of the non-constant positive steady state solutions.

Glycolysis, which occurs in the cytosol, is thought to be the archetype of a universal metabolic pathway for cellular energy requirement. The wide occurrence of glycolysis indicates that it is one of the most ancient known metabolic pathways and a common way of providing limited energy for the organism in living nature. However, its significance lies in that it can supply the energy with a rapid speed, but more importantly under oxygen free conditions such as strenuous exercise and high altitude hypoxia. Glycolysis model turns out to be a classic and representative system in biochemical reaction. All glycolysis models are based on the same reaction scheme. The difference between the models stems from the difference in the mechanism for key enzyme reaction. The first model of glycolysis was proposed by Higgins [7], and then studied by Bhargava [8] and Peng et al. [9]. The second model was presented by Sel'kov [10] and further analyzed in [11–13]. The reaction mechanisms and the positive steady states for these two models are showed in the corresponding papers above.

☆ The work is supported by the National Natural Science Foundation of China (No. 11271236), the Fundamental Research Funds for the Central Universities (GK201401004) and the Foundations of Shaanxi Educational Committee (No. 14JK1862).

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http://dx.doi.org/10.1016/j.nonrwa.2014.08.003
1468-1218/

In the present paper, we deal with the positive steady state solutions of the following glycolysis system

$$\begin{aligned} \frac{\partial U}{\partial t} &= d_1 \frac{\partial^2 U}{\partial \xi^2} + \delta - kU - UV^2, \quad \xi \in (0, l),\ t > 0, \\ \frac{\partial V}{\partial t} &= d_2 \frac{\partial^2 V}{\partial \xi^2} + kU - V + UV^2, \quad \xi \in (0, l),\ t > 0, \end{aligned} \tag{1.1}$$

subject to the boundary conditions

$$U = \frac{\delta}{k + \delta^2}, \qquad V = \delta, \quad \text{at } \xi = 0, l,\ t > 0, \tag{1.2}$$

and the initial conditions

$$U(\xi, 0) = U_0(\xi) \geq 0, \qquad V(\xi, 0) = V_0(\xi) \geq 0, \quad \xi \in (0, l). \tag{1.3}$$

Here U and V represent chemical concentrations, d_1 and d_2 are diffusion coefficients, δ is the dimensionless input flux, and k is the dimensionless rate constant for the low activity state. The reaction mechanism of model (1.1) and the generic class of models to which (1.1) belongs are given in [14–16]. Concerning this model for a two cell system, there are some stability results (see [14,17]). For $k = 0$, the model with homogeneous Neumann boundary condition was studied in [10–13] which illustrated the existence of the steady state solutions. To our knowledge, there is few research on the model (1.1). Throughout this paper we assume that all constants d_1, d_2, δ and k are positive and $0 < k < 1/8$ which is the range of rational experiment data.

The main purpose of this paper is to study the bifurcation from the constant positive steady states of (1.1)–(1.3). From the neutral curve we shall describe, the bifurcation may be from either a simple eigenvalue or a double eigenvalue. The emphasis of this paper is mainly placed in the discussion of the latter case, and the related results are given in Section 4. Our major attempt is to deal with the difficulty in the application of Lyapunov–Schmidt reduction and singularity theory for the case of double bifurcation.

To facilitate the analysis, we introduce the incremental variables

$$u = U - \frac{\delta}{k + \delta^2}, \qquad v = V - \delta.$$

Then (1.1) and (1.2) can be transformed into

$$\frac{\partial}{\partial t}\begin{pmatrix} u \\ v \end{pmatrix} = L\begin{pmatrix} u \\ v \end{pmatrix} + N(u, v), \quad \xi \in (0, l),\ t > 0 \tag{1.4}$$

and

$$u = 0, \qquad v = 0, \quad \text{at } \xi = 0, l,\ t > 0, \tag{1.5}$$

respectively, where the linear part

$$L\begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} d_1 \dfrac{\partial^2}{\partial \xi^2} & 0 \\ 0 & d_2 \dfrac{\partial^2}{\partial \xi^2} \end{pmatrix}\begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} -k - \delta^2 & -\dfrac{2\delta^2}{k + \delta^2} \\ k + \delta^2 & \dfrac{\delta^2 - k}{k + \delta^2} \end{pmatrix}\begin{pmatrix} u \\ v \end{pmatrix}$$

and the nonlinear part

$$N(u, v) = \left(\frac{\delta}{k + \delta^2} v^2 + 2\delta uv + uv^2\right)\begin{pmatrix} -1 \\ 1 \end{pmatrix}.$$

For the sake of simplicity, we denote

$$f_0 = -k - \delta^2 < 0, \qquad f_1 = -\frac{2\delta^2}{k + \delta^2} < 0, \qquad g_0 = k + \delta^2 > 0, \qquad g_1 = \frac{\delta^2 - k}{k + \delta^2} < 1,$$

which show that the model (1.4) is an activator–substrate system whenever $\delta^2 > k$. That is, u is substrate which is consumed by activator v. Afterwards, we always assume $\delta^2 > k$.

The rest of the present paper is organized as follows. In Section 2, we study the Turing's instability of the constant steady state solution, which plays an important role in the later bifurcation analysis. In Section 3, we investigate the global bifurcation from a simple eigenvalue which is summarized in Theorem 3.2 and implies the existence of non-constant positive steady state solutions for d_1, suitably large. In Section 4, we illustrate the local bifurcation from a double eigenvalue. This is the central part of this paper. In this case, the Crandall–Rabinowitz theorem can no longer be applied, and we give conditions for the bifurcation structure in Theorem 4.1 throughout Theorem 4.6 by use of Lyapunov–Schmidt procedure and singularity theory. Finally in Section 5, numerical simulations are done to confirm the analytic results.