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Global attractivity of equilibrium in Gierer–Meinhardt system with activator production saturation and gene expression time delays☆

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ABSTRACT

In this work we investigate a diffusive Gierer–Meinhardt system with gene expression time delays in the production of activators and inhibitors, and also a saturation in the activator production, which was proposed by Seirin Lee et al. (2010) [10]. We rigorously consider the basic kinetic dynamics of the Gierer–Meinhardt system with saturation. By using an upper and lower solution method, we show that when the saturation effect is strong, the unique constant steady state solution is globally attractive despite the time delays. This result limits the parameter space for which spatiotemporal pattern formation is possible.

1. Introduction

Since the pioneering work of Turing [1], Reaction–Diffusion systems have been used to demonstrate morphogenetic pattern formation [2–7]. During the process of cell division and differentiation, gene expressions control the establishment of stable patterns of differentiated cell types. Recent experimental studies have shown that timing of the pattern-forming events may have important implications in the development of the patterns [8,9,4,5,10,11]. In particular, there exists a considerable delay between the start of protein signal transduction (ligand–receptor binding) and the result (a gene production) via gene expression regulations [10].

In 1972, Gierer and Meinhardt [12] proposed a nonlinear reaction–diffusion model to describe the interaction dynamics of two chemical substances: (see [12, Eq. (12)])

$$\begin{cases} \dfrac{\partial a}{\partial t} = \rho_0 \ell_a + c\ell_a \dfrac{a^p}{h^q} - \nu_a a + D_a \dfrac{\partial^2 a}{\partial x^2}, \\ \dfrac{\partial h}{\partial t} = c'\ell_h \dfrac{a^r}{h^s} - \nu_h h + D_h \dfrac{\partial^2 h}{\partial x^2}, \end{cases} \tag{1.1}$$

where $a(x, t)$ and $h(x, t)$ are the concentrations of the activator and the inhibitor respectively; the reactions of activators and inhibitors are assumed to be power functions of a and h, and at the same time both substances are removed at a linear rate; the activator a and the inhibitor h diffuse in the environment with diffusion constant D_a and D_h respectively, and it is assumed that h diffuses faster than a; finally a constant source term for a initiates the whole reaction. Here ℓ_a, ρ_0, ℓ_h, c, ν_a, c', ν_h are all positive constant parameters, and the exponents p, q, r, s are all nonnegative. One of particular examples of exponents

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they considered was $q = 1, s = 0$, and $p = r = 2$. That is, two molecules of activator are necessary to activate, and one molecule of inhibitor is needed for inhibit; and the activators activate both substances and the inhibitors only inhibit the activator source.

On the other hand, by assuming a saturation of activator production for the case $q = 1, s = 0$, and $p = r = 2$ in (1.1), Gierer and Meinhardt [12] also considered (see [12, Eq. (16)])

$$\begin{cases} \dfrac{\partial a}{\partial t} = \rho_0 \ell_a + c\ell_a \dfrac{a^2}{(1+\kappa a^2)h} - \nu_a a + D_a \dfrac{\partial^2 a}{\partial x^2}, \\ \dfrac{\partial h}{\partial t} = c'\ell_h a^2 - \nu_h h + D_h \dfrac{\partial^2 h}{\partial x^2}. \end{cases} \tag{1.2}$$

For system (1.2), the activator concentration is limited to a maximum value so that the activated area forms an approximately constant proportion of the total structure size. Numerical simulation of concentration patterns were obtained in [12] as well as [13,14] for one and two-dimensional spatial domains.

Since then, the Gierer–Meinhardt system has been regarded as one of the prototype reaction–diffusion models of spatiotemporal pattern formation [15,16], and extensive research has been done for a more general Gierer–Meinhardt system in the form of (with $\kappa = 0$ or $\kappa > 0$)

$$\begin{cases} \dfrac{\partial u}{\partial t} = \epsilon^2 \Delta u - u + \rho_a \dfrac{u^p}{(1+\kappa u^p)v^q} + \sigma_a, & x \in \Omega,\ t > 0, \\ \tau \dfrac{\partial v}{\partial t} = D\Delta v - v + \rho_h \dfrac{u^r}{v^s} + \sigma_h, & x \in \Omega,\ t > 0, \\ \dfrac{\partial u(x,t)}{\partial \nu} = \dfrac{\partial v(x,t)}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x) > 0, \quad v(x,0) = v_0(x) > 0, & x \in \Omega. \end{cases} \tag{1.3}$$

Here, Ω is a bounded smooth region in $\mathbb{R}^n$, $n \geq 1$ and the Laplace operator $\Delta w(x,t) = \sum_{i=1}^n \frac{\partial^2 w(x,t)}{\partial x_i^2}$ for $w = u, v$ shows the diffusion effect; $\frac{\partial w(x,t)}{\partial \nu}$ is the outer normal derivative of $w = u, v$, and a no-flux boundary condition is imposed; the coefficients ϵ, τ and D are positive constants, whereas κ is a nonnegative constant; the basic production terms $\sigma_a = \sigma_a(x)$, $\sigma_h = \sigma_h(x)$ are nonnegative, and the interaction coefficients $\rho_a = \rho_a(x)$, $\rho_h = \rho_h(x)$ are positive over $\overline{\Omega}$. Up to now, there are many research results on the nonhomogeneous steady state solutions (such as multi-peak steady state solutions, etc.) of the Gierer–Meinhardt system (1.1), (see Refs. [17–25]) and the Gierer–Meinhardt system with saturation (1.2), (see Refs. [26–29]), and the *a priori* estimates, global existence and asymptotic behavior of the solution [30–35].

In this paper we assume that σ_a, ρ_a and ρ_h are positive constants, the basic production term $\sigma_h(x) \equiv 0$, and the saturation parameter κ is a positive constant. Then system (1.3) becomes:

$$\begin{cases} \dfrac{\partial u}{\partial t} = \epsilon^2 \Delta u - u + \rho_a \dfrac{u^p}{(1+\kappa u^p)v^q} + \sigma_a, & x \in \Omega,\ t > 0, \\ \tau \dfrac{\partial v}{\partial t} = D\Delta v - v + \rho_h \dfrac{u^r}{v^s}, & x \in \Omega,\ t > 0, \\ \dfrac{\partial u(x,t)}{\partial \nu} = \dfrac{\partial v(x,t)}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,0) = u_0(x) > 0, \quad v(x,0) = v_0(x) > 0, & x \in \Omega \end{cases} \tag{1.4}$$

where $\rho_a, \kappa, \sigma_a, \rho_h, \epsilon, \tau$ and D are positive constants. We show that when the saturation constant κ is large then the unique constant steady state solution is globally attractive, hence no spatiotemporal pattern is possible. In [28] assuming $p = r = 2, s = 0$ and $q = 1$, Morimoto showed that system (1.4) admits a radially symmetric steady state solution when κ is small, and the global stability proved here implies that (1.4) cannot have such radially symmetric steady state solution when κ is large.

In recent studies Gaffney and Monk [8] and Seirin Lee et al. [10] (see also [36,37]) considered the effect of gene expression time delays on morphogenesis and pattern formation. The time delays in the feedback can be caused by the signal transduction, gene transcription and mRNA translation in the process of gene expression [10]. Here we consider the Gierer–Meinhardt system with gene expression time delays and saturation of activator induced activator production as proposed in [10] (model I with saturation of activator induced activator production in [10]):

$$\begin{cases} \dfrac{\partial u}{\partial t} = D_1 \dfrac{\partial^2 u}{\partial x^2} + k_1 - k_2 u(x,t) + k_3 \dfrac{u^2(x,t-\gamma)}{(1+\kappa u^2(x,t-\gamma))v(x,t-\gamma)}, \\ \dfrac{\partial v}{\partial t} = D_2 \dfrac{\partial^2 v}{\partial x^2} + k_4 u^2(x,t-\gamma) - k_5 v(x,t), \end{cases} \tag{1.5}$$