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DYNAMICS AND PATTERNS OF AN ACTIVATOR-INHIBITOR MODEL WITH CUBIC POLYNOMIAL SOURCE

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Abstract. The dynamics of an activator-inhibitor model with general cubic polynomial source is investigated. Without diffusion, we consider the existence, stability and bifurcations of equilibria by both eigenvalue analysis and numerical methods. For the reaction-diffusion system, a Lyapunov functional is proposed to declare the global stability of constant steady states, moreover, the condition related to the activator source leading to Turing instability is obtained in the paper. In addition, taking the production rate of the activator as the bifurcation parameter, we show the decisive effect of each part in the source term on the patterns and the evolutionary process among stripes, spots and mazes. Finally, it is illustrated that weakly linear coupling in the activator-inhibitor model can cause synchronous and anti-phase patterns.

Keywords: activator-inhibitor model; cubic polynomial source; Turing pattern; global stability; weakly linear coupling

MSC 2010: 35B32, 35B35, 35B40, 92C15

1. Introduction

Turing's reaction-diffusion theory [15] in 1952 pointed out that the morphological formation of the biological patterns is generally determined by a class of chemical substances named morphogens. A stably spatial heterogeneity is eventually formed, because various morphogens are simultaneously reacted and diffused in the organism, which can lead the undifferentiated cells to be directed to redistribute and differentiate into the corresponding morphological patterns. According to the interaction

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of morphogens, Turing proposed and demonstrated that classical reaction-diffusion models can be used to describe the process of pattern formation.

Reaction-diffusion models have been applied to a variety of specific biological processes by establishing appropriate reaction items. At present, there are three kinds of typical reaction-diffusion models related to biological processes, including autocatalytic [13], activator-inhibitor [8], [12] and substrate consumption models [4].

The activator-inhibitor model is a kind of reaction-diffusion equation which is widely used to describe the pattern formation of tissue differentiation. It was proposed in 1972 by Gierer and Meinhardt in view of Turing's reaction-diffusion theory and is one of the specific models for the differentiation stage of biological development. A large number of embryonic biological phenomena indicates that the formation of the biological morphological patterns is mainly related to three crucial substances: a short-acting activator (with smaller velocity), a long-acting inhibitor (with larger velocity) and a source material that secures both morphogens above, which is a specific kind of cells in general. Finally, a pattern formation of the tissue is caused by the interaction of the three substances.

There are now numerous examples linking Gierer-Meinhardt activator-inhibitor model. J. Wang et al. [16], [20], [14], [19] gained the existence of stripes and spots in the model with several sources. In addition, the occurrence of spike clusters has also attracted some scholars' vision [17], [18]. Another significant aspect causing lots of focuses is the property of solutions for this model with different boundary conditions [9], [2]. Furthermore, regarding the pattern formation of reaction-diffusion equations, it is of a high value to consider the major effects of the strength or means of diffusion and reaction on their patterns [1], [22], [3], [21], [6].

As a result, the purpose of this paper is to study an activator-inhibitor model with the general cubic polynomial reaction term, i.e., activator owning polynomial source. In fact, the concrete differential equation corresponding with the model is as follows:

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1\nabla^2 u + a_{11}u - a_{21}v + Cu^3 + Qu^2, \\ \dfrac{\partial v}{\partial t} = d_2\nabla^2 v + a_{12}u - a_{22}v \end{cases} \tag{1.1}$$

with periodic boundary conditions, where $u = u(x, y, t)$, $v = v(x, y, t)$, $(x, y) \in \Omega = (0, 2\pi) \times (0, 2\pi)$, the activator or inhibitor sources are respectively cubic polynomial $a_{11}u + Cu^3 + Qu^2$ or linear term $a_{12}u$, a_{12}, a_{21}, a_{22} are production and degradation rates, and all the parameters are positive except for C. In detail, we discuss how the activator source affects the stability of the constant steady-state solution, bifurcations or patterns of system (1.1) or weakly linearly coupled system.

The rest of the paper is organized as follows. In Section 2, we declare the existence of constant steady states and different bifurcations for the ordinary differential equation (ODE). Specially, its bifurcation diagram and some specific solutions are demonstrated by numerical simulation. For the reaction-diffusion equation, the Lyapunov functional is constructed to prove the global stability of constant steady-state solutions in Section 3, while Turing instability will occur if the stability above is not obeyed. We focus on the interesting patterns of single or coupled activator-inhibitor systems with a square domain in the final parts (Sections 4 and 5), such as stripes, mazes as well as spots.

2. Stability and bifurcations of ODE model

In the beginning, it is vital to consider the dynamics of the model without diffusion

$$
\begin{cases} \dfrac{\mathrm{d}u}{\mathrm{d}t} = a_{11}u - a_{21}v + Cu^3 + Qu^2, \\ \dfrac{\mathrm{d}v}{\mathrm{d}t} = a_{12}u - a_{22}v. \end{cases} \tag{2.1}
$$

Set $f(u,v) = a_{11}u - a_{21}v + Cu^3 + Qu^2$ and $g(u,v) = a_{12}u - a_{22}v$ and it is obvious that the equilibria can be determined by $f(u,v) = 0$, $g(u,v) = 0$. Thus, the system has fixed point $E(u^*, v^*)$, where $u^* = v^* = 0$ or u^* satisfies

$$
Cu^2 + Qu + \frac{a_{11}a_{22} - a_{12}a_{21}}{a_{22}} = 0
$$

together with

$$
v^* = \frac{a_{12}u^*}{a_{22}}.
$$

In fact, $f(u,v) = 0$ gives an explicit function

$$
v = \frac{C}{a_{21}}u^3 + \frac{Q}{a_{21}}u^2 + \frac{a_{11}}{a_{21}}u \doteq h(u)
$$

which is a third-order polynomial. On the basis of its properties

$$
h(0) = 0, \quad h'(u) = \frac{1}{a_{21}}(3Cu^2 + 2Qu + a_{11}), \quad h'(0) = a_{11} > 0
$$

and the number of extreme points, the form of function $h(u)$ is as in the three cases in Figure 1.

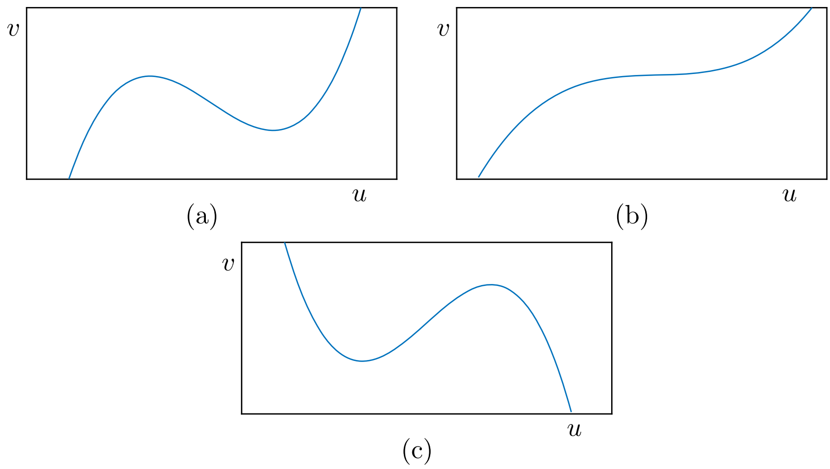


Figure 1. The possible images of explicit function $h(u)$.

It is well known that the stability of equilibrium E depends on the eigenvalues of Jaccobi matrix

$$J = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix} \Big|_{(u^*,v^*)},$$

that is, if

$$\operatorname{tr} J = (f_u + g_v)\big|_{(u^*,v^*)} < 0, \quad \det J = (f_u g_v - f_v g_u)\big|_{(u^*,v^*)} > 0,$$

then E is stable. Certainly, $f_u(u^*,v^*) = a_{21}h'(u^*)$, $f_v(u^*,v^*) = -a_{21} < 0$, $g_u(u^*,v^*) = a_{12} > 0$, $g_v(u^*,v^*) = -a_{22} < 0$. Thus, $h'(u^*) \leqslant 0$ leads to a stable equilibrium, which numerically implies that E lies at the middle part in Figure 1(a) or on the left and right in Figure 1(c). On the contrary, if $h'(u^*) > 0$, that is to say, E is at other parts, the stability needs to be further judged.

More specifically, $\operatorname{tr} J = a_{21}h'(u^*) - a_{22} < 0$, $\det J = a_{12}a_{21} - a_{22}a_{21}h'(u^*) > 0$ claims the stability of E. Similarly, the bifurcations can be discussed by $\operatorname{tr} J$ and $\det J$. We can get Theorem 2.1 about the stability of equilibria and bifurcations.

Theorem 2.1.

(1) *If $h'(u^*) < \min\{a_{22}/a_{21},\ a_{12}/a_{22}\}$, then the equilibrium $E(u^*,v^*)$ is locally asymptotically stable,*

(2) *$h'(u^*) = a_{22}/a_{21} > a_{12}/a_{22}$ brings about Hopf bifurcation at $E(u^*,v^*)$,*

(3) *$h'(u^*) = a_{12}/a_{22} \neq a_{22}/a_{21}$ leads to the bifurcation of the fixed point at $E(u^*,v^*)$,*

(4) *Bogdanov-Takens bifurcation at $E(u^*,v^*)$ occurs as $h'(u^*) = a_{22}/a_{21} = a_{12}/a_{22}$.*

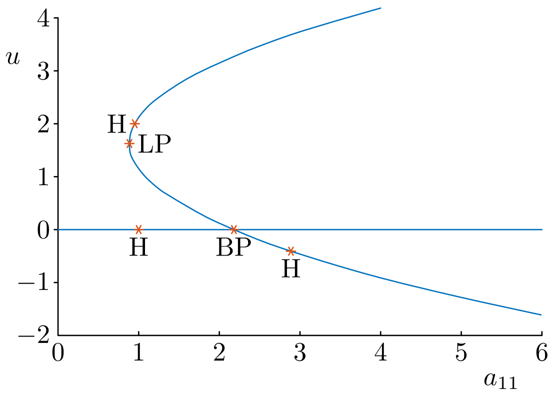


Figure 2. The bifurcation diagram for system (2.1) with parameters $a_{21} = 2$, $a_{12} = a_{22} = 1$, $C = -0.5$, $Q = 1.5$, where H, LP and BP represent Hopf, fold and branch points, respectively.

As an example, the bifurcation diagram between u and a_{11} at $a_{21} = 2$, $a_{12} = a_{22} = 1$, $C = -0.5$, $Q = 1.5$ is demonstrated in Figure 2 applying MatCont and $a_{11} = 0.9$ implies the phase plot in Figure 3.

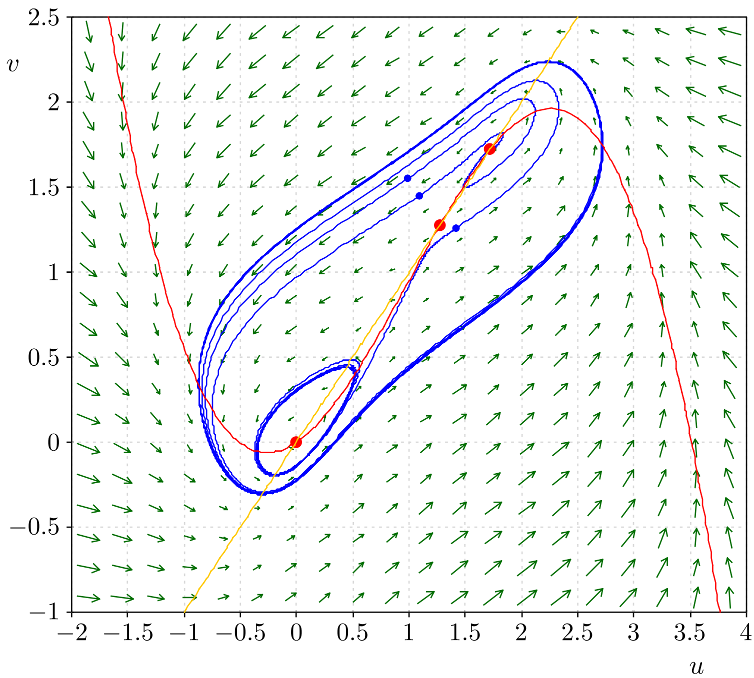


Figure 3. The phase plot at $a_{11} = 0.9$ based on parameters in Figure 2. The red and yellow curves are nullclines whose intersections are the equilibria. The outer limit cycle is stable, whereas the inner one is unstable.

In this section, we focus on global stable constant steady states and Turing instability in reaction-diffusion model.

3.1. Global stability of constant steady states. The Lyapunov functional is a powerful method to obtain the stability of infinite-dimensional dynamical systems. Therefore, mentioning the reference [7], the Lyapunov functional is constructed to prove the stability of system (1.1), which is shown in Theorem 3.1.

Theorem 3.1. *If*

$$a_{22} > \max\Big\{\frac{3Ca_{11} - Q^2}{3Ca_{21}}, a_{12}\Big\} \tag{S1}$$

is satisfied, then $E(u^*, v^*)$ *is globally asymptotically stable to system* (1.1).

P r o o f. Construct the Lyapunov functional as follows:

$$\begin{aligned} V(u(x,t), v(x,t)) = \int_\Omega \Big(&\frac{1}{2a_{21}}\Big(\frac{\partial u}{\partial t}\Big)^2 + \frac{1}{2a_{12}}\Big(\frac{\partial v}{\partial t}\Big)^2 + \frac{d_1 a_{22}}{2a_{21}}|\nabla u|^2 - \frac{d_2 a_{22}}{2a_{12}}|\nabla v|^2 \\ &- a_{22}H(u) - a_{22}uv - \frac{a_{22}^2}{2a_{12}}v^2\Big)\,\mathrm{d}x, \end{aligned} \tag{3.1}$$

where $H'(u) = h(u)$.

It is apparent that $V \to \infty$ as $\|u\|_{L^2(\Omega)}$, $\|v\|_{L^2(\Omega)}$, $\|\nabla u\|_{L^2(\Omega)}$ or $\|\nabla v\|_{L^2(\Omega)}$ goes to infinity, that is $V(u,v)$ is radially unbounded.

Next we need to check whether $V_t(u,v) \leqslant 0$ with $V_t(u,v) = 0$ only at equilibria. By calculation,

$$\begin{aligned} V_t(u,v) &= \int_\Omega \Big(\frac{1}{a_{21}}u_t u_{tt} + \frac{1}{a_{12}}v_t v_{tt} - \frac{d_1 a_{22}}{a_{21}}\Delta u u_t + \frac{d_2 a_{22}}{a_{12}}\Delta v v_t - a_{22}h(u)u_t \\ &\quad + a_{22}(uv_t + u_t v) - \frac{a_{22}^2}{a_{12}}vv_t\Big)\,\mathrm{d}x \\ &= \int_\Omega \Big(u_t\Big(h'(u)u_t + \frac{d_1}{a_{21}}\Delta u_t\Big) + v_t\Big(-\frac{a_{22}}{a_{12}} + \frac{d_2}{a_{12}}\Delta v_t\Big) - \frac{d_1 a_{22}}{a_{21}}\Delta u u_t \\ &\quad + \frac{d_2 a_{22}}{a_{12}}\Delta v v_t - a_{22}h(u)u_t + a_{22}(uv_t + u_t v) - \frac{a_{22}^2}{a_{12}}vv_t\Big)\,\mathrm{d}x \\ &= \int_\Omega \Big(-\frac{d_1}{a_{21}}|\nabla u_t|^2 + h'(u)u_t^2 - \frac{d_2}{a_{12}}|\nabla v_t|^2 - \frac{a_{22}}{a_{12}}v_t^2 \\ &\quad - a_{22}\Big(\frac{d_1}{a_{21}}\Delta u + h(u) - v\Big)u_t + \frac{a_{22}}{a_{12}}(d_2\Delta v + a_{12}u - a_{22}v)v_t\Big)\,\mathrm{d}x \\ &= -\int_\Omega \Big(\frac{d_1}{a_{21}}|\nabla u_t|^2 + \frac{d_2}{a_{12}}|\nabla v_t|^2 + (a_{22} - h'(u))u_t^2 + \Big(\frac{a_{22}}{a_{12}} - 1\Big)v_t^2\Big)\,\mathrm{d}x. \end{aligned} \tag{3.2}$$

As a result, $a_{22} > \max\{\sup_{u\in\mathbb{R}} h'(u), a_{12}\}$, i.e. $\max\{(3Ca_{11} - Q^2)/3Ca_{21}, a_{12}\}$ implies $V_t \leqslant 0$ along the orbits of system. And $V_t = 0$ if and only if $u_t^2 = v_t^2 = |\nabla u_t|^2 = |\nabla v_t|^2 = 0$, i.e. $V_t = 0$ only at equilibria. Referring to the conclusions in [5], [11], [10], the global stability of constant steady states follows. □

3.2. Turing instability of reaction-diffusion model. Next, our main objective is to investigate the variation of dynamics caused by diffusion, so it is essential to suppose (S1) in Theorem 3.1 is not satisfied.

In order to analyze Turing bifurcation of system (1.1), it is necessary to write its linearized operator corresponding to $E(u^*, v^*)$

$$L := \begin{pmatrix} d_1\Big(\dfrac{\partial^2}{\partial x^2} + \dfrac{\partial^2}{\partial y^2}\Big) + f_u(u^*, v^*) & f_v(u^*, v^*) \\ g_u(u^*, v^*) & d_2\Big(\dfrac{\partial^2}{\partial x^2} + \dfrac{\partial^2}{\partial y^2}\Big) + g_v(u^*, v^*) \end{pmatrix}. \tag{3.3}$$

If $\nu = \varphi \mathrm{e}^{\mu t}\mathrm{e}^{\mathrm{i}nx}\mathrm{e}^{\mathrm{i}my}$ is the eigenvector of L, then we obtain

$$L_{q^2}\varphi = \mu\varphi, \tag{3.4}$$

where φ is a two-dimensional vector and

$$L_{q^2} = \begin{pmatrix} -d_1(n^2+m^2) + f_u(u^*, v^*) & f_v(u^*, v^*) \\ g_u(u^*, v^*) & -d_2(n^2+m^2) + g_v(u^*, v^*) \end{pmatrix} \tag{3.5}$$

with $q^2 = n^2 + m^2$.

It follows that

$$\begin{aligned} \operatorname{tr} L_{q^2} &= -(d_1+d_2)q^2 + \operatorname{tr} J = -(d_1+d_2)q^2 + a_{21}h'(u^*) - a_{22}, \\ \det L_{q^2} &= d_1 d_2 q^4 - (d_2 f_u(u^*, v^*) + d_1 g_v(u^*, v^*))q^2 + \det J \\ &= d_1 d_2 q^4 - (d_2 a_{21} h'(u^*) - d_1 a_{22})q^2 + a_{21}(a_{12} - a_{22}h'(u^*)). \end{aligned} \tag{3.6}$$

As in the case of stable equilibria in ODE, it must be $\operatorname{tr} L_{q^2} < 0$ for all q, therefore if exists $q_0 \neq 0$ makes $\det L_{q_0^2} \leqslant 0$, then Turing bifurcation occurs. It leads to the fact that $\det L_{q^2} = 0$ has at least one positive root about q^2, that is

$$d_2 a_{21} h'(u^*) - d_1 a_{22} > 0$$

and

$$\Delta = (d_2 a_{21} h'(u^*) - d_1 a_{22})^2 - 4 d_1 d_2 a_{21}(a_{12} - a_{22}h'(u^*)) \geqslant 0.$$

Combining the conditions above gives:

Theorem 3.2. *If*

$$\text{(S2)} \qquad \max\left\{\frac{d_1}{d_2}\frac{a_{22}}{a_{21}},\ 2\sqrt{\frac{d_1}{d_2}\frac{a_{12}}{a_{21}}} - \frac{d_1}{d_2}\frac{a_{22}}{a_{21}}\right\} < h'(u^*) < \min\left\{\frac{a_{22}}{a_{21}},\ \frac{a_{12}}{a_{22}}\right\}$$

is correct, then system (1.1) *undergoes Turing instability.*

4. Simulation of patterns in system (1.1)

This part aims at the diversity of patterns in (1.1) at zero equilibrium and a_{11} is taken as the bifurcation parameter. The previous discussion tells us that $a_{11} = a_{22}$ and

$$a_{11} = 2\sqrt{\frac{d_1}{d_2}\frac{a_{12}}{a_{21}}} - \frac{d_1}{d_2}\frac{a_{22}}{a_{21}}$$

are the critical values of Hopf and Turing bifurcations, respectively. For explanation, at the case of $a_{12} = 2$, $a_{21} = 1$, $d_1 = 1.28$, $d_2 = 16$, Figure 4 shows the bifurcation diagram in the $a_{11} - a_{22}$ plane.

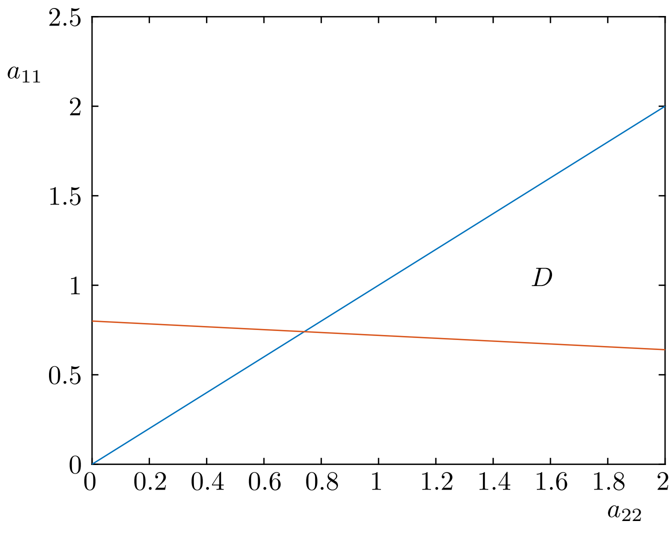
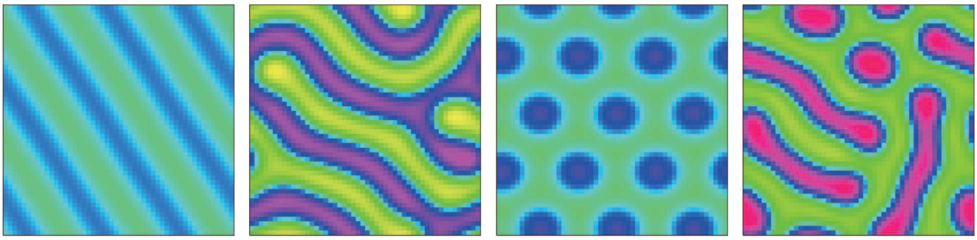


Figure 4. Bifurcation diagram in the $a_{11} - a_{22}$ plane with $a_{12} = 2$, $a_{21} = 1$, $d_1 = 1.28$, $d_2 = 16$. The red and blue lines are Turing and Hopf curves, respectively.

For this kind of cubic polynomial source in system (1.1), one can find that $C \geqslant 0$ leads to no patterns and $Q = 0$ only causes stripes. Thus, in the following, we demonstrate the pattern formation according to the points in D for $C < 0$ and

$Q \neq 0$. Assume $a_{22} = 1.5$, $C = -1$ and other parameters are the same as in Figure 4, then we have different patterns—stripes, mazes and spots—in the spatial square domain $[0, 2\pi] \times [0, 2\pi]$ for (1.1) alternating to bifurcation parameter a_{11} and coefficient Q of the quadratic term (see Figure 5).



(a) (b) (c) (d)

Figure 5. (a) The perfect stripes as $a_{11} = 0.7$, $Q = 0.08$; (b) The maze patterns with $a_{11} = 1$, $Q = 0.08$; (c) The spots cause by $a_{11} = 0.7$, $Q = 0.4$; (d) The coexistence of spots and mazes at $a_{11} = 1$, $Q = 0.4$.

5. Effect of weakly linear coupling on patterns

It is the last problem to look into the effect of weakly linear coupling between two same systems like (1.1) on pattern formation, that is, we need to consider the following system

$$
(5.1) \qquad \begin{cases}
\dfrac{\partial u_1}{\partial t} = a_{11}u_1 - a_{21}v_1 + Cu_1^3 + Qu_1^2 + d_1\nabla^2 u_1 + \varepsilon^2 K_{11}(u_2 - u_1) \\
\qquad\qquad + \varepsilon^2 K_{12}(v_2 - v_1), \\
\dfrac{\partial v_1}{\partial t} = a_{12}u_1 - a_{22}v_1 + d_2\nabla^2 v_1 + \varepsilon^2 K_{21}(u_2 - u_1) + \varepsilon^2 K_{22}(v_2 - v_1), \\
\dfrac{\partial u_2}{\partial t} = a_{11}u_2 - a_{21}v_2 + Cu_2^3 + Qu_2^2 + d_1\nabla^2 u_2 + \varepsilon^2 K_{11}(u_1 - u_2) \\
\qquad\qquad + \varepsilon^2 K_{12}(v_1 - v_2), \\
\dfrac{\partial v_2}{\partial t} = a_{12}u_2 - a_{22}v_2 + d_2\nabla^2 v_2 + \varepsilon^2 K_{21}(u_1 - u_2) + \varepsilon^2 K_{22}(v_1 - v_2),
\end{cases}
$$

where $\varepsilon \ll 1$.

Next, we complete the simulation of system (5.1) in the square domain $(0, 2\pi) \times (0, 2\pi)$. Referring to parameter sets in previous section, we investigate the influence of positive and negative weakly linear coupling on patterns, for example, take $\varepsilon^2 K_{11} = 0.01$ or -0.01, and $K_{12} = K_{21} = K_{22} = 0$.

From Figures 6 and 7, when perfect Turing patterns like stripes and spots appear in system (1.1), positive and negative weakly linear couplings make them synchronous and anti-phase, respectively. However, for analogous Turing patterns like mazes and coexistence of stripes and spots, the rule is violated.

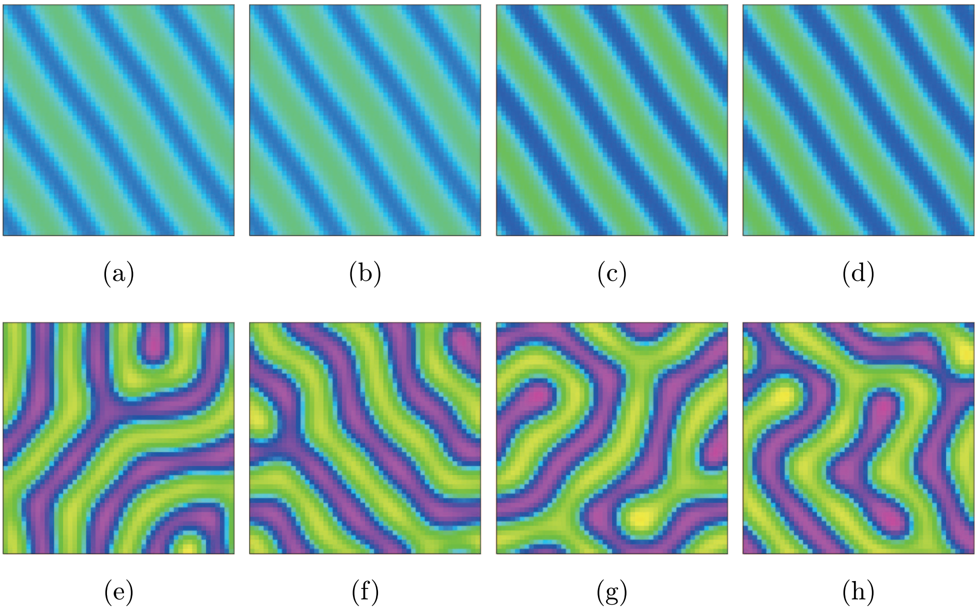
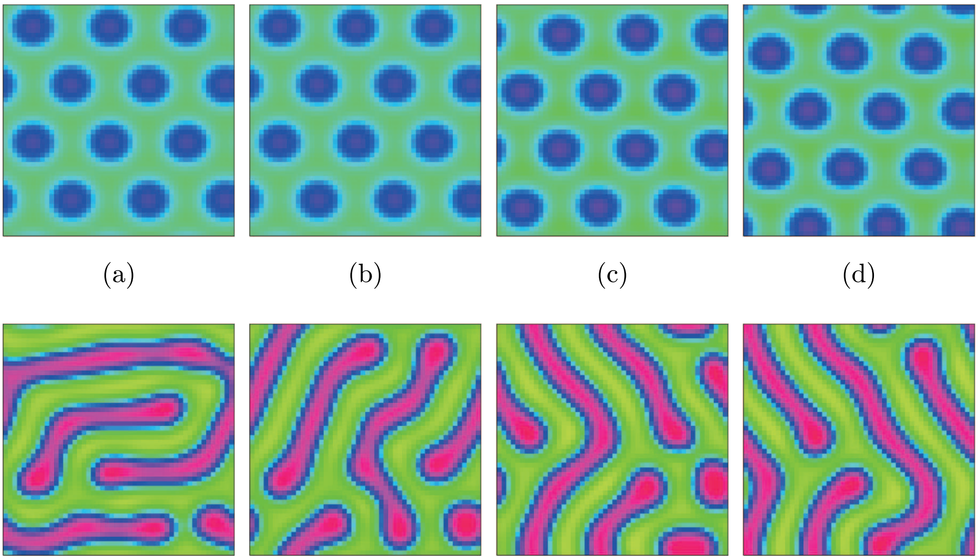


Figure 6. (a)–(d) Synchronous and anti-phase stripes with coupled coefficients 0.01 and -0.01; (e)–(h) Mazes under positive and negative couplings.

6. Conclusion

Our paper focuses on the dynamics of an activator-inhibitor model with general cubic polynomial source. For this kind of activator source, we study how and which part in it may have an effect on the kinetic behavior of the model. Our results provide useful insights into the effect mechanism that morphogen reaction mode works on pattern formation. Originally, the investigation is started from the ODE by removing the diffusion in (1.1), and we observe that all the properties, such as the existence of steady states, their stability and bifurcations, are decided by the relationship among $h'(u^*)$, a_{22}/a_{21}, and a_{12}/a_{22}. In other words, the derivative at steady states of activator source term, the production rate of the inhibitor and both degradation rates are critical factors for the ODE model. Moreover, the bifurcation diagram in Figure 2 and phase plot in Figure 3 give an intuitive display of the bifurcation



(a) (b) (c) (d)

(e) (f) (g) (h)

Figure 7. (a)–(d) Synchronous and anti-phase spots with coupled coefficients 0.01 and −0.01; (e)–(h) Analogous Turing patterns under positive and negative couplings.

cases. After that, in Theorem 3.1, the global stability of steady states in reaction-diffusion model is demonstrated using the Lyapunov functional. And it is another time to prove the crucial function of activator source term. In addition, the change from stable to unstable steady states because of diffusion gives us Turing instability, whose supposition (S2) involving activator source is shown in Theorem 3.2. As the last part of the present paper, the numerical simulation is carried out to illustrate the patterns in a spatially square domain of system (1.1). The results show that in the activator source, the relation between cubic term C and 1 distinguishes quiet from patterns, and the appearance of quadratic term Q makes patterns except for stripes possible. Certainly, since the production rate of activator is also an important aspect for pattern evolution, we choose it as the bifurcation parameter. Adding weakly linear coupling, we observe that positive or negative couplings induce Turing patterns (stripes and spots) to be synchronous or anti-phase. Also, some analogous patterns (mazes) are found but the function of coupling is not noticeable.

Competing interests. The authors declare that they have no competing interests.

Author's contributions. Yanqiu Li carried out all the studies, including dynamics of ODE and PDE, as well as patterns of the coupled system. Juncheng

Jiang conceived of the study, and participated in its design and coordination and helped to draft the manuscript. Both authors read and approved the final manuscript.

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