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Turing pattern amplitude equation for a model glycolytic reaction-diffusion system

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Abstract For a reaction-diffusion system of glycolytic oscillations containing analytical steady state solution in complicated algebraic form, Turing instability condition and the critical wavenumber at the Turing bifurcation point, have been derived by a linear stability analysis. In the framework of a weakly nonlinear theory, these relations have been subsequently used to derive an amplitude equation, which interprets the structural transitions and stability of various forms of Turing structures. Amplitude equation also conforms to the expectation that time-invariant amplitudes are independent of complexing reaction with the activator species.

Keywords Turing patterns · Reaction-Diffusion systems · Amplitude equation · Glycolytic oscillations

1 Introduction

Turing structures [1–6] are self-organized concentration patterns in reaction-diffusion (R-D) systems, which are formed when the steady states become unstable to inhomogeneous perturbations, but remain stable to homogeneous perturbations. To facilitate Turing structure formation, the inhibitor species must diffuse much faster than the activator species. Although, Turing patterns may be directly computed from the R-D equations by setting the parameters appropriately, the structural transitions and the

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stability of various forms of Turing patterns can be well-interpreted by an amplitude equation (AE), which is derived in the framework of a weakly nonlinear theory.

AE [1,2] for Turing pattern selection [3–6] has been derived in the past for a few R-D systems including Brusselator and other models [7–13]. AE has also been derived for the Swift-Hohenberg model [14], which has been widely used for a qualitative description of the convective structures induced by Benard-Marangoni instability or non-Boussinesq Benard convection [15,16]. Although, the AE derivation is, itself, a lengthy process, only those R-D systems have been chosen for AE derivation, for which the kinetic steady state is analytically solvable and simple-looking in algebraic form. In this paper, we have derived the AE for the reversible Sel'kov model [17,18], a kinetic model of glycolytic [19] R-D system, in which the steady state from the reaction kinetics, is required to be obtained by the solution of a cubic equation using Cardon's method [20]—the analytical solution of such a steady state being highly complicated. For such a R-D model [17,18], we have attempted to derive the AE, which may become useful in interpreting the structural transitions and stability of various Turing patterns.

Section 2 has discussed the reversible Sel'kov model leading to the formation of the R-D equations as given in equations (2.13) and (2.14). Section 3 has undertaken the linear stability analysis of the R-D equations to obtain Turing instability condition as presented in Eqs. (3.10) and (3.11) and the corresponding critical wavenumber (k_c) at the Turing instability point presented in Eq. (3.13). Section 4 has discussed the separation of the R-D equation into linear and nonlinear parts as shown in Eq. (4.4). In Sect. 5, nonlinear analysis is presented—this is based on the expansion of the evolution of the inhomogeneous perturbations in terms of the amplitude of the branching solution for κ (say) in the neighborhood of κ_c (see the text for details about κ and κ_c) and the derivation of two solvability conditions from order 2 and order 3 terms of the nonlinear part. In Sect. 6, the amplitude equation has been derived by incorporating the two solvability conditions derived in Sect. 5 into the expanded form (see Eq. 5.5) of the partial time derivative of amplitude. Section 7 has discussed about the interpretation of the amplitude equation in Turing structure selection problem and the new results summarized at the end of this section.

2 The model

Sel'kov [19] has proposed a simple kinetic model (1) of enzyme catalysis with product activation of the enzyme, which exhibits limit cycle oscillations. Here, the substrate S (ATP) supplied by a certain source at a constant rate (v_1) is converted irreversibly into a product P (ADP). The product P (ADP) is removed by an irreversible sink at another constant rate (v_2.). The free enzyme E (PFK1) is inactive by itself, but becomes active after combination with γ product molecules to form the complex EP^γ.

$$\begin{aligned} &\text{Source} \xrightarrow{v1} \text{S} \;+\; \text{EP}^\gamma \leftrightarrows \text{SEP}^\gamma,\\ &\text{SEP}^\gamma \rightarrow \text{EP}^\gamma + \text{P} \xrightarrow{v2} \text{Sink},\\ &\gamma\text{P} + \text{E} = \text{EP}^\gamma. \end{aligned} \tag{1}$$

Based on Sel'kov model, Richter et al. [17] have proposed the following three reversible kinetic steps (2.1 to 2.3), known as the reversible Sel'kov model,

$$A \leftrightarrows S \tag{2.1}$$

$$S + 2P \leftrightarrows 3P \tag{2.2}$$

$$P \leftrightarrows B \tag{2.3}$$

where A and B are controllable source and sink concentrations respectively—$k_{\pm i}$ (i = 1, 2, 3) are, respectively, the rate constants of the three steps (+ and − subscripts are, respectively, for forward and reverse reactions). It is worthwhile to note that the reversible Sel'kov model steps account for only the oscillatory part of the mechanism, not the complete glycolytic mechanism itself, which is rather complicated. When described in terms of activator/inhibitor model, the autocatalyst P is the activator and S, the inhibitor. The R-D equations [18,20] in one dimension are given by:

$$\partial P/\partial t = k_2SP^2 - k_{-2}P^3 - k_3P + k_{-3}B + D_p\left(\partial^2 P/\partial x^2\right) \tag{2.4}$$

$$\partial S/\partial t = k_1A - k_{-1}S - k_2SP^2 + k_{\_2}P^3 + D_s\left(\partial^2 S/\partial x^2\right) \tag{2.5}$$

where P and S represent the concentrations of the respective species, D's are diffusion coefficients and x is the geometrical coordinate. Since the specific rate constants of the model steps are not known, it is necessary to scale the reaction part [17,18] and diffusion part [22] appropriately as given below in Eqs. (2.6a) and (2.6b) respectively,

$$\begin{aligned}&k_3t = \tau; \quad S/N = \hat{s}; \quad P/N = \hat{p}; \quad N = (k_3/k_2)^{1/2};\\ &a = (k_1A)/(k_3N); \quad b = (k_{-3}B)/(k_3N); \quad \kappa = (k_{-1}/k_3); \\ &K_2 = (k_{-2}/k_2)\end{aligned} \tag{2.6a}$$

$$\rho = x\left(k_3/D_p\right)^{1/2} \tag{2.6b}$$

One, therefore, obtains the dimensionless R-D equations in the form

$$\partial\hat{p}/\partial\tau = f\left(\hat{p}, \hat{s}\right) + \left(\partial^2\hat{p}/\partial\rho^2\right) \tag{2.7}$$

$$\partial\hat{s}/\partial\tau = g\left(\hat{p}, \hat{s}\right) + d\left(\partial^2\hat{s}/\partial\rho^2\right) \tag{2.8}$$

where,

$$f(\hat{p}, \hat{s}) = -\hat{p} + b + \hat{s}\hat{p}^2 - K_2\hat{p}^3 \tag{2.9}$$

$$g\left(\hat{p}, \hat{s}\right) = a - \kappa\hat{s} - \hat{s}\hat{p}^2 + K_2\hat{p}^3 \tag{2.10}$$

$$d = D_s/D_p \tag{2.11}$$

where, $\hat{p}$ and $\hat{s}$ are scaled concentrations and τ, the scaled time.

2.1 Complex formation with the activator

If the activator P (ADP) is supposed to be involved in a complexing reaction [3,21,22] similar to that reported in the Turing structure experiments and modeling of the CIMA reaction [4–6], we have the chemical equilibrium as given below.

$$\mathrm{P} + \mathrm{C} \leftrightarrows \mathrm{PC} \tag{2.12a}$$

where the activator P is captured partially producing the complex PC by reaction with the chemical species C. The possible nature of the complexing species is an unexplored problem which is left open for future investigation. The equilibrium constant K for this complex formation reaction is given by,

$$\mathrm{K} = \mathrm{pc/p.c} \tag{2.12b}$$

where pc, p, and c are the equilibrium concentrations of the complex PC, the activator P and the complexing agent C respectively. If we use the complexing agent in large excess, such that the initial concentration (c_o) of the complexing agent is almost equal to its concentration (c) at chemical equilibrium, one can define a new constant K' such that.

$$\mathrm{K}' = \mathrm{K.c_o} \tag{2.12c}$$

Therefore, due to complexing reaction of the activator P, the new R-D equations take the form as given below.

$$\partial \hat{p}/\partial \tau' = \mathrm{f}\left(\hat{p}, \hat{s}\right) + \left(\partial \hat{p}/\partial \rho^2\right) \tag{2.13}$$

$$\partial \hat{s}/\partial \tau' = \left(1 + K'\right)\left[\mathrm{g}\left(\hat{p}, \hat{s}\right) + \mathrm{d}\left(\partial^2 \hat{s}/\partial \rho^2\right)\right] \tag{2.14}$$

where

$$\tau = \left(1 + \mathrm{K}'\right)\tau', \tag{2.15}$$

3 Linear stability analysis

From the dimensionless R-D Eqs. (2.13–2.14), we have

$$\begin{aligned}
\mathrm{f}_{11} &= f'_{\hat{p}} = -1 + 2\mathrm{s_o p_o} - 3\mathrm{K_2 p_o^2} \\
\mathrm{f}_{12} &= f'_{\hat{s}} = \mathrm{p_o^2} \\
\mathrm{f}_{21} &= \left(1 + \mathrm{K}'\right) g'_{\hat{p}} = \left(1 + \mathrm{K}'\right).\left(-2\mathrm{s_o p_o} + 3\mathrm{K_2 p_o^2}\right) \\
\mathrm{f}_{22} &= \left(1 + \mathrm{K}'\right) g'_{\hat{s}} = \left(1 + \mathrm{K}'\right).\left(-\kappa - \mathrm{p_o^2}\right)
\end{aligned} \tag{3.1}$$

where s_o, p_o are the dimensionless steady states. Applying the linear operator

$$f_{ij}(k) = f_{ij} - D_i k^2 \delta_{ij} \tag{3.2}$$

where k is the wavenumber and D's are diffusion constants, the characteristic equation for the dimensionless partial differential Eqs. (2.13–2.14) may be written as:

$$\omega_k^2 + \left(k^2 d + k^2 + k^2 dK' - f_{11} - f_{22}\right)\omega_k + \det \mathbf{F} - \left(f_{22} + df_{11} + dK' f_{11}\right)k^2 + d\left(1 + K'\right)k^4 = 0 \tag{3.3}$$

From the characteristic Eq. (3.3) for nonzero k mode, the condition for Hopf-wave bifurcation is given by

$$k_{\text{Hopf}}^2 \le \frac{f_{11} + f_{22}}{1 + (1 + K')\, d} \tag{3.4}$$

where

$$\det \mathbf{F} - \left(f_{22} + df_{11} + df_{11}K'\right)k^2 + d\left(1 + K'\right)k^4 > 0 \tag{3.5}$$

For Turing instability to set in [23,24], the constant term of the characteristic Eq. (3.3) must vanish. i.e.,

$$\det \mathbf{F} - \left(f_{22} + df_{11} + df_{11}K'\right)k^2 + d\left(1 + K'\right)k^4 = 0 \tag{3.6}$$

provided that,

$$f_{22} + d f_{11} + df_{11}K' > 0 \quad \text{and} \quad f_{11} + f_{22} < 0 \tag{3.7}$$

Substituting the values of f_{11} and f_{22} from Eqs. (3.1), one obtains

$$g'_{\hat{s}} + d f'_{\hat{p}}. > 0$$

and,

$$\kappa\left(1 + K'\right) + K' p_o^2 > -1 + 2 s_o p_o - 3K_2 p_o^2 - p_o^2 \tag{3.8}$$

The critical wavelength (wavenumber) is determined by the degenerate root of Eq. (3.6). Therefore, we have

$$\left(f_{22} + df_{11} + dK' f_{11}\right)^2 \ge 4d\left(1 + K'\right)\det \mathbf{F} \tag{3.9}$$

which is the condition for Turing instability—the equality being the critical condition. Substituting the values of f_{11}, f_{22} and det **F** from Eq. (3.1), Turing instability condition (3.9) takes the following form in terms of the dimensionless steady state concentrations of P and S.

$$\left[-\kappa - \mathrm{p}_\mathrm{o}^2 + \mathrm{d}\left(-1 + 2\mathrm{s}_\mathrm{o}\mathrm{p}_\mathrm{o} - 3\mathrm{K}_2\mathrm{p}_\mathrm{o}^2\right)\right]^2 \geq 4\mathrm{d}\left[\left(-1 + 2\mathrm{s}_\mathrm{o}\mathrm{p}_\mathrm{o} - 3\mathrm{K}_2\mathrm{p}_\mathrm{o}^2\right) \cdot \left(-\kappa - \mathrm{p}_\mathrm{o}^2\right) - \mathrm{p}_\mathrm{o}^2\left(-2\mathrm{s}_\mathrm{o}\mathrm{p}_\mathrm{o} + 3\mathrm{K}_2\mathrm{p}_\mathrm{o}^2\right)\right] \tag{3.10}$$

Equation (3.10), on algebraic manipulation gives for $\kappa = \kappa_c$,

$$\kappa_c = -\mathrm{p}_\mathrm{o}^2 - \mathrm{d}\left(-1 + 2\mathrm{s}_\mathrm{o}\mathrm{p}_\mathrm{o} - 3\mathrm{K}_2\mathrm{p}_\mathrm{o}^2\right) + 2\mathrm{p}_\mathrm{o}\mathrm{d}^{1/2}\left(2\mathrm{s}_\mathrm{o}\mathrm{p}_\mathrm{o} - 3\mathrm{K}_2\mathrm{p}_\mathrm{o}^2\right)^{1/2} \tag{3.11}$$

Equation (3.11) gives the value of κ_c to be satisfied at the Turing bifurcation point.

3.1 Critical wavenumber (k_c)

For degenerate root of Eq. (3.6), we have from Eqs. (3.6) and (3.9), the critical wavenumber k_c given by the expression

$$\mathrm{k}_\mathrm{c}^2 = (1/2) \cdot \left(-1 + 2\mathrm{s}_\mathrm{o}\mathrm{p}_\mathrm{o} - 3\mathrm{K}_2\mathrm{p}_\mathrm{o}^2\right) + (1/2\mathrm{d}) \cdot \left(-\kappa_\mathrm{c} - \mathrm{p}_\mathrm{o}^2\right) \tag{3.12}$$

Substituting the value of κ_c from Eq. (3.11) into Eq. (3.12), one obtains

$$\kappa_\mathrm{c}^2 = \left(-1 + 2\mathrm{s}_\mathrm{o}\mathrm{p}_\mathrm{o} - 3\mathrm{K}_2\mathrm{p}_\mathrm{o}^2\right) - \mathrm{p}_\mathrm{o}\mathrm{d}^{-1/2}\left(2\mathrm{s}_\mathrm{o}\mathrm{p}_\mathrm{o} - 3\mathrm{K}_2\mathrm{p}_\mathrm{o}^2\right)^{1/2} \tag{3.13}$$

Equation (3.13) gives the value of critical wavenumber (k_c) to be satisfied at the Turing bifurcation point.

4 Separation into linear and nonlinear parts

Since (p_o, s_o) is the steady state solution of the R-D Eqs. (2.13–2.14), we have

$$-\mathrm{p}_\mathrm{o} + \mathrm{b} + \mathrm{s}_\mathrm{o}\mathrm{p}_\mathrm{o}^2 - \mathrm{K}_2\mathrm{p}_\mathrm{o}^3 = 0 \tag{4.1}$$

$$\mathrm{a} - \kappa\mathrm{s}_\mathrm{o} - \mathrm{s}_\mathrm{o}\mathrm{p}_\mathrm{o}^2 + \mathrm{K}_2\mathrm{p}_\mathrm{o}^3 = 0 \tag{4.2}$$

Let the inhomogeneous perturbation (p, s) around the stable steady state (p_o, s_o) be represented by the following relations

$$\mathrm{p} = \hat{p} - \mathrm{p}_\mathrm{o}; \quad \mathrm{s} = \hat{s} - \mathrm{s}_\mathrm{o} \tag{4.3}$$

Substituting the values of $\left(\hat{p},\ \hat{s}\right)$ from Eq. (4.3) into Eqs. (2.13) and (2.14) and incorporating the steady state condition Eqs. (4.1) and (4.2), one obtains the R-D Eqs. (2.13) and (2.14) divided into linear and nonlinear parts as given below.

$$\partial_{\tau'}(\mathrm{p,s})^{\mathbf{T}} = \left[\mathbf{L}_{\mathrm{c}} + \left(1+\mathrm{K}'\right)\cdot(\kappa_c-\kappa)\,\mathbf{M}\right].(\mathrm{p,s})^{\mathbf{T}} + \left[2\mathrm{p_o sp} + \left(\mathrm{s_o} - 3\mathrm{K_2 p_o}\right)\mathrm{p}^2 + \mathrm{sp}^2 - \mathrm{K_2 p}^3\right] \cdot\left[+1,\left(-1+\mathrm{K}'\right)\right]^{\mathrm{T}} \tag{4.4}$$

where

$$\mathbf{L}_{\mathrm{c}} = \begin{bmatrix} -1+2\mathrm{s_o p_o} - 3K_2\mathrm{p_o^2} + \nabla_\rho^2 & \mathrm{p_o^2} \\ \left(1+K'\right).\left(-2s_{\mathrm{o}}\mathrm{p_o} + 3K_2\mathrm{p_o^2}\right) & \left(1+K'\right).\left(-\kappa_c - \mathrm{p_o^2} + d\nabla_\rho^2\right) \end{bmatrix} \tag{4.5}$$

$$\mathbf{M} = \begin{bmatrix} 0 & 0 \\ 0 & 1 \end{bmatrix} \tag{4.6}$$

and the symbol $\partial_{\tau'} \Rightarrow \partial/\partial\tau'$

5 Nonlinear bifurcation approach

Let the Turing structures constitute the superposition of three pairs of modes $\left(\vec{k}_i, -\vec{k}_i\right)_{i=1,2,3}$ making angles of $2\pi/3$, such that $\left|\vec{k}_i\right| = \mathrm{k_c}$ and $\vec{k}_1 + \vec{k}_2 + \vec{k}_3 = 0$ - the evolution of the inhomogeneous perturbations, $(p, s)^{\mathrm{T}}$being represented in terms of three amplitudes as given by

$$(\mathrm{p,s})^{\mathbf{T}} = \sum_{i=1}^{3}\left(\mathrm{A}_i^{\mathrm{p}}, \mathrm{A_i^s}\right)^{\mathbf{T}} \exp\left(i\vec{k}_i\cdot\rho\right) + \mathrm{c.c} \tag{5.1}$$

where $\mathrm{A_i}$'s are the amplitudes, and c.c. indicates the complex conjugate terms. The nonlinear analysis is based on the following expansion in terms of the amplitude of the branching solutions for κ(say) in the neighborhood of κ_c.

$$(\mathrm{p,\,s})^{\mathbf{T}} = \varepsilon\left(\mathrm{p_1, s_1}\right)^{\mathbf{T}} + \varepsilon^2\left(\mathrm{p_2, s_2}\right)^{\mathbf{T}} + \ldots \tag{5.2}$$

where,

$$\kappa_c - \kappa = \varepsilon\kappa^{(1)} + \varepsilon^2\kappa^{(2)} + \ldots \tag{5.3}$$

$$\partial_{\tau'} = \partial_{\tau_0'} + \varepsilon\partial_{\tau_1'} + \varepsilon^2\partial_{\tau_2'} + \ldots \tag{5.4}$$

$$\partial_{\tau'}\mathrm{A} = \varepsilon\left(\partial\mathrm{A}/\partial_{\tau_1}'\right) + \varepsilon^2\left(\partial\mathrm{A}/\partial\tau_2'\right) + \ldots. \tag{5.5}$$

where A is the amplitude and the $\left(\partial\mathrm{A}/\partial\tau_0'\right)$ term is neglected since the slow variable at zero time is time-invariant.

Substituting Eqs. (5.2) to (5.4) into Eq. (4.4) and equating the coefficients of the order of ε, ε^2, and ε^3 on both sides, one obtains:

$$\varepsilon : \mathbf{L_c.}\left(\mathrm{p}_1, \mathrm{s}_1\right)^{\mathbf{T}} = 0 \tag{5.6}$$

$$\begin{aligned}\varepsilon^2 : \mathbf{L_c}\left(\mathrm{p}_2,\ \mathrm{s}_2\right)^{\mathbf{T}} &= -\left(1+K'\right)\kappa^{(1)}\left(0, s_1\right)^{\mathbf{T}} \\ &\quad -\left[2\mathrm{p_o}\mathrm{p}_1\mathrm{s}_1 + \left(\mathrm{s_o} - 3K_2\mathrm{p}_o\right)\mathrm{p}_1^2\right] \\ &\quad \cdot\left[+1, -\left(1+\mathrm{K}'\right)\right]^{\mathbf{T}} + \partial_{\tau_1'}\left(\mathrm{p}_1, \mathrm{s}_1\right)^{\mathbf{T}} \\ &= \left(\mathrm{F_p}, \mathrm{F_s}\right)^{\mathbf{T}}\ (\text{say})\end{aligned} \tag{5.7}$$

$$\begin{aligned}\varepsilon^3 : \mathbf{L_c}\left(\mathrm{p}_3, \mathrm{s}_3\right)^{\mathbf{T}} &= -\left(1+K'\right)\cdot\left[\kappa^{(1)}\left(0, \mathrm{s}_2\right)^{\mathbf{T}} + \kappa^{(2)}\left(0, \mathrm{s}_1\right)^{\mathbf{T}}\right] \\ &\quad -\left[2\mathrm{p}_0\left(\mathrm{s}_1\mathrm{p}_2 + \mathrm{s}_2\mathrm{p}_1\right) + \left(\mathrm{s_o} - 3K_2\mathrm{p_o}\right)\cdot 2\mathrm{p}_1\mathrm{p}_2 + \mathrm{s}_1\mathrm{p}_1^2 - K_2\mathrm{p}_1^3\right] \\ &\quad \cdot\left[+1, -\left(1+\mathrm{K}'\right)\right]^{\mathbf{T}} \\ &\quad + \partial_{\tau_1'}\left(\mathrm{p}_2, \mathrm{s}_2\right)^{\mathbf{T}} + \partial_{\tau_2'}\left(\mathrm{p}_1, \mathrm{s}_1\right)^{\mathbf{T}} = \left(\mathrm{G_p}, \mathrm{G_s}\right)^{\mathbf{T}}\ (\text{say})\end{aligned} \tag{5.8}$$

Order 1 From Eq. (5.6), we have $(\mathrm{p}_1, \mathrm{s}_1)^{\mathbf{T}}$ proportional to the right eigenvectors of $\mathbf{L_c}$ with zero eigenvalue, i.e., to the critical mode (at $\kappa = \kappa_c$, $\left|\vec{k}_i\right| = \mathrm{k_c}$). However, because of the degeneracy, $(\mathrm{p}_1, \mathrm{s}_1)^{\mathbf{T}}$ is written as a linear combination of such eigenvectors as given below with the help of critical wavenumber Eq. (3.13).

$$\left(\mathrm{p}_1, \mathrm{s}_1\right)^{\mathbf{T}} = \left[\sum_i \mathrm{W_i}\exp\left(\mathrm{i}\vec{k}_i\cdot\rho\right) + \text{c.c.}\right]\cdot\left[-\left(p_o d/\left(2\mathrm{s_o} - 3K_2 p_o\right)\right)^{1/2}, 1\right]^{\mathbf{T}} \tag{5.9}$$

Order 2 The solvability condition from Eqs. (5.7) requires that the inhomogeneous term $\left(\mathrm{F_p^i}, \mathrm{F_s^i}\right)^{\mathbf{T}}$ be orthogonal to the left (row) eigenvectors of $\mathbf{L_c}$ with zero left eigenvalue. To obtain the left eigenvctors of $\mathbf{L_c}$ with zero eigenvalue, we simply have to transpose the right eigenvectors of $\mathrm{L_c^{\mathbf{T}}}$with zero eigenvalue. Therefore, we have

$$\mathrm{L_c^{\mathbf{T}}}\cdot\left(\mathrm{p}_2, \mathrm{s}_2\right)^{\mathbf{T}} = 0 \tag{5.10}$$

The right eigenvector from Eq. (5.10) can be obtained using the value of k_c from Eq. (3.13)—this right eigenvecor, on transposing, gives the left eigenvector with zero eigenvalue as given below in Eq. (5.11).

$$\left(\mathrm{p}_2, \mathrm{s}_2\right) = \left[\left(1+K'\right)\left\{d\left(2\mathrm{s_o} - 3K_2\mathrm{p_o}\right)/\mathrm{p_o}\right\}^{1/2}, 1\right]\cdot\left[\sum_i \mathrm{W_i}\exp\left(\mathrm{i}\vec{k}_i\cdot\rho\right) + \text{c.c.}\right] \tag{5.11}$$

Let us calculate $\left(\mathrm{F}_{\mathrm{p}}^{1}, \mathrm{F}_{\mathrm{s}}^{1}\right)^{\mathbf{T}}$, the coefficient of exp $\left(\mathrm{i}\vec{k}_1 \cdot \rho\right)$ from Eq. (5.7). On algebraic simplification one obtains it in the form as given in Eq. (5.12).

$$\begin{aligned}\left(\mathrm{F}_{\mathrm{p}}^{(1)}, \mathrm{F}_{\mathrm{s}}^{(1)}\right)^{\mathbf{T}} = &-\left(1+K'\right)\kappa^{(1)}\left(0, W_1\right)^{\mathbf{T}} + 2\bar{W}_2\bar{W}_3\left(\mathrm{p_o}d\right)\cdot\left(2\mathrm{s_o}-3K_2\mathrm{p_o}\right)^{-1}\\ &\cdot\left[2d^{-1/2}\left(2\mathrm{s_o}\mathrm{p_o}-3K_2\mathrm{p_o^2}\right)^{1/2}-\left(\mathrm{s_o}-3K_2\mathrm{p_o}\right)\right]\cdot\left(+1, -\left(1+K'\right)\right)^{\mathbf{T}}\\ &+\left(\partial W_1/\partial\tau_1'\right)\cdot\left\{-\left(\mathrm{p_o}d/\left(2s_o-3K_2\mathrm{p_o}\right)\right)^{1/2}, 1\right\}^{\mathbf{T}}\end{aligned} \tag{5.12}$$

Now, considering that the inhomogeneous term $\left(\mathrm{F}_{\mathrm{p}}^{(1)}, \mathrm{F}_{\mathrm{s}}^{(1)}\right)^{\mathbf{T}}$ from Eq. (5.12) must be orthogonal to the left eigenvector of $\mathrm{L_c}$ with zero eigenvalue as given in Eq. (5.11), one obtains the first solvability condition as given in Eq. (5.13).

$$\begin{aligned}&\left(\partial \mathrm{W}_1/\partial\tau_1'\right)\left[\left(1+K'\right)^{-1}-d\right]\\ &=\kappa^{(1)}\mathrm{W}_1+2\bar{W}_2\bar{W}_3d^{1/2}\left\{\mathrm{p_o}-d^{1/2}\left(2\mathrm{s}_o\mathrm{p}_o-3\mathrm{K_2p_o^2}\right)^{1/2}\right\}\\ &\cdot\left\{2\left(2\mathrm{s_op_o}-3\mathrm{K_2p_o^2}\right)^{1/2}-\mathrm{d}^{1/2}\left(\mathrm{s_o}-3\mathrm{K_2p_o}\right)\right\}/\left(2\mathrm{s_o}-3\mathrm{K_2p_o}\right)\end{aligned} \tag{5.13}$$

Let $(\mathrm{p}_2, \mathrm{s}_2)^{\mathbf{T}}$ in Eq. (5.7) be expressed as a combination of a series of Fourier terms as given below.

$$\begin{aligned}(p_2, s_2)^{\mathbf{T}} = &(P_o, S_o)^{\mathbf{T}} + (P_1, S_1)^{\mathbf{T}}\exp\left(\mathrm{i}\vec{k}_i\cdot\rho\right) + (P_2, S_2)^{\mathbf{T}}\exp\left(\mathrm{i}\vec{k}_2\cdot\rho\right)\\ &+(P_3, S_3)^{\mathbf{T}}\exp\left(\mathrm{i}\vec{k}_3\cdot\rho\right)+(P_{11}, S_{11})^{\mathbf{T}}\exp\left(2\mathrm{i}\vec{k}_1\cdot\rho\right)\\ &+(P_{22}, S_{22})^{\mathbf{T}}\exp\left(2\mathrm{i}\vec{k}_2\cdot\rho\right)+(P_{33}, S_{33})^{\mathbf{T}}\exp\left(2\mathrm{i}\vec{k}_3\cdot\rho\right)\\ &+(P_{12}, S_{12})^{\mathbf{T}}\exp\left(i\left(\vec{k}_1-\vec{k}_2\right)\cdot\rho\right)+(P_{23}, S_{23})^{\mathbf{T}}\exp\left(i\left(\vec{k}_2-\vec{k}_3\right)\cdot\rho\right)\\ &+(P_{31}, S_{31})^{\mathbf{T}}\exp\left(i\left(\vec{k}_3-\vec{k}_1\right)\cdot\rho\right)+\text{c.c.}\end{aligned} \tag{5.14}$$

The Fourier coefficient values were calculated as listed in Appendix A.

Order 3 Similar to the first solvability condition (5.13), the second solvability condition from Eq. (5.8) requires that the inhomogeneous term $\left(G_p^{(1)}, G_s^{(1)}\right)^{\mathbf{T}}$ be orthogonal to the left eigenvectors of $\mathbf{L}_c$ with zero eigenvalue. Therefore, we have from Eq. (5.11) that the second solvability condition should satisfy the relation:

$$\left[\left(1+K'\right)\left\{d\left(2\mathrm{s_o}-3K_2\mathrm{p_o}\right)/\mathrm{p_o}\right\}^{1/2}, 1\right]\cdot\left(G_p^{(1)}, G_s^{(1)}\right)^{\mathbf{T}} = 0 \tag{5.15}$$

Substituting the values of the Fourier coefficients from Appendix A into the inhomogeneous term $\left(G_p^{(1)}, G_s^{(1)}\right)^{\mathbf{T}}$, the coefficient of $\exp\left(\mathrm{i}\vec{k}_1 \cdot \rho\right)$, from Eq. (5.8) and making long algebraic manipulations, one obtains

$$
\begin{aligned}
\left(G_p^{(1)}, G_s^{(1)}\right)^{\mathbf{T}} = & -\left(1+K'\right)\left\{\kappa^{(1)}\left(0, \mathrm{s}_1\right)^{\mathbf{T}}+\kappa^{(2)}\left(0, W_1\right)^{\mathbf{T}}\right\} \\
& +\left(-1,\left(1+K'\right)\right)^{\mathbf{T}}\left[\left\{\mathrm{p_o}-\left(\mathrm{s_o}-3K_2\mathrm{p_o}\right)\cdot\left(\mathrm{p_o}d/\left(2\mathrm{s_o}-3K_2\mathrm{p_o}\right)\right)^{1/2}\right\}\right. \\
& \cdot\left\{-4\mathrm{d}^{1/2}\kappa^{(1)}\bar{W}_2\bar{W}_3/\left(\mathrm{p_o}\left(2\mathrm{s_o}\mathrm{p_o}-3K_2\mathrm{p_o^2}\right)^{1/2}-d^{1/2}\left(2\mathrm{s_o}\mathrm{p_o}-3K_2\mathrm{p_o^2}\right)\right)\right\} \\
& -2\left(\bar{S}_2\bar{W}_3+\bar{S}_3\bar{W}_2\right)\cdot\left(\mathrm{p_o}d/\left(2\mathrm{s_o}-3K_2\mathrm{p_o}\right)\right)^{1/2}\cdot\{\mathrm{p_o}+\mathrm{p_o}-\left(\mathrm{s_o}-3K_2\mathrm{p_o}\right) \\
& \left.\cdot\left(\mathrm{p_o}d/(2\mathrm{s_o}-3K_2\mathrm{p_o})\right)^{1/2}\}+\mathrm{C}_1|\mathrm{W}_1|^2\mathrm{W}_1+\mathrm{C}_{23}\left(|\mathrm{W}_2|^2+|\mathrm{W}_3|^2\right)\mathrm{W}_1\right] \\
& +\left[\left\{-\mathrm{p_o}\left(\partial\mathrm{W}_1/\partial\tau_2'\right)-\kappa^{(1)}\left(\partial\mathrm{W}_1/\partial\tau_1'\right)/\left(\mathrm{p_o}-d^{1/2}\left(2\mathrm{s_o}\mathrm{p_o}-3K_2\mathrm{p_o^2}\right)^{1/2}\right)\right.\right. \\
& \left.\left.-\mathrm{p_o}\left(\partial\mathrm{S}_1/\partial\tau_1'\right)\right\}.\left(d^{1/2}/\left(2\mathrm{s_o}\mathrm{p_o}-3K_2\mathrm{p_o^2}\right)^{1/2}\right),\quad\left(\partial\mathrm{W}_1/\partial\tau_2'\right)+\left(\partial\mathrm{S}_1/\partial\tau_1'\right)\right]^{\mathbf{T}}
\end{aligned}
\tag{5.16}
$$

where C_1 and C_{23} are the expressions included in Appendix B. Substituting the values of $G_p^{(1)}$ and $G_s^{(1)}$ from Eqs. (5.16) into Eq. (5.15), one obtains the second solvability condition as given in Eq. (5.17).

$$
\begin{aligned}
& \left[\left(1+K'\right)^{-1}-\mathrm{d}\right].\left[\left(\partial\mathrm{S}_1/\partial\tau_1'\right)+\left(\partial\mathrm{W}_1/\partial\tau_2'\right)\right] \\
& -\mathrm{dp_o^{-1}}\kappa^{(1)}\left(\partial\mathrm{W}_1/\partial\tau_1'\right)/\left\{\mathrm{p_o}-\mathrm{d}^{1/2}\left(2\mathrm{s_o}\mathrm{p_o}-3\mathrm{K}_2\mathrm{p}_o^2\right)^{1/2}\right\}=\kappa^{(1)}\mathrm{S}_1+\kappa^{(2)}\mathrm{W}_1 \\
& +4\mathrm{p_o^{-1}}\mathrm{d}^{1/2}\kappa^{(1)}\bar{W}_2\bar{W}_3\left\{\mathrm{p_o}-\left(\mathrm{s_o}-3\mathrm{K}_2\mathrm{p_o}\right)\cdot\left(\mathrm{p_o}\mathrm{d}/(2\mathrm{s_o}\mathrm{p_o}-3\mathrm{K}_2\mathrm{p_o})\right)^{1/2}\right\} \\
& /\left(2\mathrm{s_o}\mathrm{p_o}-3\mathrm{K}_2\mathrm{p_o^2}\right)^{1/2}+2\mathrm{p_o^{-1}}\left(\mathrm{p_o}\mathrm{d}/(2\mathrm{s_o}-3\mathrm{K}_2\mathrm{p_o})\right)^{1/2} \\
& \cdot\left\{\mathrm{p_o}-\mathrm{d}^{1/2}\left(2\mathrm{s_o}\mathrm{p_o}-3\mathrm{K}_2\mathrm{p_o^2}\right)^{1/2}\right\} \\
& \cdot\left\{2\mathrm{p_o}-\left(\mathrm{s_o}-3\mathrm{K}_2\mathrm{p_o}\right)\cdot\left(\mathrm{p_o}\mathrm{d}/(2\mathrm{s_o}-3\mathrm{K}_2\mathrm{p_o})\right)^{1/2}\right\} \\
& \cdot\left(\bar{S}_2\bar{W}_3+\bar{S}_3\bar{W}_2\right)-\mathrm{p_o^{-1}}\left\{\mathrm{p_o}-\mathrm{d}^{1/2}\left(2\mathrm{s_o}\mathrm{p_o}-3\mathrm{K}_2\mathrm{p_o^2}\right)^{1/2}\right\} \\
& \cdot\left\{\mathrm{C}_1|\mathrm{W}_1|^2\mathrm{W}_1+\mathrm{C}_{23}\left(|\mathrm{W}_2|^2+|\mathrm{W}_3|^2\right)\mathrm{W}_1\right\}
\end{aligned}
\tag{5.17}
$$

6 Amplitude equation

From Eqs. (5.5) we have for the amplitude A_1,

$$
\partial\mathrm{A}_1/\partial\tau'=\varepsilon\left(\partial\mathrm{A}_1/\partial\tau_1'\right)+\varepsilon^2\left(\partial\mathrm{A}_1/\partial\tau_2'\right)+\ldots. \tag{6.1}
$$

We substitute the values of $(p_1, s_1)^{\mathbf{T}}$ and $(p_2, s_2)^{\mathbf{T}}$ from Eqs. (5.9) and (5.14) into Eq. (5.2) and equate the coefficients of $\exp\left(i\vec{k}_i \cdot \rho\right)$ from Eqs. (5.1) and (5.2) to obtain the expression for amplitudes as given below using Eq. (A3) from Appendix A.

$$\begin{aligned}
(A_i,\ A_i, s)^{\mathbf{T}} &= (A_i, p,\ A_i, s)^{\mathbf{T}=\varepsilon}\left[-\left(p_o d/\left(2s_o-3K_2p_o\right)\right)^{1/2}, 1\right]^{\mathbf{T}} W_i+\varepsilon^2(P_i, S_i)^{\mathbf{T}} \\
&= \varepsilon\begin{bmatrix} -\left(p_o d/\left(2s_o-3K_2p_o\right)\right)^{1/2} \\ 1 \end{bmatrix} W_i+\varepsilon^2 \\
&= \left[-d^{1/2}\kappa^{(1)}W_i/\left\{p_o\left(2s_op_o-3K_2p_o^2\right)^{1/2}-d^{1/2}\left(2s_op_o-3K_2p_o^2\right)\right\}\right. \\
&\quad \left. -\left(p_o d/\left(2s_o-3K_2p_o\right)\right)^{1/2} S_i,\quad S_i\right]^{\mathbf{T}} \qquad (6.2)
\end{aligned}$$

Substituting the value of A_1 from Eq. (6.2) into Eq. (6.1), one obtains (neglecting terms of order ε^3 and higher),

$$\begin{aligned}
\partial A_1/\partial\tau' &= -\left(p_o d/\left(2s_o-3K_2p_o\right)\right)^{1/2}\varepsilon^2\left(\partial W_1/\partial\tau_1'\right) \\
&\quad -\left(p_o d/\left(2s_o-3K_2p_o\right)\right)^{1/2}\varepsilon^3[\kappa^{(1)}p_o^{-1}\left(\partial W_1/\partial_{\tau_1'}\right)\Big/\Big\{\ p_o-d^{1/2} \\
&\quad \left(2s_op_o-3K_2p_o^2\right)^{1/2}\Big\}+\left(\partial S_1/\partial\tau_1'\right)+\left(\partial W_1/\partial\tau_2'\right)] \qquad (6.3)
\end{aligned}$$

Incorporating the solvability conditions, Eqs. (5.13) and (5.17), into Eq. (6.3), we obtain the amplitude equation in its standard form as given below with the help of Eqs. (5.3) and (6.2) – neglecting terms of order ε^3 and higher.

$$\tau_o(\partial A_1/\partial\tau) = \mu A_1+\bar{v}\bar{A}_2\bar{A}_3-g|A_1|^2A_1-\ h\left(|A_2|^2+|A_3|^2\right)A_1 \qquad (6.4)$$

where,

$$\tau_o = \left[d\left(1+K'\right)-1\right]/\kappa_c \qquad (6.5)$$

$$\mu = \left(\kappa-\kappa_c\right)/\kappa_c \qquad (6.6)$$

which, is a normalized distance from onset,

$$\begin{aligned}
\bar{v} &= (2/\kappa_c p_o)\cdot\left\{p_o-d^{1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2}\right\} \\
&\quad \cdot\left\{2p_o-\left(s_o-3K_2p_o\right)\cdot\left(p_o d/\left(2s_o-3K_2p_o\right)\right)^{1/2}\right\} \qquad (6.7)
\end{aligned}$$

$$g = -(C_1/dp_o^2\kappa_c)\cdot\left(2s_o-3K_2p_o\right)\cdot\left\{p_o-d^{1/2}\left(2s_op_o-\ 3K_2p_o^2\right)^{1/2}\right\} \qquad (6.8)$$

$$h = -(C_{23}/dp_o^2\kappa_c)\cdot\left(2s_o-3K_2p_o\right)\cdot\left\{p_o-d^{1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2}\right\} \qquad (6.9)$$

Similar equations for A_2 and A_3 can be obtained by circular permutation of the indices.

7 Results and discussion

Amplitudes in Eq. (6.4) can be written as

$$A_j = R_j \exp\left(i\phi_j\right) \tag{7.1}$$

From linear stability analysis [25–28] (the eigenvalue properties), the amplitude Eq. (6.4) may possess three types of solutions: i) steady state, ii) stripe patterns of amplitude $R_1 = (\mu/g)^{1/2}$, $R_2 = R_3 = 0$ and iii) hexagonal patterns [1,29] H_o or H_π ($R_1 = R_2 = R_3$, with $\phi = \phi_1 + \phi_2 + \phi_3 = 0$ or π respectively). The bifurcation scenario for the amplitude Eq. (6.4) is presented below in the form of amplitude as a function of the bifurcation parameter μ (the normalized distance from onset) for stripe state (R_S) and hexagon state (R_H) respectively—μ_i's given by

$$\begin{aligned} \mu_{H1} &= -\bar{v}^2/4(g+2h); \quad \mu_S = \bar{v}^2 g/\,(h-g)^2 \\ \mu_{H2} &= (2g+h)\bar{v}^2/(h-g)^2 \end{aligned} \tag{7.2}$$

The stable branch is $H_o(H_\pi)$ if $\bar{v} > 0\,(\bar{v} < 0)$ for Turing pattern amplitude Eq. (6.4) [1,29]. A subcritical hexagonal branch appears at $\mu_{H1} < 0$, and remains stable until $\mu_{H2} > 0$. The supercritical stripe branch is unstable near the critical point, but becomes stable for $\mu > \mu_S$. Both branches (stripes and hexagons) are stable in the range $\mu_S < \mu < \mu_{H2}$. This bistable region produces either stable stripes or stable hexagon pattern, which is decided by the prior history of the change of the bifurcation parameter μ.

The present manuscript has reported the derivation of Turing instability condition by a linear stability analysis of the reversible Sel'kov model in terms of the critical value κ_c (of the parameter κ) and the critical wavenumber $k_c$at the Turing bifurcation point as shown in Eqs. (3.11) and (3.13) respectively. These values of κ_c and k_c have been subsequently used during the derivation of amplitude Eq. (6.4) for this model R-D system in the framework of a weakly nonlinear theory. This amplitude equation interprets the structural transitions and the stability of various forms of Turing structures. The interesting aspect of this amplitude equation derivation from mathematical point of view is that, the analytical steady state of this model system is highly complicated [20] in algebraic form, whereas only those R-D systems have been chosen for amplitude equation derivation in the past [1,2,7–13], for which the kinetic steady states have simple-looking analytical solution.

The amplitude Eq. (6.4) clearly indicates that time-invariant amplitudes are independent of K' (degree of complexing reaction with the activator species ADP)—K' included only in the expression for τ_o. This result is reminiscent of that obtained in Eq. (3.13) and other models [21,24] showing that Turing pattern wavelength is independent of complexing reaction with the activator species.

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Appendix A

$$P_o = (2N/D)\cdot\left\{p_o^2 + d\left(-1+2s_op_o-3K_2p_o^2\right) - 2p_o d^{1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2}\right\}$$
$$\cdot\left(|W_1|^2+|W_2|^2+|W_3|^2\right) \quad (A1)$$

$$S_o = (2N/D)\cdot\left(|W_1|^2+|W_2|^2+|W_3|^2\right) \quad (A2)$$

$$P_1\left\{p_o d^{-1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2} + \left(-2s_op_o+3K_2p_o^2\right)\right\}$$
$$+S_1\left\{p_o^2 - p_o d^{1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2}\right\} = -\kappa^{(1)}W_1 \quad (A3)$$

$$P_{11} = (N/9D)\cdot\left\{p_o^2 - 3d\left(-1+2s_op_o-3K_2p_o^2\right) + 2p_o d^{1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2}\right\}$$
$$W_1^2 \quad (A4)$$

$$S_{11} = (N/9D)\cdot\left\{-3+8s_op_o-12K_2p_o^2-4p_o d^{-1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2}\right\}W_1^2 \quad (A5)$$

$$P_{12} = (N/2D)\cdot\left\{p_o^2 - 2d\left(-1+2s_op_o-3K_2p_o^2\right) + p_o d^{1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2}\right\}$$
$$W_1\bar{W}_2 \quad (A6)$$

$$S_{12} = (N/2D)\cdot\left\{-2+6s_op_o-9K_2p_o^2-3p_o d^{-1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2}\right\}$$
$$W_1\bar{W}_2 \quad (A7)$$

where,

$$N = 2p_o\left(p_o d/\left(2s_o-3K_2p_o\right)\right)^{1/2} - (p_o d)\left(s_o-3K_2p_o\right)/\left(2s_o-3K_2p_o\right) \quad (A8)$$

$$D = p_o^2\left(2s_op_o-3K_2p_o^2\right) + d\left(-1+2s_op_o-3K_2p_o^2\right)^2$$
$$-2p_o d^{1/2}\left(-1+2s_op_o-3K_2p_o^2\right)\cdot\left(2s_op_o-3K_2p_o^2\right)^{1/2} \quad (A9)$$

Appendix B

$$C_1 = (4N/D)\cdot\left\{p_o - \left(s_o-3K_2p_o\right)\cdot\left(p_o d/\left(2s_o-3K_2p_o\right)\right)^{1/2}\right\}$$
$$\cdot\left\{p_o^2 + d\left(-1+2s_op_o-3K_2p_o^2\right) - 2p_o d^{1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2}\right\}$$

$$+(2N/9D)\cdot\left\{p_o-\left(s_o-3K_2p_o\right)\cdot\left(p_od/\left(2s_o-3K_2p_o\right)\right)^{1/2}\right\}$$
$$\cdot\left\{p_o^2-3d\left(-1+2s_op_o-3K_2p_o^2\right)+2p_od^{1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2}\right\}$$
$$-(4p_oN/D)\cdot\left(p_od/\left(2s_o-3K_2p_o\right)\right)^{1/2}-\left(2p_oN/9D\right)\cdot\left(p_od/\left(2s_o-3K_2p_o\right)\right)^{1/2}$$
$$\left\{-3+8s_op_o-12K_2p_o^2-4p_od^{-1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2}\right\}$$
$$+3\left\{\left(p_od/\left(2s_o-3K_2p_o\right)\right)+K_2\left(p_od/\left(2s_o-3K_2p_o\right)\right)^{3/2}\right\}\qquad\text{(B1)}$$

$$C_{23}=(4N/D)\cdot\left\{p_o-\left(s_o-3K_2p_o\right)\cdot\left(p_od/\left(2s_o-3K_2p_o\right)\right)^{1/2}\right\}$$
$$\cdot\left\{p_o^2+d\left(-1+2s_op_o-3K_2p_o^2\right)-2p_od^{1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2}\right\}$$
$$+(N/D)\cdot\left\{p_o-\left(s_o-3K_2p_o\right)\cdot\left(p_od/\left(2s_o-3K_2p_o\right)\right)^{1/2}\right\}$$
$$\cdot\left\{p_o^2-2d\left(-1+2s_op_o-3K_2p_o^2\right)+p_od^{1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2}\right\}$$
$$-(4p_oN/D)\cdot\left(p_od/\left(2s_o-3K_2p_o\right)\right)^{1/2}-\left(p_oN/D\right)\cdot\left(p_od/\left(2s_o-3K_2p_o\right)\right)^{1/2}$$
$$\left\{-2+6s_op_o-9K_2p_o^2-3p_od^{-1/2}\left(2s_op_o-3K_2p_o^2\right)^{1/2}\right\}$$
$$+6\left\{\left(p_od/\left(2s_o-3K_2p_o\right)\right)+K_2\left(p_od/\left(2s_o-3K_2p_o\right)\right)^{3/2}\right\}\qquad\text{(B2)}$$

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