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A Turing model with correlated random walk*

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Abstract. If in the classical Turing model the diffusion process (Brownian motion) is replaced by a more general correlated random walk, then the parameters describing spatial spread are the particle speeds and the rates of change in direction. As in the Turing model, a spatially constant equilibrium can become unstable if the different species have different turning rates and different speeds. Furthermore, a Hopf bifurcation can be found if the reproduction rate of the activator is greater than its rate of change of direction, and oscillating patterns are possible.

Key words: Random walk – Pattern formation – Hyperbolic system

1 Introduction

Reaction–diffusion equations

$$u_t = D\triangle u + f(u) \tag{1}$$

model the interaction of particles moving in space, where $u(t, x) = (u_1(t, x), \ldots, u_n(t, x))$ is a vector of densities of n types of particles.

The reaction alone is described by the reaction equation

$$\dot{u} = f(u)\ , \tag{2}$$

where $f: \mathbb{R}^n \to \mathbb{R}^n$ is continuously differentiable. Spatial spread is governed by the diffusion equation

$$u_t = D\triangle u\ .$$

The diffusion coefficient $D = \mathrm{diag}(d_1, \ldots, d_n)$ is a diagonal matrix with non-negative entries $d_j \geqq 0, j = 1, \ldots, n$.

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Reaction–diffusion equations have been studied both theoretically and in connection with applications by numerous authors (see, in particular the monographs by Henry [10], Rothe [20], Smoller [21], Temam [23] and others).

A natural approach is to first study the pure reaction equation. If there is a stable stationary solution one might guess that the reaction diffusion system (1) has a stable equilibrium as well. As Turing [24] pointed out, this conjecture is wrong even for linear systems. If different species have different diffusion rates then pattern formation may occur.

Of course the deterministic system (1) is based on the assumption that the particle number is large and the mean free path length is small. In the diffusion equation it is assumed that the particle speed can be arbitrarily large. This assumption may be appropriate in chemical reactions but in other contexts, e.g. biological populations such as microorganisms or bacteria, the assumption of finite speed is more appropriate. Consequently other models for motion should be studied, e.g. correlated random walks. In this paper we address the question of Turing instabilities, if the diffusion process is replaced by correlated random walk.

Correlated random walks for a single species in one space dimension, and the corresponding hyperbolic system, have been studied in detail by Taylor [22], Goldstein [6] and Kac [13]; see also Zauderer [25]. Kac has found an equivalence with the telegraph equation. In connection with problems of reaction and spatial spread rather general systems (velocity jump processes) have been studied by Othmer, Dunbar and Alt [17].

Dunbar and Othmer [2], and Dunbar [1] studied correlated random walks in connection with branching random walk processes and McKean's probability of the most advanced particle. They derived semilinear hyperbolic systems that describe this probability.

Holmes [12] considered a hyperbolic analog of Fisher's equation [3] which describes population growth and motion according to a correlated random walk.

Hadeler [7, 8] defined several such problems and derived corresponding reaction telegraph equations. He proved the existence of travelling front solutions.

1.1 Correlated random walk

First we consider a correlated random walk of one species on the real axis. We assume that particles with density u have constant speed γ and constant turning rate μ. We split $u = \alpha + \beta$ into a particle density α of particles that move to the right and a particle density β of particles that move to the left. The correlated random walk is described by the following system,

$$\begin{aligned} \alpha_t + \gamma\alpha_x &= \mu(\beta - \alpha) \ , \\ \beta_t - \gamma\beta_x &= \mu(\alpha - \beta) \ . \end{aligned} \tag{3}$$

The conservation laws $\alpha_t + \gamma\alpha_x = 0$ and $\beta_t - \gamma\beta_x = 0$ describe particles moving with constant speed γ to the right or left, respectively. The right hand side of this system can be interpreted in terms of a birth–death process. An α particle that moves to the right dies with rate μ and is reborn as a particle moving to the left.

The diffusion equation appears as a limiting case. Indeed, if we differentiate the equations with respect to t and x, eliminate the mixed derivatives α_{tx}, β_{tx} and consider $u = \alpha + \beta$, then we get a telegraph equation $u_{tt} + 2\mu u_t = \gamma^2 u_{xx}$ (Kac [13]). If we divide this equation by 2μ and consider the formal limit $\gamma, \mu \to \infty$, $\lim \gamma^2/2\mu = d < \infty$, we obtain the diffusion equation $u_t = d\, u_{xx}$.

In the correlated random walk model we have finite speed and finite turning rates. In the limit of Brownian motion we have particles that move very fast and turn very often. One can conjecture that the solutions of (3) are close to solutions of the diffusion equation if μ and γ are large and $\gamma^2/2\mu \approx d$. On the other hand one expects that (3) and the diffusion equation behave very differently if γ is large and μ is small. Overall one will expect that correlated random walk systems show a greater variety of phenomena than reaction diffusion systems.

1.2 Correlated random walk with reaction

Now we consider the reaction diffusion equation for one species in one space dimension

$$u_t = du_{xx} + f(u) \tag{4}$$

with a positive diffusion coefficient d.

Following [8] we distinguish several ways in which the reaction term interacts with motion. Whereas in the transition of the ordinary differential equation (2) to the reaction diffusion equation (4) the reaction term is not affected, in the correlated random walk case, due to the partition according to velocity, the nonlinearity can be split in various ways depending on the following modeling assumptions.

(a) First we assume that reaction does not depend on the direction of motion and we further assume that new particles choose either direction with the same probability. Then the system reads

$$\begin{aligned} \alpha_t + \gamma\alpha_x &= \mu(\beta - \alpha) + \tfrac{1}{2} f(\alpha + \beta)\ , \\ \beta_t - \gamma\beta_x &= \mu(\alpha - \beta) + \tfrac{1}{2} f(\alpha + \beta)\ . \end{aligned} \tag{5}$$

(b) If, however, we assume that the reaction is described by a birth–death process $\dot{u} = f(u) = h(u) - ug(u)$, where $h(u)$ is the reproduction term and $g(u)$ is the mortality, then in the first equation only particles that move to the right will disappear. The model equations are then

$$\begin{aligned} \alpha_t + \gamma\alpha_x &= \mu(\beta - \alpha) + \tfrac{1}{2} h(\alpha + \beta) - \alpha\, g(\alpha + \beta)\ , \\ \beta_t - \gamma\beta_x &= \mu(\alpha - \beta) + \tfrac{1}{2} h(\alpha + \beta) - \beta\, g(\alpha + \beta)\ . \end{aligned} \tag{6}$$

(c) If we assume that the direction of newborn particles is correlated to the direction of mother particles we arrive at the following system

$$\begin{aligned} \alpha_t + \gamma\alpha_x &= \mu(\beta - \alpha) + (\tau\alpha + (1-\tau)\beta)\, m(\alpha+\beta) - \alpha g(\alpha+\beta) \ , \\ \beta_t - \gamma\beta_x &= \mu(\alpha - \beta) + ((1-\tau)\alpha + \tau\beta)\, m(\alpha+\beta) - \beta g(\alpha+\beta) \ . \end{aligned} \tag{7}$$

Here the reproduction term is written as $h(u) = u\, m(u)$. The parameter τ, $0 \leqq \tau \leqq 1$, measures the correlation. The uncorrelated case corresponds to $\tau = \frac{1}{2}$, large values of τ describe positive correlation.

We will call each of the systems (5), (6) and (7) a **reaction random walk equation**. In the sequel we only investigate system (5), see also [8] for discussion of travelling front solutions for equations (5) and (6).

From the point of view of modeling physical processes the distinctions make sense only if the reaction process and the motion process act on similar time scales.

1.3 Neumann boundary conditions

We consider equation (4) on a compact interval $[0, l]$ and we assume homogeneous Neumann boundary conditions, i.e.

$$u_x(t, 0) = u_x(t, l) = 0 \ . \tag{8}$$

The Neumann boundary condition describes reflection at the boundary $x = 0$ and $x = l$. We define the corresponding boundary conditions for the hyperbolic system (5). As we have split the total amount of u into particles that move to the right or left we must now assume that particles α arriving at $x = l$ are reflected and thus turned into particles β and similarly at $x = 0$. Thus the appropriate Neumann boundary condition for the reaction random walk equation (5) reads

$$\alpha(t, 0) = \beta(t, 0), \qquad \beta(t, l) = \alpha(t, l) \ . \tag{9}$$

If α and β satisfy (5) with boundary conditions (9) then the particle density $u = \alpha + \beta$ and the net particle flow density $v = \alpha - \beta$ satisfy the equation

$$\begin{aligned} u_t + \gamma v_x &= f(u) \ , \\ v_t + \gamma u_x &= -2\mu v \ , \end{aligned} \tag{10}$$

with boundary condition

$$v(t, 0) = v(t, l) = 0 \ . \tag{11}$$

On the other hand, if (u, v) is a solution of (10), (11) then $\alpha := (u + v)/2$ and $\beta := (u - v)/2$ satisfy (5), (9).

We assume that u and v are twice continuously differentiable solutions of (10). We differentiate the first equation of (10) with respect to t, the second equation with respect to x and eliminate the derivatives v_{tx} and v_x to get a **reaction telegraph equation**

$$u_{tt} + (2\mu - f'(u))\, u_t = \gamma^2 u_{xx} + 2\mu f(u) \ . \tag{12}$$

The boundary condition (9) transforms as follows. Since $v(t, 0) = 0$ for all $t \geqq 0$ also $v_t(t, 0) = 0$ for all $t \geqq 0$. From the second equation of (10) one gets $u_x(t, 0) = 0$, similarly for $x = l$. The transformed boundary condition is exactly the Neumann condition (8)

$$u_x(t, 0) = u_x(t, l) = 0 \ . \tag{13}$$

For systems (6) and (7) the transition to a reaction telegraph equation is not possible in general.

The correspondence of system (10) and equation (12) is as follows. We assume that all solutions are twice continuously differentiable:

(a) If (u, v) is a solution of (10) then u is a solution of (12).

(b) If u is a solution of (12) there exists a one parameter family of functions $\{v_c\}_{c \in \mathbb{R}}$ such that (u, v_c) solves (10).

(c) If (u, v) solves (10) with Neumann boundary conditions (11) then u satisfies (12) with boundary condition (13).

(d) If u is a solution of (12), (13) then there exists a function v such that (u, v) is a solution of (10), (11) if and only if the following compatibility condition for the initial data is satisfied

$$\int_0^l (f(u(0, x)) - u_t(0, x))\, dx = 0 \ .$$

2 Reaction random walk systems

Now we return to the reaction diffusion equation (1) for n species moving in one space dimension $x \in \mathbb{R}$. Writing (1) in coordinates one has

$$u_{jt} = d_j u_{jxx} + f_j(u_1, \ldots, u_n) \ ,$$

where the subscript $j = 1, \ldots, n$ numbers the species and the subscripts t and x denote partial derivatives.

We split each particle density $u_j = \alpha_j + \beta_j$ into particle densities for left and right moving particles and consider for each $j = 1, \ldots, n$ in analogy to (5) the corresponding reaction random walk equation

$$\begin{aligned} \alpha_{jt} + \gamma_j \alpha_{jx} = &\quad \mu_j(\beta_j - \alpha_j) + \tfrac{1}{2} f_j(\alpha_1 + \beta_1, \ldots, \alpha_n + \beta_n) \ , \\ \beta_{jt} + \gamma_j \beta_{jx} = &\quad \mu_j(\alpha_j - \beta_j) + \tfrac{1}{2} f_j(\alpha_1 + \beta_1, \ldots, \alpha_n + \beta_n) \ . \end{aligned} \tag{14}$$

Each species has a speed $\gamma_j > 0$ and a turning rate $\mu_j > 0$.

We introduce diagonal matrices

$$\Gamma := \begin{pmatrix} \gamma_1 & & \\ & \ddots & \\ & & \gamma_n \end{pmatrix}, \qquad M := \begin{pmatrix} \mu_1 & & \\ & \ddots & \\ & & \mu_n \end{pmatrix},$$

vectors of the dependent variables

$$a := (\alpha_1, \ldots, \alpha_n)^T \ , \qquad b := (\beta_1, \ldots, \beta_n)^T$$

and a function $f\colon \mathbb{R}^n \to \mathbb{R}^n$

$$f(u) = (f_1(u_1, \ldots, u_n), \ldots, f_n(u_1, \ldots, u_n))^T ,$$

to get the more transparent notation for (14)

$$\begin{aligned} a_t + \Gamma a_x &= M(b-a) + \tfrac{1}{2} f(a+b) \ , \\ b_t - \Gamma b_x &= M(a-b) + \tfrac{1}{2} f(a+b) \ . \end{aligned} \tag{15}$$

This equation is called a **reaction random walk system**.

We introduce Neumann boundary conditions at $[0, l]$

$$a(t,0) = b(t,0), \qquad b(t,l) = a(t,l) \ . \tag{16}$$

We can proceed as before to arrive at a reaction telegraph system. Introduce $u := a + b$ and $v := a - b$ as new dependent variables; then the system reads

$$\begin{aligned} u_t + \Gamma v_x &= f(u) \ , \\ v_t + \Gamma u_x &= -2Mv \ , \end{aligned} \tag{17}$$

with boundary conditions equivalent to (16)

$$v(t,0) = v(t,l) = 0 \ . \tag{18}$$

If we differentiate the first equation of (17) with respect to t, the second equation of (17) with respect to x and eliminate the derivatives v_{tx} and v_x, then we arrive at the **reaction telegraph system**

$$u_{tt} + (2M - f'(u))\, u_t = \Gamma^2 u_{xx} + 2M f(u) \tag{19}$$

where $f'(u)$ is the Jacobian of f at u. To consider the limit of Brownian motion we multiply this equation by $(2M)^{-1}$

$$(2M)^{-1} u_{tt} + (I - (2M)^{-1} f'(u))\, u_t = (2M)^{-1} \Gamma^2 u_{xx} + f(u) \ .$$

We let the speeds γ_j and the turning rates μ_j go to infinity in such a way that the limits $\gamma_j^2/(2\mu_j) \to d_j$ exist. Define $D = \operatorname{diag}(d_1, \ldots, d_n)$. As a formal limit we obtain the reaction diffusion equation (1).

2.1 Linear analysis

Let the reaction equation $\dot{u} = f(u)$ have a stationary state $\hat{u} \in \mathbb{R}^n$ and let $A := f'(\hat{u})$ be the Jacobian of f at this point. Then there is a steady state for the corresponding reaction random walk system (15) with Neumann boundary conditions (16)

$$(\bar{a}(x), \bar{b}(x)) = \left(\frac{\hat{u}}{2}, \frac{\hat{u}}{2} \right) .$$

In the u, v notation the equilibrium of (17) with boundary conditions (18) is

$$(\bar{u}(x), \bar{v}(x)) = (\hat{u}, 0) \ .$$

The linearisation of (17) with boundary condition (18) at this point is

$$\begin{aligned} u_t + \Gamma v_x &= Au \ , \\ v_t + \Gamma u_x &= -2Mv \ , \end{aligned} \tag{20}$$

with boundary condition

$$v(t, 0) = v(t, l) = 0 \ . \tag{21}$$

Using the Lumer–Phillips-Theorem (see Pazy [18]) one can show that (20) with (21) defines an operator semigroup in $(L^2[0, l] \times L^2[0, l])^n$ ([11]). The generator has a pure point spectrum. A similar result was pointed out by Neves, Ribeiro and Lopes [16]. Thus the stability of the spatially constant solution is determined by eigenvalues λ of the corresponding eigenvalue problem

$$\begin{aligned} \lambda u + \Gamma v_x &= Au \ , \\ \lambda v + \Gamma u_x &= -2Mv \ , \end{aligned} \tag{22}$$

with boundary condition

$$v(0) = v(l) = 0 \ . \tag{23}$$

If all eigenvalues of (22), (23) have negative real parts then the zero solution of (20), (21) is stable. If there is an eigenvalue λ with $\operatorname{Re}\lambda > 0$ then it is unstable.

We solve for the derivatives and put

$$R(\lambda) := -\Gamma^{-1}(2M + \lambda I), \qquad S(\lambda) := \Gamma^{-1}(A - \lambda I) \ ,$$

where I is the identity. The eigenvalue problem assumes the form

$$\begin{pmatrix} u \\ v \end{pmatrix}' = \begin{pmatrix} 0 & R(\lambda) \\ S(\lambda) & 0 \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}, \tag{24}$$

with boundary condition

$$v(0) = v(l) = 0 \ , \tag{25}$$

where we used $'$ for the spatial derivative.

Since we are interested in the possible existence of eigenvalues λ with $\operatorname{Re}\lambda \geqq 0$ we can assume that $\operatorname{Re}\lambda > \max_{j=1,\ldots,n}\{-2\mu_j\}$. Then $R(\lambda)$ is regular. From (24) we have $u'(x) = R(\lambda)\, v(x)$, then the boundary condition (25) for v is equivalent to the boundary condition

$$u'(0) = u'(l) = 0 \ . \tag{26}$$

It is useful to consider the second derivative of (u, v)

$$\begin{pmatrix} u \\ v \end{pmatrix}'' = \begin{pmatrix} R(\lambda)S(\lambda) & 0 \\ 0 & S(\lambda)R(\lambda) \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}, \tag{27}$$

with boundary conditions (25) and (26). Here the equations for u and v are separated, and one may write the solution of (24) as

$$\begin{pmatrix} u(x) \\ v(x) \end{pmatrix} = \exp\left(x \begin{pmatrix} 0 & R(\lambda) \\ S(\lambda) & 0 \end{pmatrix} \right) \begin{pmatrix} u(0) \\ v(0) \end{pmatrix}.$$

We evaluate this solution at $x = l$, use the boundary conditions (25), write down the exponential series and sort even and odd exponents. Then we arrive at a nonlinear equation in λ

$$\det\left(\sum_{k=0}^{\infty} \frac{l^{2k+1}}{(2k+1)!}(S(\lambda)R(\lambda))^k S(\lambda)\right) = 0 \ . \tag{28}$$

Lemma 2.1 *The complex number* λ with $\operatorname{Re}\lambda > \max_{j=1,\ldots,n}\{-2\mu_j\}$ *is an eigenvalue of* (22), (23) *if one of the following conditions is satisfied.*

1. (24), (25) *has a nontrivial solution,*
2. (27), (25), (26) *has a nontrivial solution,*
3. *Equation* (28) *is satisfied.*

3 The Turing model

Some interesting effects of destabilization by diffusion occur in the classical Turing model (Turing [24], Maginu [14], Murray [15])

$$\begin{aligned} u_{1t} &= D_1 u_{1xx} + f_1(u_1, u_2) \ , \\ u_{2t} &= D_2 u_{2xx} + f_2(u_1, u_2) \ , \end{aligned} \tag{29}$$

where u_1 and u_2 are densities of two species and D_1, D_2 are the corresponding diffusion rates. The functions f_1 and f_2 describe the reactions between these species

$$\begin{aligned} \dot{u}_1 &= f_1(u_1, u_2) \ , \\ \dot{u}_2 &= f_2(u_1, u_2) \ . \end{aligned} \tag{30}$$

We consider homogeneous Neumann boundary conditions on the compact interval $[0, l]$

$$u_{1x}(t, 0) = u_{1x}(t, l) = u_{2x}(t, 0) = u_{2x}(t, l) = 0 \ . \tag{31}$$

Let $(\hat{u_1}, \hat{u_2})$ be a steady state of (30). Then system (29) with boundary conditions (31) has a spatially constant equilibrium at $(\bar{u}_1(x), \bar{u}_2(x)) \equiv (\hat{u_1}, \hat{u_2})$.

Let

$$A = \begin{pmatrix} a_1 & a_2 \\ a_3 & a_4 \end{pmatrix} = \begin{pmatrix} \partial_1 f_1(\hat{u_1}, \hat{u_2}) & \partial_2 f_1(\hat{u_1}, \hat{u_2}) \\ \partial_1 f_2(\hat{u_1}, \hat{u_2}) & \partial_2 f_2(\hat{u_1}, \hat{u_2}) \end{pmatrix} \tag{32}$$

be the Jacobian of (f_1, f_2) at $(\hat{u_1}, \hat{u_2})$.

Under suitable assumptions on the parameters the spatially constant equilibrium $(\bar{u}_1, \bar{u}_2)$ of (29) can be destabilized by choosing different diffusion rates D_1, D_2. We assume

(H1) $(\hat{u_1}, \hat{u_2})$ is a stable equilibrium of (30), i.e. $a_1 + a_4 < 0$ and $a_1 a_4 - a_2 a_3 > 0$.

(H2) $a_1 > 0, \quad a_4 < 0,$

and thus $a_2 a_3 < 0$. The choice of the signs in (H2) corresponds to the usual **activator inhibitor system** (Murray [15], Gierer and Meinhardt [5]).

Theorem 3.1 (Turing) *Assume* (H1) *and* (H2) *are satisfied. The spatially constant equilibrium is unstable if and only if*

(a) $\sqrt{\frac{D_2}{D_1}} > \frac{\sqrt{\det A} + \sqrt{-a_2 a_3}}{a_1}$,

(b) *There exists a mode* $k \in \mathbb{N}$ *such that* $\frac{\sqrt{\theta_1} l}{\pi} < k < \frac{\sqrt{\theta_2} l}{\pi}$, *where*

$$\theta_{1,2} = \frac{1}{2D_1 D_2}\left(D_1 a_4 + D_2 a_1 \pm \sqrt{(D_1 a^4 - D_2 a_1)^2 + 4D_1 D_2 a_2 a_3}\right) \quad (33)$$

Remarks:

1. Turing [24] found the effect of pattern formation, but he did not really state a theorem in the above way. He modeled reacting morphogens which diffuse in a ring of cells. His model is a special case of (29) with periodic boundary conditions (Maginu [14]). The case with Neumann boundary conditions is considered in Murray [15] and stability conditions are derived. In Theorem 3.1 we use a form of the stability condition proposed by Hadeler [9].

2. This Theorem is a result of a linear stability analysis. The linearization

$$\begin{aligned} u_{1t} &= D_1 u_{1xx} + a_1 u_1 + a_2 u_2 \ , \\ u_{2t} &= D_2 u_{2xx} + a_3 u_1 + a_4 u_2 \ , \end{aligned} \quad (34)$$

of (29) at the spatially constant solution defines an operator semigroup in appropriate function spaces (e.g. $L^2([0, l])$. With boundary condition (31) the generator of (34) has pure point spectrum. Thus the stability of the spatially constant equilibrium is determined by the eigenvalues of the corresponding eigenvalue problem

$$\begin{aligned} \lambda u_1 &= D_1 u_{1xx} + a_1 u_1 + a_2 u_2 \ , \\ \lambda u_2 &= D_2 u_{2xx} + a_3 u_1 + a_4 u_2 \ , \end{aligned} \quad (35)$$

with boundary conditions (31).

The eigenvalues of (35) are discrete and correspond to **modes** $k \in \mathbb{N}$ in the following way:

λ *is an eigenvalue of* (35) *if and only if for some* $k \in \mathbb{N}$

$$\det(\lambda - A - D\theta) = 0, \quad \textit{where } \theta = \frac{k^2 \pi^2}{l^2}. \quad (36)$$

Since (36) defines a quadratic polynomial in λ for each mode $k \in \mathbb{N}$ there are two eigenvalues $\lambda(k)$. The eigenfunctions are given by

$$\begin{pmatrix} U_1 \\ U_2 \end{pmatrix}(x) = \begin{pmatrix} c_1 \\ c_2 \end{pmatrix} \cos\left(\frac{k\pi}{l} x\right). \quad (37)$$

Condition (b) of Theorem 3.1 characterizes the modes $k \in \mathbb{N}$ such that at least one of the corresponding eigenvalues $\lambda(k)$ given by (36) has positive real part.

Condition (a) of Theorem 3.1 guarantees that $\theta_{1,2} \in \mathbb{R}$.

3. To consider bifurcations one may vary the length of the interval l or one of the diffusion rates D_1, D_2. We look for bifurcations by increasing D_2, where all remaining parameters are fixed.

For small D_2 condition (a) of Theorem 3.1 is not true. If D_2 increases such that (a) is satisfied, there is an interval $(\sqrt{\theta_1}l/\pi, \sqrt{\theta_2}l/\pi)$ of possible modes $k \in \mathbb{N}$. This interval grows with increasing D_2 and there is a first mode k_0 which is contained in this interval. Then there exists an eigenvalue $\lambda(k_0)$ with positive real part and the constant solution becomes unstable. The eigenfunction (37) of $\lambda(k_0)$ dominates the shape of the solution. A cosine pattern of mode k_0 appears.

4. Eigenvalues of the linearization (34) never cross the imaginary axis with nonvanishing imaginary part. There is no Hopf bifurcation from the spatially constant solution.

5. Remark 4 does not exclude the existence of oscillating spatial patterns in general reaction diffusion systems, e.g. the Brusselator (Prigogine, Nicolis [19]). In that situation the reaction equation shows oscillatory behavior for appropriate parameters, i.e. (H1) and (H2) are not satisfied.

Furthermore secondary bifurcations may occur which lead to oscillating patterns, independent of the conditions (H1) and (H2).

Now we perform the transition to correlated random walks. For each $j = 1, 2$ split the particles into right and left moving particles $u_j = \alpha_j + \beta_j$. Assume that each particle moves with a constant speed γ_j and changes direction with rate μ_j, $j = 1, 2$. Let

$$u := \begin{pmatrix} u_1 \\ u_2 \end{pmatrix}, \qquad a := \begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix}, \qquad b := \begin{pmatrix} \beta_1 \\ \beta_2 \end{pmatrix},$$

$$\Gamma := \begin{pmatrix} \gamma_1 0 \\ 0\ \gamma_2 \end{pmatrix}, \qquad M := \begin{pmatrix} \mu_1 0 \\ 0\ \mu_2 \end{pmatrix}. \tag{38}$$

Then the reaction random walk system corresponding to (29) with boundary conditions (31) is given by (15) with Neumann boundary conditions (16).

4 Linear analysis of the random walk Turing model

For linear analysis we use the characterization 2. of Lemma 2.1 for λ to be an eigenvalue. The matrices occurring in (27) are

$$R(\lambda) = \begin{pmatrix} -\frac{1}{\gamma_1}(2\mu_1 + \lambda) & 0 \\ 0 & -\frac{1}{\gamma_2}(2\mu_2 + \lambda) \end{pmatrix},$$

$$S(\lambda) = \begin{pmatrix} \frac{1}{\gamma_1}(a_1 - \lambda) & \frac{a_2}{\gamma_1} \\ \frac{a_3}{\gamma_2} & \frac{1}{\gamma_2}(a_4 - \lambda) \end{pmatrix}.$$

With the notation

$$\begin{aligned} \kappa_1 &= \frac{1}{\gamma_1^2}(\lambda + 2\mu_1)(a_1 - \lambda) \ , & \kappa_2 &= \frac{1}{\gamma_2^2}(\lambda + 2\mu_2)(a_4 - \lambda) \ , \\ m_1 &= \frac{1}{\gamma_1}(\lambda + 2\mu_1) \ , & m_2 &= \frac{1}{\gamma_2}(\lambda + 2\mu_2) \ , \\ \tilde{a}_2 &= \frac{a_2}{\gamma_1} \ , & \tilde{a}_3 &= \frac{a_3}{\gamma_2} \ . \end{aligned} \tag{39}$$

we have

$$R(\lambda)S(\lambda) = \begin{pmatrix} -\kappa_1 & -\tilde{a}_2 m_1 \\ -\tilde{a}_3 m_2 & -\kappa_2 \end{pmatrix}, \quad S(\lambda)\, R(\lambda) = \begin{pmatrix} -\kappa_1 & -\tilde{a}_2 m_2 \\ -\tilde{a}_3 m_1 & -\kappa_2 \end{pmatrix}.$$

In system (27) as well as in the boundary conditions (25), (26) u and v separate. We investigate the equations for u alone and determine conditions on λ such that a nontrivial solution of (27) exists. Then we consider the equations for v and compare the solvability condition to the first case.

4.1 Equation for u

The equation for u in (27) is

$$\begin{pmatrix} u_1'' \\ u_2'' \end{pmatrix} = \begin{pmatrix} -\kappa_1 & -\tilde{a}_2 m_1 \\ -\tilde{a}_3 m_2 & -\kappa_2 \end{pmatrix} \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} \tag{40}$$

with boundary condition (26)

$$u_1'(0) = u_1'(l) = u_2'(0) = u_2'(l) = 0 \ , \tag{41}$$

and $\kappa_1, \kappa_2, m_1, m_2, \tilde{a}_2, \tilde{a}_3$ as in (39). Let the matrix in (40) be called B.

To solve (40) we calculate the eigenvalues and the corresponding eigenvectors of B. The eigenvalues are

$$p_{1,2} = -\frac{\kappa_1 + \kappa_2}{2} \pm \frac{1}{2}\sqrt{\mathscr{D}} \ , \tag{42}$$

with discriminant

$$\mathscr{D} = (\kappa_1 - \kappa_2)^2 + 4\tilde{a}_2\tilde{a}_3 m_1 m_2 \ .$$

It is convenient to write the corresponding eigenvectors in the form

$$\xi_1 = \begin{pmatrix} -\tilde{a}_2 m_1 \\ \frac{1}{2}(\kappa_1 - \kappa_2) + \frac{1}{2}\sqrt{\mathscr{D}} \end{pmatrix}, \qquad \xi_2 = \begin{pmatrix} -\tilde{a}_2 m_1 \\ \frac{1}{2}(\kappa_1 - \kappa_2) - \frac{1}{2}\sqrt{\mathscr{D}} \end{pmatrix}.$$

If $\mathscr{D} \neq 0$ then the two eigenvectors ξ_1, ξ_2 are linearly independent.

The discriminant is, in explicit form,

$$\mathscr{D} = \left(\frac{1}{\gamma_1^2}(\lambda + 2\mu_1)(a_1 - \lambda) - \frac{1}{\gamma_2^2}(\lambda + 2\mu_2)(a_4 - \lambda)\right)^2 + \frac{4a_2a_3}{\gamma_1\gamma_2}(\lambda + 2\mu_1)(\lambda + 2\mu_2)$$

In Sect. 2.1 we assumed $\operatorname{Re}\lambda > \max\{-2\mu_1, -2\mu_2\}$, hence $\mathscr{D} \neq 0$ and ξ_1, ξ_2 are linearly independent.

Under this assumption the general solution of (40) is

$$\begin{pmatrix} u_1 \\ u_2 \end{pmatrix}(x) = (\eta_1 e^{\sqrt{p_1}x} + \eta_2 e^{-\sqrt{p_1}x})\xi_1 + (\eta_3 e^{\sqrt{p_2}x} + \eta_4 e^{-\sqrt{p_2}x})\xi_2$$

and its first derivative is

$$\begin{pmatrix} u_1' \\ u_2' \end{pmatrix}(x) = (\sigma_1 e^{\sqrt{p_1}x} - \sigma_2 e^{-\sqrt{p_1}x})\xi_1 + (\sigma_3 e^{\sqrt{p_2}x} - \sigma_4 e^{-\sqrt{p_2}x})\xi_2, \tag{43}$$

with $\quad \sigma_1 = \eta_1\sqrt{p_1}, \quad \sigma_2 = \eta_2\sqrt{p_1}, \quad \sigma_3 = \eta_3\sqrt{p_2}, \quad \sigma_4 = \eta_4\sqrt{p_2}.$

Substituting (43) into the boundary conditions (41), we obtain the linear system for $(\sigma_1, \sigma_2, \sigma_3, \sigma_4)$:

$$\begin{aligned}
u_1'(0) = 0\colon\ & (\sigma_1 - \sigma_2)(-\tilde{a}_2 m_1) + (\sigma_3 - \sigma_4)(-\tilde{a}_2 m_1) = 0 \\
& \sigma_1 - \sigma_2 + \sigma_3 - \sigma_4 = 0 \\
u_1'(l) = 0\colon\ & (\sigma_1 e^{\sqrt{p_1}l} - \sigma_2 e^{-\sqrt{p_1}l})(-\tilde{a}_2 m_1) + (\sigma_3 e^{\sqrt{p_2}l} - \sigma_4 e^{-\sqrt{p_2}l})(-\tilde{a}_2 m_1) = 0 \\
& (\sigma_1 e^{\sqrt{p_1}l} - \sigma_2 e^{-\sqrt{p_1}l}) + (\sigma_3 e^{\sqrt{p_2}l} - \sigma_4 e^{-\sqrt{p_2}l}) = 0 \\
u_2'(0) = 0\colon\ & (\sigma_1 - \sigma_2)(\tfrac{1}{2}(\kappa_1 - \kappa_2) + \tfrac{1}{2}\sqrt{\mathscr{D}}) + (\sigma_3 - \sigma_4)(\tfrac{1}{2}(\kappa_1 - \kappa_2) - \tfrac{1}{2}\sqrt{\mathscr{D}}) = 0 \\
u_2'(l) = 0\colon\ & (\sigma_1 e^{\sqrt{p_1}l} - \sigma_2 e^{-\sqrt{p_1}l})(\tfrac{1}{2}(\kappa_1 - \kappa_2) + \tfrac{1}{2}\sqrt{\mathscr{D}}) \\
& (\sigma_3 e^{\sqrt{p_2}l} - \sigma_4 e^{-\sqrt{p_2}l})(\tfrac{1}{2}(\kappa_1 - \kappa_2) + \tfrac{1}{2}\sqrt{\mathscr{D}}) = 0
\end{aligned} \tag{44}$$

To get a more comprehensible view, we define the quantities

$$r = \tfrac{1}{2}(\kappa_1 - \kappa_2), \qquad s = \tfrac{1}{2}\sqrt{\mathscr{D}}\ .$$

Then the determinant of the linear system (44) is

$$\det\begin{pmatrix} 1 & -1 & 1 & -1 \\ e^{\sqrt{p_1}l} & -e^{-\sqrt{p_1}l} & e^{\sqrt{p_2}l} & -e^{-\sqrt{p_2}l} \\ r+s & -(r+s) & r-s & -(r-s) \\ (r+s)e^{\sqrt{p_1}l} & -(r+s)e^{-\sqrt{p_1}l} & (r-s)e^{\sqrt{p_2}l} & -(r-s)e^{-\sqrt{p_2}l} \end{pmatrix}$$

$$= \det \begin{pmatrix} 1 & -1 & 1 & -1 \\ e^{\sqrt{p_1}l} & -e^{-\sqrt{p_1}l} & e^{\sqrt{p_2}l} & -e^{-\sqrt{p_2}l} \\ 0 & 0 & -2s & 2s \\ 0 & 0 & -2se^{\sqrt{p_2}l} & 2se^{-\sqrt{p_2}l} \end{pmatrix}$$

$$= \det \begin{pmatrix} 1 & -1 \\ e^{\sqrt{p_1}l} & -e^{-\sqrt{p_1}l} \end{pmatrix} \det \begin{pmatrix} -2s & 2s \\ -2se^{\sqrt{p_2}l} & 2se^{-\sqrt{p_2}l} \end{pmatrix} \tag{45}$$

To get the first equality add $-(r+s)$ times the 1st row to the 3rd and $-(r+s)$ times the 2nd row to the 4th.

System (44) has a nontrivial solution for $(\sigma_1, \sigma_2, \sigma_3, \sigma_4)$ if the determinant (45) is zero. Since $s \neq 0$, this is equivalent to

$$-e^{-\sqrt{p_1}l} = -e^{\sqrt{p_1}l}, \quad \text{or} \quad -e^{-\sqrt{p_2}l} = -e^{\sqrt{p_2}l}$$

$$\Leftrightarrow \quad e^{2\sqrt{p_1}l} = 1, \quad \text{or} \quad e^{2\sqrt{p_2}l} = 1$$

$$\Leftrightarrow \exists k \in Z\colon\ 2\sqrt{p_1}l = 2k\pi i, \quad \text{or} \quad 2\sqrt{p_2}l = 2k\pi i \tag{46}$$

$$\Leftrightarrow \exists k \in \mathbb{N}\colon\ -\frac{1}{2}(\kappa_1 + \kappa_2) + \frac{1}{2}\sqrt{\mathscr{D}} = -\frac{k^2\pi^2}{l^2}, \quad \text{or}$$

$$-\frac{1}{2}(\kappa_1 + \kappa_2) - \frac{1}{2}\sqrt{\mathscr{D}} = -\frac{k^2\pi^2}{l^2},$$

$$\Leftrightarrow \exists k \in \mathbb{N}\colon\ (\kappa_1 - \kappa_2)^2 + 4\tilde{a}_2\tilde{a}_3 m_1 m_2 = \left(\kappa_1 + \kappa_2 - \frac{2k^2\pi^2}{l^2}\right)^2$$

$$\Leftrightarrow \exists k \in \mathbb{N}\colon\ -4\kappa_1\kappa_2 + 4\tilde{a}_2\tilde{a}_3 m_1 m_2 + 4(\kappa_1 + \kappa_2)\frac{k^2\pi^2}{l^2} - 4\frac{k^4\pi^4}{l^4} = 0 \tag{47}$$

The terms of this equation contain λ in several ways, see (39). We recall the terms for the trace and determinant and for $k \in \mathbb{N}$ we introduce θ

$$\tau = -(a_1 + a_4), \qquad \delta = a_1 a_4 - a_2 a_3, \qquad \theta = \frac{k^2\pi^2}{l^2}.$$

After some calculations we get a statement equivalent to (47).

Lemms 4.1 *For given λ with $\operatorname{Re}\lambda > \max(-2\mu_1, -2\mu_2)$ the system* (44) *has a nontrivial solution if and only if there is a $k \in \mathbb{N}$, and thus a θ, such that $F(\lambda) = 0$, where*

$$F(\lambda) = \lambda^4 + F_3\lambda^3 + F_2\lambda^2 + F_1\lambda + F_0\,,$$

with

$$\begin{aligned} F_0 &= 4\delta\mu_1\mu_2 - 2\theta(\gamma_2^2\mu_1 a_1 + \gamma_1^2\mu_2 a_4) + \gamma_1^2\gamma_2^2\theta^2\,, \\ F_1 &= 2\delta(\mu_1 + \mu_2) + 4\tau\mu_1\mu_2 - \theta[\gamma_2^2(a_1 - 2\mu_1) + \gamma_1^2(a_4 - 2\mu_2)]\,, \\ F_2 &= \delta + 2(\mu_1 + \mu_2)\tau + 4\mu_1\mu_2 + (\gamma_1^2 + \gamma_2^2)\theta\,, \\ F_3 &= 2(\mu_1 + \mu_2) + \tau\,. \end{aligned} \tag{48}$$

If λ satisfies $F(\lambda)=0$ then the coefficients $\sigma_1, \ldots, \sigma_4$, resp. $\eta_1, \ldots, \eta_4$ can be determined as follows.

From the 1st and the 3rd equation of (44) it directly follows that $\sigma_1=\sigma_2$ and $\sigma_3=\sigma_4$.

From (46) it follows that $k\pi i/l=\sqrt{p_1}$ or $k\pi i/l=\sqrt{p_2}$.

In the case $k\pi i/l=\sqrt{p_1}$ a solution is given by $\eta_1=\eta_2, \eta_3=0, \eta_4=0$:

$$\begin{pmatrix} u_1 \\ u_2 \end{pmatrix}(x)=\eta_1(e^{ik\pi x/l}+e^{-ik\pi x/l})\,\xi_1=\frac{\eta_1}{2}\cos\left(\frac{k\pi}{l}x\right)\xi_1\,.$$

If $k\pi i/l=\sqrt{p_2}$ then the solution is

$$\begin{pmatrix} u_1 \\ u_2 \end{pmatrix}(x)=\frac{\eta_3}{2}\cos\left(\frac{k\pi}{l}x\right)\xi_2\,.$$

In general we have

Lemma 4.2 *Let k and λ satisfy $F(\lambda)=0$ then*

$$\begin{pmatrix} u_1 \\ u_2 \end{pmatrix}(x)=\begin{pmatrix} c_1 \\ c_2 \end{pmatrix}\cos\left(\frac{k\pi}{l}x\right)$$

is a solution of (40). *The quotient c_1/c_2 depends on λ.*

4.2 Equation for v

We recall (27) and consider the system for v

$$\begin{pmatrix} v_1'' \\ v_2'' \end{pmatrix}=\begin{pmatrix} -\kappa_1 & -\tilde{a}_2 m_2 \\ -\tilde{a}_3 m_1 & -\kappa_2 \end{pmatrix}\begin{pmatrix} v_1 \\ v_2 \end{pmatrix}, \tag{49}$$

with boundary condition (25)

$$v_1(0)=v_2(0)=v_1(l)=v_2(l)=0\,.$$

Let the matrix in (49) be called C. The eigenvalues and eigenvectors of C are as follows (again $\mathscr{D}$ is the discriminant (42)).

$$q_{1,2}=-\frac{\kappa_1+\kappa_2}{2}\pm\frac{1}{2}\sqrt{\mathscr{D}}=p_{1,2}\,,$$

$$\zeta_1=\begin{pmatrix} -\tilde{a}_2 m_2 \\ \frac{1}{2}(\kappa_1-\kappa_2)+\frac{1}{2}\sqrt{\mathscr{D}} \end{pmatrix}, \qquad \zeta_2=\begin{pmatrix} -\tilde{a}_2 m_2 \\ \frac{1}{2}(\kappa_1-\kappa_2)-\frac{1}{2}\sqrt{\mathscr{D}} \end{pmatrix}.$$

The general solution of (49) is

$$\begin{pmatrix} v_1 \\ v_2 \end{pmatrix}(x)=(\eta_1 e^{\sqrt{q_1}x}+\eta_2 e^{-\sqrt{q_1}x})\,\zeta_1+(\eta_3 e^{\sqrt{q_2}x}+\eta_4 e^{-\sqrt{q_2}x})\,\zeta_2\,.$$

Now we introduce $\sigma_1=\eta_1, \sigma_2=-\eta_2, \sigma_3=\eta_3, \sigma_4=-\eta_4$, evaluate the boundary conditions and compare with the result for the u–equation (43), (44).

We get exactly the same results as before (44)-(46) and straightforwardly we get the same condition for existence of an eigenvalue $F(\lambda) = 0$.

The corresponding solution is

$$\begin{pmatrix} v_1 \\ v_2 \end{pmatrix}(x) = \begin{pmatrix} c_1 \\ c_2 \end{pmatrix} \sin\left(\frac{k\pi}{l}\, x\right).$$

We summarize the above observations in a theorem.

Theorem 4.3 *λ is an eigenvalue of the linearization* (20), (21) *if and only if there is a mode $k \in \mathbb{N}$ such that $F(\lambda) = 0$, where*

$$F(\lambda) = \lambda^4 + F_3\lambda^3 + F_2\lambda^2 + F_1\lambda + F_0\ ,$$

with coefficients as in (48).

The corresponding eigenfunction is of the type

$$\begin{aligned} u_1(x) &= c_1 \cos\left(\frac{k\pi}{l}\, x\right), \qquad u_2(x) = c_2 \cos\left(\frac{k\pi}{l}\, x\right)\ , \\ v_1(x) &= c_3 \sin\left(\frac{k\pi}{l}\, x\right), \qquad v_2(x) = c_4 \sin\left(\frac{k\pi}{l}\, x\right)\ . \end{aligned} \tag{50}$$

For each mode $k \in \mathbb{N}$ there are four eigenvalues $\lambda(k)$ of the linearization (20), (21), given by the roots of $F(\lambda)$.

5 Discussion of the characteristic equation

5.1 Stability domain

We are interested in situations where the uniform stationary state changes its stability. A bifurcation can occur if roots of $F(\lambda)$ cross the imaginary axis. The roots of the polynomial

$$F(\lambda) = \lambda^4 + F_3\,\lambda^3 + F_2\,\lambda^2 + F_1\,\lambda + F_0$$

have all negative real parts if and only if the Routh–Hurwitz criterion is satisfied (Gantmacher [4]).

$$\begin{aligned} \triangle_1 &= F_3 > 0\ , \\ \triangle_2 &= F_2F_3 - F_1 > 0\ , \\ \triangle_3 &= (F_2F_3 - F_1)\,F_1 - F_3^2F_0 > 0\ , \\ \triangle_4 &= F_0\,\triangle_3 > 0\ . \end{aligned} \tag{51}$$

One immediately sees that these conditions are equivalent to

$$\begin{aligned} &F_0 > 0, \quad F_1 > 0, \quad F_2 > 0, \quad F_3 > 0, \\ &F_1F_2F_3 - F_3^2F_0 - F_1^2 > 0\ . \end{aligned} \tag{52}$$

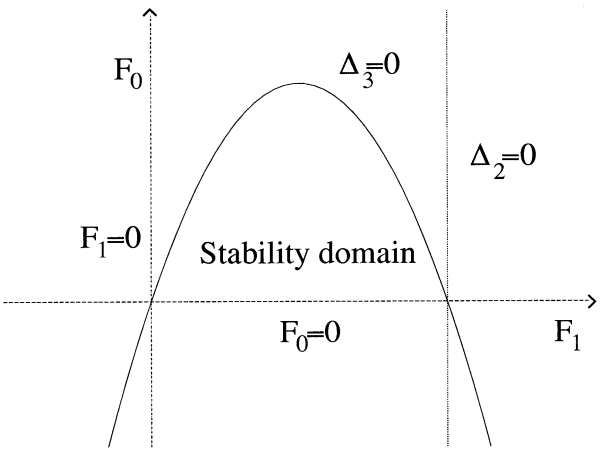


Fig 1. Stability domain

All these expressions are polynomials of maximal degree 2 in the variable θ. The condition (51) or (52) describes the stability domain. If we start from within the stability domain and vary the parameters we will eventually leave this domain. Then at least one of these conditions is violated. Therefore one should consider the change of only one single inequality in that region, whereas the other inequalities remain satisfied.

Since τ and δ are positive ((H1), (H2)) F_2 and F_3 are positive for all positive θ. Hence we can describe the stability domain by the following inequalities:

(a) $F_0 > 0$,
(b) $F_1 > 0$,
(c) $\triangle_2 = F_2 F_3 - F_1 > 0$,
(d) $\triangle_3 = (F_2 F_3 - F_1) F_1 - F_3^2 F_0 > 0$.

In Fig. 1 we show the stability domain for fixed F_2, F_3 in an (F_1, F_0)–plane.

The conditions (b) and (c) are redundant. Indeed, assuming that (a) and (d) are satisfied, it follows that $(F_2F_3 - F_1)F_1 > 0$. Since F_2 and F_3 are positive, the factors $F_2F_3 - F_1$ and F_1 are not simultaneously negative. Thus they are both positive.

The stability domain is determined by conditions (a) and (d), and the boundary of the stability domain is given by

(a) $F_0 = 0$ and $0 \leqq F_1 \leqq F_2F_3$ at the F_1–axis, and
(b) $F_0 > 0$ and $F_0 = (F_2F_3 - F_1)F_1/F_3^2$ at the parabolic arc.

In the next lemma we show that this boundary consists of bifurcation points.

Lemma 5.1. 1. *If* $F_0 = 0$ *and* $0 \leqq F_1 \leqq F_2F_3$ *then* $F(\lambda)$ *has a root at* $\lambda = 0$.
2. *If* $F_0 > 0$ *and* $F_0 = (F_2F_3 - F_1)F_1/F_3^2$ *then* $F(\lambda)$ *has a root* $\lambda = iv \neq 0$.

Proof. 1. $F_0 = 0 \Rightarrow F(\lambda) = \lambda(\lambda^3 + F_3\lambda^2 + F_2\lambda + F_1)$.

2. Since $F_2, F_3 > 0$ and $(F_2F_3 - F_1)F_1 = F_0F_3^2 > 0$ it follows that $F_1 > 0$.

We show that $\lambda = iv$ with $v^2 = F_1/F_3$ is a purely imaginary root of $F(\lambda)$.

$$\begin{aligned} F(iv) &= v^4 - v^2 F_2 + F_0 + iv(F_1 - v^2 F_3) \\ &= \frac{1}{F_3^2} F_1(F_1 - F_2 F_3) + F_0 \\ &= 0 . \end{aligned}$$

□

5.2 Stability conditions

Now we keep all parameters fixed, assume (H1) and (H2) and discuss stability in terms of θ. Here we ignore the fact that θ attains discrete values $k^2 l^2/\pi^2$, $k \in \mathbb{N}$ only and treat θ as a nonnegative continuous parameter. We recall the conditions (a) and (d).

The stability conditions are

(S1) $F_0(\theta) = 4\delta\mu_1\mu_2 - 2\theta(\gamma_2^2\mu_1 a_1 + \gamma_1^2\mu_2 a_4) + \gamma_1^2\gamma_2^2\theta^2 > 0$,

(S2) $\triangle_3(\theta) = q_0 + q_1\theta + q_2\theta^2 > 0$, with

$$\begin{aligned} q_2 &= 2(\gamma_1^2 - \gamma_2^2)^2 (a_1 - 2\mu_1)(a_4 - 2\mu_2), \\ q_1 &= 2F_3^2(\gamma_2^2\mu_1 a_1 + \gamma_1^2\mu_2 a_4) + F_3(\gamma_1^2 + \gamma_2^2)(2\delta(\mu_1 + \mu_2) + 4\tau\mu_1\mu_2) \\ &\quad - W\,[2\tau(\mu_1 + \mu_2) F_3 + (2(\mu_1 + \mu_2) - \tau)(4\mu_1\mu_2 - \delta)], \\ q_0 &= 2(\mu_1 + \mu_2)\tau\,[(\delta + 4\mu_1\mu_2)^2 + 2(\mu_1 + \mu_2)(\delta + 4\mu_1\mu_2)\tau + 4\tau^2\mu_1\mu_2 \\ &\quad + 4\delta(\mu_1 - \mu_2)^2], \end{aligned}$$

with $W := \gamma_2^2(a_1 - 2\mu_1) + \gamma_1^2(a_4 - 2\mu_2)$ and $F_3 = 2(\mu_1 + \mu_2) + \tau$.

From assumption (H1) it follows that q_0 is positive.

We check successively the conditions (S1) and (S2):

(S1) Since we are interested in the sign of F_0 we consider $G(\theta) = F_0(\theta)/(4\mu_1\mu_2)$ and identify $d_j = \gamma_j^2/(2\mu_j)$, $j = 1, 2$. The stability condition is

$$G(\theta) = \theta^2 d_1 d_2 - \theta(d_2 a_1 + d_1 a_4) + \delta > 0 .$$

Let $T = d_2 a_1 + d_1 a_4$ then the roots of $G(\theta)$ are $\theta_{1,2} = (2d_1 d_2)^{-1}$ $(T \pm \sqrt{T^2 - 4d_1 d_2 \delta})$.

(a) If $T < 0$ then there is no positive root of G and $G(\theta) > 0$ for all $\theta \geqq 0$.

(b) If $T \geqq 0$ and $T^2 - 4d_1 d_2 \delta < 0$ then there are no real roots and again $G(\theta) > 0$ for all $\theta \geqq 0$.

(c) If $T > 0$ and $T^2 - 4d_1 d_2 \delta > 0$ then $G(\theta) < 0$ for all $\theta \in (\theta_1, \theta_2)$.

We write these conditions in terms of the original model parameters.

Lemma 5.2 (violation of (S1)) *There exists an interval of θ such that condition* (S1) *is violated if and only if*

$$\sqrt{\frac{\gamma_2^2}{2\mu_2}\frac{2\mu_1}{\gamma_1^2}} > \frac{\sqrt{\delta}+\sqrt{-a_2a_3}}{a_1}. \tag{53}$$

The maximal interval is given by $[\theta_1, \theta_2]$, *where*

$$\theta_{1,2} = \frac{1}{2d_1d_2}\left(d_2a_1 + d_1a_4 \pm \sqrt{(d_2a_1 - d_1a_4)^2 + 4d_1d_2a_2a_3}\right), \tag{54}$$

with $d_j = \gamma_j^2/2\mu_j, j = 1, 2.$

(S2) $\triangle_3(\theta)$ is a quadratic polynomial in θ. We know $\triangle_3(0) = q_0 > 0$. The shape of $\triangle_3(\theta)$ depends on the sign of the leading coefficient q_2.

(a) If $q_2 < 0$ then there is exactly one $\theta_3 > 0$ such that $\triangle_3(\theta_3) = 0$ and (S2) is violated for all $\theta > \theta_3$.

(b) Assume $q_2 \geqq 0$.

Lemma 5.3 *If* $q_2 \geqq 0$ *then* $q_1 \geqq 0$.

Proof. First assume that $\gamma_1 \neq \gamma_2$. Then $q_2 \geqq 0 \Leftrightarrow \mu_1 \geqq a_1/2$.

We introduce new notations and recall old notations.

$$\delta = a_1a_4 - a_2a_3, \qquad \tau = -a_1 - a_4, \qquad m = 4\mu_1\mu_2, \qquad s = 2(\mu_1 + \mu_2),$$

$$L = \gamma_2^2\mu_1a_1 + \gamma_1^2\mu_2a_4, \qquad W = \gamma_2^2(a_1 - 2\mu_1) + \gamma_1^2(a_4 - 2\mu_2),$$

with $\delta, \tau, m, s > 0$ and $W > 0$ since $\mu_1 \geqq a_1/2$. L can be of either sign. Then q_1 as a function of τ is

$$q_1(\tau) = 2L(s+\tau)^2 + (\gamma_1^2 + \gamma_2^2)(s+\tau)(\delta s + \tau m) - W\left[\tau s(s+\tau) + (s-\tau)(m-\delta)\right].$$

We show (I) $q_1(0) > 0$ and (II) $dq_1(\tau)/d\tau > 0$.

(I) Let $\tau = 0$. We sort the terms of γ_1^2 and γ_2^2 $q_1(0) = s(\gamma_1^2g_1 + \gamma_2^2g_2)$, with

$$g_1 = (2\mu_1 - a_1)(\delta + 4\mu_2^2)$$

$$g_2 = (2\mu_2 + a_1)(\delta + 4\mu_1^2),$$

where we used $a_1 = -a_4$ $(\tau = 0)$.

Since $\mu_1 \geqq a_1/2$ we have $g_1 \geqq 0$ and $g_2 > 0$, hence $q_1(0) > 0$.

(II) $dq_1(\tau)/d\tau = \gamma_1^2f_1 + \gamma_2^2f_2$, with

$$f_1 = 4\mu_2a_4(s+\tau) + \delta s + 2\tau m + sm - (a_4 - 2\mu_2)\left[s(s+\tau) + \tau s - m + \delta\right]$$

$$f_2 = 4\mu_1a_1(s+\tau) + \delta s + 2\tau m + sm - (a_1 - 2\mu_1)\left[s(s+\tau) + \tau s - m + \delta\right].$$

It is easy to check that $df_1/d\tau > 0$, $df_1/d\delta > 0$ and $f_1|_{\tau=0,\delta=0} > 0$, hence $f_1 > 0$.

Since $\mu_1 \geqq a_1/2$ it follows that $f_2 > 0$.

Since $q_1 > 0$ for all parameter configurations satisfying $\gamma_1 \neq \gamma_2$ and $\mu_1 \geqq a_1/2$, by a continuity argument, $q_1 \geqq 0$ for $\gamma_1 = \gamma_2$. □

If $q_2 = 0$ then $\triangle_3(\theta)$ is linear with slope $q_1 \geqq 0$. Since $\triangle_3(0) = q_0 > 0$, condition (S2) is satisfied for all $\theta \geqq 0$.

If $q_2 > 0$ then $q_1 \geqq 0$ (Lemma 5.3) and there are no positive roots of $\triangle_3(\theta)$. Hence condition (S2) is satisfied for all $\theta \geqq 0$.

We summarize these observations

Lemma 5.4 (violation of (S2)) 1. *q_2 is negative if and only if $\gamma_1 \neq \gamma_2$ and $\mu_1 < a_1/2$. Then for all $\theta \geqq \theta_3$ condition* (S2) *is violated, where* $\theta_3 = (-q_1 - \sqrt{q_1^2 - 4q_2q_0})/(2q_2) > 0$.

2. *If $q_2 \geqq 0$ then condition* (S2) *is always satisfied.*

Remember that $\theta = k^2l^2/\pi^2$ attains discrete values corresponding to the modes $k \in \mathbb{N}$. Instability of the constant solution in this context means that there is a mode $k \in \mathbb{N}$ such that $\theta = k^2l^2/\pi^2$ violates one of the conditions (S1), (S2).

Theorem 5.5 (instability) *Assume* (H1) *and* (H2). *The spatially constant solution of* (15), (16) *is linear unstable if and only if one of the following conditions is satisfied*

(i) $$\sqrt{\frac{\gamma_2^2}{2\mu_2}\frac{2\mu_1}{\gamma_1^2}} > \frac{\sqrt{\delta} + \sqrt{-a_2a_3}}{a_1}$$

and there exists a mode $k \in \mathbb{N}$ such that $\sqrt{\theta_1}l/\pi < k < \sqrt{\theta_2}l/\pi$, with θ_1, θ_2 as in (54).

(ii) *$\mu_1 < a_1/2$ and $\gamma_1 \neq \gamma_2$. All modes $k \in \mathbb{N}$ with $k > \sqrt{\theta_3}l/\pi$, with θ_3 as in Lemma* 5.4, *are unstable.*

Remarks.

1. With the identification $D_j = d_j = \gamma_j^2/(2\mu_j)$, $j = 1, 2$ condition (*i*) of this theorem coincides with the classical situation (Theorem 3.1). Moreover, in this situation the random walk Turing system (15) with Neumann boundary conditions produces the same unstable modes k as the well known Turing model (29). It is remarkable that the instability depends on the quotients D_j only.

2. The condition (*ii*) has no analogue in the classical situation. This condition means that the rate of reversing direction $2\mu_1$ is smaller than the linearized reproduction rate a_1 of the activator.

5.3 Bifurcations

Now we consider bifurcations. We choose a parameter set $(\gamma_1, \mu_1, \gamma_2, \mu_2)$ in the stability region, i.e. such that the conditions (S1) and (S2) are satisfied, and

vary some parameters. Except for degenerate situations there are two qualitatively different ways to leave the stability domain (see Fig 1).

(a) The first is to satisfy condition (*i*) of Theorem 5.5, i.e. to cross the F_1-axis (see Fig 1). An eigenvalue crosses the imaginary axis at $\lambda = 0$ (Lemma 5.1). As in the classical Turing model (Theorem 3.1, Remark 3) the spatial constant equilibrium loses its stability if there is a mode $k_0 \in \mathbb{N}$ with $\theta_0 = k_0^2\pi^2/l^2$, $\theta_0 \in (\theta_1, \theta_2)$. An eigenvalue of the linearization (20), (21) has $\operatorname{Re}\lambda > 0$ and the corresponding eigenfunction is given by (50) (Theorem 4.3). A cosine pattern of mode k_0 for (u_1, u_2) and a sine pattern of this mode for (v_1, v_2) establishes itself.

(b) A second way to destabilize the spatially constant solution is to satisfy condition (*ii*) of Theorem 5.5, i.e. to cross the parabola $\triangle_3 = 0$ in Fig 1. An eigenvalue crosses the imaginary axis at $\lambda = iv$, $v \neq 0$ (Lemma 5.1) and we observe a Hopf bifurcation. There are infinitely many modes $k \geqq \sqrt{\theta_3}l/\pi$, with θ_3 given in Lemma 5.4. The remaining patterns are oscillating Fourier series of these modes.

In this case a rigorous nonlinear analysis is necessary to figure out the dominating modes and the stable oscillating states.

This effect does not occur in the classical Turing model (Theorem 3.1, Remark 4).

5.4 Conclusions

In this paper we have investigated the effects of introducing finite particle speeds into reaction diffusion mechanisms of morphogenesis, e.g. the Turing model.

It turns out (Theorem 5.5) that the effect of finite speeds is negligible if the turning rate of the activator is sufficiently large, i.e. $\mu_1 > a_1/2$, since both systems, the classical Turing model (29) and the random walk Turing model (15), produce the same instabilities.

If $\mu_1 < a_1/2$ there is a qualitative difference between these models. One observes a Hopf bifurcation for (15), which is excluded for solutions of (29).

What happens becomes clearer if one considers the linearization of the telegraph equation (19) corresponding to the random walk system (15). Remember that $u = (u_1, u_2)$ is a two component vector and the matrices A, M and Γ are defined in (32) and (38).

In the linear situation one can assume that $u_2 = 0$, and assume that the activator does not produce any inhibitor (i.e. $a_3 = 0$), then u_1 satisfies

$$u_{1tt} + (2\mu_1 - a_1)u_{1t} = \gamma_1^2 u_{1xx} + 2\mu_1 a_1 u_1 \ . \tag{55}$$

(a) If $\mu_1 > a_1/2$ equation (55) is a wave equation with damping term $(2\mu_1 - a_1) > 0$. Moreover if μ_1 is large then the u_{1t}–term dominates the u_{1tt}–term (see above) and the equation (55) has diffusion character.

(b) If the damping term is zero (i.e. $\mu_1 = a_1/2$), then (55) is a undamped wave equation and has wave character.

(c) If $2\mu_1 - a_1 < 0$ then the damping is negative and is enhancing. Oscillating behavior can result.

In other words, one can say that in the situation (*ii*) of Theorem 5.5 the random walk system has more wave character than diffusion character. Thus it is not surprising that oscillations occur.

The analogous term $(2\mu_2 - a_4)$ for the inhibitor is always positive, since we assumed in (H2) that $a_4 < 0$. If this condition is removed (e.g. Brusselator models), we expect additional effects for $\mu_2 < a_4/2$ (e.g. oscillations or turbulence).

6 Simulations

In simulations we compare the stationary patterns in the situation of Theorem 5.5(i) with the corresponding patterns for the classical reaction diffusion Turing model (29). We choose a cubic nonlinearity often used in biological applications (e.g. Maginu [14])

$$f_1(u_1, u_2) = -u_1^3 + a_1 u_1 - u_2$$

$$f_2(u_1, u_2) = u_1 - u_2$$

with $a_1 = 0.6$. The constant solution $(u_1, u_2) = (0, 0)$ is a stable equilibrium of the reaction equation (2).

We have $a_1 = 0.6, a_2 = -1, a_3 = 1, a_4 = -1, \delta = 0.4,$ and $\tau = 0.4$, hence the hypotheses (H1) and (H2) are satisfied.

For numerical simulations of the correlated random walk (3) we use a grid with time steps $h > 0$ and space discretisation $\rho > 0$ such that $\gamma = \rho/h$. Then an approximation to the correlated random walk equation (3) is given by

$$\begin{aligned} u^+((n+1)h, x) &= pu^+(nh, x-\rho) + qu^-(nh, x-\rho) \\ u^-((n+1)h, x) &= pu^-(nh, x+\rho) + qu^+(nh, x+\rho), \end{aligned} \tag{56}$$

with the probability of changing the direction $q := \mu h$ and the probability of keeping the direction $p = 1 - q$ (see Goldstein [6]).

The initial data are

$$u_1(0, x) = \begin{cases} 0.05 & \text{if } l/2 \leqq x < l/2 + \gamma_1 h \ , \\ 0 & \text{otherwise} \ , \end{cases}$$

$$u_2(0, x) = 0, \qquad v_1(0, x) = 0, \qquad v_2(0, x) = 0 \ .$$

In Fig. 2 we show the time evolution of the activator density u_1 in a situation, where condition (*i*) of Theorem 5.5 is satisfied. The corresponding diffusion rates $D_1 = 0.0625$ and $D_2 = 4$ lead to unstable modes $k \in \{1, 2, 3\}$.

We have shown in Theorem 5.5 that the stability of the mode k depends only on the ratios $D_j = \gamma_j^2/(2\mu_j)$, $j = 1, 2$, but not on the model parameters

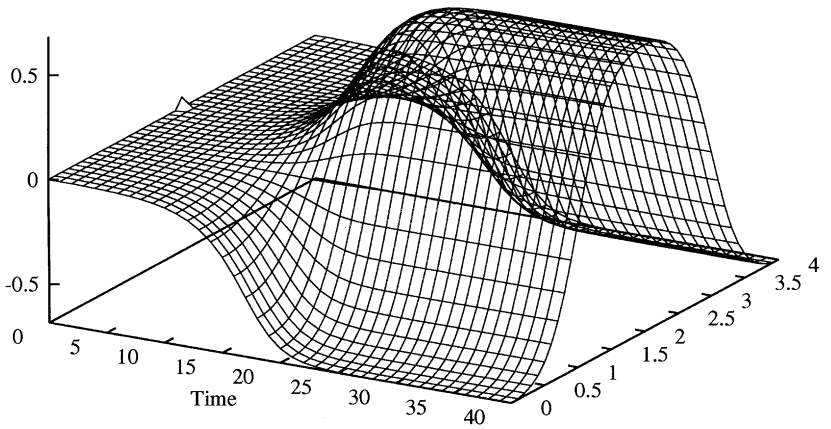
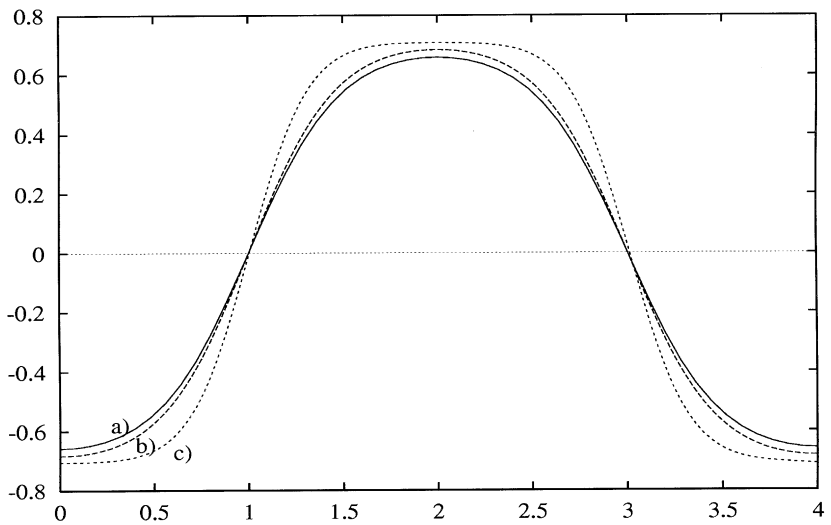


Fig 2. $\mu_1 = 2, \gamma_1 = 0.5, \mu_2 = 0.125, \gamma_2 = 1, l = 4, a_1 = 0.6$



	Activator		Inhibitor	
(a)	$D_1 = 0.0625$		$D_2 = 4$	
	μ_1	γ_1	μ_2	γ_2
(b)	2	0.5	0.125	1
(c)	32	2	0.125	1

Fig 3.

$\mu_1, \gamma_1, \mu_2, \gamma_2$ separately. As we see in the next figure (Fig. 3) the shape of the resulting pattern depends on all four parameter values $(\mu_1, \gamma_1, \mu_2, \gamma_2)$.

The curves (a), (b) and (c) in Fig. 3 show the activator density u_1 at a time $t = 40$. In (b) we have chosen the same parameter configurations as in Fig. 2, whereas in (c) we increased the turning rate μ_1 by a factor 16 and the speed γ_1 by a factor 4 such that again $D_1 = 0.0625$. In (a) we show the resulting pattern for the classical Turing model, where we used a standard discretisation routine for reaction diffusion systems. The modes of the patterns are the same but the shapes are different. Observe the plateau at the maximum level for the activator density in (c). In this case the activator is very fast and turns very often, thus maintaining near the maximum level but not affecting the pattern structure.

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