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Spatial instabilities in reaction random walks with direction-independent kinetics

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We study spatial instabilities in reacting and diffusing systems, where diffusion is modeled by a persistent random walk instead of the usual Brownian motion. Perturbations in these reaction walk systems propagate with finite speed, whereas in reaction-diffusion systems localized disturbances affect every part instantly, albeit with heavy damping. We present evolution equations for reaction random walks whose kinetics do not depend on the particles' direction of motion. The homogeneous steady state of such systems can undergo two types of transport-driven instabilities. One type of bifurcation gives rise to stationary spatial patterns and corresponds to the Turing instability in reaction-diffusion systems. The other type occurs in the ballistic regime and leads to oscillatory spatial patterns; it has no analog in reaction-diffusion systems. The conditions for these bifurcations are derived and applied to two model systems. We also analyze the stability properties of one-variable systems and find that small wavelength perturbations decay in an oscillatory manner. [S1063-651X(99)07409-7]

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I. INTRODUCTION

Dispersal of particles or individuals, such as molecules or organisms, and their interaction with each other play an important role in physics, chemistry, biology, and other sciences. Dispersal is generally modeled by a simple diffusion process, Brownian motion. In a mean-field continuum description, dispersal is described by the diffusion equation

$$\frac{\partial u}{\partial t}=D\Delta u \tag{1.1}$$

for the density u. Reactions or interactions are generally modeled by rate equations, whose reaction term is often in the form of a birth-and-death process,

$$\frac{du}{dt}=f(u)=b(u)-d(u)u. \tag{1.2}$$

Dispersal and reactions acting together can produce spatial patterns: traveling waves, such as propagating fronts of invading species [1] or chemical activity [2], or stationary patterns, such as coat patterns in mammals [3] or striped patterns in the chlorite-iodide-malonic acid reaction [4]. These phenomena are modeled by combining the diffusion equation and the rate equation to obtain a reaction-diffusion equation

$$\frac{\partial u}{\partial t}=D\Delta u+f(u). \tag{1.3}$$

The evolution equations (1.1)–(1.3) must possess certain properties to be acceptable descriptions of reacting and dispersing systems. A density u cannot be negative, and evolution equations for densities must preserve positivity, i.e., $u(r,0)\geqslant 0$ for all r at time $t=0$ implies $u(r,t)\geqslant 0$ for all r for all times $t>0$. It is well known that the diffusion equation (1.1) possesses this required feature. The rate equation (1.2) and the reaction-diffusion equation (1.3) will preserve positivity if

$$f(0)\geqslant 0. \tag{1.4}$$

The diffusion equation has, however, the unrealistic feature of infinitely fast propagation. The fundamental solution of Eq. (1.1) with a point source at $r=0$ and $t=0$ is given by

$$u(r,t)=\frac{1}{\sqrt{4\pi Dt}}\exp\left[-\frac{r^2}{4Dt}\right],\quad t>0. \tag{1.5}$$

No matter how small t and how large r, the density u will be nonzero, though exponentially small. This pathology can be traced back to the lack of inertia of Brownian particles; their direction of motion in successive time intervals is uncorrelated. This lack of correlation has two consequences: (i) The particles move with infinite velocity. There is some probability, though exponentially small, that a dispersing individual will travel an infinite distance from its current position in a small but nonzero amount of time. Clearly, this cannot be true for molecules or organisms. (ii) The motion of the dispersing individuals is unpredictable even on the smallest time scales. Again, this cannot be true, either for molecules or organisms. It is therefore desirable to adopt a model for dispersion that leads to more predictable motion with finite speed at smaller time scales and approaches diffusive motion on larger time scales. The natural choice is a persistent random walk, also known as a correlated random walk. It was introduced by Fürth [5], and further studied by Taylor [6] and Goldstein [7], as the simplest generalization of the ordinary random walk. In the persistent random walk the particles have a well-defined finite speed. However, the average velocity of the particles vanishes, and no convective flow occurs in the system.

Brownian motion, or the diffusion equation, ceases to be a good model for dispersal at scales where particles or individuals have a well-defined velocity. In most physical or chemical applications, the limiting scale is determined by the

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mean free path. In liquids, the mean free path is a fraction of the molecular diameter, and persistence or inertia effects are negligible even on mesoscopic scales. Velocity is not a relevant variable in these situations, and the position of the particle is determined by many independent effects. Dispersal has therefore a strongly diffusive character, and reaction-diffusion equations are an appropriate description for chemical reactions in aqueous solutions. In gases, the mean free path can be several orders of magnitude larger than the molecular diameter, depending on gas pressure. The velocity of particles is well defined on scales between the molecular and the mean free path scale; persistence or inertia effects are not negligible. They can be taken into account in a simplified way by using a persistent random walk to model dispersal. Turbulent diffusion and dispersal of animals, especially bacteria, are two other areas where the velocity of particles or organisms is well defined, and persistence effects are not negligible, on macroscopic scales. Section 10.6 of [8] presents the persistent random walk as a model for turbulent diffusion and discusses the inadequacy of the classical diffusion equation in this context. The persistent random walk also provides a better description for spatial spread in population dynamics than the often used diffusion equation [9–11]. Microorganisms and animals tend to continue moving in the same direction in successive time intervals. Velocity is well defined and persistence effects are important on macroscopic scales. In fact, Fürth [5] applied his theory to experiments on the motion of bacteria.

Besides these practical considerations, describing the motion of particles or individuals by a persistent random walk has several advantages from a theoretical viewpoint: (i) The persistent random walk is a generalization of Brownian motion; it contains the latter as a limiting case as shown in Sec. II B. (ii) The persistent random walk overcomes the pathological feature of Brownian motion or the diffusion equation discussed above; it fulfills the physical requirement of bounded velocity. (iii) The persistent random walk provides a unified treatment that covers the whole range of transport, from the diffusive limit to the ballistic limit.

Reaction random walks also allow us to investigate the role of transport in spatial pattern formation. A mechanism that has attracted particular attention is the Turing instability. Turing showed in his seminal paper [12] that a homogeneous steady state of reaction-diffusion systems can undergo a diffusion-driven instability, caused by a coupling between transport and chemical kinetics. Such a bifurcation gives rise to steady patterns with an intrinsic ''wavelength,'' i.e., a characteristic length that is *independent* of the boundary and initial conditions. The study of Turing bifurcations produced an abundant theoretical literature, for reviews see, for example, [3,13–15]. The first experimental observations of a Turing instability in open chemical reactors were reported less than ten years ago [16–19]. Modeling dispersing and reacting systems by reaction random walks, we can address the following two fundamental questions.

(i) How do the transport characteristics affect spatial instabilities in dispersing and reacting systems? As mentioned above, the persistent random walk allows us to consider particle motion that varies from the *ballistic* regime to the *diffusive* regime. Since the Turing instability is a diffusion-driven instability, it is of particular interest to explore how this bifurcation responds to changes in the dispersal process. Up to now, only the effects of different kinetics on pattern formation and selection have been studied, see, for instance, [20–22].

(ii) How does a finite speed of propagation of perturbations affect Turing instabilities and other spatial instabilities? As shown above, the diffusion equation implies an infinite speed for the transport of matter in the sense that any localized density disturbance *instantly* propagates to every part of the system, though with exponential damping.

This paper is organized as follows. In Sec. II we present a review of Cattaneo systems and reaction random walks. In Sec. III, the conditions for transport-driven spatial instabilities in reaction random walks with direction-independent kinetics are derived, and we apply our results to two model systems. We then investigate the stability properties of the homogeneous steady state in one-species systems in Sec. IV and conclude in Sec. V with a discussion of our results.

II. REACTING AND DISPERSING SYSTEMS

A. Reaction-Cattaneo systems and reaction-telegraph equations

Before introducing the persistent random walk, we will present a brief overview of previous approaches to address the unrealistic features of the diffusion equation or Brownian motion discussed in the Introduction.

The macroscopic description of spatially extended systems is based on the conservation or continuity equation for the density u,

$$\frac{\partial u}{\partial t} = -\frac{\partial J}{\partial r} + f(u). \tag{2.1}$$

For ease of presentation, we consider only spatially one-dimensional systems (spatial coordinate r). This equation needs to be closed via a constitutive equation for the flux J. If we use Fick's first law

$$J = -D\frac{\partial u}{\partial r}, \tag{2.2}$$

we obtain the reaction-diffusion equation (1.3). Cattaneo and others, for a review see [23], have argued that the flux should adjust to the gradient with some small but nonzero relaxation time τ. We replace Fick's first law by the Cattaneo equation

$$\tau\frac{\partial J}{\partial t} + J = -D\frac{\partial u}{\partial r}, \tag{2.3}$$

and eliminate J by differentiating Eq. (2.1) with respect to t and Eq. (2.3) with respect to r (assuming constant D), to obtain a hyperbolic equation, the reaction-telegraph equation

$$\tau\frac{\partial^2 u}{\partial t^2} + [1 - \tau f'(u)]\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial r^2} + f(u). \tag{2.4}$$

In the formal limit $\tau \to 0$, the reaction-telegraph equation goes to the parabolic reaction-diffusion equation (1.3). This statement can be placed on a rigorous footing. The solution of the telegraph equation

$$\tau \frac{\partial^2 u}{\partial t^2} + \frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial r^2}, \tag{2.5}$$

with a point source at $r=0$ and $t=0$, is

$$u(r,t) = \begin{cases} \frac{1}{\mathcal{N}} \exp\left[-\frac{t}{2\tau} \right] I_0 \left[\frac{1}{\mathcal{N}} \sqrt{\xi} \right] & \text{for } |r| < \sqrt{\frac{D}{\tau}} t \\ 0 \quad \text{otherwise} \end{cases} \tag{2.6}$$

and converges to the solution (1.5) of the diffusion equation as $\tau \rightarrow 0$, see [24], p. 388. Here I_0 is the modified Bessel function, $\xi = (D/\tau)t^2 - r^2$, and $\mathcal{N} = \sqrt{4D\tau}$. Equation (2.6) also shows explicitly that perturbations governed by the telegraph equation spread with a finite speed $\sqrt{D/\tau}$, as expected for a damped wave equation.

Gallay and Raugel [25–28] have studied propagating front solutions to reaction-telegraph equations without the $-\tau f'(u)$ term. Traveling wave fronts for the full reaction-telegraph equation (2.4) have been investigated by several authors [9,29–31]. The reaction-telegraph equation overcomes the pathological feature of the reaction-diffusion equation and has a finite speed of propagation, but it suffers from other drawbacks: (i) Hyperbolic equations typically do not preserve positivity. Even if $u(r,0) \geqslant 0$, the solution $u(r,t)$ of Eq. (2.4) will in general assume also negative values [11], which is unacceptable for a true density. (ii) In order to ensure the dissipative character of the reaction-telegraph equation (2.4), the damping coefficient $1 - \tau f'(u)$ must be positive, i.e.,

$$f'(u) < \frac{1}{\tau} \quad \text{for all} \quad u. \tag{2.7}$$

This relation between the relaxation time τ of the flux and the time scale $1/f'(u)$ of the reaction appears to be a purely mathematical requirement. The following microscopic approach will shed light on the foundational problems of the reaction-Cattaneo system (2.1) and (2.3) and the reaction-telegraph equation (2.4) hinted at by points (i) and (ii).

B. Reaction random walks

At the microscopic level, the pathologies of the diffusion equation are remedied by replacing the underlying Brownian motion with a persistent random walk, as discussed above. In the correlated or persistent random walk [32], a particle or individual takes steps of length Δr and duration Δt. The particle continues in its previous direction with probability $\alpha = 1 - \mu \Delta t$ and reverses direction with probability $\beta = \mu \Delta t$. In the continuum limit $\Delta r \rightarrow 0$ and $\Delta t \rightarrow 0$ such that

$$\lim_{\Delta r, \Delta t \rightarrow 0} \frac{\Delta r}{\Delta t} = \gamma = \text{const}, \tag{2.8}$$

we obtain the following set of equations for the density of particles going to the right, $u^+(r,t)$, and the density of particles going to the left, $u^-(r,t)$,

$$\frac{\partial u^+}{\partial t} + \gamma \frac{\partial u^+}{\partial r} = \mu(u^- - u^+), \tag{2.9a}$$

$$\frac{\partial u^-}{\partial t} - \gamma \frac{\partial u^-}{\partial r} = \mu(u^+ - u^-). \tag{2.9b}$$

In other words, the particles travel with speed γ and turn with the frequency μ. The persistent random walk is characterized by two parameters in contrast to the ordinary random walk or Brownian motion, which is completely characterized by the diffusion coefficient D. The persistent random walk spans the whole range of dispersal from ballistic motion, in the limit $\mu \rightarrow 0$, to diffusive motion, in the limit $\gamma \rightarrow \infty$, $\mu \rightarrow \infty$ such that $\lim \gamma^2/2\mu = D = \text{const}$, see below. We define the total density

$$u(r,t) = u^+(r,t) + u^-(r,t), \tag{2.10}$$

and the ''flow'' (the flow J is proportional to v: $J = \gamma v$)

$$v(r,t) = u^+(r,t) - u^-(r,t), \tag{2.11}$$

and obtain from Eq. (2.9) the following Cattaneo system:

$$\frac{\partial u}{\partial t} + \gamma \frac{\partial v}{\partial r} = 0, \tag{2.12a}$$

$$\frac{\partial v}{\partial t} + \gamma \frac{\partial u}{\partial r} = -2\mu v. \tag{2.12b}$$

Eliminating v by differentiating Eq. (2.12a) with respect to t and Eq. (2.12b) with respect to r, we obtain the telegraph equation

$$\frac{\partial^2 u}{\partial t^2} + 2\mu \frac{\partial u}{\partial t} = \gamma^2 \frac{\partial^2 u}{\partial r^2}. \tag{2.13}$$

Dividing on both sides by 2μ and comparing the resulting equation with Eq. (2.5), we find that the diffusive limit corresponds to the limit given above.

If the particles moving according to a persistent random walk interact or react with each other, the evolution equations for the densities (2.9) must be modified to include a kinetic rate term

$$\frac{\partial u^+}{\partial t} + \gamma \frac{\partial u^+}{\partial r} = \mu(u^- - u^+) + f^+(u^+, u^-), \tag{2.14a}$$

$$\frac{\partial u^-}{\partial t} - \gamma \frac{\partial u^-}{\partial r} = \mu(u^+ - u^-) + f^-(u^+, u^-). \tag{2.14b}$$

The problem then arises of how to ''distribute'' the kinetic term $f(u)$ of the reaction-diffusion equation to the left and right going densities u^+ and u^-. All previous authors [9–11,29,33], with one exception, have used exclusively the so-called *isotropic reaction walk system*

$$f^+(u^+, u^-) = f^-(u^+, u^-) = \frac{1}{2} f(u). \tag{2.15}$$

This choice is based on the assumption that $f(u)$ is a source term for the particles, that the reaction does not depend on the direction of motion, and that new particles choose either direction with equal probability. With Eq. (2.15) we obtain from Eq. (2.14) the reaction-Cattaneo system

$$\frac{\partial u}{\partial t}+\gamma\frac{\partial v}{\partial r}=f(u), \tag{2.16a}$$

$$\frac{\partial v}{\partial t}+\gamma\frac{\partial u}{\partial r}=-2\mu v. \tag{2.16b}$$

From the reaction-Cattaneo system we derive the reaction-telegraph equation

$$\frac{\partial^2 u}{\partial t^2}+[2\mu-f'(u)]\frac{\partial u}{\partial t}=\gamma^2\frac{\partial^2 u}{\partial r^2}+2\mu f(u). \tag{2.17}$$

The form (2.15) is unsound; it violates a basic principle of kinetics: The rate of removal or death of particles of a given type must go to zero as the density of those particles goes to zero. If we assume that (i) the particles undergo a birth-and-death process that is independent of the direction of motion and (ii) daughter particles choose either direction with equal probability, then the proper form of the kinetic terms in Eq. (2.14) is given by

$$f^+(u^+,u^-)=\frac{1}{2}b(u)-d(u)u^+, \tag{2.18a}$$

$$f^-(u^+,u^-)=\frac{1}{2}b(u)-d(u)u^-, \tag{2.18b}$$

with $b(u)\geqslant 0$ and $d(u)\geqslant 0$. We will call a persistent random walk with these kinetics a *direction-independent reaction walk*. The evolution equations (2.14) with Eq. (2.18) preserve positivity, whereas with Eq. (2.15) positivity is not guaranteed. Though direction-independent kinetics have been mentioned by Hadeler [11,29,33] and Hillen [10], these authors have only investigated the isotropic reaction walk (2.15), with the exception of [29], where an existence theorem for traveling fronts in direction-independent reaction walks is proven. Other choices for the kinetic terms of reaction random walks, in particular, kinetics that depend on the relative direction of motion, will be considered elsewhere [34].

III. TRANSPORT-DRIVEN INSTABILITIES

A. Turing bifurcations in reaction-diffusion systems

Before investigating the stability properties of reaction random walks, we briefly summarize the main features of the Turing bifurcation in reaction-diffusion systems. Consider the two-species system

$$\frac{\partial x}{\partial t}=D_x\frac{\partial^2 x}{\partial r^2}+f(x,y), \tag{3.1a}$$

$$\frac{\partial y}{\partial t}=D_y\frac{\partial^2 y}{\partial r^2}+g(x,y), \tag{3.1b}$$

with no-flow boundary conditions on the interval $[0,L]$,

$$\frac{\partial x}{\partial r}(0,t)=\frac{\partial x}{\partial r}(L,t)=0, \tag{3.2a}$$

$$\frac{\partial y}{\partial r}(0,t)=\frac{\partial y}{\partial r}(L,t)=0. \tag{3.2b}$$

Let $(\overline{x},\overline{y})$ be a steady state of the homogeneous system

$$\frac{dx}{dt}=f(x,y), \tag{3.3a}$$

$$\frac{dy}{dt}=g(x,y), \tag{3.3b}$$

namely,

$$f(\overline{x},\overline{y})=g(\overline{x},\overline{y})=0, \tag{3.4}$$

and let A be the Jacobian at the steady state,

$$A=\begin{pmatrix}A_{11} & A_{12}\\ A_{21} & A_{22}\end{pmatrix}=\begin{pmatrix}\frac{\partial f}{\partial x}(\overline{x},\overline{y}) & \frac{\partial f}{\partial y}(\overline{x},\overline{y})\\ \frac{\partial g}{\partial x}(\overline{x},\overline{y}) & \frac{\partial g}{\partial y}(\overline{x},\overline{y})\end{pmatrix}. \tag{3.5}$$

Then

$$(\hat{x}(r),\hat{y}(r))=(\overline{x},\overline{y}) \tag{3.6}$$

is a homogeneous steady state of the reaction-diffusion system (3.1). It is stable against homogeneous perturbations, if $(\overline{x},\overline{y})$ is a stable steady state of the homogeneous system, i.e., if

$$T=\mathrm{tr}\ A=A_{11}+A_{22}<0 \tag{3.7}$$

and

$$\Delta=\det A=A_{11}A_{22}-A_{12}A_{21}>0. \tag{3.8}$$

A Turing bifurcation corresponds to a diffusion-driven instability of a stable homogeneous steady state, where a spatial perturbation with wave number $k_c\neq 0$ becomes unstable. (For a review of the Turing instability see, for instance, [3]). For a one-dimensional system, the spectrum of possible wave numbers is given by $k=m\pi/L$, where $m=0,1,2,\ldots$. To simplify the presentation, we will treat k as a continuous variable and assume that the system can accommodate a pattern with intrinsic wave number k_c. This represents no restriction of generality, since one can ensure that any given k is in the spectrum by an appropriate choice of the system size L. A necessary but not sufficient condition for a Turing bifurcation is

$$D_yA_{11}+D_xA_{22}>0. \tag{3.9}$$

In light of Eq. (3.7), a Turing bifurcation can therefore occur only if (i) the coefficients A_{11} and A_{22} do not have the same sign, and (ii) if the diffusion coefficients are not equal. We will assume that

$$A_{11} > 0, \quad A_{22} < 0, \tag{3.10}$$

and consequently $|A_{22}| > A_{11}$ since $T < 0$ and $A_{12}A_{21} < 0$ since $\Delta > 0$. With this choice, we will call X an activator and Y an inhibitor in the broad sense. (In the strict sense, X is an activator and Y an inhibitor if also $A_{21} > 0$ and $A_{12} < 0$.) Defining

$$\Theta = \frac{D_y}{D_x}, \tag{3.11}$$

we obtain from Eq. (3.9)

$$\Theta > \frac{-A_{22}}{A_{11}} > 1. \tag{3.12}$$

The stable homogeneous steady state undergoes a Turing bifurcation with critical wave number

$$k_c^2 = \sqrt{\frac{\Delta}{D_x D_y}} \tag{3.13}$$

for parameter values of the system such that

$$D_y A_{11} + D_x A_{22} = \sqrt{4 D_x D_y \Delta}, \tag{3.14}$$

or equivalently, at the critical ratio of diffusion coefficients

$$\Theta_c = \left[\frac{1}{A_{11}} \left(\sqrt{\Delta} + \sqrt{-A_{12}A_{21}} \right) \right]^2. \tag{3.15}$$

B. Stability analysis of direction-independent reaction walks

Hillen [10] has studied the Turing instability for the isotropic reaction walk,

$$\frac{\partial x^+}{\partial t} + \gamma_x \frac{\partial x^+}{\partial r} = \mu_x (x^- - x^+) + \frac{1}{2} f(x,y), \tag{3.16a}$$

$$\frac{\partial x^-}{\partial t} - \gamma_x \frac{\partial x^-}{\partial r} = \mu_x (x^+ - x^-) + \frac{1}{2} f(x,y), \tag{3.16b}$$

$$\frac{\partial y^+}{\partial t} + \gamma_y \frac{\partial y^+}{\partial r} = \mu_y (y^- - y^+) + \frac{1}{2} g(x,y), \tag{3.16c}$$

$$\frac{\partial y^-}{\partial t} - \gamma_y \frac{\partial y^-}{\partial r} = \mu_y (y^+ - y^-) + \frac{1}{2} g(x,y), \tag{3.16d}$$

and found the surprising result that with

$$D_x = \frac{\gamma_x^2}{2\mu_x}, \quad D_y = \frac{\gamma_y^2}{2\mu_y} \tag{3.17}$$

the stability properties of isotropic reaction walks are identical to those of reaction-diffusion systems if $2\mu_x > A_{11}$. The Turing conditions (3.14) or (3.15) and the critical wave number (3.13) also govern the bifurcation to steady patterns in the reaction random walk (3.16), unless the motion is in the ballistic regime, i.e., the chemical time scale of activation $\tau_{\text{chem}} = 1/A_{11}$ is shorter than the correlation time $\tau = 1/2\mu_x$ of the switching process for the activator. If the motion of the activator is in the ballistic regime, $2\mu_x < A_{11}$, and if $\gamma_x \neq \gamma_y$, then all spatial modes with wave numbers bigger than some k_H undergo a Hopf bifurcation to oscillatory behavior. This instability does not occur in reaction-diffusion systems.

As discussed above, the isotropic reaction walk is unsound and violates a basic kinetic principle. The proper model for isotropic kinetics is the persistent random walk with direction-independent kinetics. We will show below that both results of [10] do not hold in this case: (i) Away from the ballistic regime, the stability properties of reaction random walks remain similar to those of reaction-diffusion systems, but the Turing condition depends *explicitly* on *both* parameters of the random walk, and not only on D_i. (ii) The spatial Hopf bifurcation may be suppressed by the kinetics of the activator.

We study the two-species direction-independent reaction walk

$$\frac{\partial x^+}{\partial t} + \gamma_x \frac{\partial x^+}{\partial r} = \mu_x (x^- - x^+) + \frac{1}{2} b(x,y) - d(x,y) x^+, \tag{3.18a}$$

$$\frac{\partial x^-}{\partial t} - \gamma_x \frac{\partial x^-}{\partial r} = \mu_x (x^+ - x^-) + \frac{1}{2} b(x,y) - d(x,y) x^-, \tag{3.18b}$$

$$\frac{\partial y^+}{\partial t} + \gamma_y \frac{\partial y^+}{\partial r} = \mu_y (y^- - y^+) + \frac{1}{2} c(x,y) - e(x,y) y^+, \tag{3.18c}$$

$$\frac{\partial y^-}{\partial t} - \gamma_y \frac{\partial y^-}{\partial r} = \mu_y (y^+ - y^-) + \frac{1}{2} c(x,y) - e(x,y) y^-, \tag{3.18d}$$

with impermeable boundaries, i.e., reflective boundary conditions, on $[0,L]$,

$$x^+(0,t) = x^-(0,t), \quad y^+(0,t) = y^-(0,t), \tag{3.19a}$$

$$x^-(L,t) = x^+(L,t), \quad y^-(L,t) = y^+(L,t). \tag{3.19b}$$

We introduce the total densities

$$x(r,t) = x^+(r,t) + x^-(r,t), \tag{3.20}$$

$$y(r,t) = y^+(r,t) + y^-(r,t), \tag{3.21}$$

and the flows

$$v(r,t) = x^+(r,t) - x^-(r,t), \tag{3.22}$$

$$w(r,t) = y^+(r,t) - y^-(r,t). \tag{3.23}$$

Adding Eqs. (3.18a) and (3.18b), we obtain the evolution equation for the total density of species X,

$$\frac{\partial x}{\partial t} + \gamma_x \frac{\partial v}{\partial r} = b(x,y) - d(x,y) x = f(x,y). \tag{3.24}$$

Subtracting Eq. (3.18b) from Eq. (3.18a), we obtain the evolution equation for the flow of species X,

$$\frac{\partial v}{\partial t} + \gamma_x \frac{\partial x}{\partial r} = -2\mu_x v - d(x,y) v. \tag{3.25}$$

Note that Eqs. (3.24) and (3.25) do not form a reaction-Cattaneo system, because of the contribution of the death rate $d(x,y)$ to the decay rate of the flow. Also, no reaction-telegraph equation can be derived for $x(r,t)$, unless $d(x,y)$ is a constant. The evolution equations for the total density and the flow of the species Y read

$$\frac{\partial y}{\partial t}+\gamma_y\frac{\partial w}{\partial r}=c(x,y)-e(x,y)y=g(x,y), \tag{3.26}$$

$$\frac{\partial w}{\partial t}+\gamma_y\frac{\partial y}{\partial r}=-2\mu_y w-e(x,y)w. \tag{3.27}$$

The boundary conditions (3.19) become

$$v(0,t)=v(L,t)=0, \tag{3.28a}$$

$$w(0,t)=w(L,t)=0. \tag{3.28b}$$

The homogeneous steady state of Eqs. (3.24)–(3.27) is given by

$$\hat{x}(r)=\overline{x},\quad \hat{y}(r)=\overline{y}, \tag{3.29a}$$

$$\hat{v}(r)=\hat{w}(r)=0, \tag{3.29b}$$

i.e., it coincides with the homogeneous steady state (3.6) of the reaction-diffusion system (3.1).

We now carry out a linear stability analysis of the homogeneous steady state of the direction-independent reaction walk by determining the growth rate of small perturbations,

$$x(r,t)=\overline{x}+\Delta X(r,t), \tag{3.30a}$$

$$y(r,t)=\overline{y}+\Delta Y(r,t), \tag{3.30b}$$

$$v(r,t)=\Delta V(r,t), \tag{3.30c}$$

$$w(r,t)=\Delta W(r,t). \tag{3.30d}$$

The linearized evolution equations for the direction-independent reaction walk are

$$\Delta\dot{X}+\gamma_x\Delta V'=A_{11}\Delta X+A_{12}\Delta Y, \tag{3.31a}$$

$$\Delta\dot{Y}+\gamma_y\Delta W'=A_{21}\Delta X+A_{22}\Delta Y, \tag{3.31b}$$

$$\Delta\dot{V}+\gamma_x\Delta X'=-[2\mu_x+d(\overline{x},\overline{y})]\Delta V, \tag{3.31c}$$

$$\Delta\dot{W}+\gamma_y\Delta Y'=-[2\mu_y+e(\overline{x},\overline{y})]\Delta W, \tag{3.31d}$$

where the dot and prime denote differentiation with respect to t and to r, respectively.

The boundary conditions (3.28) imply that the spatial modes for the flows are given by

$$\Phi(r)=\sin(kr), \tag{3.32}$$

with

$$k=\frac{m\pi}{L},\quad m=0,1,2,\ldots . \tag{3.33}$$

We evaluate Eqs. (3.25) and (3.27) at the boundaries $r=0$ and $r=L$ to obtain

$$\frac{\partial x}{\partial r}(0,t)=\frac{\partial x}{\partial r}(L,t)=0, \tag{3.34a}$$

$$\frac{\partial y}{\partial r}(0,t)=\frac{\partial y}{\partial r}(L,t)=0. \tag{3.34b}$$

This implies that the spatial modes for the densities are given by

$$\Psi(r)=\cos(kr). \tag{3.35}$$

The perturbations can now be written as

$$\Delta X(r,t)=X_0\Psi(r)\exp[\omega(k)t], \tag{3.36a}$$

$$\Delta Y(r,t)=Y_0\Psi(r)\exp[\omega(k)t], \tag{3.36b}$$

$$\Delta V(r,t)=V_0\Phi(r)\exp[\omega(k)t], \tag{3.36c}$$

$$\Delta W(r,t)=W_0\Phi(r)\exp[\omega(k)t], \tag{3.36d}$$

where $\omega(k)$ is the growth rate of a perturbation with wave number k.

The homogeneous steady state is stable, if the real part $\mathrm{Re}\,\omega(k)$ of the growth rate is negative for all k. Equations (3.7) and (3.8) imply, as in the case of the reaction-diffusion system, that $\mathrm{Re}\,\omega(0)<0$, i.e., the homogeneous steady state is stable against homogeneous perturbations. We will now consider inhomogeneous perturbations with wave number $k\neq 0$. To shorten the notation, we introduce

$$\mu=2\mu_x+d(\overline{x},\overline{y}), \tag{3.37}$$

$$\nu=2\mu_y+e(\overline{x},\overline{y}), \tag{3.38}$$

$$\gamma=\gamma_x,\quad \chi=\gamma_y. \tag{3.39}$$

The linearized equations read

$$\omega(k)\Delta X+\gamma\Delta V'=A_{11}\Delta X+A_{12}\Delta Y, \tag{3.40a}$$

$$\omega(k)\Delta Y+\chi\Delta W'=A_{21}\Delta X+A_{22}\Delta Y, \tag{3.40b}$$

$$\omega(k)\Delta V+\gamma\Delta X'=-\mu\Delta V, \tag{3.40c}$$

$$\omega(k)\Delta W+\chi\Delta Y'=-\nu\Delta W. \tag{3.40d}$$

From Eqs. (3.40c) and (3.40d) we obtain

$$\Delta X'=-\frac{\omega(k)+\mu}{\gamma}\Delta V, \tag{3.41a}$$

$$\Delta Y' = -\frac{\omega(k)+\nu}{\chi}\Delta W. \tag{3.41b}$$

We differentiate Eqs. (3.40a) and (3.40b) with respect to r and use Eq. (3.41) to eliminate ΔX and ΔY from the linearized equations

$$-\frac{\omega(k)+\mu}{\gamma}\omega(k)\Delta V + \gamma\Delta V'' = A_{11}\left(-\frac{\omega(k)+\mu}{\gamma}\right)\Delta V + A_{12}\left(-\frac{\omega(k)+\nu}{\chi}\right)\Delta W, \tag{3.42}$$

$$-\frac{\omega(k)+\nu}{\chi}\omega(k)\Delta W + \chi\Delta W'' = A_{21}\left(-\frac{\omega(k)+\mu}{\gamma}\right)\Delta V + A_{22}\left(-\frac{\omega(k)+\nu}{\chi}\right)\Delta W. \tag{3.43}$$

Since $\Delta V'' = -k^2\Delta V$ and $\Delta W'' = -k^2\Delta W$, these equations can be written after some simple algebra as

$$\begin{pmatrix} \chi[(\omega+\mu)(A_{11}-\omega)-k^2\gamma^2] & \gamma A_{12}(\omega+\nu) \\ \chi A_{12}(\omega+\mu) & \gamma[(\omega+\nu)(A_{22}-\omega)-k^2\chi^2] \end{pmatrix}\begin{pmatrix}\Delta V \\ \Delta W\end{pmatrix} = 0, \tag{3.44}$$

where we have dropped writing explicitly the dependence of ω on k. The characteristic equation is the determinant of the matrix in Eq. (3.44), and it is given by

$$\omega^4 + c_3\omega^3 + c_2\omega^2 + c_1\omega + c_0 = 0, \tag{3.45}$$

with

$$c_3 = \mu + \nu - T, \tag{3.46}$$

$$c_2 = \Delta - T(\mu+\nu) + \mu\nu + (\chi^2+\gamma^2)k^2, \tag{3.47}$$

$$c_1 = \Delta(\mu+\nu) - T\mu\nu - [\chi^2(A_{11}-\mu) + \gamma^2(A_{22}-\nu)]k^2, \tag{3.48}$$

$$c_0 = \Delta\mu\nu - [\mu\chi^2 A_{11} + \nu\gamma^2 A_{22}]k^2 + \gamma^2\chi^2 k^4. \tag{3.49}$$

C. Turing bifurcations in reaction walks

A Turing bifurcation corresponds to $\omega(k_c)=0$ for some $k_c \neq 0$. This requires that $c_0 = 0$,

$$\Delta\mu\nu - [\mu\chi^2 A_{11} + \nu\gamma^2 A_{22}]k^2 + \gamma^2\chi^2 k^4 = 0, \tag{3.50}$$

or

$$k^4 - \left(\frac{A_{11}}{\mathcal{D}_x} + \frac{A_{22}}{\mathcal{D}_y}\right)k^2 + \frac{\Delta}{\mathcal{D}_x\mathcal{D}_y} = 0, \tag{3.51}$$

with

$$\mathcal{D}_x = \frac{\gamma^2}{\mu}, \quad \mathcal{D}_y = \frac{\chi^2}{\nu}. \tag{3.52}$$

The solutions of this equation are

$$k^2_{+,-} = \frac{1}{2\mathcal{D}_x\mathcal{D}_y}[(\mathcal{D}_y A_{11} + \mathcal{D}_x A_{22}) \pm \sqrt{d}], \tag{3.53}$$

where

$$d = (\mathcal{D}_y A_{11} + \mathcal{D}_x A_{22})^2 - 4\mathcal{D}_x\mathcal{D}_y\Delta. \tag{3.54}$$

These roots need to be positive, which requires

$$\mathcal{D}_y A_{11} + \mathcal{D}_x A_{22} > 0. \tag{3.55}$$

The Turing bifurcation corresponds to a double root, which requires the discriminant d to be zero,

$$\mathcal{D}_y A_{11} + \mathcal{D}_x A_{22} = \sqrt{4\mathcal{D}_y\mathcal{D}_x\Delta}. \tag{3.56}$$

This Turing condition can be rewritten after some algebra as a condition on the random walk parameters

$$\left(\frac{\mathcal{D}_y}{\mathcal{D}_x}\right)_c = \left[\frac{1}{A_{11}}(\sqrt{\Delta} + \sqrt{-A_{12}A_{21}})\right]^2. \tag{3.57}$$

The critical wave number for the Turing bifurcation, i.e., the double root of Eq. (3.51), is

$$k_c^2 = \sqrt{\frac{\Delta}{\mathcal{D}_x\mathcal{D}_y}}. \tag{3.58}$$

Contrary to appearances, these conditions are not identical with the Turing conditions for the reaction-diffusion system, since the $\mathcal{D}_i$ differ from the diffusion coefficients D_i,

$$\mathcal{D}_x = \frac{\gamma_x^2}{2\mu_x + d(\overline{x},\overline{y})} \tag{3.59a}$$

$$= D_x\left(1 + \frac{d(\overline{x},\overline{y})}{2\mu_x}\right)^{-1} \tag{3.59b}$$

and

$$\mathcal{D}_y = \frac{\gamma_y^2}{2\mu_y + e(\overline{x},\overline{y})} \tag{3.60a}$$

$$= D_y\left(1 + \frac{e(\overline{x},\overline{y})}{2\mu_y}\right)^{-1}. \tag{3.60b}$$

Let Θ_c^{RD} be the critical ratio of diffusion coefficients given by Eq. (3.15). Then the Turing condition for the direction-independent reaction walk can be written as

$$\Theta_c^{\mathrm{DIRW}} = \left(\frac{D_y}{D_x}\right)_c = \frac{1 + [e(\overline{x},\overline{y})/(2\mu_y)]}{1 + [d(\overline{x},\overline{y})/(2\mu_x)]}\Theta_c^{\mathrm{RD}}. \tag{3.61}$$

The critical wave number is given by

$$k_c^{2,\mathrm{DIRW}} = \sqrt{\frac{\Delta}{D_x D_y}}\sqrt{\frac{4\mu_x\mu_y}{[2\mu_x + d(\overline{x},\overline{y})][2\mu_y + e(\overline{x},\overline{y})]}}, \tag{3.62}$$

$$k_c^{2,\mathrm{DIRW}} = k_c^{2,\mathrm{RD}}\sqrt{\frac{4\mu_x\mu_y}{[2\mu_x + d(\overline{x},\overline{y})][2\mu_y + e(\overline{x},\overline{y})]}}. \tag{3.63}$$

We draw several conclusions from these equations: (i) The Turing condition for the reaction walk with proper direction-independent kinetics depends on the parameters of the persistent random walk not only through the combination $D_i = \gamma_i^2/(2\mu_i)$ but also explicitly on the turning rates μ_i, in contrast to the isotropic reaction walk [10]. (ii) The Turing bifurcation will be advanced or delayed compared to the reaction-diffusion case, depending if μ_x/μ_y is smaller or larger than $d(\overline{x},\overline{y})/e(\overline{x},\overline{y})$. (iii) The critical wave number is always shifted to smaller values, or the intrinsic length of the Turing pattern to larger values, compared with the reaction-diffusion system.

D. Spatial Hopf bifurcation

In contrast to reaction-diffusion systems, the homogeneous steady state of a direction-independent reaction walk, like that of an isotropic reaction walk, may undergo an instability to oscillating spatial patterns. Such a Hopf bifurcation occurs when the real part of the growth rate $\omega(k)$ becomes zero, while the imaginary part is nonzero, $\omega(k_H) = i\Omega$. Inserting this form into Eq. (3.45), we find from the real and imaginary part of the equation

$$\Omega^4 - ic_3\Omega^3 - c_2\Omega^2 + ic_1\Omega + c_0 = 0, \tag{3.64}$$

the frequency Ω,

$$\Omega^2 = \frac{c_1}{c_3}, \tag{3.65}$$

and the Hopf condition,

$$c_1^2 - c_1c_2c_3 + c_0c_3^2 = 0. \tag{3.66}$$

Since T is negative, c_3 is always positive. Appendix B shows that c_1 is positive at the Hopf bifurcation, and therefore the right hand side of Eq. (3.65) is indeed positive. Gathering terms of equal powers in k, we rewrite the Hopf condition as

$$\rho_2 k^4 + \rho_1 k^2 + \rho_0 = 0, \tag{3.67}$$

where, after some algebra,

$$\rho_2 = -(A_{11} - \mu)(A_{22} - \nu)(\chi^2 - \gamma^2)^2, \tag{3.68}$$

$$\rho_0 = TS[\Delta(\mu^2 + \nu^2) - TS(M + \Delta) + M^2 + \Delta^2 + T^2M], \tag{3.69}$$

and

$$\rho_1 = -2(\Delta S - TM)B_1 - (S - T)(\Delta S - TM)(\chi^2 + \gamma^2) + (S - T)B_1(\Delta - TS + M) - (S - T)^2B_2. \tag{3.70}$$

Here

$$S = \mu + \nu, \quad M = \mu\nu, \tag{3.71}$$

$$B_1 = \chi^2(A_{11} - \mu) + \gamma^2(A_{22} - \nu), \tag{3.72}$$

and

$$B_2 = \mu\chi^2A_{11} + \nu\gamma^2A_{22}. \tag{3.73}$$

Since $\mu > 0$, $\nu > 0$, $\Delta > 0$, and $T < 0$, we have that ρ_0 is always negative. We also have that ρ_2 is negative, if $\gamma \neq \chi$ and $\mu > A_{11}$. Lengthy calculations, see Appendix A, show that ρ_1 is negative if ρ_2 is negative. Thus for $\mu > A_{11}$, Eq. (3.67) has no real roots, since all coefficients are negative. In other words, a Hopf bifurcation can only occur in the ballistic regime. If $\mu < A_{11}$ and $\gamma \neq \chi$, then ρ_2 is positive, and Eq. (3.67) has a positive root k_H. The existence of this Hopf bifurcation depends, however, on the kinetics. The Hopf condition reads

$$\mu < A_{11}, \tag{3.74}$$

or

$$2\mu_x < A_{11} - d(\overline{x},\overline{y}). \tag{3.75}$$

Clearly, the Hopf bifurcation can only occur if the right hand side is positive, i.e., if the rate of activation is bigger than the death rate of the activator in the steady state. As we will see in the next subsection, this is not the case in commonly studied model systems.

A Routh-Hurwitz analysis of the characteristic equation (3.45), see Appendix B, shows that the Turing bifurcation and the Hopf bifurcation are the only instabilities possible for the homogeneous steady state. In summary, we have the following.

If the steady state $(\overline{x},\overline{y})$ of the homogeneous system (3.3) is stable, i.e., if the conditions (3.7) and (3.8) are fulfilled, then the homogeneous steady state of Eq. (3.18) or the equivalent system (3.24)–(3.27) is linearly unstable, if and only if one of the following two conditions is satisfied.

(1) Turing instability

$$\frac{\gamma_y^2[2\mu_x+d(\overline{x},\overline{y})]}{\gamma_x^2[2\mu_y+e(\overline{x},\overline{y})]}>\left[\frac{1}{A_{11}}(\sqrt{\Delta}+\sqrt{-A_{12}A_{21}})\right]^2. \tag{3.76}$$

All spatial modes with wave numbers k in the interval (k_-,k_+) are unstable.

(2) Hopf instability

$$2\mu_x<A_{11}-d(\overline{x},\overline{y}). \tag{3.77}$$

All spatial modes with wave numbers bigger than k_H, the positive root of Eq. (3.67), are unstable.

E. Model systems

We apply the results of the preceding stability analysis to two model systems, commonly used to study spatial pattern formation in reaction-diffusion systems. The kinetic terms for the Brusselator [13] are given by

$$f(x,y)=p-(q+1)x+x^2y, \tag{3.78}$$

$$g(x,y)=qx-x^2y, \tag{3.79}$$

where p and q are positive constants. The decay rates of activator and inhibitor are

$$d(x,y)=q+1, \quad e(x,y)=x^2. \tag{3.80}$$

The Brusselator has a unique homogeneous steady state

$$\overline{x}=p, \quad \overline{y}=\frac{q}{p}, \tag{3.81}$$

with the Jacobian

$$A=\begin{pmatrix} q-1 & p^2 \\ -q & -p^2 \end{pmatrix} \tag{3.82}$$

and

$$T=q-1-p^2, \quad \Delta=p^2. \tag{3.83}$$

Note that for all parameter values, $\Delta>0$ and $A_{22}<0$. The trace T is negative if $q<1+p^2$, and $A_{11}>0$ if $q>1$. The conditions (3.7), (3.8), and (3.10) are fulfilled for

$$1<q<1+p^2. \tag{3.84}$$

A Turing bifurcation occurs in a direction-independent reaction walk with Brusselator kinetics at

$$\left(\frac{D_y}{D_x}\right)_c=\frac{1+[p^2/(2\mu_y)]}{1+[(q+1)/(2\mu_x)]}\,\frac{p^2}{(q-1)^2}(1+\sqrt{q})^2, \tag{3.85}$$

$$\left(\frac{D_y}{D_x}\right)_c=\frac{1+[p^2/(2\mu_y)]}{1+[(q+1)/(2\mu_x)]}\,\Theta_c^{\mathrm{RD}}, \tag{3.86}$$

and the critical wave number is given by

$$k_c^2=\sqrt{\frac{p^2}{D_xD_y}}\sqrt{\frac{4\mu_x\mu_y}{(2\mu_x+q+1)(2\mu_y+p^2)}}, \tag{3.87}$$

$$k_c^2=k_c^{2,\mathrm{RD}}\sqrt{\frac{4\mu_x\mu_y}{(2\mu_x+q+1)(2\mu_y+p^2)}}. \tag{3.88}$$

For the Brusselator, the spatial Hopf condition reads

$$2\mu_x+q+1<q-1, \tag{3.89}$$

or

$$\mu_x<-1, \tag{3.90}$$

which can never be fulfilled since the turning rate is nonnegative. The Brusselator kinetics suppress the spatial Hopf bifurcation.

The Gierer-Meinhardt model [35] has the following kinetics:

$$f(x,y)=1-x+p\frac{x^2}{y}, \tag{3.91}$$

$$g(x,y)=q(x^2-y), \tag{3.92}$$

where p and q are positive parameters. The decay rates of the activator and inhibitor are

$$d(x,y)=1, \quad e(x,y)=q. \tag{3.93}$$

This model also has a unique homogeneous steady state

$$\overline{x}=1+p, \quad \overline{y}=(1+p)^2, \tag{3.94}$$

and the Jacobian is

$$A=\begin{pmatrix} (p-1)/(p+1) & -p/(1+p)^2 \\ 2q(1+p) & -q \end{pmatrix}, \tag{3.95}$$

and

$$T=\frac{p-1}{p+1}-q, \quad \Delta=q. \tag{3.96}$$

For all parameter values, the determinant Δ is positive and A_{22} is negative. The trace T is negative if $(p-1)/(p+1)<q$, and A_{11} is positive for $p>1$. The conditions (3.7), (3.8), and (3.10) are fulfilled for

$$\frac{p-1}{p+1}<q, \quad p>1. \tag{3.97}$$

A Turing bifurcation occurs in direction-independent reaction walks with Gierer-Meinhardt kinetics at

$$\left(\frac{D_y}{D_x}\right)_c=\frac{1+[q/(2\mu_y)]}{1+[1/(2\mu_x)]}\Theta_c^{\mathrm{RD}}, \tag{3.98}$$

where

$$\Theta_c^{\mathrm{RD}}=\left(\frac{p+1}{p-1}\right)^2q\left(1+\sqrt{\frac{2p}{1+p}}\right)^2. \tag{3.99}$$

The critical wave number is given by

$$k_c^2 = \sqrt{\frac{q}{D_x D_y}} \sqrt{\frac{4\mu_x \mu_y}{(2\mu_x + 1)(2\mu_y + q)}}, \tag{3.100}$$

$$k_c^2 = k_c^{2,\mathrm{RD}} \sqrt{\frac{4\mu_x \mu_y}{(2\mu_x + 1)(2\mu_y + q)}}. \tag{3.101}$$

The condition for the spatial Hopf bifurcation is

$$2\mu_x + 1 < \frac{p-1}{p+1}, \tag{3.102}$$

$$\mu_x < -\frac{1}{p+1}, \tag{3.103}$$

which can never be true.

Kinetics suppress the spatial Hopf bifurcation in both the Brusselator and the Gierer-Meinhardt model, since $A_{11} - d(\overline{x},\overline{y})$ is negative. These two models are representative of the behavior of other activator-inhibitor models commonly used to describe pattern formation. The Schnakenberg model [3,36], $f(x,y) = p - x + x^2 y$, $g(x,y) = q - x^2 y$, the glycolytic model [37,38], $f(x,y) = qy + yx^2 - x$, $g(x,y) = p - qy - yx^2$, and the Lengyel-Epstein model [39], $f(x,y) = p - x - 4xy/(1 + x^2)$, $g(x,y) = q[x - xy/(1 + x^2)]$, all have $A_{11} - d(\overline{x},\overline{y}) < 0$, and the spatial Hopf bifurcation cannot occur. For the Gray-Scott model [40], $f(x,y) = yx^2 - (p + q)x$, $g(x,y) = -yx^2 + q(1 - y)$, we find that $A_{11} - d(\overline{x},\overline{y}) = 0$, and again the spatial Hopf bifurcation is suppressed by the kinetics. If this model is modified and the third order autocatalysis replaced by a rather unrealistic fourth order, $f(x,y) = yx^3 - qx$, $g(x,y) = -yx^3 + q(1 - y)$, then for sufficiently small q the model has a nontrivial stable homogeneous steady state, for which $A_{11} - d(\overline{x},\overline{y}) = q$. A spatial Hopf bifurcation occurs for $2\mu_x < q$. In conclusion, the existence of a spatial Hopf bifurcation in the ballistic regime is an interesting theoretical possibility, but studies of activator-inhibitor models show that it is unlikely to occur for realistic kinetics.

IV. STABILITY PROPERTIES OF ONE-SPECIES SYSTEMS

It is instructive to analyze the stability properties of one-species systems. Such systems cannot undergo transport-driven instabilities, but their study sheds light on the behavior of large wave number or small wavelength perturbations. Consider the one-species reaction-diffusion system

$$\frac{\partial x}{\partial t} = D \frac{\partial^2 x}{\partial r^2} + f(x), \tag{4.1}$$

with no-flow boundary conditions on the interval $[0,L]$,

$$\frac{\partial x}{\partial r}(0,t) = \frac{\partial x}{\partial r}(L,t) = 0. \tag{4.2}$$

Let $\overline{x}$ be a stable steady state of the homogeneous system, i.e.,

$$f(\overline{x}) = 0, \quad \text{with } \frac{df}{dx}(\overline{x}) \equiv \omega_0 < 0. \tag{4.3}$$

The linearized evolution equation for small perturbations is

$$\omega(k)\Delta X = -Dk^2 \Delta X + \omega_0 \Delta X, \tag{4.4}$$

which yields the spectrum of growth rates

$$\omega(k) = \omega_0 - Dk^2. \tag{4.5}$$

For a one-species system, diffusion has the intuitively expected effect; it is always stabilizing.

The corresponding direction-independent reaction walk gives rise to the following equations for the total density and flow:

$$\frac{\partial x}{\partial t} + \gamma \frac{\partial v}{\partial r} = b(x) - d(x)x = f(x), \tag{4.6a}$$

$$\frac{\partial v}{\partial t} + \gamma \frac{\partial x}{\partial r} = -2\tilde{\mu} v - d(x) v. \tag{4.6b}$$

The homogeneous steady state is given by

$$\hat{x}(r) = \overline{x}, \quad \hat{v}(r) = 0, \tag{4.7}$$

and the linearized evolution equations are

$$\omega(k)\Delta X + \gamma \Delta V' = \omega_0 \Delta X, \tag{4.8a}$$

$$\omega(k)\Delta V + \gamma \Delta X' = -\mu \Delta V, \tag{4.8b}$$

where

$$\mu = 2\tilde{\mu} + d(\overline{x}). \tag{4.9}$$

We eliminate ΔX and obtain

$$[(\omega + \mu)(\omega_0 - \omega) - \gamma^2 k^2]\Delta V = 0, \tag{4.10}$$

or the characteristic equation

$$\omega^2 + (\mu - \omega_0)\omega - \mu\omega_0 + \gamma^2 k^2 = 0. \tag{4.11}$$

The spectrum of growth rates is given by

$$\omega(k)_{\pm} = \frac{1}{2}\left[\omega_0 - \mu \pm \sqrt{(\omega_0 + \mu)^2 - 4\gamma^2 k^2}\right]. \tag{4.12}$$

For

$$k < k_c = \frac{1}{2\gamma}|\omega_0 + \mu|, \tag{4.13}$$

the growth rates are real and negative. At $k = k_c$, a double root occurs, $\omega(k_c) = \frac{1}{2}(\omega_0 - \mu)$, and for $k > k_c$, the growth rates become complex. The real part is equal to $\omega(k_c)$ and negative. Perturbations with wave numbers bigger than k_c exhibit damped oscillations. These perturbations decay with a rate that is the mean of the decay rate of the flow, $-\mu$, and of the chemical decay rate ω_0. They oscillate with a frequency $\Omega(k) = \sqrt{|(\omega_0 + \mu)^2 - 4\gamma^2 k^2|}$. This behavior is qualitatively different from the reaction-diffusion system, where perturbations of all wave numbers decay monotonely. As expected, k_c goes to infinity in the diffusive limit

$$k_c \to \frac{\tilde{\mu}}{\gamma} = \frac{\gamma}{2D} \to \infty, \tag{4.14}$$

as $\gamma \to \infty$, $\tilde{\mu} \to \infty$ with $D = \gamma^2/(2\tilde{\mu})$. In the ballistic limit, $\tilde{\mu} \to 0$, the wave number k_c goes to

$$k_c = \frac{|\omega_0 + d(\overline{x})|}{2\gamma}. \tag{4.15}$$

Note that if the decay rate of the flow, $\mu = 2\tilde{\mu} + d(\overline{x})$, coincides with chemical decay rate $|\omega_0|$, i.e., $\mu = |\omega_0|$, then $k_c = 0$, and perturbations with all wave numbers k exhibit damped oscillations. This phenomenon foreshadows the spatial Hopf condition for two-species activator-inhibitor systems, $\mu = A_{11}$.

V. CONCLUSIONS

Direction-independent reaction walks provide a unified description of reacting and dispersing systems, covering the full range of particle motion from the ballistic to the diffusive regime. As is well known, the persistent random walk can be described by a Cattaneo system or a telegraph equation. This is not the case for a reaction random walk with proper kinetic terms, i.e., the direction-independent reaction walk. The decay rate of the flow is no longer solely given by the turning rate of the particles; the death rate provides an extra additive contribution. To our knowledge, no microscopic basis for reaction-Cattaneo systems or reaction-telegraph equations has been established.

Our studies of direction-independent reaction walks show that the Turing bifurcation is remarkably robust. Only quantitative changes occur as the system moves away from the diffusive limit and persistence or inertia effects become important. The critical wavelength shifts to larger values, and the critical ratio of effective diffusion coefficients may decrease or increase. These changes occur because the critical wavelength and the Turing condition depend not only on the effective diffusion coefficients, $D_i = \gamma_i^2/(2\mu_i)$, but also on the turning rates μ_i. The Turing bifurcation persists all the way to the ballistic limit, if the kinetics suppress the spatial Hopf bifurcation, as is the case in the two model systems studied here and other activator-inhibitor models with realistic kinetics. Remarkably, the Turing bifurcation neither disappears nor do other instabilities occur. Transport characteristics affect details of the Turing mechanism, but not its essence.

Reaction walks differ from reaction-diffusion systems in that small wavelength perturbations exhibit damped oscillations, as shown explicitly for one-species systems in the preceding section. A similar phenomenon occurs in reaction-diffusion-convection systems with linear shear flow [41]. There the oscillatory time scales are the result of the interaction of diffusion with convection. Here the oscillatory time scales for short wavelength modes are the result of the ballistic character of the motion on small length scales. It will be interesting to investigate what role these time scales may play in conjunction with other effects. For instance, oscillatory spatial patterns may appear if the homogeneous steady state is perturbed by spatially and temporally broadband noise.

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APPENDIX A: SIGN OF ρ_1

The approach to determine the sign of ρ_1 is analogous to the one used in [10] for the isotropic reaction walk. Consider ρ_1 as a function of the trace T of the Jacobian. Let $T=0$, i.e., $A_{11} = -A_{22} \equiv a$. Then we obtain after some algebra

$$\rho_1(0) = S[-\chi^2(\Delta + \mu^2)(a+\nu) + \gamma^2(\Delta + \nu^2)(a-\mu)]. \tag{A1}$$

Since $S>0$, $\Delta>0$, $a>0$, $\mu>0$, and $\nu>0$, we have that $\rho_1(0)<0$ if $\mu>a$, i.e., $\mu>A_{11}$.

The derivative of $\rho_1(T)$ with respect to T is given by

$$\frac{d\rho(T)}{dT} = \chi^2[(A_{11}-\mu)C_1 - \mu A_{11}C_2 + C_3] + \gamma^2[(A_{22}-\nu)C_1 - \nu A_{22}C_2 + C_3], \tag{A2}$$

with

$$C_1 = M - S^2 - \Delta + 2TS, \tag{A3}$$

$$C_2 = 2T - 2S, \tag{A4}$$

$$C_3 = SM + \Delta S - 2TM. \tag{A5}$$

Recall that $\Delta>0$ and $T<0$. We have that

$$C_1 = -\mu^2 - \mu\nu - \nu^2 - \Delta + 2TS, \tag{A6}$$

which is negative, since all terms are negative. Note that $C_2<0$ and $C_3>0$, and recall that $A_{11}>0$. Therefore the coefficient of χ^2 is positive, if $\mu>A_{11}$. The sign of the coefficient of γ^2 is not as easily determined, because $A_{22}<0$. Consider the coefficient of γ^2 to be a function of T and Δ,

$$F(T,\Delta) = (A_{22}-\nu)C_1 - \nu A_{22}C_2 + C_3, \tag{A7}$$

and take the partial derivative with respect to T,

$$\frac{\partial F}{\partial T} = (A_{22}-\nu)2S - \nu A_{22}2 - 2M, \tag{A8}$$

$$\frac{\partial F}{\partial T} = 2\mu A_{22} - 2\mu\nu - 2\nu^2 - 2\mu - 2\nu < 0, \tag{A9}$$

and with respect to Δ,

$$\frac{\partial F}{\partial \Delta} = -(A_{22}-\nu) + S, \tag{A10}$$

$$\frac{\partial F}{\partial \Delta} = -A_{22} + \mu + 2\nu > 0. \tag{A11}$$

At $T=0$ and $\Delta=0$ we have

$$F(0{,}0)=(A_{22}-\nu)(M-S^2)-\nu A_{22}(-2S)+SM, \tag{A12}$$

$$F(0{,}0)=(-a+2\mu)(\mu\nu+\nu^2)+a\mu^2+\nu^3, \tag{A13}$$

which is positive if $\mu>a/2$. Taking into account this result, the signs of the partial derivatives, and recalling that the relevant quadrant in parameter space is given by $T<0,\Delta>0$, we find that the coefficient of γ^2 in Eq. (A2) is positive, and therefore $d\rho_1(T)/dT$ is positive, for $\mu>A_{11}$. Together with $\rho_1(0)<0$ if $\mu>A_{11}$, this implies that $\rho_1(T)$ for negative values of T is negative if $\mu>A_{11}$. Therefore, $\rho_1<0$ if $\rho_2<0$.

APPENDIX B: ROUTH-HURWITZ STABILITY CRITERION

The necessary and sufficient conditions for all roots of the characteristic equation

$$\omega^4+c_3\omega^3+c_2\omega^2+c_1\omega+c_0=0 \tag{B1}$$

to have a negative real part are given by the Routh-Hurwitz conditions, see, for instance, [3], and read as follows:

$$c_0>0, \tag{B2}$$

$$\Delta_1=c_3>0, \tag{B3}$$

$$\Delta_2=c_3c_2-c_1>0, \tag{B4}$$

$$\Delta_3=c_3c_2c_1-c_3^2c_0-c_1^2>0, \tag{B5}$$

$$\Delta_4=c_0\Delta_3>0. \tag{B6}$$

It follows from Eqs. (3.46) and (3.47) that $c_3>0$ and $c_2>0$ is always true. Equations (B2) and (B5) imply Eq. (B6). The condition (B5) can be written as

$$c_1(c_3c_2-c_1)>c_3^2c_0, \tag{B7}$$

where the right hand side is positive due to condition (B2). From Eq. (B7) we can conclude that

$$c_3c_2>c_1>0, \tag{B8}$$

since both c_3 and c_2 are always positive. The Routh-Hurwitz conditions therefore reduce to two conditions, and the homogeneous steady state of the direction-independent reaction walk is stable if and only if

$$c_0>0, \tag{B9}$$

and

$$c_3c_2c_1-c_3^2c_0-c_1^2>0. \tag{B10}$$

Violation of the first condition corresponds to the condition for the Turing bifurcation (3.50), and violation of the second condition corresponds to the condition for the Hopf bifurcation (3.74).

[1] A. Okubo, P. K. Maini, M. H. Williamson, and J. D. Murray, Proc. R. Soc. London, Ser. B **238**, 113 (1989).

[2] *Oscillations and Traveling Waves in Chemical Systems*, edited by R. J. Field and M. Burger (Wiley, New York, 1985).

[3] J. D. Murray, *Mathematical Biology* (Springer-Verlag, Berlin, 1989).

[4] P. De Kepper, J. Boissonade, and I. R. Epstein, J. Phys. Chem. **94**, 6525 (1990).

[5] R. Fürth, Z. Phys. **2**, 244 (1920).

[6] G. I. Taylor, Proc. London Math. Soc. Ser. 2 **20**, 196 (1921).

[7] S. Goldstein, Q. J. Mech. Appl. Math. **4**, 129 (1951).

[8] A. S. Monin and A. M. Yaglom, *Statistical Fluid Mechanics* (The MIT Press, Cambridge, MA, 1971).

[9] E. E. Holmes, Am. Nat. **142**, 779 (1993).

[10] T. Hillen, J. Math. Biol. **35**, 49 (1996).

[11] K. P. Hadeler, in *Mathematics Inspired by Biology*, edited by V. Capasso and O. Diekman, Lecture Notes in Mathematics (Springer-Verlag, Berlin, in press) [preprint available as Sonderforschungsbereich 382, Universities Tübingen and Stuttgart Report No. 97 (1998) at http://www.uni-tuebingen.de/uni/opx/reports.html].

[12] A. M. Turing, Philos. Trans. R. Soc. London, Ser. B **237**, 37 (1952).

[13] G. Nicolis and I. Prigogine, *Self-Organization in Nonequilibrium Systems* (Wiley, New York, 1977).

[14] P. Gray and S. K. Scott, *Chemical Oscillations and Instabilities* (Clarendon Press, Oxford, 1990).

[15] H. Meinhardt, Rep. Prog. Phys. **55**, 797 (1992).

[16] V. Castets, E. Dulos, J. Boissonade, and P. De Kepper, Phys. Rev. Lett. **64**, 2953 (1990).

[17] Q. Ouyang and H. L. Swinney, Nature (London) **352**, 610 (1991).

[18] Q. Ouyang and H. L. Swinney, Chaos **1**, 411 (1991).

[19] I. Lengyel, S. Kádár, and I. R. Epstein, Phys. Rev. Lett. **69**, 2729 (1992).

[20] A. J. Koch and H. Meinhardt, Rev. Mod. Phys. **66**, 1481 (1994).

[21] V. Dufiet and J. Boissonade, J. Chem. Phys. **96**, 664 (1992).

[22] G. Dewel *et al.*, Physica A **213**, 181 (1995).

[23] D. D. Joseph and L. Preziosi, Rev. Mod. Phys. **61**, 41 (1989).

[24] E. Zauder, *Partial Differential Equations of Applied Mathematics*, 2nd ed. (Wiley, New York, 1989).

[25] Th. Gallay and G. Raugel, ZAMP **48**, 451 (1997).

[26] Th. Gallay and G. Raugel, e-print patt-sol/9809007.

[27] Th. Gallay and G. Raugel, e-print patt-sol/9812007.

[28] Th. Gallay and G. Raugel, J. Diff. Eqns. **150**, 42 (1998).

[29] K. P. Hadeler, Can. Appl. Math. Quart. **2**, 27 (1994).

[30] V. Méndez and J. Camacho, Phys. Rev. E **55**, 6476 (1997).

[31] V. Méndez and A. Compte, Physica A **260**, 90 (1998).

[32] G. H. Weiss, *Aspects and Applications of the Random Walk* (North-Holland, Amsterdam, 1994).

[33] K. P. Hadeler, in *Stochastic and Spatial Structures of Dynami-*

cal Systems, edited by S. van Strien and S. V. Lunel (North-Holland, Amsterdam, 1996), p. 133.

[34] W. Horsthemke (unpublished).

[35] L. A. Segel, *Modeling Dynamic Phenomena in Molecular and Cellular Biology* (Cambridge University Press, Cambridge, England, 1984).

[36] J. Schnakenberg, J. Theor. Biol. **81**, 389 (1979).

[37] R. Dillon, P. K. Maini, and H. G. Othmer, J. Math. Biol. **32**, 345 (1994).

[38] C. Varea, J. L. Aragón, and R. A. Barrio, Phys. Rev. E **56**, 1250 (1997).

[39] I. Lengyel and I. R. Epstein, Acc. Chem. Res. **26**, 235 (1993).

[40] P. Gray and S. K. Scott, J. Phys. Chem. **89**, 22 (1985).

[41] C. R. Doering and W. Horsthemke, Phys. Lett. A **182**, 227 (1993).