

EXISTENCE OF TURING INSTABILITIES IN A TWO-SPECIES FRACTIONAL REACTION-DIFFUSION SYSTEM*

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Abstract. We introduce a two-species fractional reaction-diffusion system to model activator-inhibitor dynamics with anomalous diffusion such as occurs in spatially inhomogeneous media. Conditions are derived for Turing-instability induced pattern formation in these fractional activator-inhibitor systems whereby the homogeneous steady state solution is stable in the absence of diffusion but becomes unstable over a range of wavenumbers when fractional diffusion is present. The conditions are applied to a variant of the Gierer–Meinhardt reaction kinetics which has been generalized to incorporate anomalous diffusion in one or both of the activator and inhibitor variables. The anomalous diffusion extends the range of diffusion coefficients over which Turing patterns can occur. An intriguing possibility suggested by this analysis, which can arise when the diffusion of the activator is anomalous but the diffusion of the inhibitor is regular, is that Turing instabilities can exist even when the diffusion coefficient of the activator exceeds that of the inhibitor.

Key words. reaction-diffusion, Turing pattern, anomalous diffusion, inhomogeneous media

AMS subject classifications. 35K57, 26A33, 35B40, 82D30

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1. Introduction. Promulgated by the theoretical paper of Turing [1], physical mechanisms of pattern formation modelled by reaction-diffusion systems have become an area of intense research, particularly during the last decade [2, 3, 4, 5, 6, 7]. These models provide a general theoretical framework for describing pattern formation in systems from many diverse disciplines including (but not limited to) biology [2, 3, 8, 6], chemistry [9, 6], neuroscience [10], physics [11], and optics [12, 13]. While standard reaction-diffusion models provide a good description of pattern formation in homogeneous media, few realistic physical and biological systems are spatially homogeneous.

There are now numerous experimental examples of Turing pattern formation which have clearly been influenced by inhomogeneities in the media. Indeed, the first experimental evidence for a Turing pattern [9] (in the chlorite-iodide-malonic acid reaction) was subsequently revealed [14, 15, 16] to be strongly affected by spatial inhomogeneities (iodide-starch reactions), which effectively reduced the diffusion coefficient of the activator. Recent examples of Turing patterns affected by inhomogeneities include convection in liquid crystals [17], catalytic surface reactions where crystal symmetry provides a natural anisotropy [18], thermal convection in porous media [19], and pattern formation in biological media such as cardiac tissue with anisotropic fiber orientation [20].

There have been a number of different theoretical approaches to modelling pattern formation in inhomogeneous media. One of these approaches has been based on an ad hoc replacement of some of the system parameters (for example, the diffusion

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constant, or coupling constants) with spatially varying parameters [21, 22, 23, 24, 25, 26, 27] or species dependent parameters [28]. In another phenomenological approach, nonlinearity has been introduced into the diffusion term by taking the Laplacian of a power of the dependent variable [29, 30, 31], i.e., ∇u^m where $m = 1$ is standard diffusion, $m > 1$ is interpreted as slow diffusion, and $m < 1$ is interpreted as fast diffusion.

Despite the above attempts to model more realistic physical media, no general theory for pattern formation in random, fractal, or other inhomogeneous media has yet been established. On the other hand, there has been considerable progress toward obtaining a theoretical framework for diffusion without reactions in inhomogeneous media. In particular, fractional diffusion equations, i.e., diffusion equations with fractional order temporal and/or spatial derivatives, have proven useful in describing anomalous diffusion processes in which the mean-square displacement of the diffusing particles scales as a power law $\langle r^2(t) \rangle \sim t^\gamma$ with exponent $\gamma \neq 1$ [32, 33, 34, 35, 36, 37, 38, 39]. While the fractional diffusion equation that describes anomalous superdiffusion ($\gamma > 1$) remains essentially phenomenological in origin [33], the fractional diffusion equation for anomalous subdiffusion ($\gamma < 1$), such as occurs in inhomogeneous media [40, 41], has been derived from a continuous-time random walk model with temporal memory [34, 42, 39]. A fractional Fokker–Planck equation has also been derived under similar conditions to model anomalous diffusion in an external force field [43].

Recently, we derived a fractional reaction-diffusion (FRD) equation

$$(1.1) \quad \frac{\partial \mathbf{n}(\mathbf{r}, t)}{\partial t} = C \left(\frac{\partial^{1-\gamma}}{\partial t^{1-\gamma}} \nabla^2 \mathbf{n}(\mathbf{r}, t) + \mathcal{L}^{-1} \left(\frac{\partial^{-\gamma}}{\partial t^{-\gamma}} \nabla^2 \mathbf{n}(\mathbf{r}, t) \Big|_{t=0} \right) \right) + \mathbf{f}(\mathbf{n}(\mathbf{r}, t))$$

from a continuous-time random walk model with temporal memory and sources [44]. In this equation the exponent $\gamma \in [0, 1]$; the expression

$$\frac{d^{-\gamma} y(t)}{dt^{-\gamma}} = \frac{1}{\Gamma(\gamma)} \int_0^t \frac{y(s)}{(t-s)^{1-\gamma}} ds$$

denotes the Riemann–Liouville fractional integral, and the expression

$$\frac{d^{1-\gamma} y(t)}{dt^{1-\gamma}} = \frac{d}{dt} \frac{d^{-\gamma} y(t)}{dt^{-\gamma}}$$

denotes the Riemann–Liouville fractional derivative. With the further identification that the components of the vector $\mathbf{n}(\mathbf{r}, t)$ denote the number density of the different species, the FRD equation models a reaction-diffusion process in which the diffusion is anomalous subdiffusion. It should be pointed out that the exponent γ in (1.1) may be different for each different species; an exponent $\gamma = 1$ represents standard diffusion for that species.

Equation (1.1), derived from a continuous-time random walk with temporal memory, complements other nonstandard reaction-diffusion systems derived from correlated random walks [45, 46, 47] and from reinforced random walks [48, 49].

Our first investigation of (1.1) considered the special case of single species FRD in one dimension (i.e., $\mathbf{n}(\mathbf{r}, t) = n(x, t)$) and showed that, similar to the case of regular reaction-diffusion in one dimension, Turing-instability induced pattern formation cannot occur. In this paper, we have considered the FRD equation for the case of two species and one spatial dimension, representing an activator-inhibitor system. Our

main result in this work is to derive conditions for Turing-instability induced pattern formation in fractional activator-inhibitor systems in one spatial dimension.

In section 2 we employ the Laplace transform method to review conditions for Turing-instability induced pattern formation in regular activator-inhibitor systems in one dimension. In section 3 we introduce the general fractional activator-inhibitor system and use a spatial Fourier transform and a temporal Laplace transform to decouple the linearized system in preparation for Turing-instability analysis. Further progress from this point involves an inversion of the Laplace transforms. In the appendix we provide details for carrying out an inverse Laplace transform for this general system. This results in series expansions in (fractional) powers of t to describe the temporal evolution of perturbations about the homogeneous steady state. While these series expansions are exact, they do not reveal the asymptotic large t behavior which is required for the Turing-instability analysis. To simplify this, in section 4 we consider three special cases of fractional activator-inhibitor systems in one dimension. These special cases are characterized by a fractional diffusion scaling exponent $\gamma = 1/2$. We employ direct contour integration methods to obtain the inverse Laplace transform in these cases, and we derive expressions for the asymptotic large t behavior of perturbations about the homogeneous steady state. We then derive conditions for a Turing instability in these systems and apply the conditions to variants of the Gierer–Meinhardt model [50], which have been generalized to incorporate anomalous diffusion in one or both of the activator and inhibitor variables.

We conclude with a summary and discussion in section 5.

2. Regular activator-inhibitor system. In the case of regular diffusion, the activator-inhibitor system in nondimensionalized and scaled form can be written [2]

$$(2.1) \quad \frac{\partial n_1(x, t)}{\partial t} = \lambda f_1(n_1, n_2) + \nabla^2 n_1(x, t),$$

$$(2.2) \quad \frac{\partial n_2(x, t)}{\partial t} = \lambda f_2(n_1, n_2) + d\nabla^2 n_2(x, t),$$

where $n_1(x, t)$ is the number density of particles of the activator variable, $n_2(x, t)$ is the number density of particles of the inhibitor variable, f_1 and f_2 are (generally nonlinear) functions describing the reaction kinetics, $d > 0$ is the ratio of the diffusion coefficients of activator and inhibitor variables, and $\lambda > 0$ is a scaling variable which can be interpreted as the linear size of the spatial domain, or as the relative strength of the reaction terms. Following Murray [2], we will assume zero-flux boundary conditions and prescribed initial conditions. A Turing instability occurs when a homogeneous steady state solution of the reaction system is linearly stable to perturbations in the absence of the diffusion terms but linearly unstable to small spatial perturbations in the presence of diffusion. Conditions on the system parameters for which a Turing instability occurs define a domain in parameter space called the Turing space [2].

The linear stability equations for the time evolution of perturbations

$$(\Delta n_1(x, t), \Delta n_2(x, t))$$

about a homogeneous steady state (n_1^*, n_2^*) in the regular activator-inhibitor system are

$$(2.3) \quad \frac{\partial \Delta n_1(x, t)}{\partial t} = \lambda a_{11} \Delta n_1 + \lambda a_{12} \Delta n_2 + \nabla^2 \Delta n_1(x, t),$$

$$(2.4) \quad \frac{\partial \Delta n_2(x, t)}{\partial t} = \lambda a_{21} \Delta n_2 + \lambda a_{22} \Delta n_2 + d \nabla^2 \Delta n_2(x, t),$$

where $a_{ij} = \frac{\partial f_i}{\partial n_j} |_{(n_1^*, n_2^*)}$. It is a simple matter to find the exact algebraic solution of these equations subject to the governing boundary conditions and thus to infer stability properties. Here we consider an approach based on Laplace transform methods which is also convenient for finding Turing conditions in the case when the diffusion is anomalous. After applying a temporal Laplace transform and a spatial Fourier transform, the transformed perturbations decouple as

$$(2.5) \quad \widehat{\Delta n_1}(q, s) = \frac{(s + dq^2 - \lambda a_{22}) \widetilde{\Delta n_1}(q, t = 0) + \lambda a_{12} \widetilde{\Delta n_2}(q, t = 0)}{(s + q^2 - \lambda a_{11})(s + dq^2 - \lambda a_{22}) - \lambda^2 a_{12} a_{21}},$$

$$(2.6) \quad \widehat{\Delta n_2}(q, s) = \frac{(s + q^2 - \lambda a_{11}) \widetilde{\Delta n_2}(q, t = 0) + \lambda a_{21} \widetilde{\Delta n_1}(q, t = 0)}{(s + q^2 - \lambda a_{11})(s + dq^2 - \lambda a_{22}) - \lambda^2 a_{12} a_{21}},$$

where s is the Laplace transform variable, q is the Fourier transform variable, a hat denotes a Laplace transformed variable, and a tilde denotes a Fourier transformed variable. The temporal growth of the perturbations can now be found by inverting the Laplace transforms, which follows directly after factorizing the denominator

$$(2.7) \quad (s + q^2 - \lambda a_{11})(s + dq^2 - \lambda a_{22}) - \lambda^2 a_{12} a_{21} = (s - z_1(q))(s - z_2(q))$$

and using partial fractions. If the two roots are distinct, then the canonical expression to be inverted has the form

$$\widehat{\Delta n}(q, s) = \sum_{j=1}^2 \frac{\alpha_j(q)}{s - z_j(q)},$$

and the inverse Laplace transform yields

$$\widetilde{\Delta n}(q, t) = \sum_{j=1}^2 \alpha_j(q) e^{z_j(q)t}.$$

Hence the homogeneous steady state is linearly unstable if one or more of the roots has a real component greater than zero but is linearly stable otherwise. It is straightforward to show that a similar result holds if the two roots are equal. The conditions for a Turing instability can thus be summarized as follows.

Condition (i).

$$(2.8) \quad \Re(z_1(q = 0)) < 0, \quad \Re(z_2(q = 0)) < 0.$$

Condition (ii).

$$(2.9) \quad \Re(z_1(q > 0)) > 0 \quad \text{and/or} \quad \Re(z_2(q > 0)) > 0,$$

where z_k are the zeros of the quadratic

$$(2.10) \quad f(z) = (z + q^2 - \lambda a_{11})(z + dq^2 - \lambda a_{22}) - \lambda^2 a_{12} a_{21}.$$

Note that the roots are functions of the wavenumber q , so in a physical reaction-diffusion problem on a finite domain some modes may be stable and others unstable. From (2.7) it follows that condition (i) is consistent with the conditions

$$(2.11) \quad a_{11} + a_{22} < 0,$$

$$(2.12) \quad a_{11} a_{22} - a_{12} a_{21} > 0;$$

and condition (ii) cannot be realized in conjunction with condition (i) if $d = 1$. Furthermore, for activator reaction kinetics with $a_{11} > 0$, conditions (i) and (ii) cannot be achieved simultaneously if $d \leq 1$. Physically, this means that a necessary condition for Turing-instability induced pattern formation is that the inhibitor diffuses faster than the activator.

3. General fractional activator-inhibitor systems. We now consider the fractional activator-inhibitor system (a special case of (1.1))

$$(3.1) \quad \frac{\partial n_1(x, t)}{\partial t} = \lambda f_1(n_1, n_2) + \mathcal{D}^{1-\gamma_1} n_1(x, t),$$

$$(3.2) \quad \frac{\partial n_2(x, t)}{\partial t} = \lambda f_2(n_1, n_2) + d\mathcal{D}^{1-\gamma_2} n_2(x, t),$$

where $0 < \gamma_1 \leq 1$ is the anomalous diffusion exponent of the activator, $0 < \gamma_2 \leq 1$ is the anomalous diffusion exponent of the inhibitor, and, as demonstrated in [44],

$$(3.3) \quad \mathcal{D}^{1-\gamma} n(x, t) = \frac{\partial^{1-\gamma}}{\partial t^{1-\gamma}} \nabla^2 n(x, t) + \mathcal{L}^{-1} \left\{ \frac{\partial^{-\gamma}}{\partial t^{-\gamma}} \nabla^2 n(x, t) \Big|_{t=0} \right\}$$

is the appropriate generalization of the diffusion operator from regular to fractional. The term $\mathcal{L}^{-1} \{ \frac{\partial^{-\gamma}}{\partial t^{-\gamma}} \nabla^2 n(x, t) \Big|_{t=0} \}$ automatically precludes the introduction of unphysical terms when solving the equation by the Laplace transform method.

Proceeding as in the previous section, we consider perturbations about the homogeneous steady state (n_1^*, n_2^*) . The linearized system in this case is

$$(3.4) \quad \frac{\partial \Delta n_1(x, t)}{\partial t} = \lambda a_{11} \Delta n_1 + \lambda a_{12} \Delta n_2 + \mathcal{D}^{1-\gamma_1} \Delta n_1(x, t),$$

$$(3.5) \quad \frac{\partial \Delta n_2(x, t)}{\partial t} = \lambda a_{21} \Delta n_1 + \lambda a_{22} \Delta n_2 + d\mathcal{D}^{1-\gamma_2} \Delta n_2(x, t).$$

Applying a temporal Laplace transform and a spatial Fourier transform, we obtain

$$(3.6) \quad \begin{aligned} s\widehat{\Delta n_1}(q, s) - \Delta \tilde{n}_1(q, t=0) &= \lambda a_{11} \widehat{\Delta n_1}(q, s) + \lambda a_{12} \widehat{\Delta n_2}(q, s) \\ &\quad - s^{1-\gamma_1} q^2 \widehat{\Delta n_1}(q, s), \end{aligned}$$

$$(3.7) \quad \begin{aligned} s\widehat{\Delta n_2}(q, s) - \Delta \tilde{n}_2(q, t=0) &= \lambda a_{21} \widehat{\Delta n_1}(q, s) + \lambda a_{22} \widehat{\Delta n_2}(q, s) \\ &\quad - s^{1-\gamma_2} q^2 \widehat{\Delta n_2}(q, s), \end{aligned}$$

which decouples as

$$(3.8) \quad \widehat{\Delta n_1}(q, s) = \frac{(s + s^{1-\gamma_2} dq^2 - \lambda a_{22}) \widehat{\Delta n_1}(q, t=0) + \lambda a_{12} \widehat{\Delta n_2}(q, t=0)}{(s + s^{1-\gamma_1} q^2 - \lambda a_{11})(s + s^{1-\gamma_2} dq^2 - \lambda a_{22}) - \lambda^2 a_{12} a_{21}},$$

$$(3.9) \quad \widehat{\Delta n_2}(q, s) = \frac{(s + s^{1-\gamma_1} q^2 - \lambda a_{11}) \widehat{\Delta n_2}(q, t=0) + \lambda a_{21} \widehat{\Delta n_1}(q, t=0)}{(s + s^{1-\gamma_1} q^2 - \lambda a_{11})(s + s^{1-\gamma_2} dq^2 - \lambda a_{22}) - \lambda^2 a_{12} a_{21}}.$$

The conditions for a Turing instability in this system are obtained by inverting the Laplace transforms and deducing the large t asymptotic behavior. In this general case, the inversion results in a series expansion in (fractional) powers of t ; however, the resulting expression (which is derived in the appendix) is too complicated to be of much use in extracting the asymptotic large t properties. In the next section, we

introduce three reductions of the general problem in which the fractional diffusion, when it is present, has the scaling exponent $\gamma = 1/2$. In these special cases, we have employed contour integration methods to carry out the Laplace inversions in a form which allows simple deduction of the large t asymptotic behaviors.

4. Half fractional activator-inhibitor systems. We now consider special reductions of the fractional-activator inhibitor system described by (3.1)–(3.2) for the case when the fractional diffusion has a scaling exponent $\gamma = 1/2$. A key physical requirement for Turing-instability induced pattern formation in standard reaction-diffusion systems is that the inhibitor diffuses faster than the activator [2] (see also section 2). We consider the three possibilities for half fractional activator-inhibitor systems: (1) Half fractional subdiffusion for the activator ($\gamma_1 = 1/2$) but regular diffusion for the inhibitor ($\gamma_2 = 1$); (2) half fractional subdiffusion for both the activator and the inhibitor ($\gamma_1 = \gamma_2 = 1/2$); (3) regular diffusion for the activator ($\gamma_1 = 1$) but half fractional subdiffusion for the inhibitor ($\gamma_2 = 1/2$). From (3.8)–(3.9), the decoupled Fourier and Laplace transforms for the perturbations about the homogeneous steady state reduce to the canonical form

$$(4.1) \quad \widehat{\Delta n}(q, s) = \frac{\alpha(q)s + \beta(q)s^{\frac{1}{2}} + \gamma(q)}{\prod_{i=1}^4 (s^{\frac{1}{2}} - z_i)},$$

where $\alpha(q), \beta(q), \gamma(q)$ are real valued functions of q and the denominator is defined by the following.

Case 1.

$$(4.2) \quad \prod_{i=1}^4 (s^{\frac{1}{2}} - z_i) = (s + s^{\frac{1}{2}}q^2 - \lambda a_{11})(s + dq^2 - \lambda a_{22}) - \lambda^2 a_{12} a_{21}.$$

Case 2.

$$(4.3) \quad \prod_{i=1}^4 (s^{\frac{1}{2}} - z_i) = (s + s^{\frac{1}{2}}q^2 - \lambda a_{11})(s + s^{\frac{1}{2}}dq^2 - \lambda a_{22}) - \lambda^2 a_{12} a_{21}.$$

Case 3.

$$(4.4) \quad \prod_{i=1}^4 (s^{\frac{1}{2}} - z_i) = (s + q^2 - \lambda a_{11})(s + s^{\frac{1}{2}}dq^2 - \lambda a_{22}) - \lambda^2 a_{12} a_{21}.$$

4.1. Inverse Laplace transform. The inverse Laplace transform of the expression in (4.1) can be evaluated using the standard complex inversion formula

$$(4.5) \quad \widehat{\Delta n}(q, t) = \frac{1}{2\pi i} \int_{c-i\infty}^{c+i\infty} \frac{\alpha(q)s + \beta(q)s^{\frac{1}{2}} + \gamma(q)}{\prod_{i=1}^4 (s^{\frac{1}{2}} - z_i)} e^{st} ds$$

$$(4.6) \quad = \frac{1}{2\pi i} \int_{c-i\infty}^{c+i\infty} \frac{(\alpha(q)s + \beta(q)s^{\frac{1}{2}} + \gamma(q)) \prod_{i=1}^4 (s^{\frac{1}{2}} + z_i) e^{st} ds}{\prod_{i=1}^4 (s - z_i^2)},$$

where the real number c lies to the right of all singularities. To evaluate the integral, we will consider the Bromwich contour modified with a branch cut from the branch point at $s = 0$ (see Figure 1). Thus we restrict the values of s to $s = re^{i\theta_p + 2n\pi}$ with $-\pi < \theta_p \leq \pi$.

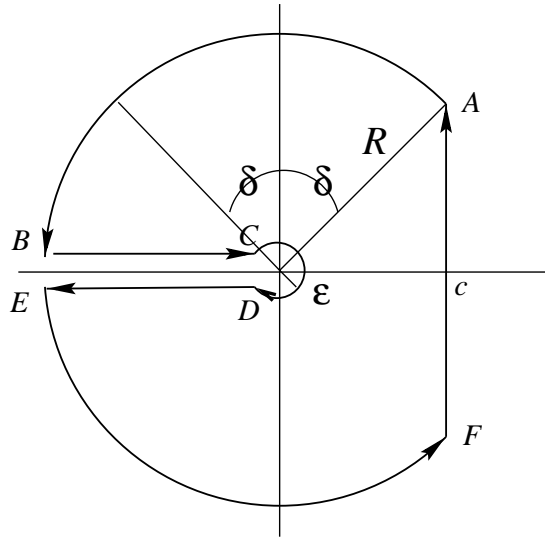


FIG. 1. Modified Bromwich contour Γ for the complex inversion formula.

For convenience, we define

$$\Phi(s) = \frac{(\alpha(q)s + \beta(q)s^{\frac{1}{2}} + \gamma(q)) \prod_{i=1}^4 (s^{\frac{1}{2}} + z_i)}{\prod_{i=1}^4 (s - z_i^2)},$$

and we let the principal branch define $s^{\frac{1}{2}} = r^{\frac{1}{2}} e^{i\frac{\theta_p}{2}}$.

We can express the inverse Laplace transform in terms of contour integrals along the modified Bromwich contour Γ as follows:

$$\begin{aligned} (4.7) \quad \widetilde{\Delta}n(q, t) &= \lim_{R \rightarrow \infty} \frac{1}{2\pi i} \int_{FA} \Phi(s) e^{st} ds, \\ &= \frac{1}{2\pi i} \left(\lim_{\epsilon \rightarrow 0} \lim_{R \rightarrow \infty} \int_{\Gamma} \Phi(s) e^{st} ds - \lim_{R \rightarrow \infty} \int_{AB} \Phi(s) e^{st} ds \right. \\ &\quad - \lim_{\epsilon \rightarrow 0} \lim_{R \rightarrow \infty} \int_{BC} \Phi(s) e^{st} ds - \lim_{\epsilon \rightarrow 0} \int_{CD} \Phi(s) e^{st} ds \\ (4.8) \quad &\quad \left. - \lim_{\epsilon \rightarrow 0} \lim_{R \rightarrow \infty} \int_{DE} \Phi(s) e^{st} ds - \lim_{R \rightarrow \infty} \int_{EF} \Phi(s) e^{st} ds \right). \end{aligned}$$

First, we establish that all of the integrals along the circular arcs vanish. Along the small circular arc CD ,

$$(4.9) \quad \lim_{\epsilon \rightarrow 0} \frac{1}{2\pi i} \int_{CD} \Phi(s) e^{st} ds = \lim_{\epsilon \rightarrow 0} \frac{1}{2\pi} \int_{\pi}^{-\pi} \Phi(\epsilon e^{i\theta}) e^{\epsilon e^{i\theta} t} \epsilon e^{i\theta} d\theta.$$

Taking the limit under the integral sign and noting that $\lim_{\epsilon \rightarrow 0} \Phi(\epsilon e^{i\theta})$ is equal to a constant yield the required result.

Now consider the integral along the large arc AB :

$$(4.10) \quad \lim_{R \rightarrow \infty} \frac{1}{2\pi i} \int_{AB} \Phi(s) e^{st} ds \leq \lim_{R \rightarrow \infty} \left(\max_{\frac{\pi}{2} - \delta \leq \theta \leq \pi} \right) |\Phi(R e^{i\theta})| \left(\frac{R}{2\pi} \int_{\frac{\pi}{2} - \delta}^{\pi} |e^{R e^{i\theta} t}| d\theta \right).$$

The bound can be simplified further by noting that

$$(4.11) \quad \frac{R}{2\pi} \int_{\frac{\pi}{2}-\delta}^{\pi} |e^{Re^{i\theta}t}|d\theta = \frac{R}{2\pi} \int_{\frac{\pi}{2}-\delta}^{\frac{\pi}{2}+\delta} e^{tR\cos\theta}d\theta + \frac{R}{2\pi} \int_{\frac{\pi}{2}+\delta}^{\pi} e^{tR\cos\theta}d\theta$$

$$(4.12) \quad \leq \frac{R}{2\pi} \left(2\delta e^{tc} + \frac{\pi}{2Rt} e^{-\frac{2tR\delta}{\pi}} - \frac{\pi}{2Rt} e^{-Rt} \right)$$

$$(4.13) \quad \leq \frac{2c}{\pi} + \frac{1}{4t} e^{-\frac{2tR\delta}{\pi}} - \frac{1}{4t} e^{-Rt}$$

$$(4.14) \quad \leq K \quad (\text{a constant for fixed } t).$$

The inequality in (4.12) follows by replacing $R \cos \theta \leq c$ in the first integral on the right-hand side of (4.11) and $\cos \theta \leq \frac{2}{\pi}(\frac{\pi}{2} - \theta)$ in the second integral on the right-hand side of (4.11); and the further inequality in (4.13) follows by replacing $\delta \leq \frac{2c}{R}$ (for small δ). The result, that the integral along the arc AB vanishes, now immediately follows from (4.10) using (4.14) together with

$$(4.15) \quad \lim_{R \rightarrow \infty} \left(\max_{\frac{\pi}{2}-\delta \leq \theta \leq \pi} \right) |\Phi(Re^{i\theta})| = 0.$$

In a similar fashion, it is straightforward to show that the integral along the arc EF also vanishes.

Equation (4.8) now reduces to

$$(4.16) \quad \begin{aligned} \widetilde{\Delta n}(q, t) = & \frac{1}{2\pi i} \left(\lim_{\epsilon \rightarrow 0} \lim_{R \rightarrow \infty} \int_{\Gamma} \Phi(s)e^{st} ds \right. \\ & \left. - \lim_{\epsilon \rightarrow 0} \lim_{R \rightarrow \infty} \int_{BC} \Phi(s)e^{st} ds - \lim_{\epsilon \rightarrow 0} \lim_{R \rightarrow \infty} \int_{DE} \Phi(s)e^{st} ds \right). \end{aligned}$$

We will use the Cauchy residue theorem to evaluate the first integral in (4.16):

$$(4.17) \quad \frac{1}{2\pi i} \int_{\Gamma} \Phi(s)e^{st} ds = \sum_{k=1}^4 \text{Res}(\Phi(s)e^{st}),$$

where the sum is over the residues for the four poles $s = z_k^2$ of $\Phi(s)$. Some care needs to be exercised in evaluating the residues depending on the sign of the real component of the zeros z_k of (4.2)–(4.3). If the real component is positive, then on the principal branch, $s^{\frac{1}{2}} = z_k$. On the other hand, if the real component is negative, then on the principal branch, $s^{\frac{1}{2}} = -z_k$. We can thus write the sum over residues as

$$(4.18) \quad \frac{1}{2\pi i} \int_{\Gamma} \Phi(s)e^{st} ds = \sum_{k=1}^4 \frac{(\alpha z_k^2 + \beta \text{csgn}(z_k)z_k + \gamma)(\text{csgn}(z_k)z_k + z_k)e^{tz_k^2}}{\prod_{i=1, i \neq k}^4 (z_k - z_i)},$$

where csgn is the complex sign function defined by

$$(4.19) \quad \text{csgn}(z) = \begin{cases} 1, & \Re(z) > 0, \quad \text{or} \quad \Re(z) = 0 \quad \text{and} \quad \Im(z) > 0; \\ -1, & \Re(z) < 0, \quad \text{or} \quad \Re(z) = 0 \quad \text{and} \quad \Im(z) < 0. \end{cases}$$

Note that for a zero with a positive real component the residue of the corresponding pole contains an exponential factor that grows in time if $\Re(z_k^2) > 0$, whereas for a zero with a negative real component the residue is zero.

We now consider the second and fourth terms on the right-hand side of (4.16). Along the line segment BC , $s = xe^{i\pi} = -x$; $s^{\frac{1}{2}} = e^{i\frac{\pi}{2}}x^{\frac{1}{2}} = ix^{\frac{1}{2}}$; $ds = -dx$; $S =$

$-R \rightarrow x = +R; s = -\epsilon \rightarrow x = +\epsilon$. Thus we can write

$$\begin{aligned}
 & -\frac{1}{2\pi i} \lim_{\epsilon \rightarrow 0} \lim_{R \rightarrow \infty} \int_{BC} \Phi(s) e^{st} ds = -\frac{1}{2\pi i} \lim_{\epsilon \rightarrow 0} \lim_{R \rightarrow \infty} \int_R^\epsilon \Phi(x e^{i\pi}) e^{-xt} (-dx) \\
 (4.20) \quad & = -\frac{1}{2\pi i} \int_0^\infty \frac{(-\alpha(q)x + i\beta(q)x^{\frac{1}{2}} + \gamma(q)) \prod_{i=1}^4 (ix^{\frac{1}{2}} + z_i) e^{-xt}}{\prod_{i=1}^4 (x + z_i^2)} dx.
 \end{aligned}$$

Along the line segment DE , $s = x e^{-i\pi} = -x; s^{\frac{1}{2}} = e^{-i\frac{\pi}{2}} x^{\frac{1}{2}} = -ix^{\frac{1}{2}}; ds = -dx; S = -R \rightarrow x = +R; s = -\epsilon \rightarrow x = +\epsilon$. Similarly, we now have

$$\begin{aligned}
 & -\frac{1}{2\pi i} \lim_{\epsilon \rightarrow 0} \lim_{R \rightarrow \infty} \int_{DE} \Phi(s) e^{st} ds = -\frac{1}{2\pi i} \lim_{\epsilon \rightarrow 0} \lim_{R \rightarrow \infty} \int_\epsilon^R \Phi(x e^{-i\pi}) e^{-xt} (-dx) \\
 (4.21) \quad & = \frac{1}{2\pi i} \int_0^\infty \frac{(-\alpha(q)x - i\beta(q)x^{\frac{1}{2}} + \gamma(q)) \prod_{i=1}^4 (-ix^{\frac{1}{2}} + z_i) e^{-xt}}{\prod_{i=1}^4 (x + z_i^2)} dx.
 \end{aligned}$$

Combining the results of (4.20)–(4.21), we have

$$\begin{aligned}
 & -\frac{1}{2\pi i} \lim_{\epsilon \rightarrow 0} \lim_{R \rightarrow \infty} \left(\int_{BC} \Phi(s) e^{st} ds + \int_{DE} \Phi(s) e^{st} ds \right) = -\frac{1}{\pi} \int_0^\infty \frac{x^{\frac{1}{2}} e^{-xt}}{\prod_{i=1}^4 (x + z_i^2)} P_2(x) dx, \\
 (4.22) \quad & \text{where}
 \end{aligned}$$

$$\begin{aligned}
 (4.23) \quad P_2(x) = & \left(\beta(q) + \alpha(q) \sum_{i=1}^4 z_i \right) x^2 \\
 & + \left(-\gamma(q) \sum_{i=1}^4 z_i - \alpha(q) \sum_{i=1, j \neq i, k \neq j}^4 z_i z_j z_k - \beta(q) \sum_{i=1, j \neq i}^4 z_i z_j \right) x \\
 & + \left(\gamma(q) \sum_{i=1, j \neq i, k \neq j}^4 z_i z_j z_k + \beta(q) \prod_{i=1}^4 z_i \right)
 \end{aligned}$$

is a degree two polynomial in x .

Finally, combining the results of (4.16), (4.18), and (4.22), we obtain

$$\begin{aligned}
 (4.24) \quad \widetilde{\Delta n}(q, t) = & \sum_{k=1}^4 \frac{(\alpha z_k^2 + \beta \text{csgn}(z_k) z_k + \gamma) (\text{csgn}(z_k) z_k + z_k) e^{t z_k^2}}{\prod_{i=1, i \neq k}^4 (z_k - z_i)} \\
 & - \frac{1}{\pi} \int_0^\infty \frac{x^{\frac{1}{2}} e^{-xt}}{\prod_{i=1}^4 (x + z_i^2)} P_2(x) dx,
 \end{aligned}$$

where z_k are the zeros defined by (4.2)–(4.3). The above expression can be written equivalently as

$$\begin{aligned}
 (4.25) \quad \widetilde{\Delta n}(q, t) = & \sum_{k=1, \Re(z_k) > 0}^4 \frac{(\alpha z_k^2 + \beta z_k + \gamma) (2z_k) e^{t z_k^2}}{\prod_{i=1, i \neq k}^4 (z_k - z_i)} \\
 & - \frac{1}{\pi} \int_0^\infty \frac{x^{\frac{1}{2}} e^{-xt}}{\prod_{i=1}^4 (x + z_i^2)} P_2(x) dx,
 \end{aligned}$$

where the sum over the contributions from the poles is restricted to those for which the corresponding zeros have positive real components.

4.2. Asymptotic results—Turing conditions. It is a simple matter to extract the large t asymptotic behavior from (4.25). An asymptotic series for the integral in (4.25) follows as a special case of Watson’s lemma [51]:

$$(4.26) \quad \int_0^\infty \frac{x^{\frac{1}{2}} e^{-xt}}{\prod_{i=1}^4 (x + z_i^2)} P_2(x) dx \sim \sum_{n=0}^\infty \frac{d^n}{dx^n} \left(\frac{P_2(x)}{\prod_{i=1}^4 (x + z_i^2)} \right) \Big|_{x=0} \frac{\Gamma(\frac{3}{2} + n)}{n! t^{\frac{3}{2} + n}}.$$

Using the explicit form of $P_2(x)$ given by (4.23), we have the leading order behavior

$$(4.27) \quad \int_0^\infty \frac{x^{\frac{1}{2}} e^{-xt}}{\prod_{i=1}^4 (x + z_i^2)} P_2(x) dx \sim - \left(\frac{\beta(q)}{\prod_{i=1}^4 z_i} + \frac{\gamma(q) \sum_{i=1, j \neq i, k \neq j} z_i z_j z_k}{\prod_{i=1}^4 z_i^2} \right) \frac{\Gamma(\frac{3}{2})}{\pi t^{\frac{3}{2}}},$$

which shows that this term decays in time. Hence the only possible source of instability is the first term in (4.25). From this term we see that perturbations about the homogeneous steady state solutions will be unstable in the presence of half fractional diffusion if any of the zeros z_k and the corresponding poles z_k^2 have a positive real component but will be stable otherwise.

The conditions for a Turing instability in half fractional activator-inhibitor systems can thus be summarized as follows.

Condition (i).

$$(4.28) \quad \Re(z_k(q = 0)) < 0 \quad \forall k.$$

Condition (ii).

$$(4.29) \quad \Re(z_k(q > 0)) > 0 \quad \text{and} \quad \Re(z_k^2(q > 0)) > 0 \quad \text{for some } z_k,$$

where z_k are the zeros of the quartic defined by the following.

Case 1.

$$(4.30) \quad f_1(z) = (z^2 + zq^2 - \lambda a_{11})(z^2 + dq^2 - \lambda a_{22}) - \lambda^2 a_{12} a_{21}.$$

Case 2.

$$(4.31) \quad f_2(z) = (z^2 + zq^2 - \lambda a_{11})(z^2 + zdq^2 - \lambda a_{22}) - \lambda^2 a_{12} a_{21}.$$

Case 3.

$$(4.32) \quad f_3(z) = (z^2 + q^2 - \lambda a_{11})(z^2 + zdq^2 - \lambda a_{22}) - \lambda^2 a_{12} a_{21}.$$

The first condition, which is independent of the nature of the diffusion (regular or fractional) and results in the parameter restrictions (2.11)–(2.12), is best described as a precondition for a Turing instability. The second condition, however, does depend on the nature of the diffusion, and this condition, under the constraint of the precondition, defines the Turing space.

4.3. Turing space. It is possible to obtain explicit expressions for the zeros of the quartics defined in (4.30)–(4.32) using an algebraic computer package such as Maple or Mathematica. For general systems, however, the resultant expressions are too unwieldy to be practically useful for extracting the Turing space (parameter ranges that permit a Turing instability) or the maximally unstable mode (the mode q for which $\Re(z_k^2(q)) > 0$ is a maximum, where z_k is a zero of the quartic, with

$\Re(z_k(q)) > 0$). In this subsection, we describe limited results about the Turing space that can be obtained without explicit expressions for the zeros of the quartics. We will assume at the outset that $a_{11} > 0, a_{22} < 0, a_{12} < 0, a_{21} > 0$ in correspondence with the standard activator-inhibitor system [2] and that the precondition (4.28) for a Turing instability is met so that (2.11)–(2.12) are satisfied.

Our results in this section are based on simple applications of the Routh–Hurwitz theorem and Descartes’s rule of signs (see, for example, Murray [2, Appendix 2]). In the case of a quartic

$$(4.33) \quad f(z) = z^4 + b_1 z^3 + b_2 z^2 + b_3 z + b_4$$

with real coefficients b_j , the Routh–Hurwitz theorem asserts that all zeros have negative real parts if and only if

$$\begin{aligned} b_1 &> 0, \\ b_1 b_2 - b_3 &> 0, \\ b_1 b_2 b_3 - b_1^2 b_4 - b_3^2 &> 0, \\ b_4 &> 0. \end{aligned}$$

Descartes’s rule of signs asserts that if the coefficients of the quartic have n changes of sign (starting with the positive coefficient of z^4), then the quartic has $n, n - 2$, or zero positive real zeros.

4.3.1. Case 1. The coefficients of the quartic (4.30) are

$$\begin{aligned} b_1 &= q^2, \\ b_2 &= dq^2 - \lambda(a_{11} + a_{22}), \\ b_3 &= dq^4 - \lambda a_{22} q^2, \\ b_4 &= -\lambda a_{11} dq^2 + \lambda^2(a_{11} a_{22} - a_{12} a_{21}). \end{aligned}$$

Clearly, $b_1 > 0, b_2 > 0$, and $b_3 > 0$, but $b_1 b_2 - b_3 = -\lambda q^2 a_{11}$ is less than zero independently of the value of d . Hence the Routh–Hurwitz conditions are not met in this case, and at least one of the zeros of the quartic has a real component greater than or equal to zero. It is trivial to show that the quartic (4.30) has no purely imaginary zeros (with standard activator-inhibitor values for a_{ij}), and hence at least one of the zeros, z_k , has a strictly positive real component. This ensures a Turing instability for parameters where the real component of z_k^2 is also strictly positive. One parameter regime where this occurs is

$$(4.34) \quad q > q_1^* \equiv \left\{ \lambda \left(\frac{a_{11} a_{22} - a_{12} a_{21}}{a_{11} d} \right) \right\}^{\frac{1}{2}},$$

since in this case $b_4 < 0$ so that there is one change of sign among the coefficients of the quartic (4.30), and hence from Descartes’s rule there is one positive real zero. It follows that all wavenumbers above a cut-off q_1^* , (4.34), are destabilized by the fractional activator diffusion. Moreover, this range of destabilized wavenumbers increases with increasing d .

For wavenumbers below the cut-off q_1^* , we have $b_4 > 0$, and hence from Descartes’s rule there are no positive real zeros, and (interchanging z with $-z$) there are four or two or zero negative real zeros. Combining this result with the result of the Routh–Hurwitz theorem, which asserts that at least one of the zeros has a positive real

component in this case, we have that either all zeros are complex or two are complex and two are negative real. Significantly, at least one of the zeros is of the form $z_k = |\alpha_k| + i\beta_k$, where α_k and β_k are real numbers. Hence a Turing instability could occur in modes $q < q_1^*$ for which $\alpha_k^2 - \beta_k^2 > 0$.

4.3.2. Case 2. First, we note that a Turing instability cannot occur in the Case 2 fractional activator-inhibitor system if $d = 1$. This is a simple extension of Turing’s result for standard activator-inhibitor systems, that unequal diffusion is a necessary condition for pattern formation, to the case where the diffusion is anomalous subdiffusion with scaling exponent $1/2$. To see this, note that if $d = 1$, we can factor the quartic (4.30) as

$$(4.35) \quad f_2(z) = (z^2 + zq^2 - z^+)(z^2 + zq^2 - z^-),$$

where

$$(4.36) \quad z^\pm = \frac{\lambda}{2} \left((a_{11} + a_{22}) \pm \sqrt{(a_{11} + a_{22})^2 - 4(a_{11}a_{22} - a_{12}a_{21})} \right).$$

However, we have from (4.28) that each of the zeros defined by (4.36) must have a negative real part so that the zeros of the quartic satisfy quadratics of the form

$$(4.37) \quad z^2 + zq^2 = -|\alpha| + i\beta,$$

where α and β are real. But (4.37) cannot have a solution for which both z and z^2 have positive real parts, in violation of the requirement (4.29).

In Case 2, the coefficients of the quartic (4.31) are

$$\begin{aligned} b_1 &= dq^2 + q^2, \\ b_2 &= dq^4 - \lambda(a_{11} + a_{22}), \\ b_3 &= -\lambda q^2(a_{22} + a_{11}d), \\ b_4 &= \lambda^2(a_{11}a_{22} - a_{12}a_{21}). \end{aligned}$$

We note that if $d > \frac{|a_{22}|}{|a_{11}|} > 1$, then $b_3 < 0$, and with $b_4 > 0$ (from Condition (i) for a Turing instability (4.28)) the Routh–Hurwitz conditions are again not met, and at least one of the zeros of the quartic has a strictly positive real component. (There are no purely imaginary zeros in this case.) Descartes’s rule of signs provides no unambiguous result about the existence of real positive zeros in this case.

However, if $d < \frac{|a_{22}|}{|a_{11}|}$, then $b_3 > 0$, and it is a simple exercise to show that the Routh–Hurwitz conditions are met for wavenumbers

$$(4.38) \quad q > q_2^* \equiv \left\{ \frac{\lambda}{d} \left(\frac{a_{11} + da_{22}}{d + 1} + \frac{(d + 1)(a_{11}a_{12} - a_{12}a_{21})}{-a_{22} - a_{11}d} \right) \right\}^{\frac{1}{4}}.$$

From Descartes’s rule, there are no real positive zeros for the wavenumbers $q < q_2^*$, where the Routh–Hurwitz conditions are not met; however, again the possibility of Turing instabilities arising from complex zeros cannot be ruled out.

4.3.3. Case 3. The coefficients of the quartic (4.32) are

$$\begin{aligned} b_1 &= dq^2, \\ b_2 &= q^2 - \lambda(a_{11} + a_{22}), \\ b_3 &= dq^4 - \lambda a_{11}dq^2, \\ b_4 &= -q^2\lambda a_{22} + \lambda^2(a_{11}a_{22} - a_{12}a_{21}). \end{aligned}$$

In this case, $b_1 > 0, b_2 > 0, b_4 > 0, b_1 b_2 - b_3 = -dq^2 \lambda a_{22} > 0$. Since $a_{12} a_{21}$ must be negative to make $\det(A) > 0$ (see (2.12)), we have $b_3(b_1 b_2 - b_3) - b_1^2 b_4 = d^2 q^4 \lambda^2 a_{12} a_{21} < 0$ so that the Routh–Hurwitz conditions are violated for standard activator-inhibitor parameters a_{ij} . Since this quartic has no purely imaginary zeros, at least one of the zeros has a positive real component.

4.4. Fractional diffusion Gierer–Meinhardt models. The Gierer–Meinhardt model [50] is one of the simplest and most widely studied [2] models for the reaction kinetics of an activator-inhibitor system. One version of this model has the reaction kinetics

$$(4.39) \quad f_1(n_1, n_2) = 1 - n_1 + 3 \frac{n_1^2}{n_2},$$

$$(4.40) \quad f_2(n_1, n_2) = n_1^2 - n_2,$$

from which we deduce the unique homogeneous steady state

$$(4.41) \quad (n_1^*, n_2^*) = (4, 16)$$

with linear stability parameters

$$(4.42) \quad a_{11} = \frac{1}{2}, \quad a_{12} = -\frac{3}{16}, \quad a_{21} = 8, \quad a_{22} = -1.$$

The preconditions for a Turing instability (2.11)–(2.12) are clearly met in this model system. Furthermore it can be shown that in the standard reaction-diffusion system a necessary requirement for the further condition for a Turing instability (2.9) to be satisfied is [2]

$$(4.43) \quad d > \left(\frac{1}{a_{11}} (\sqrt{a_{11} a_{22} - a_{12} a_{21}} + \sqrt{-a_{12} a_{21}}) \right)^2,$$

which, in the case of the Gierer–Meinhardt reaction kinetics (4.39)–(4.40), gives the lower bound $d = (2 + \sqrt{6})^2 \approx 19.79$.

We now consider the half fractional reaction-diffusion systems considered in section 4 with the Gierer–Meinhardt reaction kinetics (4.39)–(4.40) and the scaling parameter $\lambda = 1$. It is a simple matter to find the zeros of the quartics (4.30)–(4.32) numerically for prescribed values of d and thus to determine if the conditions (4.29) for Turing instabilities at these values of d are met. Using this approach, we have explored a range of $d \in [1/100, 100]$, and we have been able to deduce the following.

Case 1. Turing instabilities persist for all d in the range explored. Thus anomalous diffusion in the activator but regular diffusion in the inhibitor provide an enhancement of diffusion in the inhibitor relative to the activator sufficient to precipitate a Turing instability, independent of the ratio of the diffusion coefficients.

Case 2. Turing instabilities occur for $d \gtrsim 12$ but not for $d \lesssim 12$ in the range explored. In this case, with anomalous diffusion in both the activator and the inhibitor, the threshold ratio of diffusion coefficients d for a Turing instability is reduced in comparison to the standard diffusion case.

Case 3. Turing instabilities occur for $d \gtrsim 32$ but not for $d \lesssim 32$ in the range explored. In comparison to the standard diffusion case, the higher threshold value for d in Case 3 is necessary to compensate for the anomalous diffusion of the inhibitor, which has been effectively reduced relative to the standard diffusion of the activator.

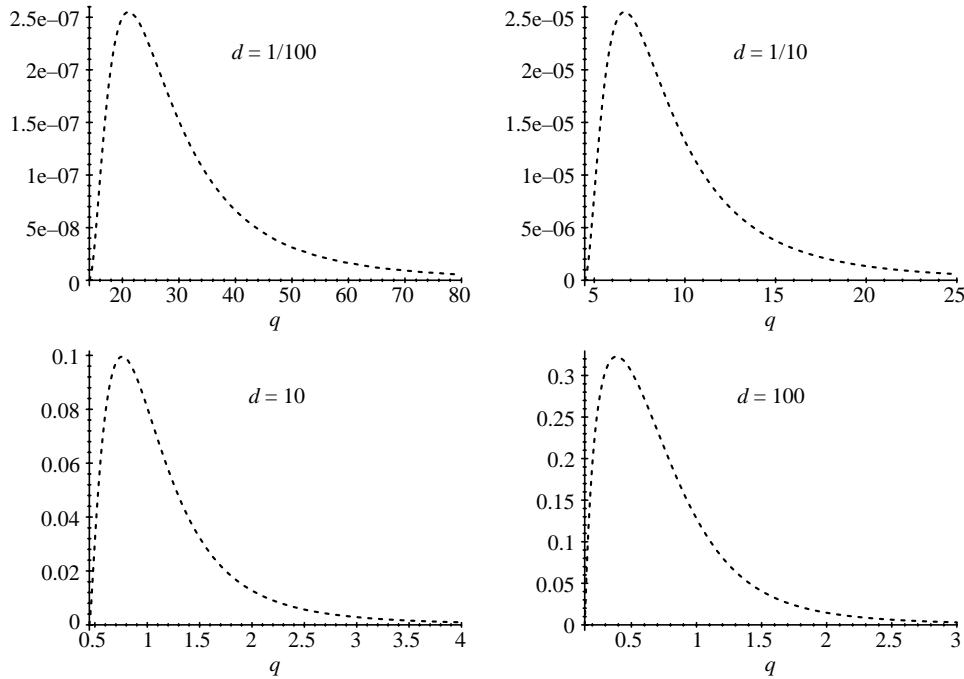


FIG. 2. Plots of $Re(z_k^2(q))$ versus q for the zero with $z_k(q) > 0$ in the Case 1 FRD model with Gierer–Meinhardt reaction kinetics. As d increases, both the magnitude and the wavelength of the maximally unstable mode increase.

One of the most intriguing results in the analysis of the FRD systems considered above is the existence of Turing instabilities in Case 1 for an extended range of values of d including $d < 1$. This means that fractional diffusion in the activator variable is by itself sufficient to precipitate a Turing instability in a two-species FRD system with regular diffusion in the inhibitor variable, irrespective of the value of d . We note, however, that the existence of a Turing instability is a necessary but not a sufficient condition for Turing pattern formation. If all modes were approximately equally destabilized by the fractional diffusion or if the destabilization were sufficiently weak, for example, then no Turing pattern would be observed. Further insight into the conditions for Turing patterns is provided in Figure 2, which plots $Re(z_k^2(q))$ versus q for Case 1 for a range of values of $q > q_1^*$, (4.34), at selected values of d . Note the similar shapes but very different scales in these plots. The particular zero z_k shown in this figure corresponds to the zero identified in our earlier analysis which is real and positive for $q > q_1^*$. In addition, Figure 2 demonstrates that not all modes are equally destabilized above the threshold value $q > q_1^*$. For each value of d , there is a well-defined maximally unstable mode. Furthermore, the amplitude of the modes with wavenumber above the maximally unstable mode decreases monotonically with wavenumber. However, this attenuation of the short wavelength modes may not be sufficient to result in a Turing pattern. In recent work, Kuramoto, Nakao, and Battogtokh [52] have reported that in nonlinear systems where fluctuations of arbitrarily short wavelengths are linearly unstable the system is characterized by multiscaled turbulence. This may also be the case for the FRD system considered here. As an additional remark, we note that the amplitude of the maximally unstable mode decreases with decreasing d , and the range of unstable modes with half the amplitude

of the maximally unstable mode increases with decreasing d . Taken together, these two effects suggest that Turing instabilities (manifest as either Turing patterns or turbulence) can occur over the entire range of d but that they will become more diffuse as d is reduced.

A more thorough numerical investigation of Turing pattern formation or turbulence in the FRD with Gierer–Meinhardt reaction kinetics and related fractional activator-inhibitor systems will be presented in a future publication.

5. Summary and discussion. Turing-instability induced pattern formation in standard reaction-diffusion equations is one of the best understood and most widely applicable mechanisms for pattern formation. In recent years, numerous examples have appeared in the literature of diffusive systems in which the diffusion is anomalous—indeed, anomalous diffusion is ubiquitous in inhomogeneous or fractal media. This study is part of an ongoing program to understand how anomalous diffusion and inhomogeneities in the diffusing medium influence reaction-diffusion systems and pattern formation. The equations describing the evolution of the number density of species in such systems are FRD equations involving fractional order temporal differential operators [44].

In this paper, we have employed Laplace transform methods to derive conditions for Turing instabilities in a two-species fractional activator-inhibitor system in one dimension in which the mean-square displacement between diffusing species scales as $\langle r^2(t) \rangle \sim t^{\frac{1}{2}}$. The conditions summarized in (4.28)–(4.29) are simply defined in terms of the zeros of quartic polynomials (4.30)–(4.32). We anticipate that similar conditions, but pertaining to higher degree polynomials, would apply whenever the scaling exponent was any rational fraction.

The existence of conditions for Turing instabilities in systems with anomalous diffusion indicates that the Turing mechanism for pattern formation or turbulence is robust under different physical conditions, including diffusion in inhomogeneous or fractal media. Indeed, our numerical analysis of the fractional Turing conditions (4.29) in the case of the FRD with Gierer–Meinhardt reaction kinetics revealed that anomalous diffusion extends the range of diffusion coefficients over which Turing instabilities can occur. The finding that Turing instabilities can exist in an FRD system, even in cases where the diffusion coefficient of the activator is greater than that of the inhibitor, provides further insight into possible mechanisms of pattern formation in physical and biological systems. In particular, it suggests that even when the reaction kinetics are well understood, knowledge of the intrinsic diffusibility of a substance alone is not sufficient to predict how it will interact with another substance in a natural physical environment. Knowledge of the microscopic structure of the diffusing medium is equally important in predicting the existence of spatial patterns.

The new Turing conditions for pattern formation or turbulence in an FRD system (4.29) reveal that both the Turing space and the details of the patterns are affected by the anomalous diffusion process. The further ramifications of this condition for real physical systems provide an engaging problem for future research.

Appendix. Here we consider the inverse Laplace transform for

$$(A.1) \quad \hat{\Delta}n(q, s) = \frac{s^\mu}{(s + s^{1-\gamma_1}q^2 - \lambda a_{11})(s + s^{1-\gamma_2}dq^2 - \lambda a_{22}) - \lambda^2 a_{12}a_{21}},$$

where $0 \leq \mu \leq 1$ and $\gamma_2 > \gamma_1$. First, we rewrite

$$\hat{\Delta}n(q, s) = \frac{s^\mu}{s^2 + s^{2-\gamma_1}q^2} \sum_{m=0}^\infty (-1)^m \left(\frac{\hat{a}s^{2-\gamma_2} + \hat{b}s^{2-\gamma_1-\gamma_2} + \hat{c}s^{1-\gamma_1} + \hat{d}s^{1-\gamma_2} + \hat{e}s + \hat{f}}{s^2 + s^{2-\gamma_1}q^2} \right)^m, \tag{A.2}$$

where $\hat{a} = dq^2$, $\hat{b} = dq^4$, $\hat{c} = -q^2\lambda a_{22}$, $\hat{d} = -dq^2\lambda a_{11}$, $\hat{e} = -\lambda(a_{11} + a_{22})$, and $\hat{f} = \lambda^2(a_{11}a_{22} - a_{12}a_{21})$.

Now we expand the multinomial in the numerator to obtain

$$\hat{\Delta}n(q, s) = \sum_{m=0}^\infty (-1)^m \hat{f}^m \sum_{k_1=0}^m \binom{\hat{a}}{\hat{f}}^{k_1} \sum_{k_2=0}^{m-k_1} \binom{\hat{b}}{\hat{f}}^{k_2} \sum_{k_3=0}^{m-k_1-k_2} \binom{\hat{c}}{\hat{f}}^{k_3} \sum_{k_4=0}^{m-k_1-k_2-k_3} \binom{\hat{d}}{\hat{f}}^{k_4} \sum_{k_5=0}^{m-k_1-k_2-k_3-k_4} \binom{\hat{e}}{\hat{f}}^{k_5} \frac{m!}{k_1!k_2!k_3!k_4!k_5!} \frac{s^{\gamma_1-\sigma}}{(s^{\gamma_1} + q^2)^{m+1}}, \tag{A.3}$$

where

$$\sigma = 2 - (\gamma_1 - 2)m - (2 - \gamma_2)k_1 - (2 - \gamma_1 - \gamma_2)k_2 - (1 - \gamma_1)k_3 - (1 - \gamma_2)k_4 - k_5 - \mu.$$

The inverse Laplace transform is now obtained by using known Laplace transform properties of the two-parameter Mittag-Leffler function [53]. Explicitly,

$$\tilde{\Delta}n(q, t) = \sum_{m=0}^\infty (-1)^m \hat{f}^m \sum_{k_1=0}^m \binom{\hat{a}}{\hat{f}}^{k_1} \sum_{k_2=0}^{m-k_1} \binom{\hat{b}}{\hat{f}}^{k_2} \sum_{k_3=0}^{m-k_1-k_2} \binom{\hat{c}}{\hat{f}}^{k_3} \sum_{k_4=0}^{m-k_1-k_2-k_3} \binom{\hat{d}}{\hat{f}}^{k_4} \sum_{k_5=0}^{m-k_1-k_2-k_3-k_4} \binom{\hat{e}}{\hat{f}}^{k_5} \frac{1}{k_1!k_2!k_3!k_4!k_5!} t^{\gamma_1 m + \sigma - 1} E_{\gamma_1, \sigma}^{(m)}(-q^2 t^{\gamma_1}), \tag{A.4}$$

where $E_{\gamma_1, \sigma}$ is the two-parameter Mittag-Leffler function. Using the known series expansion for this function [53], we finally obtain

$$\tilde{\Delta}n(q, t) = \sum_{m=0}^\infty (-1)^m \hat{f}^m \sum_{k_1=0}^m \binom{\hat{a}}{\hat{f}}^{k_1} \sum_{k_2=0}^{m-k_1} \binom{\hat{b}}{\hat{f}}^{k_2} \sum_{k_3=0}^{m-k_1-k_2} \binom{\hat{c}}{\hat{f}}^{k_3} \sum_{k_4=0}^{m-k_1-k_2-k_3} \binom{\hat{d}}{\hat{f}}^{k_4} \sum_{k_5=0}^{m-k_1-k_2-k_3-k_4} \binom{\hat{e}}{\hat{f}}^{k_5} \frac{1}{k_1!k_2!k_3!k_4!k_5!} \sum_{l=0}^\infty (-1)^l \frac{(l+m)! q^{2l} t^{\gamma_1 l + \gamma_1 m + \sigma - 1}}{l! \Gamma(\gamma_1 l + \gamma_1 m + \sigma)}. \tag{A.5}$$

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