Spike Pinning for the Gierer-Meinhardt Model

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Abstract

The pinning effect induced by two different types of spatial inhomogeneities on the dynamics and equilibria of a one-spike solution to the one-dimensional Gierer-Meinhardt (GM) activator-inhibitor model of morphogenesis is studied. The first problem that is treated is the shadow problem that results from taking the infinite inhibitor diffusivity limit in the GM model. For this problem, we show that an exponentially weak spatially varying activator diffusivity can stabilize an equilibrium spike-layer solution that would necessarily be unstable when the activator diffusivity was spatially uniform. The second problem that is treated is the full GM model in the presence of a spatially varying inhibitor decay rate. For this problem, we show that the equilibrium location of a one-spike solution depends on certain global properties of the inhibitor decay rate over the domain.

1 Introduction

The effect of certain spatial inhomogeneities on the dynamics of a one-spike solution to the Gierer-Meinhardt (GM) model [3] is studied. This activator-inhibitor model was introduced in [3] to try to qualitatively explain the process of morphogenesis. Over the years there has been much numerical work classifying pattern formation aspects of this model, including the development of spikes and stripes (cf. [4], [7] and the references therein). A mathematical survey of results on spike solutions to the GM model is given in [9].

In a one-dimensional domain, the dimensionless GM model reduces to the following reaction-diffusion system of activator-inhibitor type (cf. [5]):

$$a_t = \varepsilon^2 a_{xx} - a + \frac{a^p}{h^q}\,, \qquad -1 < x < 1\,, \quad t > 0\,, \tag{1.1a}$$

$$0 = D h_{xx} - \mu h + \varepsilon^{-1}\frac{a^r}{h^s}\,, \qquad -1 < x < 1\,, \quad t > 0\,, \tag{1.1b}$$

$$a_x(\pm 1, t) = h_x(\pm 1, t) = 0\,. \tag{1.1c}$$

Here a, h, ε, $D > 0$ and $\mu > 0$ represent the scaled activator concentration, inhibitor concentration, activator diffusivity, inhibitor diffusivity, and inhibitor decay rate. The exponents (p, q, r, s) in (1.1) are assumed to satisfy

$$p > 1, \qquad q > 0, \qquad r > 0, \qquad s \geq 0, \qquad 0 < \frac{p-1}{q} < \frac{r}{s+1}\,. \tag{1.2}$$

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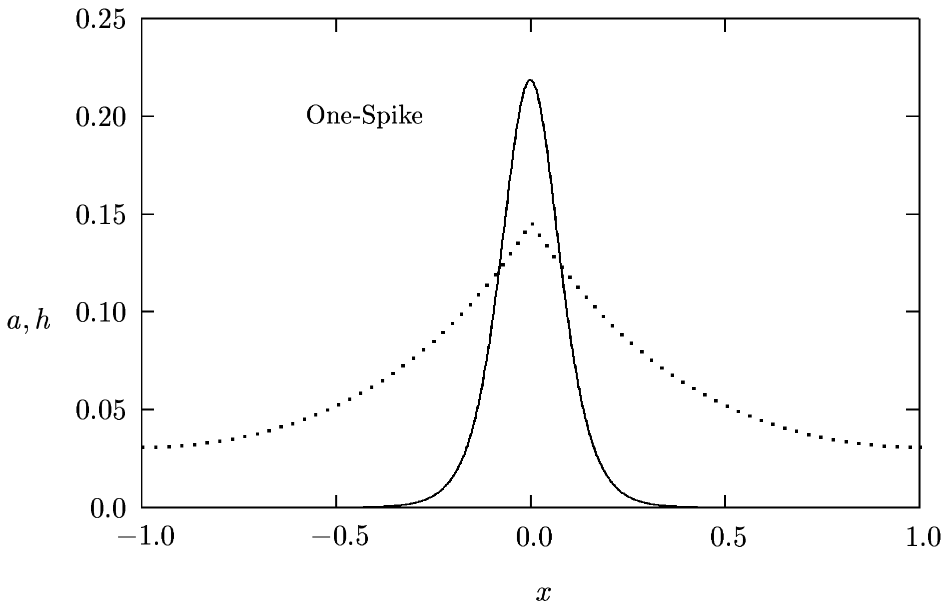

Figure 1: Plot of a one-spike equilibrium solution to (1.1) with $(p, q, r, s) = (2, 1, 2, 0)$, $\epsilon = .05$, $\mu \equiv 1.0$ and $D = .20$. The solid curve is the activator concentration and the dotted curve is the inhibitor concentration.

Here we assume that $\varepsilon \ll 1$ so that the activator diffuses more slowly than does the inhibitor.

For $\varepsilon \ll 1$, many numerical studies of the GM model (1.1) (i. e. [3], [4]) have shown that the solution to (1.1) can have one or more spikes in the activator concentration a. These spikes, which represent strong localized deviations from a constant background concentration, have a spatial extent of $O(\varepsilon)$. In Fig. 1 we plot a one-spike equilibrium solution to (1.1) for certain specific parameter values. When μ is spatially uniform, an equilibrium one-spike solution is, by symmetry considerations, centered at the midpoint of the interval as shown in Fig. 1.

In §3 we examine the effect of a spatially variable inhibitor decay rate $\mu = \mu(x) > 0$ on the dynamics and equilibrium position of a one-spike solution to (1.1). In the biological context, this term is an example of a precursor gradient. The significance of precursor gradients from a biological viewpoint is discussed in [4]. From a mathematical viewpoint, we show that the effect of a spatially varying μ is to perturb the equilibrium location for a one-spike solution away from the midpoint of the interval. The exact equilibrium location now depends on certain global properties of $\mu(x)$ over the domain. The stability behavior of the one-spike solution is independent of μ when D is large. The results for this problem are given in Proposition 3.1 and Corollary 3.1, 3.2 below.

In §2 we consider a related problem with a spatially inhomogeneous coefficient. Specifically, we now let μ be spatially uniform and we consider the shadow problem associated with (1.1) that results from taking the limit $D \to \infty$ in (1.1b). A weak spatially inhomogeneous diffusivity for the activator equation is then introduced. This leads to the perturbed shadow problem, defined by the scalar nonlocal problem

$$a_t = \frac{\varepsilon^2}{\kappa}\left(\kappa a_x\right)_x - a + \frac{a^p}{h^q}\,, \qquad -1 < x < 1\,, \quad t > 0\,, \tag{1.3a}$$

$$h = \left(\frac{\varepsilon^{-1}}{2\mu}\int_{-1}^{1} a^r\,dx\right)^{\frac{1}{s+1}}\,, \qquad a_x(\pm 1, t) = 0\,. \tag{1.3b}$$

The motivation for this form of κ is mentioned below in context with a related problem studied in [10] for the Ginzburg-Landau equation. When $\kappa \equiv 1$ in (1.3a) it was shown using formal asymptotics in [5], and then proved later in [2], that (1.3) admits a one-spike solution that drifts exponentially slowly towards the closest endpoint of the domain. In addition, the equilibrium one-spike solution, which is centered at $x = 0$, is unstable. The metastable behavior associated with (1.3) when $\kappa \equiv 1$ suggests that exponentially small changes in $\kappa - 1$ should influence the metastable dynamics greatly. Therefore, in §2 we study the dynamics of a one-spike solution for (1.3) as $\varepsilon \to 0$ for a $\kappa(x;\varepsilon)$ of the form

$$\kappa(x;\varepsilon) = 1 + \varepsilon^{\nu} g(x) e^{-\varepsilon^{-1} d}\,. \tag{1.3c}$$

Here ν and $d > 0$ are constants and $g(x)$ is smooth. When $g^{''}(x) < 0$ and $0 < d < d_c$, where d_c is some constant, we show in §2 that (1.3) can have a stable spatially inhomogeneous equilibrium one-spike solution where the spike is centered at a zero of $g^{'}(x)$. Results for this problem are given in Propositions 2.1 and 2.2 below. This effect whereby a localized structure is stabilized by a weak but spatially inhomogeneous coefficient in the differential operator is called pinning.

The effect of weak spatially inhomogeneous terms has been examined in other contexts, including the pinning of vortices in superconductivity (cf. [1], [6]) and the pinning of an interface for the Ginzburg Landau equation posed in a thin cylinder of revolution, modeled by (cf. [10])

$$u_t = \frac{\varepsilon^2}{A}\left(A u_x\right)_x + 2(u - u^3)\,, \quad -1 < x < 1\,; \qquad u_x(\pm 1, t) = 0\,. \tag{1.4}$$

This equation was derived in the thin channel limit in [10]. In this context, x is the direction along the axis of the cylinder and $A = A(x;\varepsilon)$ denotes the slowly varying cross-sectional area of the cylinder. For this problem, it was shown in [10] that an internal layer solution can be stabilized by an exponentially weak non-convex perturbation of a straight cylindrical domain by taking $A(x;\varepsilon)$ to have the form $A(x;\varepsilon) = 1 + \varepsilon^{\nu} e^{-d/\varepsilon} g(x)$, where $g^{''}(x) < 0$ and $d > 0$. A similar pinning result is obtained for spike solutions of the related problem (1.3).

2 One-Spike Dynamics: The Perturbed Shadow Problem

In this section we construct a one-spike solution to (1.3). When $\kappa \equiv 1$ in (1.3), the resulting unperturbed problem admits a quasi-equilibrium one-spike solution of the form (see [5])

$$a \sim a_e(x;x_0) \equiv h_e^{q/(p-1)} u_c\left[\varepsilon^{-1}(x-x_0)\right] , \tag{2.1a}$$

$$h \sim h_e \equiv \left(\frac{b_r}{2\mu}\right)^{\frac{p-1}{(s+1)(p-1)-qr}} , \qquad \text{where} \quad b_r \equiv \int_{-\infty}^{\infty} \left[u_c(y)\right]^r \, dy \, . \tag{2.1b}$$

Here $u_c(y)$ is the unique positive solution to

$$u_c'' - u_c + u_c^p = 0, \qquad -\infty < y < \infty \, , \tag{2.2a}$$

$$u_c'(0) = 0 ; \qquad u_c(y) \sim \alpha e^{-|y|} , \qquad \text{as} \quad y \to \pm\infty \, , \tag{2.2b}$$

for some $\alpha > 0$. The function a_e is called the quasi-equilibrium one-spike solution to (1.3) since a_e has exactly one localized maximum and it fails to satisfy the steady-state problem corresponding to (1.3) by only exponentially small terms as $\varepsilon \to 0$ for any value of x_0 in $|x_0| < 1$.

For the time-dependent problem, our goal is to derive an asymptotic differential equation for the trajectory $x = x_0(t)$ of the localized maximum of a_e, which represents the center of the spike. Since $\kappa - 1$ is exponentially small, we begin by linearizing (1.3) in the form

$$a(x,t) = a_e\left[x; x_0(t)\right] + w(x,t) \, , \tag{2.3}$$

where $w \ll a_e$. Substituting (2.3) into (1.3), we get the linearized problem for w

$$L_\epsilon w = \partial_t a_e + \partial_t w - \varepsilon^2 \kappa_x \kappa^{-1} \partial_x a_e \, , \qquad -1 < x < 1 \, , \quad t \geq 0 \, , \tag{2.4a}$$

$$w_x(\pm 1, t) = -\partial_x a_e(\pm 1; x_0) \, , \tag{2.4b}$$

where the nonlocal operator L_ε is defined by

$$L_\varepsilon \phi \equiv \frac{\varepsilon^2}{\kappa} \left(\kappa \phi_x\right)_x - \phi + p u_c^{p-1} \phi - \frac{r q \varepsilon^{-1} u_c^p}{b_r (s+1)} \int_{-1}^{1} u_c^{r-1} \phi \, dx \, . \tag{2.4c}$$

Here b_r is defined in (2.1b). The coefficients in the operator L_ε are localized near $x = x_0$ since $u_c = u_c\left[\varepsilon^{-1}(x - x_0)\right]$.

2.1 Exponentially Small Eigenvalue

Let $x_0 \in (-1,1)$ be fixed and consider the eigenvalue problem

$$L_\varepsilon \phi = \lambda \phi \qquad -1 < x < 1 ; \qquad \phi_x(\pm 1) = 0 \, . \tag{2.5}$$

When $\kappa \equiv 1$, it was shown in [5] that, under the conditions on p and r given in (2.8) below, the eigenvalue of (2.5) with the largest real part is exponentially small as $\varepsilon \to 0$ and the corresponding eigenfunction is localized near $x = x_0$. We will estimate the change in this exponentially small eigenvalue as a result of the exponentially small perturbation $\kappa - 1$. To do so, we let $\kappa = 1$ and proceed as in [5] by introducing the localized eigenvalue problem for $\Phi = \Phi(y)$ given by

$$\mathcal{L}_0 \Phi = \sigma \Phi \quad -\infty < y < \infty\,; \qquad \Phi \to 0 \quad \text{exponentially} \qquad \text{as} \quad y \to \pm\infty\,, \tag{2.6}$$

where $y = \varepsilon^{-1}(x - x_0)$. Here $\mathcal{L}_0$ is defined by

$$\mathcal{L}_0 \Phi \equiv \Phi_{yy} - \Phi + p u_c^{p-1} \Phi - \frac{r q u_c^p}{b_r (s+1)} \int_{-\infty}^{\infty} u_c^{r-1} \Phi \, dy\,, \tag{2.7}$$

where $u_c = u_c(y)$. The following rigorous result on the spectrum of (2.7) is proved in [11].
Theorem(**Wei [11]**): *Let σ_0 be the eigenvalue of (2.6) with the largest real part and let Φ_0 denote the corresponding eigenfunction. Assume that either of the following two conditions hold:*

$$\text{(i)} \quad r = 2\,, \;\; 1 < p \le 5\,, \qquad \text{or} \qquad \text{(ii)} \quad r = p + 1\,, \;\; p > 1\,. \tag{2.8}$$

Then, when (p, q, r, s) satisfy (1.2), we have

$$\sigma_0 = 0\,, \qquad \Phi_0(y) = u_c'(y)\,. \tag{2.9}$$

The assumption (2.8) holds for the two common sets of parameter values for the Gierer-Meinhardt system $(p, q, r, s) = (2, 1, 2, 0)$ and $(p, q, r, s) = (3, 2, 2, 0)$.

The effects of the exponentially small perturbation $\kappa - 1$ and of the finite domain in (2.5) perturb this eigenvalue σ_0 by exponentially small terms as $\varepsilon \to 0$. Let the perturbed eigenpair be denoted by λ_0 and ϕ_0. In order that ϕ_0 satisfy the boundary condition on $x = \pm 1$, we proceed as in [5] by constructing ϕ_0 in the boundary layer form

$$\phi_0 \sim u_c' \left[\varepsilon^{-1}(x - x_0)\right] + \phi_{L0}\left[\varepsilon^{-1}(1 + x)\right] + \phi_{R0}\left[\varepsilon^{-1}(1 - x)\right]\,, \tag{2.10a}$$

where

$$\phi_{L0}(\eta) = \alpha e^{-\varepsilon^{-1}(1 + x_0)} e^{-\eta}\,, \qquad \phi_{R0}(\eta) = -\alpha e^{-\varepsilon^{-1}(1 - x_0)} e^{-\eta}\,. \tag{2.10b}$$

To estimate λ_0 we first define the inner product $(u, v)_\kappa \equiv \int_{-1}^{1} u v \kappa \, dx$. Integrating by parts, we obtain for any two functions ϕ and ψ that

$$(L_\varepsilon \phi, \psi)_\kappa = \varepsilon^2 \kappa \left(\phi_x \psi - \phi \psi_x\right)|_{-1}^{1} + \left(\phi, L_\varepsilon^* \psi\right)\,, \tag{2.11}$$

where L_ε^* is the adjoint operator defined by

$$L_\varepsilon^* \psi \equiv \frac{\varepsilon^2}{\kappa} \left(\kappa \psi_x\right)_x - \psi + p u_c^{p-1} \psi - \frac{r q \varepsilon^{-1} u_c^{r-1}}{b_r \kappa (s+1)} \int_{-1}^{1} \kappa u_c^p \psi \, dx\,. \tag{2.12}$$

Now let $\psi = u_c^{'}$ and $\phi = \phi_0$. Then, since $\phi_{0x}(\pm 1) = 0$, we get from (2.11) that

$$\lambda_0 \left(\phi_0, u_c^{'}\right)_\kappa + \varepsilon\kappa\phi_0 u_c^{''}|_{-1}^{1} = \varepsilon \left(\frac{\kappa_x u_c^{''}}{\kappa}, \phi_0\right)_\kappa - \frac{rq\varepsilon^{-1}}{b_r(s+1)} \left(\int_{-1}^{1} \phi_0 u_c^{r-1}\, dx\right) \left(\int_{-1}^{1} \kappa u_c^p u_c^{'}\, dx\right). \tag{2.13}$$

The two terms on the left side of (2.13) can be estimated as in [5] by using (2.10) for ϕ_0 and (2.2) for $u_c^{''}(y)$ as $y \to \pm\infty$. The exponentially small perturbation $\kappa - 1$ does not affect the leading order asymptotic estimates for these quantities. Thus, for $\varepsilon \to 0$, we get

$$\left(\phi_0, u_c^{'}\right)_\kappa \sim \varepsilon\beta_0\,, \qquad \beta_0 \equiv \int_{-\infty}^{\infty} \left[u_c^{'}(y)\right]^2 \, dy\,, \tag{2.14a}$$

$$-\varepsilon\kappa\phi_0 u_c^{''}|_{-1}^{1} \sim 2\varepsilon\alpha^2 \left(e^{-2\varepsilon^{-1}(1+x_0)} + e^{-2\varepsilon^{-1}(1-x_0)}\right). \tag{2.14b}$$

Next, we use (1.3c) to asymptotically estimate the first term on the right side of (2.13) as

$$\varepsilon \left(\frac{\kappa_x u_c^{''}}{\kappa}, \phi_0\right)_\kappa \sim \varepsilon^{2+\nu} e^{-d/\varepsilon} \int_{-\infty}^{\infty} g^{'}(x_0 + \varepsilon y) u_c^{'}(y) u_c^{''}(y)\, dy\,. \tag{2.15}$$

Expanding g in a Taylor series, and using the fact that $u_c(y)$ is even, we integrate by parts to get

$$\varepsilon \left(\frac{\kappa_x u_c^{''}}{\kappa}, \phi_0\right)_\kappa \sim -\frac{\varepsilon^{2+\nu} e^{-d/\varepsilon}}{2} \sum_{j=0}^{\infty} \frac{\varepsilon^{2j+1}}{(2j)!} g^{(2j+2)}(x_0)\beta_j\,, \qquad \beta_j \equiv \int_{-\infty}^{\infty} y^{2j} \left[u_c^{'}(y)\right]^2 \, dy\,. \tag{2.16}$$

For the exponentially small perturbation $\kappa - 1$ to have a significant effect on the eigenvalue for at least some values of x_0 we must balance the exponential orders of (2.14b) and (2.16). Thus, for $\varepsilon \to 0$ we take d to satisfy

$$0 < d \leq 2 - c\varepsilon \log \varepsilon\,, \tag{2.17}$$

for some c independent of ε. With this restriction on d, the last term on the right side of (2.13) is estimated for $\varepsilon \to 0$ as

$$\frac{rq\varepsilon^{-1}}{b_r(s+1)} \left(\int_{-1}^{1} \phi_0 u_c^{r-1}\, dx\right) \left(\int_{-1}^{1} \kappa u_c^p u_c^{'}\, dx\right) = O\left(\varepsilon^q \max\left\{e^{-(r+d)\varepsilon^{-1}(1+x_0)}, e^{-(r+d)\varepsilon^{-1}(1-x_0)}\right\}\right), \tag{2.18}$$

for some q. Since $r > 0$, we conclude that the term in (2.18) is asymptotically smaller as $\varepsilon \to 0$ than the inner product term in (2.16). Finally, substituting (2.14) and (2.16) into (2.13), and neglecting the last term on the right side of (2.13), we obtain the following main result for λ_0:

Proposition 2.1: (Exponentially Small Eigenvalue) *Let (2.8) and (2.17) be satisfied. Then, for $\varepsilon \to 0$ the eigenvalue λ_0 of (2.5) with the largest real part is exponentially small and it has the asymptotic estimate*

$$\lambda_0 = \lambda_0(x_0) \sim \frac{2\alpha^2}{\beta_0}\left(e^{-2\varepsilon^{-1}(1+x_0)} + e^{-2\varepsilon^{-1}(1-x_0)}\right) - \frac{\varepsilon^{1+\nu}e^{-d/\varepsilon}}{2\beta_0}\sum_{j=0}^{\infty}\frac{\varepsilon^{2j+1}}{(2j)!}g^{(2j+2)}(x_0)\beta_j\,. \tag{2.19}$$

Here α is defined in (2.2) and β_j for $j \geq 0$ is defined in (2.16).

From the calculations above we observe that the nonlocal term in L_ε, which is not self-adjoint, does not influence the leading order asymptotic estimate for the exponentially small eigenvalue. Hence, the adjoint operator L_ε^* also has an exponentially small eigenvalue with the same estimate as that given in (2.19).

2.2 The Metastable Spike Motion

We now derive an ODE for $x_0(t)$ from (2.4). Assume that $w(x,0) = 0$ in (2.4) so that the initial condition for (1.3) is a spike-layer solution with spike center initially located at $x_0(0) = x_0^0 \in (-1,1)$. Since the principal eigenvalue of L_ε is exponentially small we can assume that the motion is quasi-steady by neglecting $\partial_t w$ in (2.4). To ensure that w is uniformly small over exponentially long time intervals, we must impose the condition that w is orthogonal to ϕ_0.

To derive an ODE for $x_0(t)$ we begin by using (2.11) with $\psi = \phi_0$ and $w = \phi$ to get

$$\left(L_\varepsilon w, \phi_0\right)_\kappa = \varepsilon^2 \kappa \phi_0 w_x|_{-1}^{1} + \left(w, L_\varepsilon^* \phi_0\right)_\kappa\,. \tag{2.20}$$

Using the remark following (2.19) above, we get $(w, L_\varepsilon^*\phi_0) \sim \lambda_0\,(w,\phi_0) = 0$ by our condition of orthogonality. From this condition, and by using (2.1a) and (2.4), (2.20) reduces to the following implicit differential equation for $x_0(t)$:

$$\left(\phi_0, \partial_t u_c\right)_\kappa + \varepsilon\kappa\phi_0 u_c'|_{-1}^{1} \sim \varepsilon\left(\frac{\kappa_x u_c'}{\kappa}, \phi_0\right)_\kappa\,. \tag{2.21}$$

The two terms on the left side of (2.21) can be estimated as in [5] by using (2.10) for ϕ_0 and (2.2) for $u_c''(y)$ as $y \to \pm\infty$. For $\varepsilon \to 0$, we get

$$\left(\phi_0, \partial_t u_c\right)_\kappa \sim -x_0'\beta_0\,, \tag{2.22a}$$

$$-\varepsilon\kappa\phi_0 u_c'|_{-1}^{1} \sim 2\varepsilon\alpha^2\left(e^{-2\varepsilon^{-1}(1+x_0)} - e^{-2\varepsilon^{-1}(1-x_0)}\right)\,. \tag{2.22b}$$

Next, for $\varepsilon \to 0$, we calculate as in (2.15) that

$$\varepsilon\left(\frac{\kappa_x u_c'}{\kappa}, \phi_0\right)_\kappa \sim \varepsilon^{2+\nu}e^{-d/\varepsilon}\int_{-\infty}^{\infty} g'(x_0+\varepsilon y)\left[u_c'(y)\right]^2 dy \sim \varepsilon^{2+\nu}e^{-d/\varepsilon}\sum_{j=0}^{\infty}\frac{\varepsilon^{2j}}{(2j)!}g^{(2j+1)}(x_0)\beta_j\,. \tag{2.23}$$

Finally, substituting (2.22) and (2.23) into (2.21), we obtain the following metastability result for $x_0(t)$:

Proposition 2.2: (Metastability) *Let (2.8) and (2.17) be satisfied. Then, for $\varepsilon \to 0$, the trajectory $x_0(t)$ of the center of the spike for a one-spike solution to (1.3) satisfies the asymptotic differential equation*

$$\frac{dx_0}{dt} \sim h(x_0) \equiv \frac{2\varepsilon\alpha^2}{\beta_0}\left(e^{-2\varepsilon^{-1}(1-x_0)} - e^{-2\varepsilon^{-1}(1+x_0)}\right) - \frac{\varepsilon^{2+\nu}e^{-d/\varepsilon}}{\beta_0}\sum_{j=0}^{\infty}\frac{\varepsilon^{2j}}{(2j)!}g^{(2j+1)}(x_0)\beta_j\,. \qquad (2.24)$$

Here α is defined in (2.2) and β_j for $j \geq 0$ is defined in (2.16).

An important remark, as observed from (2.24), is that the behavior of $x_0(t)$ depends only on pointwise values of certain derivatives of the perturbation $\kappa - 1$. This will be different from the behavior that we will observe in §3.

2.3 An Example of the Theory

We now discuss the qualitative behavior associated with (2.19) and (2.24). From (2.24) we see that $h(-1) < 0$ and $h(1) > 0$ as $\varepsilon \to 0$ when $d > 0$. Thus, there exists at least one equilibrium value x_0^e for $x_0(t)$. The existence of any other equilibria for x_0 depends on the constants d and ν and the function $g'(x)$. In particular, when $d > 0$ is sufficiently small, then (2.24) has an equilibrium point near each zero of $g^{'}(x)$. As shown in the example below, we can have other equilibrium points in the interval $[-1, 1]$ when d is near some critical value.

The next result concerns the stability of the equilibria of (2.24). Let x_0^e satisfy $h(x_0^e)=0$. Then, by comparing (2.19) and (2.24), we find that $h'(x_0^e) = 2\lambda_0(x_0^e)$. This shows that the decay rate for the differential equation (2.24) associated with infinitesimal perturbations about x_0^e is $2\lambda_0(x_0^e)$. This leads to the next result.

Corollary 2.1: (Stability of Equilibrium) *Let x_0^e satisfy $h(x_0^e) = 0$. Then (1.3) has a one-spike equilibrium solution of the form given in (2.1) and this solution is stable (unstable) if $\lambda_0(x_0^e) < 0$ ($\lambda_0(x_0^e) > 0$). Here $u_c(y)$, $\lambda_0(x_0)$ and $h(x_0)$ are given in (2.2), (2.19) and (2.24).*

Thus a one-spike equilibrium solution centered at x_0^e is unstable when $g''(x_0^e) < 0$. Since $g''(x) < 0$ corresponds to a weakly convex domain, this result predicts that there is no stable spike-layer solutions in such domains. However, when $g''(x_0^e) > 0$, then $\lambda_0(x_0^e)$ can be negative for certain choices of ν and d, resulting in a stable spike-layer solution centered at x_0^e. The key point to construct such a stable equilibrium solution is to guarantee that (2.24) has multiple equilibria corresponding to simple zeroes of $h(x_0)$. Then, we must have exactly one stable equilibrium of (2.24) between every two consecutive unstable equilibria.

To illustrate the result, let $p = 2$ for which $u_c(y) = (3/2)\,\text{sech}^2\,(y/2)$. Then, we calculate from

(2.2) and (2.14a) that $\beta_0 = 6/5$ and $\alpha = 6$. Thus, to leading order (2.19) becomes

$$\lambda_0 = \lambda_0(x_0) \sim 60\left(e^{-2\varepsilon^{-1}(1+x_0)} + e^{-2\varepsilon^{-1}(1-x_0)}\right) - \frac{\varepsilon^{\nu+2}}{2} e^{-\varepsilon^{-1}d} g''(x_0) + \cdots, \tag{2.25}$$

and (2.24) reduces to

$$x_0' \sim h(x_0) = 60\varepsilon\left(e^{-2\varepsilon^{-1}(1-x_0)} - e^{-2\varepsilon^{-1}(1+x_0)}\right) - \varepsilon^{\nu+2} e^{-\varepsilon^{-1}d} g'(x_0) + \cdots. \tag{2.26}$$

Choose $g(x) = x^2/2$, which corresponds to a non-convex domain. In this case, $x_0^e = 0$ is an equilibrium solution to (2.26) for any ν and d. This solution can be stable if d is small enough. From (2.25), we calculate $\lambda_0(0) = -\frac{\varepsilon^{\nu+2}}{2} e^{-\varepsilon^{-1}d} + 120 e^{-2\varepsilon^{-1}}$. Let d_c be the zero of $\lambda_0(0)$ as a function of d. Then, $d_c = 2 - \varepsilon \log 240 + (\nu + 2)\varepsilon \log \varepsilon$. From Corollary 2.1 it follows that the equilibrium $x_0^e = 0$ is stable (unstable) when $d < d_c$ $(d > d_c)$. When $d < d_c$ there are two other equilibrium points for (2.26) on either side of $x = 0$ that are unstable. This example clearly shows the effect of pinning whereby the exponentially weak non-convex perturbation of the original domain leads to a stable one-spike equilibrium solution to the shadow problem (1.3) centered at the midpoint of the domain.

3 One-Spike Dynamics: The Perturbed Gierer-Meinhardt Model

In this section we analyze the dynamics of a one-spike solution to (1.1). For finite inhibitor diffusivity D and for $\mu = \mu(x) > 0$, we derive a differential equation determining the location $x_0(t)$ of the maximum of the activator concentration for a one-spike solution to (1.1).

In the inner region near the spike we introduce the new variables

$$y = \varepsilon^{-1}[x - x_0(\tau)], \qquad \tilde{h}(y) = h(x_0 + \varepsilon y), \qquad \tilde{a}(y) = a(x_0 + \varepsilon y), \qquad \tau = \varepsilon^2 t. \tag{3.1a}$$

We then expand the inner solution as

$$\tilde{h}(y) = \tilde{h}_0(y) + \varepsilon \tilde{h}_1(y) + \cdots, \qquad \tilde{a}(y) = \tilde{a}_0(y) + \varepsilon \tilde{a}_1(y) + \cdots. \tag{3.1b}$$

The spike location is to satisfy $\tilde{a}_0'(0) = 0$. Substituting (3.1) into (1.1), and collecting terms that are $O(1)$ as $\varepsilon \to 0$, we get the leading order problem for $\tilde{a}_0$ and $\tilde{h}_0$:

$$\tilde{a}_0'' - \tilde{a}_0 + \tilde{a}_0^p/\tilde{h}_0^q = 0, \qquad -\infty < y < \infty, \tag{3.2a}$$

$$\tilde{h}_0'' = 0, \tag{3.2b}$$

with $\tilde{a}_0'(0) = 0$. In order to match to the outer solution, to be constructed below, we require that $\tilde{h}_0$ is independent of y. Thus, we set $\tilde{h}_0 = H$, where $H = H(\tau)$ is a function to be determined. We then write the solution to (3.2a) as

$$\tilde{a}_0 = H^\gamma u_c, \qquad \text{where} \qquad \gamma \equiv q/(p-1), \tag{3.3}$$

where u_c satisfies (2.2).

Collecting the $O(\varepsilon)$ terms in the inner region expansion, we obtain the problem for $\tilde{a}_1$ and $\tilde{h}_1$,

$$\tilde{a}_1'' - \tilde{a}_1 + \frac{p\tilde{a}_0^{p-1}}{\tilde{h}_0^q}\tilde{a}_1 = \frac{q\tilde{a}_0^p}{\tilde{h}_0^{q+1}}\tilde{h}_1 - x_0'\tilde{a}_{0y}\,, \qquad -\infty < y < \infty\,, \tag{3.4a}$$

$$D\tilde{h}_{1yy} = -\tilde{a}_0^r/\tilde{h}_0^s\,. \tag{3.4b}$$

Here $x_0' \equiv dx_0/d\tau$. Next, we write $\tilde{a}_1$ as

$$\tilde{a}_1 = H^\gamma u_1\,. \tag{3.5}$$

Using (3.3), (3.5), and $\tilde{h}_0 \equiv H$, (3.4) becomes

$$L(u_1) \equiv u_1'' - u_1 + pu_c^{p-1}u_1 = \frac{qu_c^p}{H}\tilde{h}_1 - x_0'u_c'\,, \qquad -\infty < y < \infty\,, \tag{3.6a}$$

$$D\tilde{h}_{1yy} = -H^{\gamma r - s}u_c^r\,, \tag{3.6b}$$

where u_1 is to decay exponentially as $|y| \to \infty$. Since $Lu_c' = 0$ and $u_c' \to 0$ exponentially as $|y| \to \infty$, the right side of (3.6a) must satisfy the solvability condition that it is orthogonal to u_c'. From this condition we obtain the differential equation

$$x_0' = \frac{q}{H\int_{-\infty}^{\infty}\left[u_c'(y)\right]^2\,dy}\int_{-\infty}^{\infty} u_c^p u_c' \tilde{h}_1\,dy\,. \tag{3.7}$$

If we integrate (3.7) by parts twice, and use the facts that h_1'' and u_c are even functions, we get

$$x_0' = -\frac{q}{2H(p+1)}\left(\frac{\int_{-\infty}^{\infty}\left[u_c(y)\right]^{p+1}\,dy}{\int_{-\infty}^{\infty}\left[u_c'(y)\right]^2\,dy}\right)\left[\lim_{y\to+\infty}\tilde{h}_1' + \lim_{y\to-\infty}\tilde{h}_1'\right]\,. \tag{3.8}$$

In the outer region defined at an $O(1)$ distance away from the center of the spike, a is exponentially small and we expand h as $h = h_0(x) + o(1)$ as $\varepsilon \to 0$. Then, from (1.1b), we obtain that h_0 satisfies

$$Dh_0'' - \mu h_0 = -H^{\gamma r - s}b_r\delta(x - x_0)\,, \qquad -1 < x < 1\,, \tag{3.9a}$$

$$h_0'(\pm 1) = 0\,. \tag{3.9b}$$

Here b_r is defined in (2.1b). Solving for h_0 we get

$$h_0(x) = H^{\gamma r - s}b_r G(x; x_0)\,, \tag{3.10}$$

where the Green's function $G(x;x_0)$ satisfies

$$DG_{xx} - \mu G = -\delta(x - x_0)\,, \qquad -1 < x < 1\,, \tag{3.11a}$$

$$G_x(\pm 1; x_0) = 0\,. \tag{3.11b}$$

To match with the inner solution we require that

$$h_0(x_0) = H\,, \qquad \lim_{y\to+\infty} \tilde{h}_1' + \lim_{y\to-\infty} \tilde{h}_1' = h_0'(x_{0+}) + h_0'(x_{0-})\,. \tag{3.12}$$

Substituting (3.10) into (3.12), we get

$$\lim_{y\to+\infty} \tilde{h}_1' + \lim_{y\to-\infty} \tilde{h}_1' = \frac{H}{G(x_0;x_0)}\left[G_x(x_{0+};x_0) + G_x(x_{0-};x_0)\right]\,, \tag{3.13a}$$

$$H = \left[\frac{1}{b_r G(x_0;x_0)}\right]^{1/[\gamma r - (s+1)]}\,. \tag{3.13b}$$

Finally, substituting (3.13) into (3.3), (3.8) and (3.10) and letting $\tau = \varepsilon^2 t$, we obtain the main result of this section:

Proposition 3.1: *For $\varepsilon \ll 1$, the the dynamics of a one-spike solution to (1.1) is characterized by*

$$a(x,t) \sim H^\gamma u_c\left(\varepsilon^{-1}[x - x_0(t)]\right)\,, \tag{3.14a}$$

$$h(x,t) \sim HG\left[x; x_0(t)\right]/G\left[x_0(t); x_0(t)\right]\,, \tag{3.14b}$$

where $H = H(t)$ is given in (3.13b). The spike location $x_0(t)$ satisfies the differential equation

$$\frac{dx_0}{dt} \sim -\varepsilon^2 C\left(\frac{G_x(x_{0+};x_0) + G_x(x_{0-};x_0)}{G(x_0;x_0)}\right)\,, \tag{3.14c}$$

where $C > 0$ is defined by

$$C \equiv \frac{q}{2(p+1)}\left(\frac{\int_{-\infty}^{\infty}[u_c(y)]^{p+1}\,dy}{\int_{-\infty}^{\infty}[u_c'(y)]^2\,dy}\right)\,. \tag{3.14d}$$

3.1 Case 1: $\mu(\mathbf{x}) = \mu$ is a positive constant

In the special case where $\mu(x) = \mu$ is a positive constant independent of x, we can solve (3.11) explicitly for $G(x;x_0)$ to get

$$G(x;x_0) = \begin{cases} A_0 \cosh\left[\theta(1+x)\right]/\cosh\left[\theta(1+x_0)\right]\,, & -1 < x < x_0\,, \\ A_0 \cosh\left[\theta(1-x)\right]/\cosh\left[\theta(1-x_0)\right]\,, & x_0 < x < 1\,, \end{cases} \tag{3.15a}$$

t	$\log_{10}(1+t)$	$x_0(t)$ (num.)	$x_0(t)$ (asy.)
18.0	1.279	−0.5907	−0.5913
99.0	2.000	−0.5510	−0.5538
207.0	2.318	−0.5026	−0.5079
486.0	2.688	−0.3974	−0.4073
864.0	2.937	−0.2905	−0.3035
1359.0	3.134	−0.1936	−0.2076
1881.0	3.275	−0.1265	−0.1395
2268.0	3.356	−0.0924	−0.1040

Table 1: A comparison of the asymptotic and numerical results for $x_0(t)$ corresponding to the parameter values shown in the caption of Fig. 2.

where

$$A_0 \equiv \frac{1}{\sqrt{\mu D}} \left(\tanh\left[\theta(1-x_0)\right] + \tanh\left[\theta(1+x_0)\right] \right)^{-1} , \qquad \theta \equiv (\mu/D)^{1/2} . \tag{3.15b}$$

Substituting (3.15) into (3.14c), we obtain the following result:

Corollary 3.1: *For $\varepsilon \ll 1$ and when $\mu(x) = \mu$ is a positive constant, the differential equation for the spike location is*

$$\frac{dx_0}{dt} \sim -\varepsilon^2 C \sqrt{\frac{\mu}{D}} \left[\tanh\left(\theta(1+x_0)\right) - \tanh\left(\theta(1-x_0)\right) \right] , \tag{3.16}$$

where C is defined in (3.14d).

The stable equilibrium solution for (3.16) is $x_0 = 0$. Setting $x_0 = 0$ in (3.14a) and (3.14b) we obtain a symmetric one-spike equilibrium solution for (1.1). Notice that $x_0 \to 0$ as $t \to \infty$ for any initial condition $x_0(0) = x_0^0 \in (-1, 1)$. To validate (3.16) we compared it with the corresponding full numerical result computed from (1.1) for the parameter set $(p, q, r, s) = (2, 1, 2, 0)$ using the routine D03PCF from the NAG library [8]. The initial condition was taken to be of the form (3.14a) and (3.14b) with $x_0(0) = -0.6$ and $\varepsilon = .03$, $\mu = 1.0$, and $D = 1.0$. In Fig. 2 and in Table 1 we show the favorable comparison between the numerical result for x_0 with the corresponding asymptotic result obtained by solving the differential equation (3.16) with the initial condition $x_0(0) = -0.6$. In solving the differential equation, the integrals in the definition of the constant C in (3.14d) can be evaluated explicitly since the solution to (2.2) is $u_c(y) = (3/2)\,\mathrm{sech}^2\,(y/2)$ when $p = 2$.

3.2 Case 2: $\mu(\mathbf{x}) > 0$ depends on x

In general, when μ depends on x we must compute the Green's function satisfying (3.11) to determine the dynamics as described in (3.14c). However, to illustrate qualitatively the effect of a

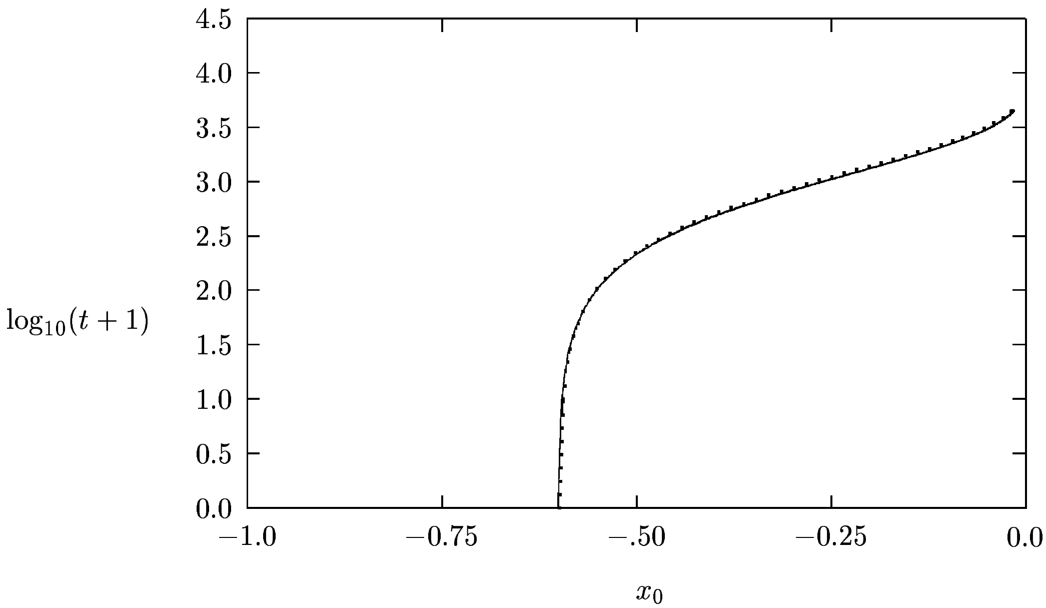

Figure 2: Plot of the trajectory $x_0(t)$ of the center of the spike for a one-spike solution with $\epsilon = .03$, $\mu = 1.0$, $D = 1.0$ and $(p,q,r,s) = (2,1,2,0)$. The solid curve is the full numerical result and the dotted curve is the asymptotic result.

spatially varying $\mu(x)$, we now derive an approximate differential equation for x_0 in the limit $D \gg 1$ with D independent of ε.

In the limit $D \gg 1$, we expand G as

$$G(x;x_0) = G_0(x;x_0) + D^{-1}G_1(x;x_0) + O\left(D^{-2}\right) . \tag{3.17}$$

Substituting (3.17) into (3.11) and collecting powers of D^{-1}, we get

$$G_{0xx} = 0 ; \qquad G_{1xx} = \mu G_0 - \delta(x - x_0) , \tag{3.18}$$

with $G_{jxx} = 0$ at $x = \pm 1$ for $j = 0, 1$. The problem for G_1 does not have a solution unless G_0 satisfies a solvability condition. In this way, we calculate that

$$G_0 = (2\mu_a)^{-1} ; \qquad G_{1x} = (2\mu_a)^{-1} \int_{-1}^{x} \mu(y)\, dy - \left\{ \begin{array}{ll} 0 & -1 < x < x_0 , \\ 1 & x_0 < x < 1 . \end{array} \right. \tag{3.19}$$

Here μ_a is the average of μ over the interval, defined by

$$\mu_a \equiv \frac{1}{2} \int_{-1}^{1} \mu(x)\, dx . \tag{3.20}$$

Substituting (3.19) into (3.14c) we obtain the following result:
Corollary 3.2: *For $\varepsilon \ll 1$ and $D \gg 1$, with D independent of ε, the differential equation for the spike location (3.14c) reduces to*

$$\frac{dx_0}{dt} \sim -\frac{2\varepsilon^2 C}{D} \left(\int_{-1}^{x_0} \mu(y)\, dy - \mu_a \right), \tag{3.21}$$

where C is defined in (3.14d).

From (3.21) we observe that the pinning effect induced by $\mu(x)$ depends on global properties of the spatial inhomogeneity $\mu(x)$, in contrast to the pointwise values as obtained in §2 for the shadow problem. Since $\mu(x) > 0$, there is a unique equilibrium spike-layer location x_{0e} for (3.21) satisfying

$$\int_{-1}^{x_{0e}} \mu(y)\, dy = \mu_a\,. \tag{3.22}$$

This equilibrium is a stable fixed point for (3.21). Notice that if $\int_0^1 \mu\, dx < \int_{-1}^0 \mu\, dx$, then the equilibrium location satisfies $x_{0e} \in (-1, 0)$. Alternatively, if there is more mass of μ on the right side of $x = 0$, then $x_{0e} \in (0, 1)$.

As an example, let $\omega > 0$ and consider the profile

$$\mu(x) \equiv \frac{1}{2} \left(1 + \frac{\omega e^{-\omega x}}{\sinh \omega} \right). \tag{3.23}$$

It is easy to see that $\mu_a = 1$ for any $\omega > 0$. Also, as $\omega \to 0$ we have $\mu(x) \to 1$. As $\omega \to \infty$ we have $\mu(x) \to 1/2 + \omega e^{-\omega(x+1)}$, which has a boundary layer near $x = -1$. For any $\omega > 0$ there is more mass of μ to the left of $x = 0$ than to the right of $x = 0$. From (3.22), x_{0e} satisfies the algebraic equation

$$x_{0e} - \frac{e^{-\omega x_{0e}}}{\sinh \omega} = 1 - \frac{e^{\omega}}{\sinh \omega}\,. \tag{3.24}$$

It is easily seen that $-1 < x_{0e} < 0$ when $\omega > 0$ and $x_{0e} \to -1$ as $\omega \to \infty$.

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