Diffusion, Cross-Diffusion, and Their Spike-Layer Steady States

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Introduction

Many mathematicians, myself included, were brought up to believe that diffusion is a smoothing and trivializing process. Indeed, this is the case for single diffusion equations. Consider the heat equation

$$(1)\quad \begin{cases} u_t = \Delta u & \text{in } \Omega \times (0, \infty), \\ u(x, 0) = u_0(x) \geq 0 & \text{in } \Omega, \\ \frac{\partial u}{\partial \upsilon} = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases}$$

where $u_t = \frac{\partial u}{\partial t}$ and $\Delta = \sum_{i=1}^{n} \frac{\partial^2}{\partial x_i^2}$ is the usual Laplace operator, Ω is a bounded smooth domain in $\mathbf{R}^n$, υ is the unit outer normal to $\partial\Omega$, and u_0 is a real-valued continuous function (not identically zero) representing the initial heat distribution. Here the boundary condition implies that (1) is an isolated system. It is well known that the solution $u(x, t)$ of (1) becomes smooth as soon as t becomes positive and eventually converges to the constant $\frac{1}{|\Omega|}\int_\Omega u_0(x)dx$ as t tends to ∞. In other words, in an isolated system, no matter what the initial heat distribution is, eventually the heat distribution becomes homogeneous. A similar result holds when a source/sink term (or a *reaction* term) is present. That is, if we replace the linear heat equation in (1) by

$$u_t = \Delta u + f(u),$$

where f is a smooth function (linear or nonlinear), then Matano and Casten-Holland in 1978–79 proved that *stable* steady states must be constants provided that the domain Ω is *convex*. Interesting results for nonconvex Ω have been obtained by Matano, Hale-Vegas, Jimbo-Morita, and others.

On the other hand, it is important to be able to use diffusion (and reaction) to model pattern formation in various branches of science (e.g., biology and chemistry). Therefore, it is rather significant that the situation becomes *drastically different* when we come to systems of diffusion equations. In fact, even as early as 1952 Alan Turing argued, in an important paper [28], that in a system of equations modeling two interactive substances, *different diffusion rates* could lead to nonhomogeneous distributions of such reactants. Since then several models in morphogenesis have developed Turing's idea. One distinctive characteristic of many of those models is that at least one of the reactants is often *highly concentrated* in small areas and thereby exhibits strikingly different patterns. In this expository paper we shall first briefly introduce the current mathematical research on those highly concentrated solutions, i.e., solutions whose graphs display narrow peaks or spikes, also known as *point-condensation* solutions, or *spike-layers.* Using an activator-inhibitor system below, with slowly diffusing activator and rapidly diffusing inhibitor, not only will we discuss the existence of such spike-layer steady states, but we will also determine the *profile* of those spikes and the *locations* of their peaks, as well as their *stability* and *instability* properties.

In contrast to those models developed from Turing's idea, in which different diffusion rates combined with suitable reaction terms produce

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nonhomogeneous patterns or spike-layers, we shall include below a classical Lotka-Volterra competition-diffusion system in population dynamics for which no nonconstant steady state could exist no matter what the diffusion rates are. However, it is *not* entirely reasonable to add just diffusions to models in population dynamics, since individuals do *not* move around randomly. In particular, while modeling segregation phenomena for two competing species, one must take into account the population pressures created by the competitors. This leads us to a "cross-diffusion" system proposed by Shigesada, Kawasaki, and Teramoto [27] in 1979 that improves the Lotka-Volterra system. Putting this in a slightly larger context, we see that "taxis," i.e., oriented movements by individuals under the influence of environmental factors, should be included in modeling population dynamics. In this framework the model in [27] turns out to be a "negative taxis" system. (Here the "negativity" refers to the "directions" of individual movements.) We will also include a chemotaxis model, due to Keller and Segel [13], that is a "positive taxis" system and, of course, also a "cross-diffusion" system. It is interesting to note that *spike-layers appear in each of those two systems* under appropriate conditions. In addition to discussing spike-layers in those two cross-diffusion systems, we shall focus on the effect of cross-diffusion versus that of diffusion. Roughly speaking, our results for the Shigesada-Kawasaki-Teramoto system indicate that, in contrast to diffusions, *the gap between the two cross-diffusions alone suffices to create nontrivial patterns.*

In the last section of this paper some open questions or conjectures and possible future directions of research are discussed.

Spike-Layers in Diffusion Systems

A far-reaching example beginning with Turing's idea, "diffusion-driven instability", is the following system (already suitably rescaled), due to Gierer and Meinhardt [11] in 1972:

$$(2)\quad \begin{cases} U_t = d_1\Delta U - U + U^p/V^q & \text{in } \Omega\times\mathbf{R}^+,\\ \tau V_t = d_2\Delta V - V + U^r/V^s & \text{in } \Omega\times\mathbf{R}^+,\\ \frac{\partial U}{\partial \upsilon} = 0 = \frac{\partial V}{\partial \upsilon} & \text{on } \partial\Omega\times\mathbf{R}^+,\end{cases}$$

where d_1, d_2, p, q, r, τ are all positive constants, $s \geq 0$, and

$$(3)\qquad 0 < \frac{p-1}{q} < \frac{r}{s+1}.$$

(The original choices in [11] of the exponents are $p = 2,\ q = 1,\ r = 2$, and $s = 0$.) This system was motivated by biological experiments on *hydra* in morphogenesis. *Hydra*, an animal of a few millimeters in length, is made up of approximately 100,000 cells of about fifteen different types. It consists of a "head" region located at one end along its length. Typical experiments on *hydra* involve removing part of the "head" region and transplanting it to other parts of the body column. Then, a new "head" will form if and only if the transplanted area is sufficiently far from the (old) head. These observations have led to the assumption of the existence of two chemical substances—a slowly diffusing (short-range) activator and a rapidly diffusing (long-range) inhibitor. Here U represents the density of the activator and V represents that of the inhibitor. To understand the dynamics of (2), it is helpful to consider first its corresponding "kinetic system"

$$(4)\quad \begin{cases} U_t &= -U + U^p/V^q,\\ \tau V_t &= -V + U^r/V^s.\end{cases}$$

This system has a unique constant steady state $U \equiv 1,\ V \equiv 1$. For $0 < \tau < \frac{s+1}{p-1}$ it is easy to see that the constant solution $U \equiv 1,\ V \equiv 1$ is stable as a steady state of (4). However, if d_1 is small and d_2 is large, it is not hard to see that the constant steady state $U \equiv 1,\ V \equiv 1$ of (2) becomes unstable and bifurcations occur. (Heuristically, this may be seen by linearizing (2) at $U \equiv 1 \equiv V$ and replacing the Laplace operator Δ by one of its eigenvalues.) This phenomenon is generally referred to as Turing's "diffusion-driven instability", as was mentioned in the introduction.

The fact that U diffuses slowly and V diffuses rapidly may be reflected by the assumption that $d_1 = \epsilon^2$ is small and d_2 is large. If we divide the second equation in (2) by d_2 and let d_2 tend to ∞, it seems reasonable to expect that, for each fixed t, V tends to a (spatially) harmonic function that must be a constant by the boundary condition. That is, as $d_2 \to \infty$, V tends to a spatially homogeneous function $\zeta(t)$. Thus, integrating the second equation in (2) over Ω, we reduce (2) to the "shadow system"

$$(5)\quad \begin{cases} U_t = \epsilon^2\Delta U - U + U^p/\zeta^q & \text{in } \Omega\times\mathbf{R}^+,\\ \tau\zeta_t = -\zeta + \frac{1}{\zeta^s|\Omega|}\int_\Omega U^r(x,t)dx & \text{in } \mathbf{R}^+,\\ \frac{\partial U}{\partial \upsilon} = 0 & \text{on } \partial\Omega\times\mathbf{R}^+.\end{cases}$$

It turns out that the steady states of (5) and their stability properties are closely related to that of the original system (2) and that the study of the steady states of (5) essentially reduces to that of the following single equation:

$$
(6) \qquad \begin{cases} \epsilon^2 \Delta u - u + u^p = 0 & \text{in } \Omega, \\ u > 0 & \text{in } \Omega, \\ \frac{\partial u}{\partial \upsilon} = 0 & \text{on } \partial\Omega. \end{cases}
$$

Since ϵ is small, (6) is a singular perturbation problem. However, the traditional method, using inner and outer expansions, simply does not apply here, because a spike-layer solution of (6) is exponentially small away from its peak. To solve (6), it is important to note that although the corresponding elliptic system for (2) does not admit a variational structure, there is a natural "energy" functional for (6) in $H_1(\Omega)$

$$
J_\epsilon(u) = \frac{1}{2}\int_\Omega (\epsilon^2 |\nabla u|^2 + u^2) - \frac{1}{p+1}\int_\Omega u_+^{p+1}
$$

where $u_+ = \max\{u, 0\}$. Thus, to solve (6) we need only to find nontrivial critical points of J_ϵ. This energy consideration of solutions turns out to be the new key ingredient. Since this functional J_ϵ is neither bounded from above nor bounded from below, instead of looking for (local) maxima or minima, we search for a *saddle* point of J_ϵ via a variational approach. This approach, due to Ding and the author [19], unifies the "mountain-pass" lemma of Ambrosetti and Rabinowitz and a constrained minimization principle of Nehari in 1960, and allows us to obtain a "least-energy" solution. The existence of a single-peaked spike-layer solution of (6), its profile, and the location of the peak are all derived from this variational approach in a series of papers [15] and [20, 21] during 1986–93.

Theorem 1 *[15, 20, 21]. Suppose that $1 < p < \frac{n+2}{n-2}$ (∞ if $n = 1$ or 2). Then for every ϵ sufficiently small (6) possesses a least-energy solution u_ϵ that has exactly one (local, thus global) maximum point P_ϵ in $\overline{\Omega}$. Moreover, the following properties hold.*
(i) $P_\epsilon \in \partial\Omega$ and $H(P_\epsilon) \to \max_{\partial\Omega} H$ as $\epsilon \to 0$, where H is the mean curvature of $\partial\Omega$.
(ii) $u_\epsilon \to 0$ everywhere in Ω and $u_\epsilon(\varphi_\epsilon(\epsilon y)) \to w(y)$ as $\epsilon \to 0$ where φ_ϵ^{-1} is a diffeomorphism straightening $\partial\Omega$ near P_ϵ and w is the unique positive solution of

$$
\begin{cases} \Delta w - w + w^p = 0 \text{ in } \mathbf{R}^n, \\ w \to 0 \text{ at } \infty, \\ w(0) = \max_{\mathbf{R}^n} w. \end{cases}
$$

In other words, although J_ϵ is not bounded from below, it does have a minimum when restricted to the set of all solutions of (6), and we call this solution a *least-energy solution*. Moreover, the least-energy solution u_ϵ has *exactly one peak*, which must be situated on the boundary $\partial\Omega$ and *near the "most curved" part of the boundary.* Heuristically speaking, the energy of a spike-layer solution concentrates on a small neighborhood of each of its peaks. Thus, a least-energy solution u_ϵ should have only one peak. Moreover, since a "boundary-peak" has roughly half the energy an "interior-peak" does, the least-energy solution u_ϵ ought to have its peak on the boundary. To determine where on the boundary this peak should be is quite delicate; we need the following energy expansion of u_ϵ, for ϵ small:

$$
J_\epsilon(u_\epsilon) = \epsilon^n \left(\frac{1}{2} I(w) - C\epsilon H(P_\epsilon) + o(\epsilon) \right),
$$

where C is a positive constant depending on n and w and

$$
I(w) = \int_{\mathbf{R}^n} \left[\frac{1}{2}(|\nabla w|^2 + w^2) - \frac{1}{p+1} w^p \right]
$$

is the energy of the entire solution w. It is now intuitively clear that in order to "minimize" $J_\epsilon(u_\epsilon)$ one needs to maximize $H(P_\epsilon)$.

From this solution u_ϵ it is straightforward to construct a steady-state solution (U_∞, ζ_∞) for the shadow system (5) as follows:

$$
U_\infty = \zeta_\infty^{q/(p-1)} u_\epsilon \text{ and } \zeta_\infty^{-\alpha} = \frac{1}{|\Omega|}\int_\Omega u_\epsilon^r,
$$

where $\alpha = \frac{qr}{p-1} - (s+1) > 0$ by (3). Returning from (U_∞, ζ_∞) to a steady-state solution (U_{d_2}, V_{d_2}), for large d_2, of the original system (2) is, however, highly nontrivial and requires very detailed knowledge of the spike-layer solution u_ϵ. This is accomplished in [22] for the special case *when Ω is axially symmetric or $n = 1$*. (It should be noted that in case $n = 1$, the system (2) was solved earlier by Takagi.)

To complete our discussion of the system (2), we include a paragraph on *the stability and instability properties of the spike-layer steady-state solution obtained above for $n = 1$*.

Again, the first step is to study the shadow system. Setting $\beta = \frac{qr}{p-1}(\frac{1}{p-1} - \frac{1}{2r})$ and recalling $\alpha = \frac{qr}{p-1} - (s+1)$, we have the following:

Theorem 2 *[23]. Assume that $n = 1$ and $\alpha > 0$.*
(i) Suppose that $\tau > \beta$. If α and ϵ are sufficiently small, then the steady-state solution (U_∞, ζ_∞) of (5) is unstable.
(ii) Suppose that $r = 2$ and $\beta > \tau > 0$. If α and ϵ are sufficiently small, then the steady-state solution (U_∞, ζ_∞) of (5) is stable.
(iii) Suppose that $r = p + 1$ and $1 < p < 5$. Then there exists $\tau_0 \geq 0$ such that if $\beta > \tau > \tau_0$ and α, ϵ are sufficiently small, then the steady-state solution (U_∞, ζ_∞) of (5) is stable.

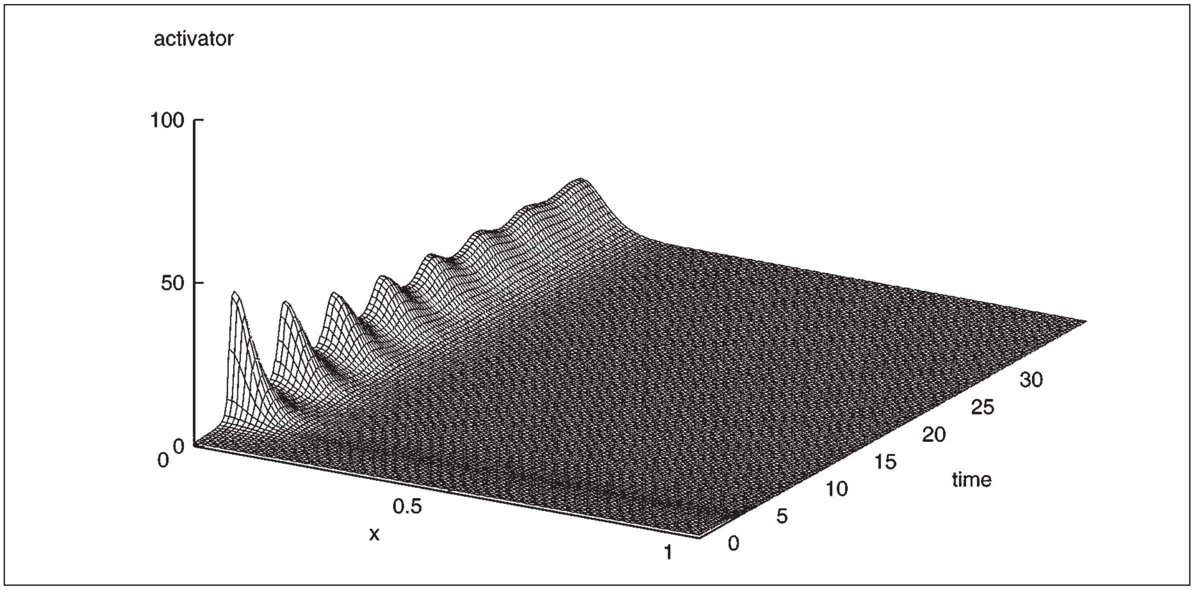

Figure 1. The numerical solution for the activator U in system (2) with $d_1 = 0.001$, $d_2 = 10$, $p = 2$, $q = 1$, $r = 2$, $s = 0$, $\tau = 0.7$, and $\Omega = (0, 1)$ and initial data

$$U(x,0) = \begin{Bmatrix} 1.1 - x, & 0 \le x \le 0.1, \\ 1, & 0.1 \le x \le 1, \end{Bmatrix} \text{ and } V(x,0) \equiv 1,\ 0 \le x \le 1$$

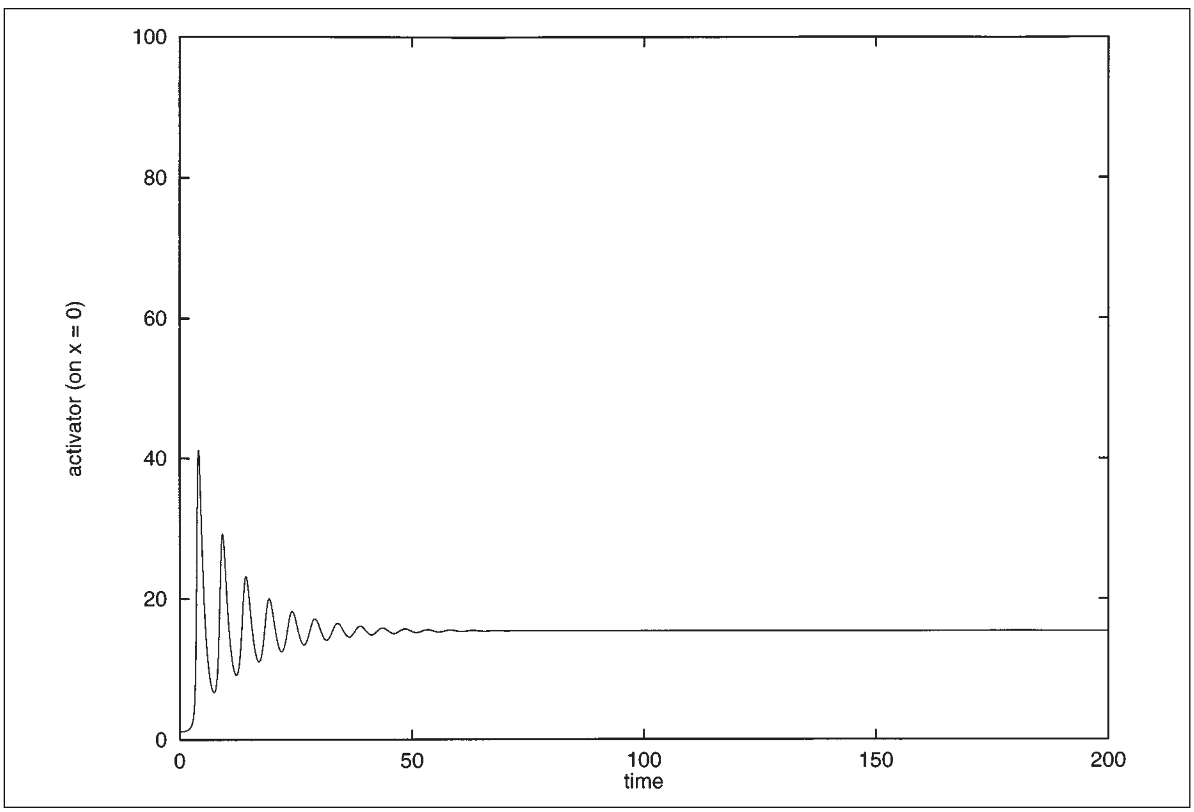

Figure 2. The graph for the peak $U(0, t)$, $0 \le t \le 200$, of the solution in Figure 1.

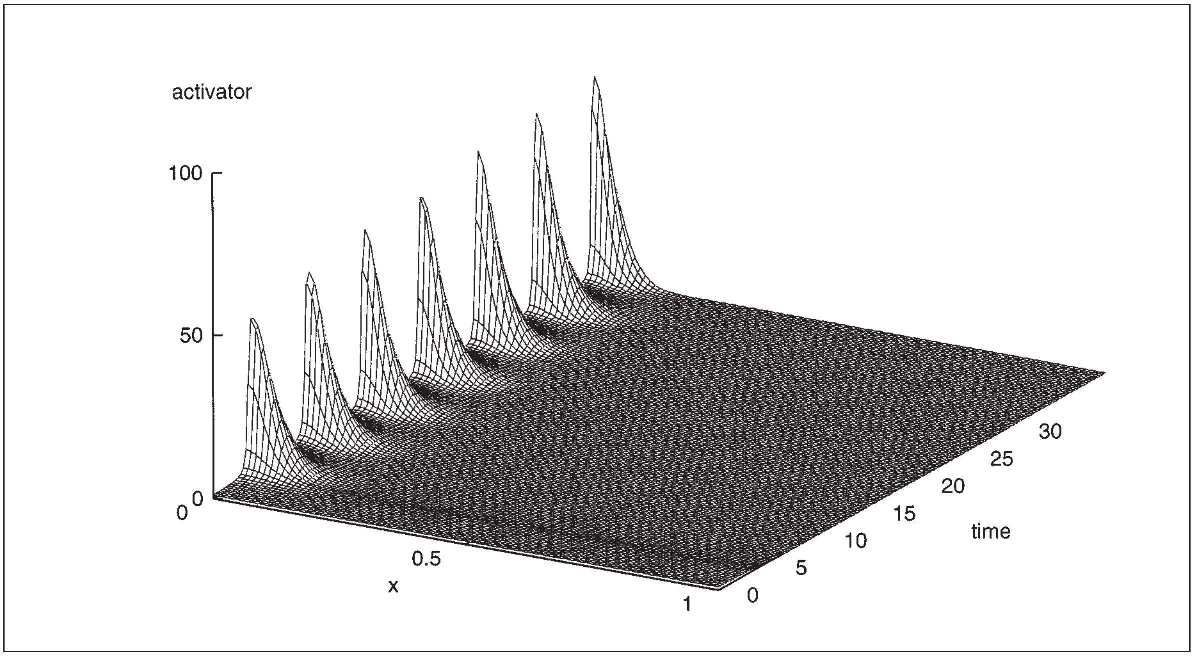

Figure 3. The numerical solution for the activator U in system (2) with the same initial value and parameters as in Figure 1 except that $\tau = 0.83$ here.

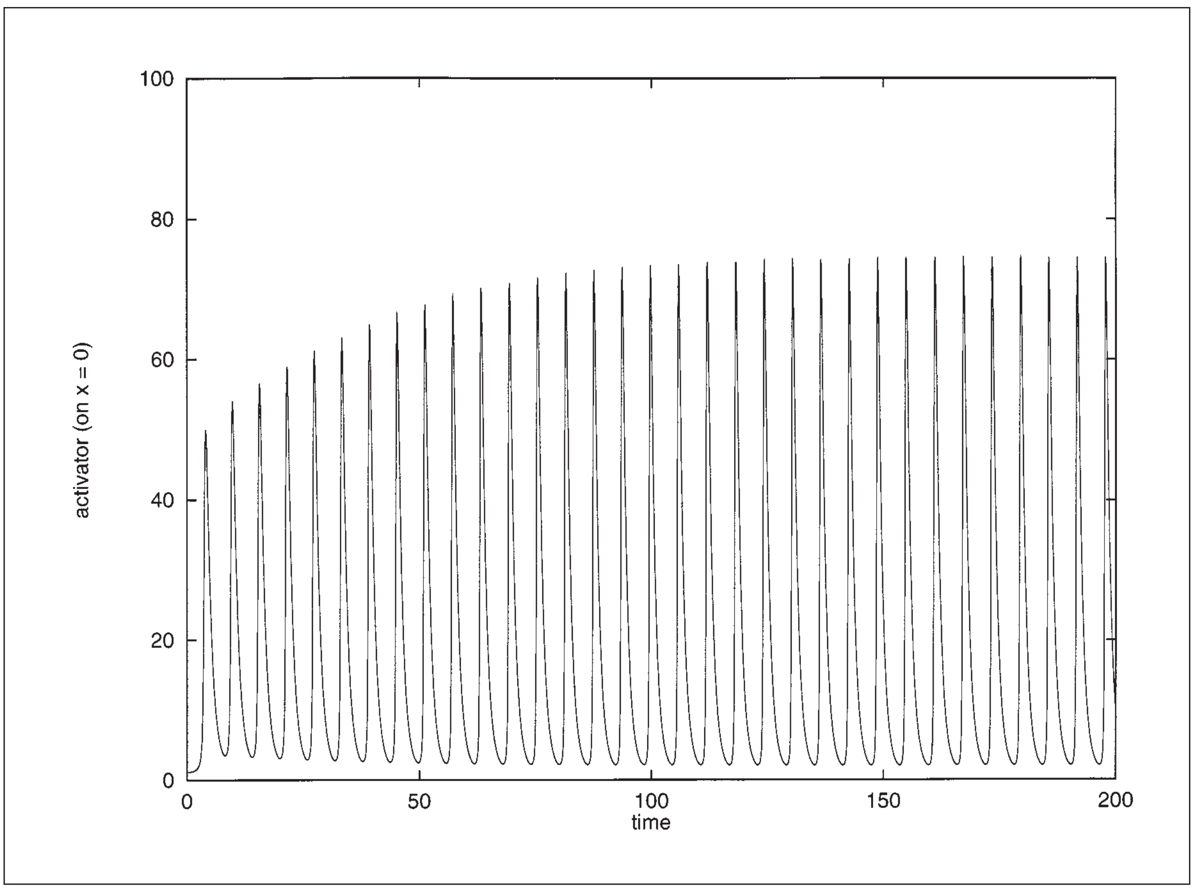

Figure 4. The graph for the peak $U(0, t)$, $0 \le t \le 200$, of the solution in Figure 3.

Theorem 2 shows that in order for the spike-layer steady state to be stable, the inhibitor needs to react fast (i.e., τ must be reasonably small) in response to the change of the activator. The proof contains detailed analysis of the characteristic equation

$$\alpha + \lambda \left[\frac{qr \int_\Omega u_\epsilon^{r-1}(L_\epsilon - \lambda)^{-1} u_\epsilon}{(p-1)\int_\Omega u_\epsilon^r} - \tau \right] = 0,$$

where $L_\epsilon = \epsilon^2 \Delta - 1 + p u_\epsilon^{p-1}$, and is quite involved.

It turns out that *exactly the same conclusions* for the shadow system (5) in Theorem 2 hold for the steady-state solution (U_{d_2}, V_{d_2}) of the original system (2) provided that d_2 is sufficiently large.

To illustrate further the role of the parameters in the dynamics of the system (2), we present some numerical simulations here done by E. Yanagida and M. Fukushima at the University of Tokyo. First, in (2) we fix the domain $\Omega = (0,1)$; the diffusion rates $d_1 = 0.001$, $d_2 = 10.0$; the exponents $p = 2$, $q = 1$, $r = 2$, $s = 0$; and the initial data

$$U(x,0) = \begin{cases} 1.1 - x, & x \in [0, 0.1] \\ 1, & x \in [0.1, 1] \end{cases}$$

and

$$V(x,0) \equiv 1, \quad x \in [0,1].$$

Note that the initial value here represents a small perturbation of the constant steady state $U \equiv 1$ and $V \equiv 1$. In Figures 1 and 2 the numerical solution for the activator U in (2) with $\tau = 0.7$ is illustrated. Note further that when τ is reasonably large, say, $\tau = 0.83$, the numerical solution seems to stabilize to a periodic motion instead, as indicated in Figures 3 and 4. The rigorous mathematical analysis for this phenomenon is currently under investigation.

Many interesting and important questions remain open, even in the case $n = 1$.

The biological experiments on *hydra* described in [11] indicate that the system (2), in the case $n = 1$, should have many *stable* spike-layer steady states—some with single peak, others with multiple peaks—and perhaps the spike-layer steady state with a single boundary peak should be the "most" stable one. Mathematically, with what we have done it is easy to construct, in case $n = 1$, spike-layer steady states to (2) with single peak or multiple peaks, and with interior peaks, boundary peaks, or their combinations. What can we say about their stability or instability? We have already proved in Theorem 2 that under suitable conditions the single-boundary-peak solution (U_{d_2}, V_{d_2}) (corresponding to the "least-energy" solution u_ϵ of (6)) *is stable if* d_2 *is sufficiently large.* It is conjectured that as d_2 decreases, more and more multipeak spike-layer steady states become stable. Heuristically, since the rapidly diffusing inhibitor suppresses the formation of new spikes close to the existing ones, the larger d_2 becomes, the fewer stable spikes are expected. The stability question for multidimensional spike-layer steady states is even more fascinating, because the geometry of domain also comes into play.

A Cross-Diffusion System with Competition

We begin our discussion with the classical Lotka-Volterra competition-diffusion system:

(7)
$$\begin{cases} u_t = d_1 \Delta u + u(a_1 - b_1 u - c_1 v) & \text{in } \Omega \times (0,\infty), \\ v_t = d_2 \Delta v + v(a_2 - b_2 u - c_2 v) & \text{in } \Omega \times (0,\infty), \\ \frac{\partial u}{\partial \upsilon} = 0 = \frac{\partial v}{\partial \upsilon} & \text{on } \partial\Omega \times (0,\infty), \end{cases}$$

where all the constants a_i, b_i, c_i, d_i, $i = 1,2$ are positive and u, v are nonnegative. Here, as is explained in [29], u and v represent the population densities of two competing species. For convenience we set $A = \frac{a_1}{a_2}$, $B = \frac{b_1}{b_2}$, and $C = \frac{c_1}{c_2}$. It is well known that in the "weak competition" case, i.e.,

$$B > A > C, \tag{8}$$

the constant steady state

$$(u_*, v_*) \equiv \left(\frac{a_1 c_2 - a_2 c_1}{b_1 c_2 - b_2 c_1}, \frac{b_1 a_2 - b_2 a_1}{b_1 c_2 - b_2 c_1} \right)$$

is *globally asymptotically stable regardless of the diffusion rates* d_1 *and* d_2. This implies, in particular, that *no nonconstant steady state can exist for any diffusion rates* d_1, d_2.

On the other hand, as was also remarked before, the pressures created by mutually competing species should be taken into account. In an attempt to model segregation phenomena between two competing species, Shigesada, Kawasaki, and Teramoto [27] proposed in 1979 the following cross-diffusion model:

$$\begin{cases} u_t = \Delta[(d_1 + \rho_{12} v)u] + u(a_1 - b_1 u - c_1 v) \\ \qquad\qquad \text{in } \Omega \times (0,T), \\ v_t = \Delta[(d_2 + \rho_{21} u)v] + v(a_1 - b_2 u - c_2 v) \\ \qquad\qquad \text{in } \Omega \times (0,T), \\ \frac{\partial u}{\partial \upsilon} = 0 = \frac{\partial v}{\partial \upsilon} \qquad \text{on } \partial\Omega \times (0,T), \end{cases} \tag{9}$$

where ρ_{12} and ρ_{21} represent the cross-diffusion pressures and are nonnegative. (In fact, the model in [27] also includes "self-diffusion" pressures that turn out to be not so different from the usual diffusion, as is shown in [16]. Here, for simplicity, we shall discuss only (9).) Considerable work has been done concerning the global existence of solutions to the system (9) under various hypotheses. However, it is worth noting that even the *local existence* question for (9) is highly nontrivial and was only recently resolved in a series of papers by H. Amann [1, 2].

We first focus on the effect of cross-diffusions on steady states. To illustrate the significance of cross-diffusions, we again go to the weak competition case (i.e., $B > A > C$), since in this case (9) has no nonconstant steady states if both $\rho_{12} = \rho_{21} = 0$.

Let $0 = \lambda_0 < \lambda_1 < \lambda_2 < \ldots$ denote the eigenvalues of $-\Delta$ subject to the same boundary condition as in (1), and let m_k be the multiplicity of λ_k.

Theorem 3 *[16]. Suppose that $B > A > (B + C)/2$ and m_k is odd for some $k \geq 1$. Then there exist positive constants $K_1 = K_1(a_i, b_i, c_i) < K_2 = K_2(a_i, b_i, c_i)$ such that for any $d_1 > 0$, $\rho_{21} \geq 0$, and $d_2 \in (K_1, K_2)$ the system (9) has at least a nonconstant steady state if $\rho_{12} \geq K_3$ for some positive constant $K_3 = K_3(a_i, b_i, c_i, d_1, \rho_{21})$.*

Thus, for every fixed $d_1 > 0$, $\rho_{21} \geq 0$, and d_2 belonging to a proper range, if we keep increasing the cross-diffusion ρ_{12}, eventually we will have a nonconstant steady state of (9). On the other hand, increasing the diffusion coefficients d_1 or d_2 while other parameters are fixed tends to eliminate any existing patterns.

Theorem 4 *[16]. Suppose that $B > A > C$. Then there exists a positive constant $K_4 = K_4(a_i, b_i, c_i)$ such that (u_*, v_*) is the only positive steady state of (9) provided that one of the following holds:*

(i) $\max\{\frac{\rho_{12}}{d_1}, \frac{\rho_{21}}{d_2}\} \leq K_4$

(ii) $\max\{\frac{\rho_{12}}{d_2}, \frac{\rho_{21}}{d_1}, \frac{\rho_{12}\rho_{21}}{d_1^2}, \frac{\rho_{12}\rho_{21}}{d_2^2}\} \leq K_4$

(iii) $\max\{\frac{\rho_{12}}{\sqrt{d_1 d_2}}, \frac{\rho_{21}}{\sqrt{d_1 d_2}}, \frac{\rho_{12}\rho_{21}}{d_1\sqrt{d_1 d_2}}, \frac{\rho_{12}\rho_{21}}{d_2\sqrt{d_1 d_2}}\} \leq K_4$.

Note that when $\rho_{21} = 0$, Theorem 4 implies that if any one of the three quantities

$$\frac{\rho_{12}}{d_1}, \frac{\rho_{12}}{d_2}, \text{ or } \frac{\rho_{12}}{\sqrt{d_1 d_2}}$$

is small, then nonconstant steady states of (9) do not exist.

In the "strong competition" case, i.e., $B < A < C$, the situation of steady-state solutions of (7) becomes more interesting and complicated and is *not* completely understood. Nonetheless, cross-diffusions still have similar effects in helping create nontrivial patterns of (9). We refer interested readers to [16] for the details.

So far in this section we have only touched upon the existence and nonexistence of nonconstant steady states. It seems a natural and important question to ask if we can derive any qualitative properties (such as the spike-layers in the previous section) of those steady states. Our first step in this direction is to classify *all the possible (limiting) steady states* when one of the cross-diffusion pressures tends to infinity.

Theorem 5 *[17]. Suppose for simplicity that $\rho_{21} = 0$. Suppose further that $B \neq A \neq C$, $n \leq 3$, and $\frac{a_2}{d_2} \neq \lambda_k$ for all k. Let (u_j, v_j) be a nonconstant steady-state solution of (9) with $\rho_{12} = \rho_{12,j}$. Then, by passing to a subsequence if necessary, either (i) or (ii) holds as $\rho_{12,j} \to \infty$, where*
(i) $(u_j, \frac{\rho_{12,j}}{d_1} v_j) \to (u, v)$ uniformly, $u > 0$, $v > 0$, and

$$\begin{cases} d_1\Delta[(1+v)u] + u(a_1 - b_1 u) = 0 & \text{in } \Omega, \\ d_2\Delta v + v(a_2 - b_2 u) = 0 & \text{in } \Omega, \\ \frac{\partial u}{\partial \upsilon} = 0 = \frac{\partial v}{\partial \upsilon} & \text{on } \partial\Omega; \end{cases}$$

and

(ii) *$(u_j, v_j) \to (\frac{\xi}{w}, w)$ uniformly, ξ is a positive constant, $w > 0$, and*

$$\begin{cases} d_2\Delta w + w(a_2 - c_2 w) - b_2\xi = 0 & \text{in } \Omega, \\ \frac{\partial w}{\partial \upsilon} = 0 & \text{on } \partial\Omega, \\ \int_\Omega \frac{1}{w}(a_1 - \frac{b_1\xi}{w} - c_1 w) = 0. \end{cases}$$

The proof is quite lengthy. The most important step in the proof is to obtain *a priori* bounds on steady states of (9) that are independent of ρ_{12}.

Incidentally, both alternatives (i) and (ii) above do occur under suitable conditions. Moreover, it turns out that both systems possess spike-layer solutions. For instance, using a suitable change of variables, the equation in (ii) may be transformed into (6) with $p = 2$. Thus, spike-layer solutions exist. Perhaps we ought to remark that in fact what is important is the ratio of cross-diffusion versus diffusion ρ_{12}/d_1 in which d_1 also varies. A deeper classification result is obtained in [17] as $\rho_{12} \to \infty$ in (9) in terms of various possibilities of ρ_{12}/d_1 and d_1.

Another Cross-Diffusion System: Chemotaxis

A basic equation in population dynamics (without the reaction term for the time being) is

$$u_t = \nabla \cdot (d\nabla u \pm u\nabla\psi(E(x,t))), \tag{10}$$

where $d > 0$, ψ is increasing, and E represents environmental influences that could also depend on u. The first term on the right-hand side of (10) is diffusion, while the second term there represents the "directed movement", or the "taxis". Examples for ψ include $\psi(E) = kE$, $k \log E$, or $kE^m/(1 + aE^m)$, where $k > 0$ and $m \in N$. When the negative sign in (10) is used, we refer to the movement as "positive taxis". When the positive sign in (10) is adopted, we have "negative taxis", as in the system (9) already discussed before.

To illustrate "positive taxis", we turn to a chemotaxis model due to Keller and Segel [13]. Chemotaxis is the oriented movement of cells in response to chemicals in their environment. Cellular slime molds (amoebae) release a certain chemical, c-AMP, move toward its higher concentration, and eventually form aggregrates. Letting $u(x,t)$ be the population of amoebae at place x and at time t and $v(x,t)$ be the concentration of this chemical, Keller and Segel proposed the following model to describe the chemotactic aggregation stage of amoebae:

$$
\text{(11)} \quad \begin{cases} u_t = d_1 \Delta u - \eta \nabla \cdot [u \nabla \psi(v)] & \text{in } \Omega \times (0,T), \\ v_t = d_2 \Delta v - av + bu & \text{in } \Omega \times (0,T), \\ \frac{\partial u}{\partial \upsilon} = 0 = \frac{\partial v}{\partial \upsilon} & \text{on } \partial\Omega \times (0,T), \\ u(x,0) = u_0(x), \; v(x,0) = v_0(x) \text{ in } \Omega, & \end{cases}
$$

where the constants η, a, and b are positive. Comparing the first equation in (11) to (10), we see that (11) is indeed an example for "positive taxis". Popular examples for the "sensitivity function" ψ include $\psi(v) = kv$, $k \log v$, or $kv^2/(1+v^2)$, where $k > 0$ is a constant. Much work has focused on the case $\psi(v) = v$. For the case $\psi(v) = k \log v$, Nagai and Senba [18] recently proved global existence for a modified parabolic-elliptic system in case $n = 2$. Observe that in (11) the total population is always conserved; that is, for all $t > 0$ we have

$$
\int_\Omega u(x,t)dx \equiv \int_\Omega u_0(x)dx.
$$

Therefore, to study the steady states of (11) for the case $\psi(v) = \log v$, we consider the following elliptic system:

$$
\text{(12)} \quad \begin{cases} d_1 \Delta u - \eta \nabla \cdot (u \nabla \log v) = 0 & \text{in } \Omega, \\ d_2 \Delta v - av + bu = 0 & \text{in } \Omega, \\ \frac{\partial u}{\partial \upsilon} = 0 = \frac{\partial v}{\partial \upsilon} & \text{on } \partial\Omega, \\ \frac{1}{|\Omega|} \int_\Omega u(x)dx = \overline{u} & \text{(prescribed).} \end{cases}
$$

With $p = \eta/d_1$ it is not hard to show that $u = \lambda v^p$ for some constant $\lambda > 0$. Thus, setting $\epsilon^2 = d_2/a$, $\mu = (b\lambda/a)^{\frac{1}{p-1}}$, and $w = \mu v$, we see that w satisfies (6); i.e.,

$$
\text{(13)} \quad \begin{cases} \epsilon^2 \Delta w - w + w^p = 0 & \text{in } \Omega, \\ \frac{\partial w}{\partial \upsilon} = 0 & \text{on } \partial\Omega, \end{cases}
$$

and our previous results for (6) apply. To obtain a solution pair for (12) from a solution of (13), simply set

$$
\text{(14)} \quad u = \frac{\overline{u}|\Omega| w^p}{\int_\Omega w^p} \quad \text{and } v = \frac{\overline{v}|\Omega| w}{\int_\Omega w}
$$

with $\overline{v} = b\overline{u}/a$. In this way *we obtain a spike-layer steady state for the chemotaxis system when d_2/a is small and $1 < \eta/d_1 < \frac{n+2}{n-2}$* ($\infty$ if $n = 1, 2$). Although many believe that this particular steady state (corresponding to the "least-energy" solution of (6)) is stable, its proof has thus far eluded us.

Concluding Remarks

In this expository paper, through several examples, we have considered mathematically the notions and mechanisms of diffusion and cross-diffusion from the point of view of pattern formation. In particular, we have considered only one type of pattern, namely, the spike-layers. Thus, it would be helpful to include a few remarks to put spike-layers in perspective.

I.) We start with equation (6). First, note that (6) always has a constant solution $u \equiv 1$. In fact, it was proved in [15] that if ϵ is large, then $u \equiv 1$ is the only solution of (6). More interestingly, as ϵ tends to 0, pushing the "energy" method developed in [15] and [19, 20, 21] further, Gui and Wei [12] showed that the number of spike-layer solutions of (6) tends to infinity. Furthermore, for particular domains, it can be verified that, when ϵ is small, (6) has layer solutions of various dimensions. More precisely, if we view spike-layers as 0-dimensional (since the set where a spike-layer does not tend to 0 as $\epsilon \to 0$ consists of isolated points), then for every integer k between 0 and $n-1$, (6) has a k-dimensional layer provided that ϵ is sufficiently small. The rich structure of solutions to (6) makes it extremely interesting and challenging to understand the entire dynamics of these related nonlinear diffusion systems. It should be remarked that the results included in this paper concerning the spike-layer solutions of (6) *do generalize to more general nonlinearities than u^p*. This kind of extension seems important both from a mathematical point of view as well as for its potential applications, as models in applied mathematics or other branches of science often involve a certain degree of uncertainty or arbitrariness and thus require some flexibility. In this connection we mention that when $p = \frac{n+2}{n-2}$, $n \geq 3$, in (6), the situation is not nearly as clear as that of the subcritical case $p < \frac{n+2}{n-2}$, and it does not seem to allow much flexibility at all. That is, the *exact* nonlinearity $u^{\frac{n+2}{n-2}}$ is required, and therefore the model in this case is not robust. We refer to [10] for some more recent developments and a brief description of previous work in this direction. For the supercritical case $p > \frac{n+2}{n-2}$, (6) remains largely open.

II.) Mathematically, it seems interesting to replace the homogeneous Neumann boundary condition in (6) by the homogeneous Dirichlet boundary condition $u = 0$ on $\partial\Omega$. First of all, it was established in [24] that the least-energy solution survives this change and it also has a unique (local) maximum point (i.e., the peak) Q_ϵ in Ω. Moreover, the profile of the spike is a rescaled version of w also. *However, the peak Q_ϵ now "converges" to the "most-centered" part of Ω; i.e.,* $\mathrm{dist}(Q_\epsilon, \partial\Omega) \to \max_{x\in\Omega} \mathrm{dist}(x, \partial\Omega)$ as $\epsilon \to 0$. In addition, since the Dirichlet boundary condition is far more rigid than the Neumann boundary condition, it allows much fewer solutions to exist. It would be very interesting to understand how solutions change while the Dirichlet boundary condition $u = 0$ is continuously deformed to the Neumann condition $\frac{\partial u}{\partial \upsilon} = 0$ on $\partial\Omega$, say, via

$$(1-\gamma)u + \gamma\frac{\partial u}{\partial \upsilon} = 0 \text{ on } \partial\Omega,$$

where γ varies from 0 to 1. When γ is close to 1, Ward [31] studied this problem by using formal asymptotic analysis.

III.) Comparing the chemotaxis model (12) to the competition model of (9), we find that the *u and v in (12) must peak together,* while our results in [17] on the systems (i), (ii) in Theorem 5 show that *the system (9) does have steady states that form segregates.* This is consistent with our intuition on "positive taxis" as well as "negative taxis".

IV.) Spike-layer solutions also appear in nonlinear Schrödinger equations. Beginning with the work of Floer and Weinstein [9], there has been much research on this topic. See, for instance, [25, 30, 5, 6]. Some of the recent work was stimulated by the development of research on the Neumann problem (6). The Ginzburg-Landau equation is yet another such example; it also exhibits concentration phenomena. Interested readers are referred to [4] and [14].

V.) Transition-layers are clearly very much related to our interest here. The studies of transition-layers began much earlier, and it seems that they are better understood. In particular, a powerful technique—the singular limit eigenvalue problem method—has been developed by several Japanese mathematicians, including Nishiura, Mimura, Fujii, and others. There is, of course, a vast literature on transition-layers; we shall only refer interested readers to Paul Fife's monograph [7] and the references therein. However, it should be mentioned that for Cahn-Hilliard equations in phase transitions (in material science), transition-layers have been studied extensively by Alikakos, Bates, Chen, Fife, Fusco, Hale, and others. Moreover, recent research [3] shows that spike-layers also appear in Cahn-Hilliard equations and are related to the "nucleation" phenomena. Although spike-layers there perhaps are unstable, they seem to have profound implications on the dynamics involved.

Finally, we would like to include some brief comments on the models used in this paper. As was pointed out by Okubo in his book [26], most, if not all, mathematical models in biology are not "realistic", but "educational". Nevertheless, there are good reasons for formulating them and for studying them. We refer to a very interesting discussion by Fife [8] on the rationale of using reaction and diffusion in modeling biological phenomena. We hope the mathematical progress in understanding diffusion, cross-diffusion, and their spike-layer solutions not only produces interesting mathematics and stimulates the development of mathematics but also enhances our ability in modeling real-world phenomena in various other branches of science.

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