Traveling Waves in Coupled Reaction-Diffusion Models with Degenerate Sources

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Abstract

We consider a general system of coupled nonlinear diffusion equations that are characterized by having degenerate source terms and thereby not having isolated rest states. Using a general form of physically relevant source terms, we derive conditions that are required to trigger traveling waves when a stable uniform steady-state solution is perturbed by a highly localized disturbance. We show that the degeneracy in the source terms implies that traveling waves have a number of surprising properties that are not present for systems with non-degenerate source terms. We also show that such systems can lead to a pair of waves that initially propagate outwards from the disturbance, slow down, and reverse direction before ultimately colliding and annihilating each other. PACS number(s): 05.45.-a, 87.15.Vv, 87.18.Pj

1 Introduction

Since the pioneering works of Hodgkin and Huxley [4] and of Turing [13] in 1952, nonlinear diffusion models have been studied extensively in the context of many different biological, chemical, and physical phenomena. Biological applications occur quite often because of diffusion effects coupled with chemical or other nonlinear 'reaction' terms.

In many different applications, highly localized disturbances of a stable rest state, e.g., large local increases in chemical or population concentrations, can lead to wave propagation. Specific examples include equations for excitable systems, e.g., the Hodgkin-Huxley equations [4] describe how the electrical potential across membranes of nerve cells and a large current input can lead to a depolarization of the potential above a threshold, thereby generating an 'action potential' wave. Another example is a wave of spreading cortical depression [2], an experimental slow wave phenomenon that occurs in the cortex of various brain structures in a variety of animals. These waves are instigated by injecting a bolus of potassium chloride into the cortex. Epidemics of disease also exhibit similar phenomena.

In this paper, we consider a class of coupled nonlinear diffusion equations that are characterized by not having isolated rest states, i.e., the rest states are not unique and depend continuously on one or more parameters. This can arise as a consequence of having locally conservative source terms.

We will study a coupled system of two nonlinear diffusion equations for quantities u and v. Without loss of generality, we rescale the time t, space x, and the population v such that the diffusion coefficient for u is unity, and the absolute magnitudes of the nonlinear source terms, $g(u, v)$, are equal

$$u_t = u_{xx} + g(u, v), \tag{1}$$

$$v_t = Dv_{xx} - g(u, v). \tag{2}$$

Here, D is the diffusion coefficient for v. We consider the evolution of u and v on the real line, $-\infty < x < \infty$. Although the quantities u and v can represent the evolution of a broad range of biological and physical variables that may take negative values, we will refer to them as 'populations'. We will assume that the function g is continuous and has the property that in the absence of diffusion, any initial state will not grow unboundedly. This is clearly a precondition for the model to be realistic. For simplicity, we also will assume that the curve $g(u, v) = 0$ represents a single continuous curve, although more complicated situations can be considered using a similar approach to that taken in this paper.

Our goal is to understand the dynamics of the solution when a stable homogeneous steady-state of such a system is subjected to an instantaneous, large amplitude, and highly localized perturbation in one of the populations. One might imagine that such perturbations could lead to traveling waves, but the nonuniqueness of the rest states raises a number of questions. Under what conditions can a traveling wave be triggered, and if a traveling wave solution develops, then to what rest state does the tail of the wave approach?

There is an extremely wide set of problems where this situation of nonunique rest states occurs, and we give two simple biological examples. The first example is associated with epidemics of non-fatal diseases. There is a mathematical formulation of this problem called the SIS model (see, e.g., Keshet [3]). Here S represents the number of susceptible people in the population, and I represents the number of infected people in the population. This model assumes that infected individuals can recover from the infection, but there is no long term immunity from reinfection at a later time. The model equations are given by:

$$\frac{\partial S}{\partial t} = D_S \frac{\partial^2 S}{\partial x^2} - rSI + bI, \tag{3}$$

$$\frac{\partial I}{\partial t} = D_I \frac{\partial^2 I}{\partial x^2} + rSI - bI. \tag{4}$$

The diffusion rates D_S and D_I are different with $D_S > D_I$ since infected individuals are

assumed to be less mobile than healthy individuals. The parameter r is the infection rate per number of susceptible individuals per infected individual per unit time. Thus rS individuals are infected by one infected individual per unit time. The parameter b is the rate at which infected individuals recover and return to the susceptible class.

The only condition on the rest state, (S_0, I_0), is $f(S_0, I_0; r, b) \equiv rS_0I_0 - bI_0 = 0$. Thus there is a family of rest states that depends continuously on one parameter. Suppose a spatially uniform state that is stable to small perturbations is perturbed by placing a large number of infected individuals into a highly localized region. A natural question to consider is how this localized outbreak will evolve and to what state the system will ultimately evolve.

The second example is a model for spreading cortical depression (SD) derived by Tuckwell and Miura (TM) [12]. Although the TM model is greatly simplified, the issue of the nonunique rest states is clearly illustrated in this case. The phenomenon of SD is a slowly propagating chemical wave (primarily potassium) in the cortex of many different brain structures and in many different animals [2]. The simplified model system in one space dimension involves only two ion populations, namely potassium (K) and calcium (C), and is given by

$$\frac{\partial K_o}{\partial t} = D_K \frac{\partial^2 K_o}{\partial x^2} + F(K_o, K_i, C_o, C_i), \tag{5}$$

$$\frac{\partial K_i}{\partial t} = -\alpha F(K_o, K_i, C_o, C_i), \tag{6}$$

$$\frac{\partial C_o}{\partial t} = D_C \frac{\partial^2 C_o}{\partial x^2} + G(K_o, K_i, C_o, C_i), \tag{7}$$

$$\frac{\partial C_i}{\partial t} = -\alpha G(K_o, K_i, C_o, C_i) \tag{8}$$

where K_o, K_i, C_o, C_i are the extracellular and intracellular concentrations of potassium and calcium, respectively, D_K and D_C are the diffusion coefficients for potassium and calcium in aqueous solution, respectively, and the functions F and G are highly nonlinear terms representing membrane ionic currents and ion currents due to metabolic pump terms that

move ions against their electrochemical gradients. The additional parameter α accounts for the difference between the intracellular and extracellular volumes.

The rest states for the four variables K_o, K_i, C_o, C_i in this model are determined only by the two equations $F(K_o, K_i, C_o, C_i) = 0 = G(K_o, K_i, C_o, C_i)$. Thus, there is a two-parameter family of rest states. Experiments often involve triggering a wave by injecting a highly localized source of potassium ions into the brain. Again, the natural question to ask is to what state will the system eventually evolve and under what conditions could a localized stimulus lead to a permanent change in the ion composition in the brain.

Systems in which bistable switching occurs for source terms that are not symmetric have been widely studied. In certain parameter regimes, the Fitzhugh-Nagumo equations have two stable states, and there exists an extensive literature that studies traveling wave fronts of these equations (see for example Rinzel and Terman [9]). The existence of bistable switching wave fronts with zero velocity has been considered by Sepulchrea and Krinsky [11]. In addition, Pazo and Perez-Munuzuri [8] considered traveling wave fronts in coupled arrays. However, despite the obvious importance of systems with symmetric source terms, to our knowledge, there has been surprisingly little work. Most of the pioneering work for these systems has been developed for a two-variable model (u and v) in which the source term $g(u, v)$ is proportional to uv. This model was proposed by Kawasaki *et al.* [5] in the context of patterns generated by the bacterium Bacillus subtilis. The focus of previous work has been on the type of traveling waves that can arise when an unstable rest state is perturbed (by a possibly infinitesimal disturbance) and is replaced by a stable rest state for this system. Billingham and Needham [1], Merkin and Needham [6], and Merkin *et al.* [7] proved a very broad range of results for the case $D = 1$ and Satnoianu *et al.* [10] have done likewise for $D = 0$.

In contrast, we examine the case where a stable rest state is perturbed by a highly localized disturbance and determine under what conditions traveling waves can replace the

initial stable rest state with a different stable rest state. We consider a very general form of the source term and derive a number of results that throw significant light on the behavior that can occur in such systems. By making a number of reasonable assumptions about the source terms, we consider what properties are required to generate traveling waves. We determine a number of conditions that must be satisfied in order for the initial disturbance to propagate outwards and evolve into a pair of traveling waves. It is well known that coupled reaction-diffusion equations with non-degenerate source terms can have traveling waves that exist for a continuous range of wave speeds. In contrast, we show that for degenerate source terms, traveling waves can only occur for discrete values of the wave speed. We show that traveling waves can abruptly cease to exist as the diffusion coefficient D is varied and that the widely studied case of $D = 1$ is a special case in the sense that it is the only value of the diffusion coefficient for which stationary waves can exist.

In Section 2, we show how the initial condition reduces the continuous family of rest states to a discrete set of rest states. In Section 2.1, we consider the nature and stability of these states and show how diffusion can destabilize the solutions. In Section 3, we consider the initial evolution of large amplitude perturbations. By making detailed estimates of the diffusion and source terms in the model, we determine the conditions that are required to trigger a traveling wave. In Section 4, we determine the properties of traveling waves, including conditions leading to the direction of propagation and determination of the population mass contained in a traveling wave. We also consider a specific example, for which some analytical solutions can be derived, and we use these to understand how the diffusion coefficient can affect traveling waves. In Section 4.3, we consider the process of establishing a traveling wave after a triggering event. We show that under certain conditions, a triggering event will lead to traveling waves, but under other conditions a triggering event can lead to a wave which initially propagates outward, continuously slows down until it eventually stops, reverses its direction, and ultimately collides with its mirror image and is annihilated.

Finally, in Section 5, we give a discussion and interpretation of our results and, in some cases, provide suggestions for experimentally determining whether propagating waves can occur and what types of initial disturbances are required to trigger them.

2 Spatially homogeneous steady states

The local conservation condition for the system (1)–(2) implies that there is a one-parameter family of possible steady states along the curve given by $g(u, v) = 0$. However, for spatially homogeneous solutions, the diffusive terms are zero, and hence the addition of the two equations imply that the quantity $u + v$ must be conserved. Therefore, solution trajectories must move along lines of constant $u + v$. The value of the constant depends on the initial state of the system at each x. If we ignore the non-generic case in which the curve $g(u, v) = 0$ is parallel to the line $u + v =$constant over a finite length, then the one-parameter family of steady states is reduced to isolated steady states corresponding to the intersections of the $g(u, v) = 0$ curve and the line $u + v =$constant.

The diffusion terms simply redistribute populations in space, and therefore, we also have a global conservation of total population. Taking the reference values of u and v to be zero at infinity, adding equations (1) and (2) and integrating over all space, we obtain

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_{-\infty}^{\infty}(u+v)\mathrm{d}x = 0.$$

Integrating with respect to time and applying the initial conditions, we obtain

$$\int_{-\infty}^{\infty}(u+v)\mathrm{d}x = K \tag{9}$$

where K is the total population deviation from the values at infinity.

We will consider a spatially uniform rest state that is perturbed by a localized disturbance.

Without loss of generality, we take the unperturbed rest state to be $(u, v) = (0, 0)$. After an excitation is introduced, we wish to determine the final state to which the system evolves. Although there is a one-parameter family of possible rest states, given by $g(u, v) = 0$, most of these states have a value of $u + v$ that is not zero. If we consider solutions that are independent of x, then states with nonzero $u + v$ cannot occur since they would cause the integral in (9) to diverge. In fact, any uniform solution must spread the initial population K over the entire real line, and so the value of $u+v$ must be the same as the initial zero rest state. This implies that the only possible spatially uniform long-term rest states correspond to the intersections of the curves $g(u, v) = 0$ and $u+v = 0$. In general, these conditions will be satisfied at a set of discrete points. In particular, if $(u, v) = (0, 0)$ is the only solution of $g(u, v) = 0$ and $u + v = 0$, then this represents the only possible rest point. If we also consider traveling waves, then a similar argument shows that the tails of the traveling waves also must tend to one of the states that represents a solution of $g(u, v) = 0$ and $u + v = 0$.

2.1 Stability of spatially homogeneous states

We consider stability of the steady state $(u, v) = (u_0, v_0)$ by adding perturbations of the form

$$(u, v) = (u_0, v_0) + (\tilde{u}, \tilde{v})e^{ikx+\lambda t}.$$

After substitution into (1)–(2) and linearization in $\tilde{u}$ and $\tilde{v}$, we obtain

$$\lambda\tilde{u} = -k^2\tilde{u} + g_{u0}\tilde{u} + g_{v0}\tilde{v},$$

$$\lambda\tilde{v} = -Dk^2\tilde{v} - g_{u0}\tilde{u} - g_{v0}\tilde{v}$$

where g_{u0} and g_{v0} are the first-order partial derivatives of g evaluated at (u_0, v_0). These equations yield the following eigenvalue equation for λ,

$$\lambda^2 + \left(g_{v0} - g_{u0} + (1+D)k^2\right)\lambda + k^2(Dk^2 - Dg_{u0} + g_{v0}) = 0.$$

If the perturbations are spatially uniform ($k = 0$), then the eigenvalues are $g_u - g_v$ and 0. In this case, the diffusive terms play no role and so the trajectories of (1)–(2) are confined to the lines $u+v$ =constant. The $\lambda = g_u - g_v$ eigenvalue corresponds to perturbations of the system along the line $u + v$ =constant. The zero eigenvalue corresponds to perturbations that are not parallel to the line $u + v$=constant and, therefore, represent changes in the initial population at each point. Such perturbations are neutrally stable because trajectories are confined to lines of constant $u + v$, and therefore, such perturbations can neither decay back to the original state nor grow.

When diffusion is present ($k \neq 0$), stability requires that $g_{v0} - g_{u0} + (1 + D)k^2 > 0$ and $Dk^2 - Dg_{u0} + g_{v0} > 0$ for all values of the wavenumber k. For sufficiently large wavenumbers, these conditions are automatically satisfied. Since our system is on an infinite domain, the wavenumber can take infinitesimal values. Therefore, the stability constraints become $g_{v0} > g_{u0}$ and $g_{v0} > Dg_{u0}$. The first constraint is the same as the stability constraint in the absence of diffusion and ensures stability of a rest point along a line of constant $u + v$. The second constraint ensures that diffusion does not destabilize the neutrally stable eigenvalue that exists in the absence of diffusion via a long-wavelength (small values of k represent the fastest growing modes) Turing instability. The presence of D in this constraint essentially means that there is only one constraint, namely $g_{v0} > g_{u0}$ if $0 < D < 1$ and $g_{v0} > Dg_{u0}$ if $D > 1$.

3 Initial evolution of disturbances

We consider an initial condition that is a perturbation in u that is localized at the origin $x = 0$. For convenience, we take a perturbation of the form

$$u(x, 0) = u_0(x) = \frac{K}{\sqrt{4\pi s}} \exp\left(\frac{-x^2}{4s}\right). \tag{10}$$

Here K represents the population contained in the perturbation and s represents the degree of localization. We assume there is no initial disturbance in v. In many settings, we are interested in the way that the system develops after a highly localized stimulus. For this reason, we consider the case in which s is small, which implies that initially the amplitude of u is large but highly concentrated near $x = 0$. We note that as $s \to 0$, the initial condition tends to a delta function with strength K.

At early times and in the case of a highly localized perturbation, the curvature of u, and hence the diffusive fluxes, are large. However, if the source term has a strong nonlinearity, then these terms also will be large, and it is unclear whether diffusion or source terms will dominate the initial evolution. Initially, $v = 0$ and u is large, so we assume that the source term has the asymptotic form

$$g(u, v) \sim -Bu|u|^{p-1} \left[1 + \text{asymptotically small corrections}\right]. \tag{11}$$

Here $B > 0$ and $p > 0$ are constants. We assume that B is positive to ensure that spatially homogeneous solutions do not grow unboundedly. If v grows to become $O(1)$ or if u decreases to become $O(1)$, then this asymptotic form will no longer be valid. In order to investigate the relative sizes of the diffusive and source terms, we approximate the source terms during early times and near $x = 0$ by its leading order term. We use this to develop two approximate solutions and then consider the validity of these approximations.

Firstly, if we neglect the source terms, then the solution is given by

$$u(x,t) = \frac{K}{\sqrt{4\pi(t+s)}} \exp\left(\frac{-x^2}{4(t+s)}\right).$$

Using this solution, the relative magnitude of the diffusive terms to the source terms is given by

$$\frac{u_{xx}}{|Bu^p|} = O\left(\frac{(t+s)^{(p-3)/2}}{K^{p-1}B}\right).$$

Initially, this ratio will be large, and the neglect of the source terms will be valid, if $p < 3$, i.e., if the nonlinearity grows more slowly than a cubic. Diffusion will continue to dominate until

$$t \sim B^{2/(p-3)} K^{2(p-1)/(p-3)},$$

at which time

$$u \sim B^{-1/(p-3)} K^{-2/(p-3)}.$$

However, we should note that when u reaches this value, the source terms may no longer be dominated by the leading order term and so the approximation would have broken down earlier.

Secondly, if we neglect the diffusion terms, then each location evolves independently of solution values at other locations, and we obtain the solution

$$u = [(p-1)Bt + u_0^{1-p}]^{1/(1-p)}.$$

To ensure that the assumption that diffusion is negligible is valid, one needs to compare the diffusive and source terms. It is easy to show that the relative size of the diffusion terms decreases as time increases and that the relative size of the diffusion terms is largest at early

times, in which case

$$\frac{u_{xx}}{|Bu^p|} = O\left(\frac{K^{1-p}s^{(p-3)/2}}{B}\right).$$

If $p > 3$, then while the expansion (11) remains valid, the source terms are always bigger than the diffusive terms.

Finally, in the borderline case, $p = 3$, neither the diffusive terms nor the source terms dominate, and there is a balance between the two. For this case, the solution can be expressed in terms of a similarity variable

$$u = \frac{\mathcal{U}(\eta)}{\sqrt{2Bt}} \quad \text{and} \quad v = \frac{\mathcal{V}(\eta)}{\sqrt{2Bt}} \tag{12}$$

where

$$\eta \equiv \frac{x}{\sqrt{2t}}.$$

For all sufficiently smooth initial conditions, the solution will tend to this similarity solution, except possibly at $x = 0$. After substituting (12) into (1)–(2), the leading order equations become

$$\mathcal{U}'' + (\eta\mathcal{U})' = \mathcal{U}^3 \quad \text{and} \quad D\mathcal{V}'' + (\eta\mathcal{V})' = -\mathcal{U}^3. \tag{13}$$

The solution is symmetric in η and the conditions specifying the total populations and requiring no population fluxes at zero and infinity are

$$\int_0^\infty (\mathcal{U} + \mathcal{V})\mathrm{d}\eta = \frac{1}{2}KB^{1/2},$$

$$\mathcal{U}'(0) + D\mathcal{V}'(0) = 0,$$

and

$$\eta\mathcal{U} \to 0 \quad \text{and} \quad \eta\mathcal{V} \to 0 \quad \text{as} \quad \eta \to \infty.$$

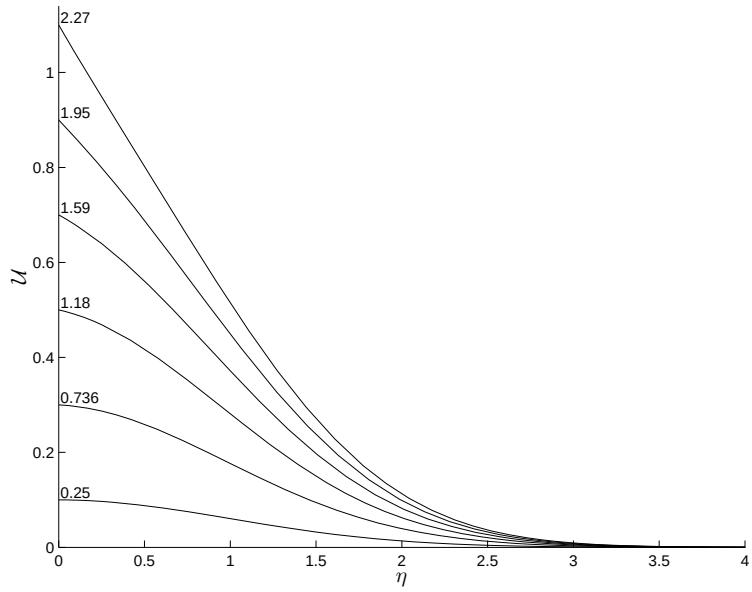

Figure 1: The similarity solution for the case when the nonlinearity in the source term is $g(u, v) = -Bu^3$. The solution is plotted for various values of B.

Since the equations (13) decouple, this problem can be solved readily using a simple numerical shooting technique. The results for $\mathcal{U}$ are shown in Figure 1 for various values of $KB^{1/2}$. As one would expect, as the strength of the nonlinearity becomes weaker, $KB^{1/2} \to 0$, the solution profile is more closely approximated by the diffusive profile in which nonlinear effects do not play a significant role.

3.1 Single rest state

With the above information, we are able to understand the initial stage of the evolution of u and v for various values of p. We begin by considering the case in which there is only a single rest point $(u, v) = (0, 0)$. For fixed values of x, we consider the trajectories in the (u, v) plane (see Figure 2). The solution trajectories will start with $v = 0$, and the segment $0 \leq u \leq K/\sqrt{4\pi s}$ will be doubly covered by the initial condition. Since we are considering the case in which the initial disturbance is highly localized (s is small), the values of u near

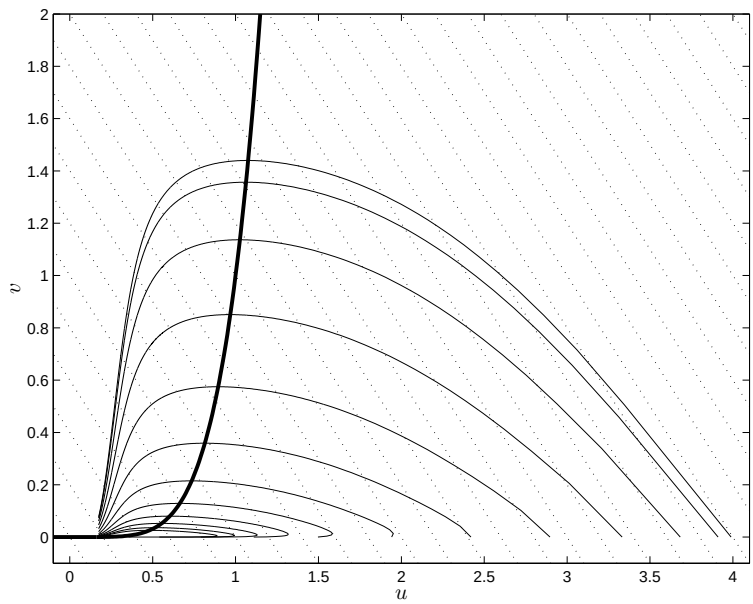

Figure 2: Trajectories of fixed spatial locations for the initial value problem with source terms $g(u, v) = v - u^5$ that initially dominate the diffusion and have only a single rest state at $(u, v) = (0, 0)$. The curve $g(u, v) = 0$ is plotted as a bold solid line and lines of constant $u + v$ are plotted as dotted lines. The trajectory that begins at the largest value of u is at $x = 0$ and neighboring trajectories are separated by 0.02.

$x = 0$ will be large.

Figure 2 shows an example with source term $g(u, v) = v - u^5$ that have $p > 3$. Initially, the diffusive terms will be negligible, and so the solution will rapidly evolve along lines of constant $u + v$ (dotted lines). This will continue until v becomes sufficiently large and/or u becomes sufficiently small that the source terms are no longer dominated by the leading order expression. At this time, the trajectory for $x = 0$, which represents the largest value of $u + v$, will have a value of v that has deviated significantly away from zero. The trajectories then evolve toward the vicinity of the curve $g(u, v) = 0$. In this vicinity, the magnitude of the source terms are small, and hence, the diffusive terms become important. Points far from $x = 0$ will have remained relatively close to $(u, v) = (0, 0)$, whereas points near $x = 0$ will have generally attained values of u and v that differ significantly from zero. Hence, there

will be significant spatial variations in u and v. Therefore, the diffusive fluxes will start to act on the solution and attempt to flatten any curvature. Diffusion acts to straighten out any local gradients, but the source terms prevent the trajectories from moving too far away from the curve $g(u, v) = 0$. Therefore, the diffusive straightening will force trajectories to slowly evolve along the curve $g(u, v) = 0$ to the unique rest state.

For $p < 3$, initially, the source term will be negligible and the solution will be dominated by diffusion. This is shown in Figure 3 for $g(u, v) = v - u$. Hence, for values of x near zero, the trajectories will rapidly move along the u-axis towards $u = 0$. This will continue until u is of order $B^{-1/(p-3)}K^{-2/(p-3)}$ or until the asymptotic corrections in the source terms become significant. Following this, there will be a balance between the source terms and the diffusive terms, and the trajectory will move partially in the direction of constant $u + v$. Trajectories will reach the vicinity of the curve $g(u, v) = 0$ and then diffusion once again will drive the solution towards the rest state.

For $p = 3$, initially, the trajectories will move at an angle in between the $u-$axis and the lines $u + v =$constant. This can be seen in Figure 4 where the source term is given by $g(u, v) = v - u^3$. For larger values of B, corresponding to larger source terms, the direction of the trajectories will become more aligned in the direction of constant $u+v$. After reaching the vicinity of the curve $g(u, v) = 0$, the dynamics are similar to the first two cases.

From the above results, we see that, for weak nonlinearities, $p < 3$, the dynamics will be dominated by diffusion and evolve with values of v that stay relatively small. However, for strong nonlinearities, $p > 3$, the evolution of the solution will be dominated by the nonlinear source terms and when the solutions evolve into the region where $u = O(1)$, the typical values of v will generally be far from zero.

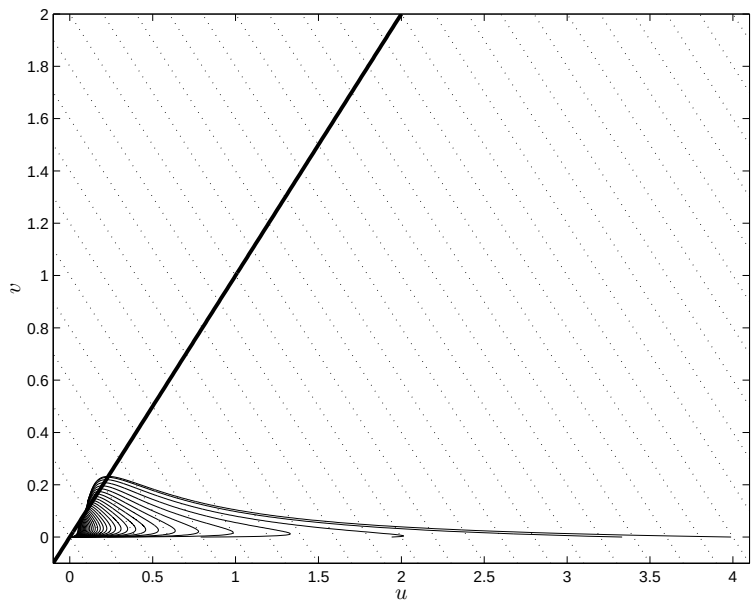

Figure 3: Trajectories of fixed spatial locations for the initial value problem with source terms $g(u, v) = v - u$ that initially dominate the diffusion and have only a single rest state at $(u, v) = (0, 0)$. The curve $g(u, v) = 0$ is plotted as a bold solid line and lines of constant $u + v$ are plotted as dotted lines. The trajectory that begins at the largest value of u is at $x = 0$ and neighboring trajectories are separated by 0.06.

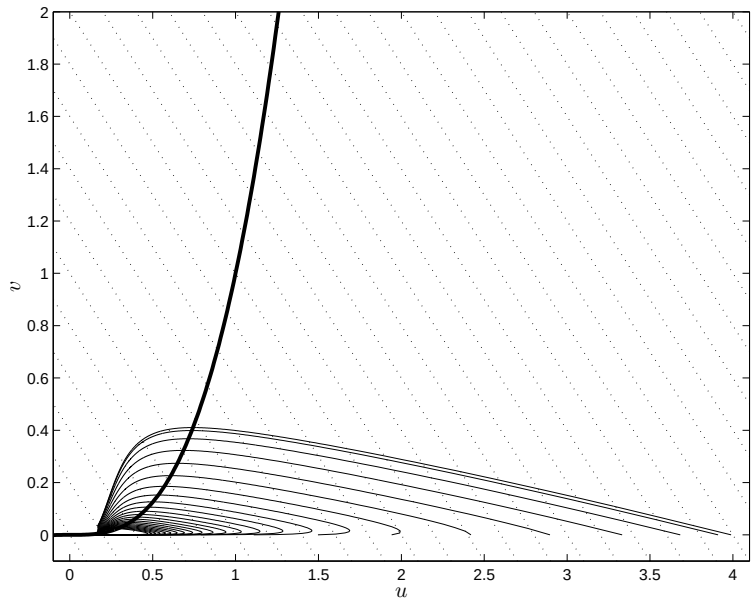

Figure 4: Trajectories of fixed spatial locations for the initial value problem with source terms $g(u, v) = v - u^3$ that have a nonlinearity for which diffusive and source terms initially have the same magnitude and only a single rest state at $(u, v) = (0, 0)$. The curve $g(u, v) = 0$ is plotted as a bold solid line and lines of constant $u + v$ are plotted as dotted lines. The trajectory that begins at the largest value of u is at $x = 0$ and neighboring trajectories are separated by 0.02.

3.2 Multiple rest states

We are particularly interested in the case in which a stable rest state is perturbed and two wave fronts propagate away from the initial perturbation leaving behind a stable rest state. In this section, we therefore consider the case in which there are multiple stable rest states. Given a spatially homogeneous stable rest state, we wish to determine what types of initial perturbations cause the region that has been significantly perturbed to evolve towards the vicinity of a different rest state. This will certainly be necessary in order to have the possibility of triggering traveling wave fronts. We consider source terms that are continuous and, in the absence of diffusion, do not lead to unbounded states. This means that the curve $g(u, v) = 0$ intersects the line $u+v$=constant at least once, for any value of the constant. We will focus on the simplest case in which this can happen, namely when the curve $g(u, v) = 0$ intersects the line $u + v = 0$ at three points, two of which must be linearly stable. We consider three possible examples of source terms.

We begin by considering the case in which the diffusive terms are absent. This implies that trajectories at a fixed location will evolve along lines of $u + v$=constant (where the constant is determined by the initial conditions) until they reach the curve $g(u, v) = 0$. For certain values of the constant, there are three possible steady state solutions, and therefore, there are three possible branches of the curve $g(u, v) = 0$. There are two stable branches (bold solid lines in Figure 5), one passing through $(u, v) = (0, 0)$, and the other passing through the other rest state, and there is an unstable branch in between (dashed lines in Figure 5).

In Case I, if we take an initial disturbance in u that has $K > 0$, then the trajectories at a fixed location will evolve along lines of constant $u + v$ until they reach the curve $g(u, v) = 0$. For $K > 0$, this means that all the trajectories will reach the same branch of the $g(u, v) = 0$ curve, and the solution will be spatially continuous. For this type of disturbance, no matter

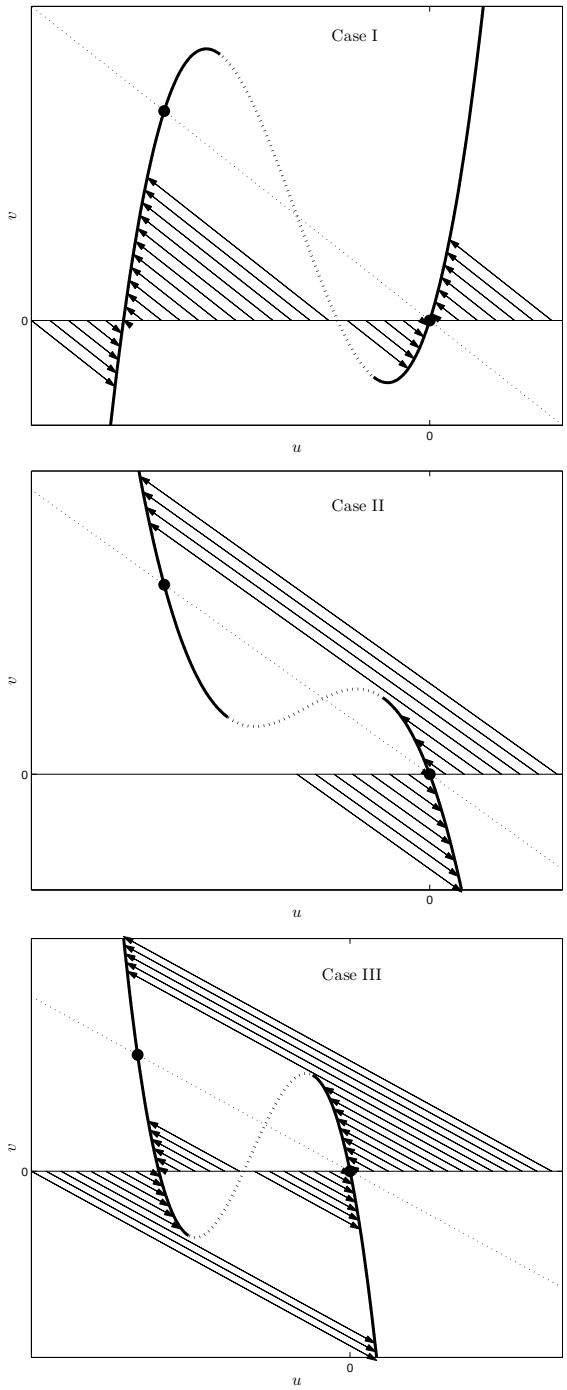

Figure 5: Schematics of trajectories at fixed locations when diffusion is ignored and so trajectories are confined to lines of constant $u + v$. For different forms of the source terms certain initial conditions can lead to discontinuous profiles.

how localized or how large the initial strength of the disturbance, trajectories cannot reach the other branch. If $K < 0$ and the peak amplitude of the disturbance is sufficiently small, the evolution will follow a similar pattern. In this case, the solution trajectories also will evolve to the same solution branch, and the solution will be spatially continuous.

However, if $K < 0$ and the peak amplitude of the disturbance is sufficiently large, the behavior is different. Trajectories associated with locations that were far from the initial perturbation will evolve toward the initial rest state whereas trajectories associated with locations that were initially near the center of the perturbation will evolve to the other solution branch. This will lead to a final solution that is spatially discontinuous.

In Case II, the behavior is broadly similar to that in Case I except that negative disturbances always evolve towards the same branch whereas positive disturbances can evolve toward the other branch if the peak disturbance is large enough.

In Case III, we illustrate that more complicated behavior than in the first two examples can arise. In this case, if the disturbance is large and negative, then a portion of the disturbance, which may not necessarily include the center, will evolve towards the other branch.

The addition of the diffusive terms will give rise to two important differences. Firstly, trajectories will not be confined to lines of constant $u + v$. Secondly, when the trajectories reach the vicinity of the curve $g(u, v) = 0$ spatially inhomogeneous solutions will experience diffusive fluxes that try to make them more spatially uniform.

If we consider Case I with source terms that have a strong nonlinearity ($p > 3$), the trajectories in the center of the disturbance move approximately along lines of $u + v$, and so the points can reach the vicinity of the other rest state. If $K > 0$ or if $K < 0$ and the peak disturbance is sufficiently small, the solution will remain on the same branch so that diffusion will act to bring all the points back to the original rest state. This is similar to the behavior observed in the case with only a single rest state in Figure 2. However, when

$K < 0$ and the peak disturbance is sufficiently large, the trajectories near the center of the disturbance may be able to reach the vicinity of the other branch, whereas locations far from the center of the disturbance will evolve toward the original branch. We note that diffusion modifies the direction of trajectories away from the lines of constant $u + v$. Therefore, the peak amplitude required to reach the other branch may be somewhat larger than the case in which diffusion is absent. When the trajectories are close to the curve $g(u, v) = 0$, the diffusive terms will become important and will act to straighten out spatial gradients. The region that was initially in the tail of the perturbation will have remained near the point $(u, v) = (0, 0)$, whereas the region that was initially in the center of the perturbation will be closer to the other stable rest state. One can think of the diffusion terms as acting to 'pull' trajectories along the curve $g(u, v) = 0$ towards a stable rest point. Therefore, there is a competition between the two different rest states, and this could lead to the triggering of outward propagating traveling waves from the center of the perturbation.

On the other hand, if the nonlinearity is weak, that is $p < 3$, then trajectories will move approximately along the $u-$axis. Hence, rather than having a chance to experience the nonlinear effects, trajectories will evolve rapidly back to the original rest state, and it becomes very difficult for the region where there was initially a significant perturbation to evolve toward the other rest state.

In the case of $p = 3$, the trajectories in the far field evolve at a fixed angle to the lines of constant $u + v$, so that the behavior is broadly similar to the case of $p > 3$ except that the peak amplitude to reach the other branch is larger. We also note that, even for $p < 3$, a balance between diffusive and source terms is reached when $u \sim B^{-1/(p-3)} K^{-2/(p-3)}$ at which point the trajectories significantly deviate from the $u-$axis. If the population mass, K, in the disturbance is sufficiently large, then the trajectories may still be able to reach the other branch. However, unlike the case of strong nonlinearities, the unstable branch cannot be reached by making the disturbance more localized since the peak value of the disturbance is

not important in this case.

4 Traveling waves

We now consider the cases in which there are multiple stable rest states and determine the properties of any resulting traveling waves. We again consider the simplest case with three steady states of which only two can be stable. If the localized disturbance leads to a replacement of the original stable steady state by the other stable steady state, it must do so by triggering a wave that propagates away from the initial disturbance. We therefore consider factors that determine the dynamics of traveling waves.

The existence and direction of propagation of steady traveling waves can be determined by the following analysis. Suppose a traveling wave front exists in the form $u = U(\xi)$ and $v = V(\xi)$ where $\xi = x - ct$ and c is the constant wave speed. Furthermore, suppose that the traveling wave front connects the stable rest states (U_-, V_-) as $\xi \to -\infty$ and (U_+, V_+) as $\xi \to \infty$. For $x > 0$, (U_+, V_+) will be the initial state and (U_-, V_-) will be the other stable rest state. Then, (1)–(2) become

$$-cU' = U'' + g(U, V), \tag{14}$$

$$-cV' = DV'' - g(U, V). \tag{15}$$

Adding (14) and (15), we obtain

$$-c(U + V)' = (U + DV)''.$$

Integrating and applying the boundary conditions, $U' \to 0$, $V' \to 0$ and $U + V \to 0$ at

infinity, we obtain

$$-c(U+V) = U' + DV'. \tag{16}$$

We consider the third-order dynamical system represented by (14) and (16). Singular points of this system are obtained by solving $U+V=0$ and $g(U,V)=0$. Any traveling wave front solution must be a heteroclinic orbit in ξ that links the two rest states. We first consider the linear stability of these singular points with respect to ξ. Introducing disturbances of the form $e^{\nu\xi}$, we obtain the following relation for the eigenvalue ν

$$D\nu^3 + c(1+D)\nu^2 + (c^2 + Dg_{u\pm} - g_{v\pm})\nu + c(g_{u\pm} - g_{v\pm}) = 0.$$

The partial derivatives $g_{u\pm}$ and $g_{v\pm}$ are evaluated at the relevant singular point, namely $(U_\pm, V_\pm)$. Since both singular states are stable with respect to time, it follows from Section 2.1 that $g_{v\pm} - g_{u\pm} > 0$ and $Dg_{v\pm} - g_{u\pm} > 0$. If $c > 0$, then the sum of the three roots of the eigenvalue relation (for either of the stable singular points) is negative and the product is positive. Hence, both singular points must have one unstable and two stable eigenvalues. If $c < 0$, then the sum of the three roots is positive and the product is negative. Hence, both singular points must have two unstable and one stable eigenvalue. In both cases, the dimension of the unstable manifold for one singular point plus the dimensionality of the stable manifold for the other singular point equals the dimensionality of the system. Therefore, for an arbitrary value of c, we do not expect the unstable manifold of (U_-, V_-) and the stable manifold of (U_+, V_+) to coincide. However, we may generically expect the stable and unstable manifolds to intersect and form a heteroclinic orbit only at discrete values of c. This is quite different from the case in which the source terms are not symmetric. In that case there is no such restriction on the dimensionality of the stable and unstable manifolds, and heteroclinic orbits can exist for continuous ranges of the wave speed.

If a heteroclinic trajectory leaves a singular point along a direction that is not orthogonal to an eigenvector with eigenvalue ν (that must be positive), then its distance along the eigenvector from the singular point decreases as $e^{\nu\xi}$ as $\xi \to -\infty$. A similar conclusion holds for a heteroclinic orbit that arrives at a singular point. Therefore, the smaller the value of ν, the broader the wave front of the traveling wave. As $c \to 0$, one of the eigenvalues, for each singular point, tends to zero. Hence, for small values of c, one of the eigenvalues for each singular point also will be small. If a heteroclinic orbit were to exist that was not orthogonal to the eigenvector associated with the small eigenvalue, then the width of the wave front becomes large. Hence, one is led to consider the case $c = 0$ in which both singular points have a zero eigenvalue.

The case of $c = 0$ is special in the sense that a solution cannot, in general, satisfy both boundary conditions. For $c = 0$, equation (16) becomes $(U + V)' + (D - 1)V' = 0$, which can be integrated to yield $(U + V) + (D - 1)V = \text{constant}$. As $x \to \pm\infty$, $U + V \to 0$ and $V \to V_{\pm}$. However, these conditions cannot be satisfied unless $D = 1$, since $V_+ \neq V_-$. We conclude that there are no stationary waves when the diffusivities are different.

4.1 Almost equal diffusivities

If the diffusivities are equal ($D = 1$), we can integrate (16) and use the boundary conditions as $\xi \to \pm\infty$ to obtain $U + V = 0$. Hence, (14) becomes

$$-cU' = U'' + g(U, -U).$$

After multiplying by U', integrating over ξ, and solving for c, we obtain

$$c = -\frac{\int_{U_-}^{U_+} g(U, -U)\mathrm{d}U}{\int_{-\infty}^{\infty} U'^2 \mathrm{d}\xi}.$$

Since the denominator of the fraction is strictly positive, the sign of c, and hence, the direction of the traveling wave, is determined by the sign of the numerator. In this case, it is possible to have a stationary wave, $c = 0$, with finite width. This can occur because one can show that the constraint $U + V = 0$ forces the heteroclinic orbit to be orthogonal to the eigenvector corresponding to the zero eigenvalue at the singular point.

The question that naturally arises is how is the wave modified by the presence of different diffusion coefficients ($D \neq 1$). We first consider the case when the diffusion coefficients are almost equal, $|D - 1| \ll 1$. We propose expansions of the form

$$U = U_{(0)} + (D-1)U_{(1)} + \dots,$$

$$V = V_{(0)} + (D-1)V_{(1)} + \dots,$$

$$c = c_{(0)} + (D-1)c_{(1)} + \dots.$$

At leading order, we obtain $U_{(0)} = -V_{(0)}$ and

$$U''_{(0)} + c_{(0)}U'_{(0)} + g(U_{(0)}, -U_{(0)}) = 0. \tag{17}$$

The trajectory must connect the two rest states, and so $U_{(0)} \to U_{\pm}$ as $\xi \to \pm\infty$. If we consider the solution of the above equation (17) for large $|\xi|$, then we can linearize the source terms about each of the two fixed points to obtain

$$U''_{(0)} + c_{(0)}U'_{(0)} + (g_{u\pm} - g_{v\pm})U_{(0)} = 0.$$

We note that $g_{v\pm} - g_{u\pm} > 0$ because both stationary points under consideration are linearly

stable with respect to time. If $c_{(0)} \geq 0$, then the behavior at large $|\xi|$ is given by

$$U_{(0)} - U_+ \sim \exp\left[\frac{\left(-c_{(0)} - \sqrt{c_{(0)}^2 + 4(g_{v+} - g_{u+})}\right)\xi}{2}\right] \qquad \text{as} \qquad \xi \to \infty,$$

and

$$U_{(0)} - U_- \sim \exp\left[\frac{\left(-c_{(0)} + \sqrt{c_{(0)}^2 + 4(g_{v-} - g_{u-})}\right)\xi}{2}\right] \qquad \text{as} \qquad \xi \to -\infty.$$

Similar expressions can be obtained for $c_{(0)} < 0$. Substituting into (16) yields

$$(U_{(1)} + V_{(1)})' + c_{(0)}(U_{(1)} + V_{(1)}) = U'_{(0)}.$$

This can be integrated and, using the boundary conditions $U_{(1)} + V_{(1)} \to 0$ as $\xi \to \pm\infty$, yields

$$U_{(1)} + V_{(1)} = e^{-c_{(0)}\xi} \int_{-\infty}^{\xi} e^{c_{(0)}y} U'_{(0)}(y)\mathrm{d}y \tag{18}$$

if $c_{(0)} > 0$ and

$$U_{(1)} + V_{(1)} = -e^{-c_{(0)}\xi} \int_{\xi}^{\infty} e^{c_{(0)}y} U'_{(0)}(y)\mathrm{d}y \tag{19}$$

if $c_{(0)} < 0$. In the case of $c_{(0)} = 0$, no solution can be found.

Now we consider the total excess population that exists in a traveling wave. At leading order, this is zero, but at first order, we obtain

$$\int_{-\infty}^{\infty} (u+v)\mathrm{d}x = (D-1)\int_{-\infty}^{\infty} \left[U_{(1)} + V_{(1)}\right]\mathrm{d}\xi + O(D-1)^2.$$

After using (18) and (19), and changing the order of integration, we obtain

$$\int_{-\infty}^{\infty} (u+v)\mathrm{d}x = \frac{(D-1)(U_+ - U_-)}{c_{(0)}} + O(D-1)^2.$$

This gives the net global population change contained in a traveling wave. This means that for $D \neq 1$, the population in the vicinity of the wave front can differ from the population far from the front.

The mechanism that allows this to happen can be understood by considering the waves in u and v separately, but remembering that they must travel together and, hence, have the same wave speed. Suppose that for $D = 1$, there is a wave propagating with $c \neq 0$. This wave speed is selected because it can balance the local mismatches between the diffusion and source terms that occur in the wave front. If the wave front in v has width of order w, then the approximate sizes of the diffusive, source, and wave propagation terms are given by Du/w^2, $g(u, v)$, and cu/w, respectively. A simple scaling analysis shows that $w \sim \sqrt{D}$ and $c \sim \sqrt{D}$. Thus, smaller diffusion leads to a narrower wave front that propagates at lower speed. So if we decrease the diffusivity of v, there is a tendency to decrease the magnitude of the wave speed of the solution for v. However, the diffusivity of u remains the same, so the diffusive fluxes in u remain comparable in magnitude. Thus, the wave speed of the solution u has a tendency to stay the same. Any wave front will have to adopt a compromise wave speed, and so we expect that v will lag behind u. When the diffusivities are equal, $u + v = 0$ everywhere, and there is no lag, but when $D < 1$, v lags slightly behind u, and so the total population contained in the wave will be dominated by the contribution from u behind the wave front.

We note that as $c_{(0)} \to 0$, the population contained in a traveling wave front for D near unity tends to infinity. This is because the rate at which the heteroclinic orbit approaches the fixed points tends to zero. Thus, the widths of the traveling waves tend to infinity, and hence the integral diverges. This explains why we cannot obtain stationary waves for $D \neq 1$.

4.2 Example system with some exact solutions

In order to understand the way in which the wave speed is affected by changes in the diffusivity D, it is instructive to consider a particular example. If we choose one of two special forms for the source terms, it is possible to obtain exact solutions to the traveling wave equations for the cases $D = 1$ and $D = 0$. We choose the simplest form that can allow for two stable rest states, namely,

$$g(u, v) = v + u - Bu(u + \gamma)(u + 1)$$

or

$$g(u, v) = -(v + u) - Bu(u + \gamma)(u + 1)$$

where $0 < \gamma < 1$ and $B > 0$ are constant parameters. These two special forms are similar to Case I and Case II in Figure 5, respectively. We note that after trivial transformations, these two cases represent the generic function with three possible steady states that is linear in v and cubic in u.

For Case I, the rest states at $(u, v) = (0, 0)$ and $(-1, -1)$ are linearly stable if

$$B \min(\gamma, 1 - \gamma) > \max\left(0, 1 - \frac{1}{D}\right).$$

For $D = 1$, $U + V = 0$ everywhere, so that (14) becomes

$$U'' + cU' - BU(U + \gamma)(U + 1) = 0. \tag{20}$$

The boundary conditions are $U \to 0$ as $\xi \to \infty$ and $U \to -1$ as $\xi \to -\infty$. This can be

solved by searching for a solution in the form

$$U = -V = -\frac{1}{2} + \frac{1}{2}\tanh(\mu\xi) \tag{21}$$

where $\mu > 0$ is a constant. Substituting (21) into (20) and equating powers of $\tanh(\mu\xi)$ yields the solution

$$\mu = \sqrt{\frac{B}{8}} \quad \text{and} \quad c = \sqrt{2B}\left(\frac{1}{2} - \gamma\right).$$

Thus the direction of the traveling wave front depends only on the parameter γ.

For zero diffusivity in v, that is $D = 0$, we can eliminate v in (16) to obtain

$$U'' + \left(c - \frac{1}{c}\right)U' - BU(U+\gamma)(U+1) = 0.$$

This equation is the same as the $D = 1$ case, but with c replaced by $c - 1/c$ and, hence, can be solved using the same method to yield

$$U = -\frac{1}{2} + \frac{1}{2}\tanh\left(\xi\sqrt{\frac{B}{8}}\right),$$

$$V = \frac{1}{2} - \frac{1}{2}\tanh\left(\xi\sqrt{\frac{B}{8}}\right) - \frac{B}{8c}\text{sech}^2\left(\xi\sqrt{\frac{B}{8}}\right),$$

and

$$c = \frac{\sqrt{B}(\frac{1}{2} - \gamma) \pm \sqrt{B(\frac{1}{2} - \gamma)^2 + 2}}{\sqrt{2}}.$$

This means that for $D = 0$, there are two possible traveling waves that propagate in opposite directions. As noted in the previous analysis, the wave speed c must always be nonzero since $D \neq 1$. It is easy to see that the rightward propagating wave is non-monotonic if $B(1-\gamma) > 1$ and the leftward propagating wave is non-monotonic if $B\gamma > 1$. These wave profiles for V are shown in Figure 6, for both the leftward and rightward propagating waves. In addition,

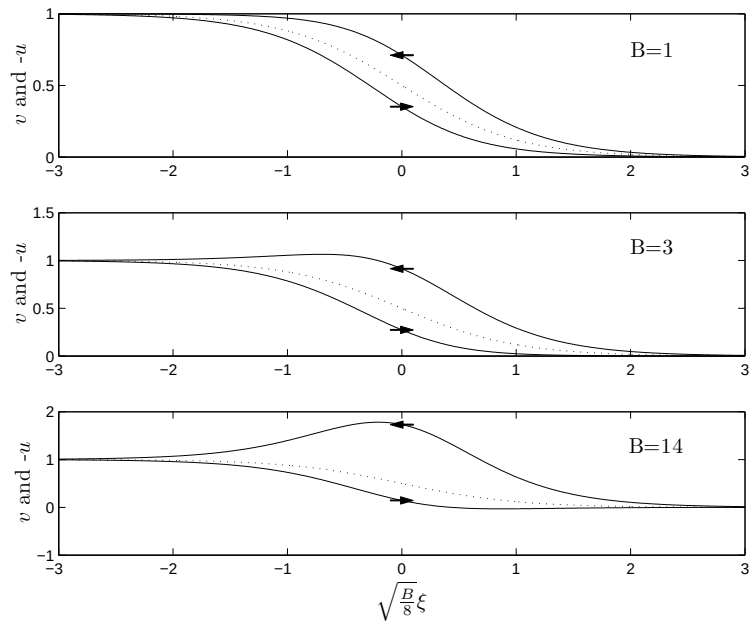

Figure 6: Traveling wave solutions for source terms $g(u,v) = v + u - Bu(u+\gamma)(u+1)$ with $\gamma = 1/2$ and $D = 0$ and various values of B. In this case, there can be two possible traveling waves, both having the same u profile (dashed line), but with different v profile (solid line). The direction of the propagating waves are indicated on the v profiles.

we also plot $-U$ on the same graph to illustrate that the lag between the U and V fields depends on the direction of the propagation. It should be noted in the above example that, although there are two waves in the case $D = 0$, there is only a single wave when $D = 1$.

For Case II, the fixed points at $(u,v) = (0,0)$ and $(-1,-1)$ are linearly stable if

$$B \min(\gamma, 1-\gamma) > \max\left(0, \frac{1}{D} - 1\right).$$

For $D = 1$, $U + V = 0$ everywhere, so the solution and wave speed are identical to those for Case I.

For $D = 0$, we can use the same procedure to obtain

$$U'' + \left(c + \frac{1}{c}\right) U' - BU(U+\gamma)(U+1) = 0.$$

This equation is the same as in the $D = 1$ case in Case I, but with c replaced by $c + 1/c$, and hence,

$$U = -\frac{1}{2} + \frac{1}{2}\tanh\left(\xi\sqrt{\frac{B}{8}}\right),$$

$$V = \frac{1}{2} - \frac{1}{2}\tanh\left(\xi\sqrt{\frac{B}{8}}\right) - \frac{B}{8c}\mathrm{sech}^2\left(\xi\sqrt{\frac{B}{8}}\right),$$

and

$$c = \frac{\sqrt{B}(\frac{1}{2} - \gamma) \pm \sqrt{B(\frac{1}{2} - \gamma)^2 - 2}}{\sqrt{2}}.$$

This means that for $D = 0$, depending on the values of B and γ, there can be two, one, or zero traveling waves. In addition, if traveling waves of this form exist, then they must have a wave speed that has the same sign as the wave in the case $D = 1$.

To further investigate traveling waves for values of D that differ from zero or unity, we adopt a simple numerical shooting method for the wave speed. If $c > 0$, then both stationary points have a one-dimensional unstable manifold. We wish to find values of c for which the unstable manifold of one of the singular points coincides with the stable manifold of the other singular point. For a given value of c, we compute the eigenvector associated with the unstable eigenvalue. Using the eigenvector to determine an initial condition that is on the unstable manifold, we numerically integrate to determine the entire unstable manifold. We then choose c to minimize the distance between this unstable manifold and the other stable rest state. If the minimum distance is zero then this value of c corresponds to a heteroclinic orbit. If $c < 0$, we adopt a similar procedure, but start on the stable manifold and integrate backwards in time.

The results in Case I are displayed in Figure 7 for fixed $B = 1$ and various values of $\gamma \geq 1/2$. The results for $\gamma < 1/2$ can be obtained by replacing γ by $1 - \gamma$ and c by $-c$. We immediately see that as D increases, the absolute magnitude of the wave speed decreases for both of the possible waves. The absolute magnitude of the wave speeds continues to decrease

until the wave speed associated with one of the traveling waves approaches zero. In the case of $\gamma = 1/2$ (Figure 7), both traveling waves end at $D = 1$, at which point a stationary wave exists, and for values of $D > 1$, no traveling waves exist.

For $\gamma \neq 1/2$, the results are quite different (Figure 7, $\gamma = 0.6$ and 0.7). In these cases, the left and rightward traveling waves end abruptly at different critical values of D. The critical values of D are, in general, not equal to unity. From the results in Section 4, the wave speed cannot equal zero for $D \neq 1$. Hence, as these critical points are approached, the wave speed tends to zero and the wave front becomes increasingly wide. For values of D larger than the critical values, the traveling waves cease to exist.

The results in Case II are displayed in Figure 8 for values of $\gamma < 1/2$. In Figure 8 ($\gamma = 0.1, B = 25$), the value of γ is sufficiently far away from 1/2 that $B(1/2 - \gamma)^2 > 2$, so that the wave speeds at $D = 0$ are real, and hence, two traveling waves exist. In Figure 8 ($\gamma = 0.2, B = 25$), the waves do not exist below a critical value of D. However, near the critical point, there are two waves that propagate in the same direction where the speed of the slower wave decreases as D increases. At a value of $D < 1$, the wave speed reaches zero, and for values of D greater than this, only the faster of the two waves exists. In Figure 8 ($\gamma = 0.4, B = 25$), there is only a single traveling wave. The speed decreases as D decreases until it becomes zero, and for sufficiently small values of D, no traveling wave exists. For $\gamma = 1/2$, the case of $D = 1$ has zero wave speed, thus traveling waves only exist for values of $D > 1$.

Finally, the stability and bifurcation properties of these traveling waves are clearly of interest, but these are beyond the scope of this paper.

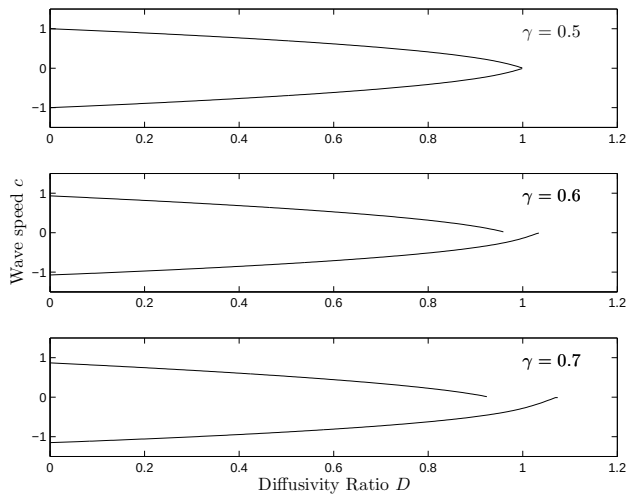

Figure 7: The wave speed of traveling waves is plotted against the diffusivity ratio for source terms $g(u, v) = v + u - Bu(u + \gamma)(u + 1)$ with $B = 1$ and values of $\gamma = 0.5,\ 0.6$, and 0.7.

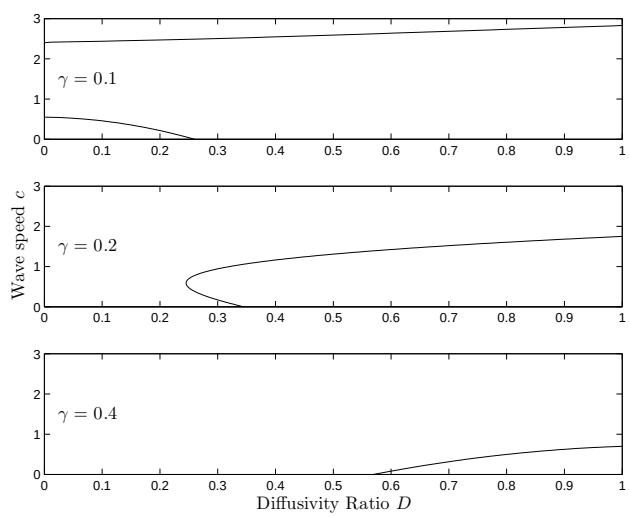

Figure 8: The wave speed of traveling waves is plotted against the diffusivity ratio for source terms $g(u, v) = -v - u - Bu(u + \gamma)(u + 1)$ with $B = 25$ and values of $\gamma = 0.1,\ 0.2$, and 0.4.

4.3 Traveling and self-annihilating waves

There is a spectrum of possible qualitative behavior that can occur for a system of equations (1)-(2) with initial perturbation (10). This behavior depends on a number of factors, including the number of intersections between the line $u + v = 0$ and the curve $g(u, v) = 0$, the stability of these rest states, the peak amplitude of the initial perturbation, the strength of the nonlinearity, and the existence and stability of any traveling waves.

We are particularly interested in the case in which the initial condition evolves into two traveling wave solutions that propagate away from the initial perturbation. Clearly a number of conditions must be met. Firstly, the line $u + v = 0$ must intersect the curve $g(u, v) = 0$ at multiple points. Secondly, the initial disturbance must be large enough and have the appropriate sign so that trajectories evolve into the vicinity of the other rest state. This can be achieved readily in the case of a strong nonlinearity ($p > 3$), but will generally be significantly more difficult for ($p < 3$). However, these two conditions are not sufficient. The region that initially evolves toward the vicinity of the other rest state must have enough population to be able to use diffusion to 'pull' populations from the original rest state. Finally, a stable traveling wave that connects the two rest states and propagates in the appropriate direction also must exist.

If these conditions are met, then we have the possibility of setting up a traveling wave. In Figure 9, we show results where the initial value problem satisfies these conditions. The problem was solved numerically using a standard Crank-Nicolson algorithm for time stepping with a Newton-Raphson method to solve the resulting algebraic equations. There is a rapid initial phase when diffusion is small and trajectories for each location move approximately along lines of constant $u + v$ until they are close to the curve $g(u, v) = 0$. The source terms in this example are sufficiently strong, that the central region of the disturbance can evolve to become close to the other rest state. Diffusion then sets up two outward propagating

waves, and as the waves move further apart, each wave front becomes increasingly close to the solution for an isolated traveling wave.

An interesting situation occurs when the disturbance is large enough to push trajectories toward the vicinity of the other rest state, but in which the only traveling wave that exists propagates inward (Figure 10). In this case, the initial transient behavior is similar to that in Figure 9. The initial disturbance sets up a wave that initially propagates outwards, but the wave cannot continue to propagate outwards because no such steady wave exists. Rather, it continuously decelerates as the profile gets closer and closer to the traveling wave profile. Eventually, after the transient wave has decayed, the wave propagates inwards until it collides with its mirror image at $x = 0$. When this collision occurs, another rapid transient phase begins, and the two waves annihilate each other. The solution then diffusively returns to the initial state.

5 Discussion

In this discussion, we will summarize our basic results and their implications for the generation of traveling waves. We have derived a number of conditions that must be met in order for a highly localized perturbation of a stable rest state of the equations (1)-(2) to evolve towards two traveling waves that propagate away from the initial perturbation.

A stable traveling wave front will connect the initial stable rest state to a different stable rest state that has the same net local population as the original rest state. Such states can exist only if the curves $g(u, v) = 0$ and $u + v = 0$ have multiple intersections. For strong nonlinearities ($p > 3$), the motion occurs in two separate stages. Firstly, each location rapidly evolves towards the values of u and v for which the source terms are zero. At the end of this phase, values of v will generally be significantly different from zero. Secondly, diffusion acts to slowly smooth out local curvature. If the initial perturbations are sufficiently large

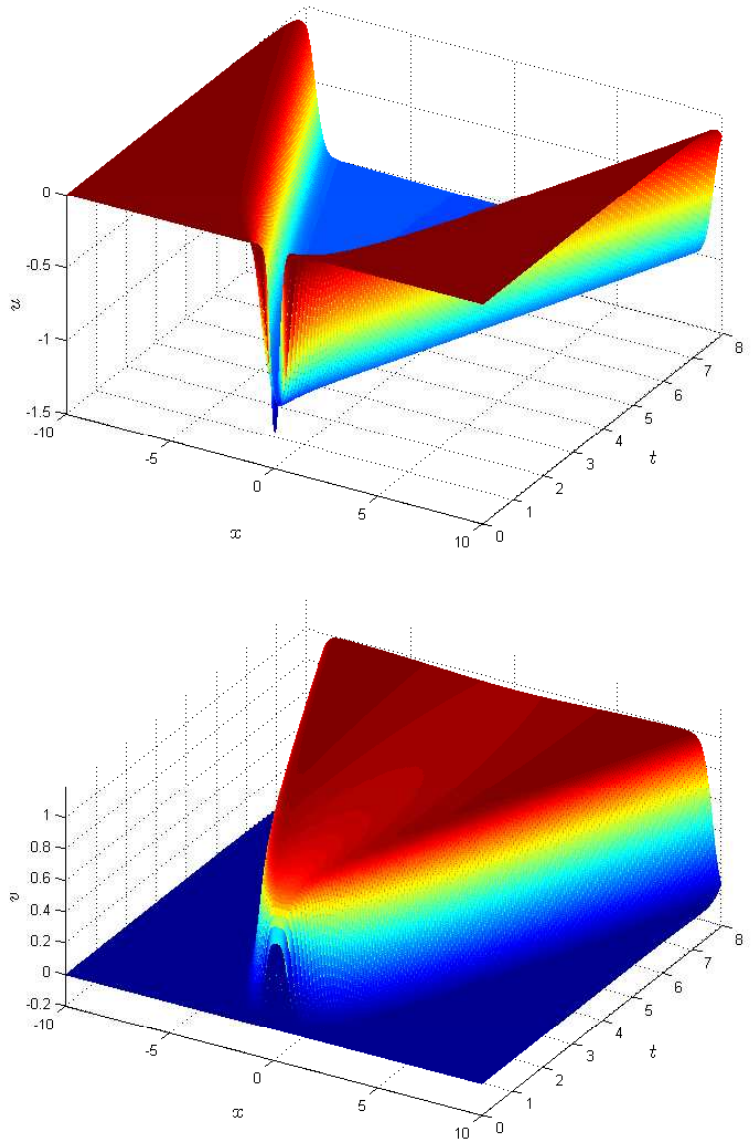

Figure 9: (Color) The values of u and v are plotted against x and t for an initial value problem with source terms $g(u, v) = v + u - Bu(u + \gamma)(u + 1)$, $B = 5$, $\gamma = 0.45$, $D = 0.9$, and an initial condition with $K = -0.7$ and $s = 0.05$.

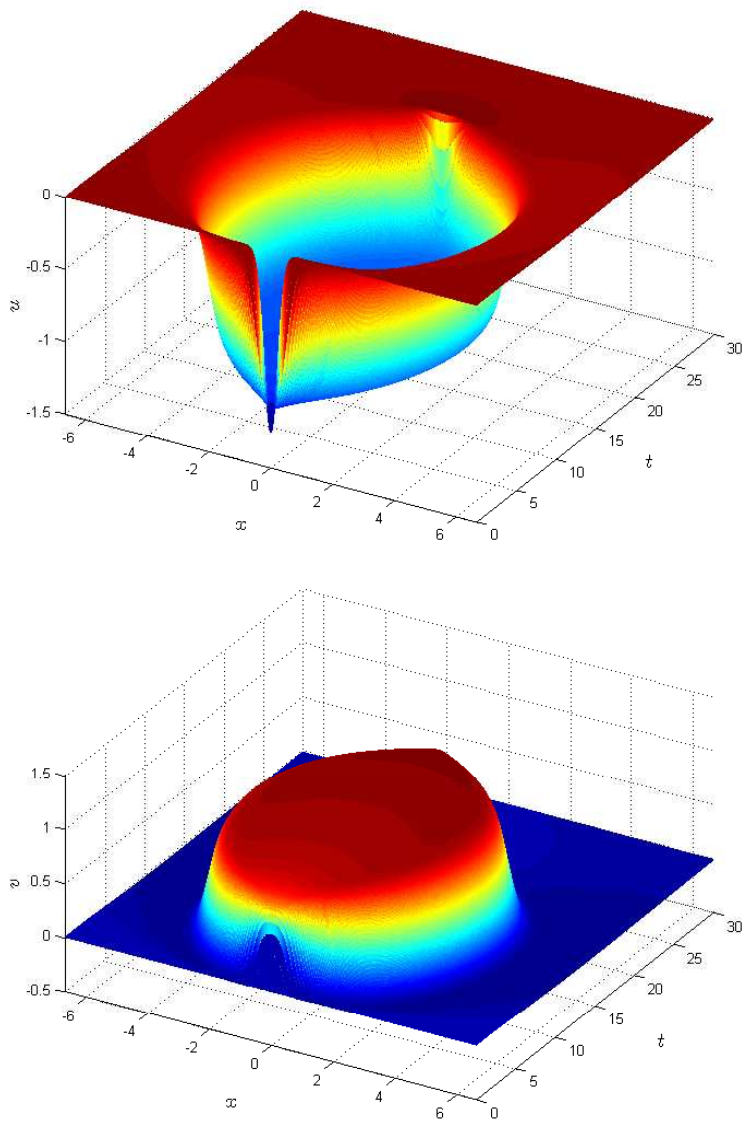

Figure 10: (Color) The values of u and v are plotted against x and t for an initial-value problem with source terms $g(u, v) = v + u - Bu(u + \gamma)(u + 1)$, $B = 5$, $\gamma = 0.55$, $D = 0.9$, and an initial condition with $K = -0.7$ and $s = 0.05$.

to overcome a 'triggering barrier', then the solution can evolve towards the vicinity of a different rest state. This then can lead to the development of traveling waves. For weak source terms ($p < 3$), the behavior is different. The motion occurs in a single slowly evolving diffusive phase. The initial perturbation will diffuse until the value of u is sufficiently small that the source terms will become important. Only then will v begin to differ significantly from zero, and trajectories have a possibility to overcome the triggering barrier.

For both weak and strong nonlinearities, if the magnitude of the initial disturbance is small, then no traveling wave will be triggered. In the case of a strong nonlinearity, the triggering problem can be overcome by increasing the stimulus amplitude, which can be done in one of two ways. Firstly, one can simply make the size of the population in the initial impulse large enough so that trajectories near $x = 0$ will evolve to the portion of the curve near the other rest state. Secondly, one can localize the disturbance until the values of the disturbance near $x = 0$ are large enough. In the case of weak nonlinearities, localizing the disturbance will not generally be helpful in overcoming the barrier.

In general, a highly localized large amplitude perturbation of a stable rest state will lead to the generation of two outward traveling waves. A particularly interesting case arises when there does not exist an outward traveling wave solution. In this case, the initially outward going waves will slow down, stop, and then propagate inwards where they will collide with each other. Furthermore, as in many problems with threshold phenomena, these colliding waves will annihilate each other.

Although one needs to know the full functional form of $g(u, v)$ in order to completely understand the dynamics of such systems it is interesting to note that a substantial amount of information can be inferred from the curve $g(u, v) = 0$. Experimentally determining the form of $g(u, v)$ is a challenging task. However, obtaining information about the curve $g(u, v) = 0$ is considerably easier. We note that for spatially uniform initial data, solutions will evolve to a stable point on the curve $g(u, v) = 0$ as $t \to \infty$. Therefore, it may be experimentally

possible to map out the stable part of this curve by performing a set of experiments that take an array of spatially homogeneous initial points in the (u, v)-space and determining the set of points to which they evolve. For a given initial rest state, one can easily determine whether the curve $g(u, v) = 0$ and the line $u + v = 0$ have multiple intersections. If multiple intersections exist, then the system is a candidate for obtaining the types of waves described in this paper. One also can determine the sign of initial disturbances that can possibly lead to the development of traveling waves (see Figure 5).

In addition, when choosing initial disturbances that can trigger traveling waves, it is useful to know whether the source terms are strong ($p > 3$) or weak ($p < 3$). This can be determined by performing an experiment with a highly localized initial disturbance in u and measuring the values of u and v at the center of the disturbance. If the disturbance initially evolves approximately along lines of constant $u+v$ then the source terms are strong, whereas if v remains approximately constant during the initial evolution then the source terms are weak. If $p > 3$, then one can obtain a rough approximation of the magnitude of the peak disturbance required to overcome the triggering barrier (see Figure 5).

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