Travelling fronts for the KPP equation with spatio-temporal delay

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Abstract

We study an integro-differential equation based on the KPP equation with a convolution term which introduces a time-delay in the nonlinearity. Special attention is paid to the question of the existence of travelling wavefront solutions connecting the two uniform steady states and their qualitative form. Motivated by the analogue between steady travelling fronts and heteroclinic orbits of an associated ordinary differential equation, we prove, using a geometric singular perturbation analysis, that steady travelling wavefront solutions persist when the delay is suitably small, for a class of convolution kernels. These travelling fronts are qualitatively similar to the well known KPP wavefront. The effect of finite and large delay is studied numerically and we find that this introduces qualitative changes to the fronts but that the front remains stable. A numerical integration of the initial-value problem confirms the qualitative shape of these fronts and suggests that – even for large delay – they may be temporally stable. Finally we show that in the discrete delay case the non-zero uniform state can be driven unstable. In this case a travelling wavefront can leave in its wake a periodic travelling wave moving with a different speed.

1. Introduction

One of the cornerstones of mathematical biology is the KPP or Fisher equation for the scalar-valued function $u(x,t)$:

$$u_t = u_{xx} + u - u^2\,, \quad x \in \mathbb{R}\,, \quad t > 0 \tag{1.1}$$

(cf. Jones & Sleeman [1983], Murray [1989], Grindrod [1991] and references therein). This equation is a prototype for modelling travelling fronts in for example population dynamics. An area of recent active interest is the improvement of this model by including temporal delay and spatial averaging acting on the nonlinearity (cf. Britton [1990], Gourley & Britton [1993,1996] and references therein). The model (1.1) is replaced by

$$u_t = u_{xx} + u - u\,(g ** u)\,, \quad x \in \mathbb{R}\,, \quad t > 0 \tag{1.2}$$

where

$$g * * u = \int_{-\infty}^{t} \int_{-\infty}^{+\infty} g(x-\xi, t-\tau)\, u(\xi, \tau)\, d\xi\, d\tau\,, \tag{1.3}$$

and the kernel $g(x,t)$ is any integrable non-negative function satisfying

$$g(-x,t) = g(x,t) \quad \text{and} \quad g * * 1 = 1\,. \tag{1.4}$$

In this paper we will consider (1.2) with a class of kernels of the form

$$g(x,t) = \frac{b}{\sqrt{4\pi t}} e^{-x^2/4t} e^{-bt}\,, \quad \text{where} \quad b > 0\,. \tag{1.5}$$

The parameter $1/b$ is representative of the delay and $b = \infty$ corresponds to zero delay. In this case the delay is spatially distributed. We shall also consider a kernel of the form

$$g(x,t) = \delta(x)\delta(t-T), \qquad T > 0$$

which gives an equation with a discrete, rather than distributed, time delay T.

In population models, temporal delays can account for the fact that a resource, once consumed, takes time to recover. Thus the model includes the effect of past populations. Spatial averaging accounts for the fact that individuals are moving around (by diffusion) and have therefore not been at the same point in space at different times in their history. A detailed derivation is provided in Britton [1990] for the use of the kernel (1.5) to account for this. Mathematically, the term $g * * u$ is non-local and therefore can modify the nature of the solutions of the PDE (1.1) dramatically.

One of the most important solutions of (1.1) is the monotone travelling front solution which exists for all $c \geq 2$ where c is the speed of the front. Although there has been a number of studies of the model (1.2), the implications of temporal delay or spatial averaging for travelling fronts have not been studied.

In this paper we will address three issues regarding the effect of temporal delay and spatial averaging on the fronts. For small temporal delay we will show, by characterising the front as a heteroclinic connection and using singular perturbation techniques from dynamical systems theory, that these fronts persist for every $c > 2$ and are qualitatively the same as the (non-delayed) KPP front. For large delay we show, by computing the heteroclinic connection numerically, that these fronts persist and change qualitatively when the temporal delay exceeds a critical speed-dependent value. For large delay these fronts lose monotonicity and develop oscillations on the lee-side of the front, but remain positive for all $x \in \mathbb{R}$ and are therefore still admissible if u represents a population.

The implications of our results for population dynamics in mathematical biology are twofold. First, the fronts are not sensitive to the addition of the non-local terms: they are robust to the addition of temporal delay and spatial averaging of the form considered here acting on the nonlinearity. Secondly, the delay and averaging introduces qualitative changes to the front such as oscillatory variation in space when the delay is large.

By defining a new variable $w = g{**}\, u$, the non-local term in (1.2) can be eliminated at the expense of adding a second PDE:

$$\begin{aligned} u_t &= u(1-w) + u_{xx} \\ w_t &= b(u-w) + w_{xx} \quad x \in \mathbb{R}\,, \quad t > 0\,. \end{aligned} \tag{1.6}$$

This system of reaction diffusion equations is the starting point for the much of the analysis in the paper. We are interested in the question of the existence of travelling wave solutions connecting the two uniform steady state solutions $(u, w) = (0, 0)$ and $(1, 1)$. We shall first formulate this as an existence question for a heteroclinic connection in $\mathbb{R}^4$. Then we shall show analytically that the desired connection does exist at least when b is large (large b means the delay is small). We then present numerical evidence that the travelling waves continue to exist when b is not large and reveal their precise form, which we compare to the KPP waves. A second numerical technique – numerical integration of the initial-value problem – provides evidence that these modified travelling fronts are temporally stable. Finally, using numerical integration of the initial-value problem, we shall consider a KPP equation with a *discrete* delay, namely

$$\frac{\partial}{\partial t}u(x,t) = \frac{\partial}{\partial x^2}u(x,t) + [1 - u(x, t-T)]u(x,t) \tag{1.7}$$

where $T > 0$ is the delay, comparable to $1/b$ in the model (1.2) with (1.5). Equation (1.7) is also a particular case of (1.2), arising when $g(x,t) = \delta(x)\delta(t-T)$. When $g(x,t)$ is given by (1.5) the uniform steady state $u = 1$ never actually loses linear stability for any $b > 0$. So the travelling waves connecting $u = 0$ and $u = 1$ simply change shape for different values of b. But in the model (1.7), as T is increased the uniform state $u = 1$ loses stability when T passes through the value $\pi/2$; the kinetic equations then have limit cycle solutions. This raises the possibility that a wavefront might exist moving out into the domain, leaving behind it an oscillatory wake. We present the results of some numerical simulations which confirm this. These are the first numerical simulations of the interaction between travelling fronts and periodic wave trains for the delayed KPP equation. We compare these results with the recent work of Sherratt et al. [1997] which found extensive interactions of this type in coupled systems of reaction-diffusion equations.

2. Characterising fronts as heteroclinic connections

Travelling wave states travelling at speed c are solutions of equation (1.6) of the form

$$u(x,t) = \tilde{u}(x-ct)\,, \quad w(x,t) = \tilde{w}(x-ct)\,. \tag{2.1}$$

We write $\xi = x - ct$ and substitute $\tilde{u}$ and $\tilde{w}$ into (1.6), resulting in the coupled system of ordinary differential equations

$$\begin{aligned} \tilde{u}_{\xi\xi} + c\tilde{u}_\xi + \tilde{u} - \tilde{u}\tilde{w} &= 0 \\ \tilde{w}_{\xi\xi} + c\tilde{w}_\xi + b(\tilde{u} - \tilde{w}) &= 0 \,. \end{aligned} \tag{2.2}$$

The above pair of ODEs is invariant under the reflection $(c, \xi) \mapsto (-c, -\xi)$ and so we assume, without loss of generality that $c > 0$. In this section, the above pair of ODEs will be formulated as a dynamical system in $\mathbb{R}^4$ and the question of existence of travelling fronts is characterised as an existence question for heteroclinic connections of a two-parameter family of ODEs in $\mathbb{R}^4$.

By defining new variables

$$\tilde{v} = \tilde{u}_\xi + \tfrac{1}{2}c\tilde{u} \quad \text{and} \quad \tilde{y} = \tilde{w}_\xi + \tfrac{1}{2}c\tilde{w} \,, \tag{2.3}$$

the system (2.2) can be formulated as

$$Z_\xi = F(Z, c, b) \,, \quad \text{with} \quad Z = \begin{pmatrix} \tilde{u} \\ \tilde{v} \\ \tilde{w} \\ \tilde{y} \end{pmatrix} \in \mathbb{R}^4 \tag{2.4}$$

and

$$F(Z, c, b) = \begin{pmatrix} -\frac{1}{2}c\tilde{u} + \tilde{v} \\ -\frac{1}{2}c\tilde{v} + \left(\frac{1}{4}c^2 - 1\right)\tilde{u} + \tilde{u}\tilde{w} \\ -\frac{1}{2}c\tilde{w} + \tilde{y} \\ -\frac{1}{2}c\tilde{y} + \left(\frac{1}{4}c^2 + b\right)\tilde{w} - b\tilde{u} \end{pmatrix} . \tag{2.5}$$

In the limit as $b \to \infty$ the above system can be shown to reduce to the second-order ODE for KPP fronts, and it is then straightforward to establish the existence of a heteroclinic connection using phase-plane techniques. When b is finite the phase space is four-dimensional, and therefore the persistence of such a heteroclinic connection is not obvious. In the remainder of this section, we will find the equilibrium points of the system (2.4) and determine the local structure in the neighbourhood of these equilibria.

There are two equilibria satisfing $F(Z, c, b) = 0$:

$$Z^0 = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix} \quad \text{and} \quad Z^1 = \frac{1}{2}\begin{pmatrix} 2 \\ c \\ 2 \\ c \end{pmatrix} . \tag{2.6}$$

Note that the two states are independent of the delay.

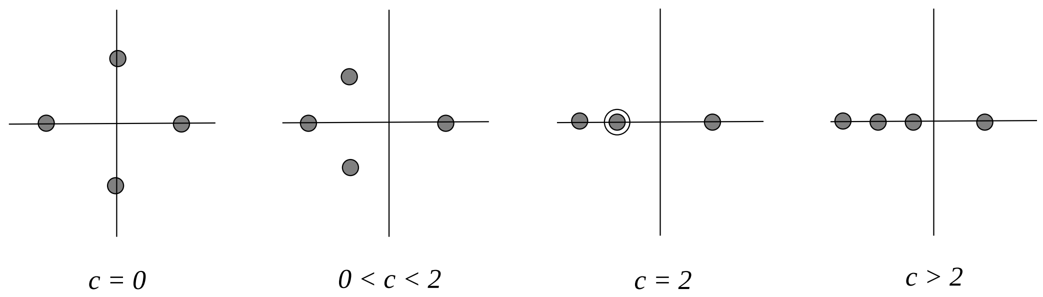

Figure 2.1: Qualitative position of the spectrum of $\mathbf{A}_0$ when $b > 0$.

The linearisation about Z^0 has the following properties. Let

$$\mathbf{A}_0 \stackrel{\text{def}}{=} DF(Z^0, c, b) = \begin{pmatrix} -\frac{1}{2}c & 1 & 0 & 0 \\ \frac{1}{4}c^2 - 1 & -\frac{1}{2}c & 0 & 0 \\ 0 & 0 & -\frac{1}{2}c & 1 \\ -b & 0 & b + \frac{1}{4}c^2 & -\frac{1}{2}c \end{pmatrix} . \tag{2.7}$$

Then the characteristic equation for $\mathbf{A}_0$ is

$$\Delta_0(\lambda) \stackrel{\text{def}}{=} \det[\lambda \mathbf{I} - \mathbf{A}_0] = (\lambda^2 + c\lambda + 1)(\lambda^2 + c\lambda - b) . \tag{2.8}$$

For all $b > 0$ the spectrum of $\mathbf{A}_0$ takes the qualitative form shown in Figure 2.1, as a function of c.

The important feature of the spectrum is that $E^s(Z^0)$, the stable subspace at Z^0, is three dimensional for all positive b and c. If c is further restricted to $c > 2$, then all four eigenvalues of $\mathbf{A}_0$ are strictly real.

For the linearization about Z^1, let

$$\mathbf{A}_1 \stackrel{\text{def}}{=} DF(Z^1, c, b) = \begin{pmatrix} -\frac{1}{2}c & 1 & 0 & 0 \\ \frac{1}{4}c^2 & -\frac{1}{2}c & 1 & 0 \\ 0 & 0 & -\frac{1}{2}c & 1 \\ -b & 0 & b + \frac{1}{4}c^2 & -\frac{1}{2}c \end{pmatrix} . \tag{2.9}$$

The characteristic equation for $\mathbf{A}_1$ is

$$\Delta_1(\lambda) \stackrel{\text{def}}{=} \det[\lambda \mathbf{I} - \mathbf{A}_1] = \lambda^4 + 2c\lambda^3 + (c^2 - b)\lambda^2 - bc\lambda + b . \tag{2.10}$$

When $c = 0$, the characteristic equation reduces to $\Delta_1(\lambda) = \lambda^4 - b\lambda^2 + b$. For all $b > 0$ the qualitative position of the roots of $\Delta_1(\lambda)$ take the form shown in Figure 2.2 in the complex $\lambda-$plane.

For all $b > 0$ the $\dim E^s(Z^1) = \dim E^u(Z^1) = 2$, when $c = 0$. When $c > 0$ the characteristic polynomial can be factorised as

$$\Delta_1(\lambda) = (\lambda^2 + c\lambda + r_-)(\lambda^2 + c\lambda + r_+) , \tag{2.11}$$

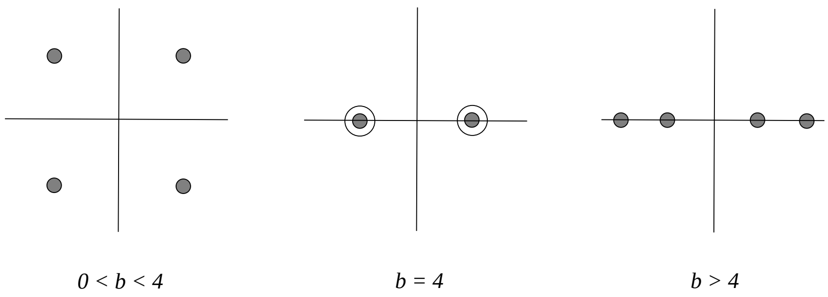

Figure 2.2: Qualitative position of the spectrum of $\mathbf{A}_1$ when $c = 0$.

where

$$r_{\pm} = \tfrac{1}{2}(-b \pm \sqrt{b(b-4)})\,. \tag{2.12}$$

Note that $r_- r_+ = b > 0$ and $r_- + r_+ = -b < 0$. Therefore with $b > 0$, the only double root of the characteristic polynomial occurs when $b = 4$; and therefore the spectrum for $c > 0$ is qualitatively represented by Figure 2.2; that is, for all b, c positive the $\dim E^u(Z^1) = 2$ and for $c > 0$ and $b > 4$ all eigenvalues of $\mathbf{A}_1$ are real.

Let $W^s(Z^0)$ and $W^u(Z^1)$ be the local stable and unstable manifolds respectively associated with Z^0 and Z^1. The argument for the existence of a heteroclinic connection between the points Z^0 and Z^1 (and hence a travelling front of the system (1.6)) is that the sum of the dimensions of $W^s(Z^0)$ and $W^u(Z^1)$ is five and therefore they can potentially intersect along a one-dimensional curve in $\mathbb{R}^4$. In §3 we will show, using a geometric singular perturbation argument, that for $\frac{1}{b}$ small such a heteroclinic connection exists. In §4, using a numerical technique we show that a heteroclinic connection persists for finite and large delay and moreover it changes qualitatively – loses monotonicity and develops oscillations – when $b < 4$, due to the change of type of the eigenvalues of $\mathbf{A}_1$.

3. Persistence of travelling fronts for small delay

In this section, geometric singular perturbation theory and Fenichel's invariant manifold theory (cf. Fenichel [1979], Jones [1995]) are used to analyse (2.4) for $b >> 1$. Let

$$\varepsilon = \frac{1}{\sqrt{b}} \qquad (b > 0)\,, \tag{3.1}$$

and define new variables with $\tilde{y}$ stretched:

$$u = \tilde{u}\,, \quad v = \tilde{v}\,, \quad w = \tilde{w} \quad \text{and} \quad y = \varepsilon \tilde{y}\,.$$

Then equation (2.4) can be cast into standard form for a singular perturbation problem

$$u_\xi \;=\; v - \tfrac{1}{2}cu$$

$$
\begin{aligned}
v_\xi &= (\tfrac{1}{4}c^2-1)u - \tfrac{1}{2}cv + uw\\
\varepsilon w_\xi &= y - \tfrac{1}{2}\varepsilon cw\\
\varepsilon y_\xi &= w - u - \tfrac{1}{2}\varepsilon cy + \tfrac{1}{4}\varepsilon^2 c^2 w\,.
\end{aligned}
\tag{3.2}
$$

The system (3.2) is called the "slow system". Let $\Xi = \xi/\varepsilon$; then the dual "fast system" associated with (3.2) is

$$
\begin{aligned}
u_\Xi &= \varepsilon(v - \tfrac{1}{2}cu)\\
v_\Xi &= \varepsilon((\tfrac{1}{4}c^2-1)u - \tfrac{1}{2}cv + uw)\\
w_\Xi &= y - \tfrac{1}{2}\varepsilon cw\\
y_\Xi &= w - u - \tfrac{1}{2}\varepsilon cy + \tfrac{1}{4}\varepsilon^2 c^2 w\,.
\end{aligned}
\tag{3.3}
$$

The classical approach to studying such singular perturbation problems for fronts is to use matched asymptotic expansions (cf. Grindrod [1991, §2.3]). However, we will show that a more complete global picture can be obtained by using dynamical systems techniques: invariant manifold theory and geometric singular perturbation theory.

Setting $\varepsilon = 0$ in (3.2) reduces it to the second-order ODE for KPP fronts. But, more importantly, this ODE, when $\varepsilon = 0$, is restricted to an invariant set $\{w = u,\ y = 0\} \subset \mathbb{R}^4$ which is a normally-hyperbolic two-dimensional submanifold of $\mathbb{R}^4$. We will show that this set satisfies the hypotheses of Fenichel's invariant manifold theorem and therefore persists for ε sufficiently small. Denoting this manifold by $\mathcal{M}_\varepsilon$, we then show that a restriction of (3.2) to $\mathcal{M}_\varepsilon$ reduces to a *regular perturbation*. Persistence of the heteroclinic connection then reduces to a Melnikov-type argument.

To be precise, $\mathcal{M}_0$ is any compact subset of

$$
\{\ (u,v,w,y) \in \mathbb{R}^4\ :\ u = w \text{ and } y = 0\ \}\,. \tag{3.4}
$$

Note that $\dim \mathcal{M}_0 = 2$.

Definition (Fenichel [1979]:) the manifold $\mathcal{M}_0$ is said to be *normally hyperbolic* if the linearisation of the *fast system* (3.3), restricted to $\mathcal{M}_0$, has exactly $\dim \mathcal{M}_0$ eigenvalues on the imaginary axis, with the remainder of the spectrum hyperbolic.

The linearisation of (3.3), restricted to $\mathcal{M}_0$, reduces to

$$
\begin{pmatrix} 0 & 0 & 0 & 0\\ 0 & 0 & 0 & 0\\ 0 & 0 & 0 & 1\\ -1 & 0 & 1 & 0 \end{pmatrix}, \tag{3.5}
$$

which has exactly two zero eigenvalues and the other two are strictly hyperbolic. By Fenichel's invariant manifold theorem (Fenichel [1979], Theorem 9.1), for $\varepsilon > 0$ but sufficiently small, there exists a submanifold of $\mathbb{R}^4$, $\mathcal{M}_\varepsilon$, that lies within $\mathcal{O}(\varepsilon)$ of $\mathcal{M}_0$

and is diffeomorphic to $\mathcal{M}_0$. It is invariant under the flow of (3.3) and $\mathcal{C}^r$ smooth for any $r < +\infty$.

In fact, since $\mathcal{M}_0$ can be characterised as the graph of a function, we have that

$$\mathcal{M}_\varepsilon = \{ \, (u,v,w,y) \in \mathbb{R}^4 \ : \ w = h(u,v,\varepsilon) \text{ and } y = g(u,v,\varepsilon) \, \} \,, \tag{3.6}$$

where g, h depend smoothly on ε and satisfy

$$h(u,v,0) = u \quad \text{and} \quad g(u,v,0) = 0 \,. \tag{3.7}$$

Substitution of g, h into (3.2), to obtain a differential equation on $\mathcal{M}_\varepsilon$, results in a *regular perturbation*.

In other words, on $\mathcal{M}_\varepsilon$, (3.2) reduces to

$$\begin{aligned} u_\xi &= v - \tfrac{1}{2}cu \\ v_\xi &= \left(\tfrac{1}{4}c^2 - 1\right) u - \tfrac{1}{2}cv + uh(u,v,\varepsilon) \,. \end{aligned} \tag{3.8}$$

Let $c > 2$ be fixed and denote the solution of (3.8) with $\varepsilon = 0$ by (u_0, v_0); then (u_0, v_0) satisfies

$$\begin{aligned} (u_0)_\xi &= v_0 - \tfrac{1}{2}cu_0 \\ (v_0)_\xi &= \left(\tfrac{1}{4}c^2 - 1\right) u_0 - \tfrac{1}{2}cv_0 + u_0^2 \,, \end{aligned} \tag{3.9}$$

which is the well-known equation for travelling fronts of the KPP equation. A phase-plane argument shows that for all $c > 2$, there exists a monotone heteroclinic connection between the points $(0,0)$ and $(1, \frac{1}{2}c)$. What we will prove, using a Melnikov-type argument is that, *for every $c > 2$, and $\varepsilon > 0$ sufficiently small, there exists a heteroclinic orbit of (3.2) in $\mathbb{R}^4$ – but on $\mathcal{M}_\varepsilon$ – connecting Z^0 and Z^1.* In fact, the fronts for $0 < c < 2$ also persist but they are of less interest in biological models because $u(\xi)$ can take negative values.

The system (3.8) can be written in the form

$$U_\xi = f(U) + \varepsilon^2 G(U,\varepsilon) \,, \quad U = \begin{pmatrix} u \\ v \end{pmatrix} \in \mathbb{R}^2 \,, \tag{3.10}$$

with

$$f(U) = \begin{pmatrix} v - \frac{1}{2}cu \\ (\frac{1}{4}c^2 - 1)u - \frac{1}{2}cv + u^2 \end{pmatrix} \tag{3.11}$$

and

$$G(U,\varepsilon) = \begin{pmatrix} 0 \\ u(h(u,v,\varepsilon) - u)/\varepsilon^2 \end{pmatrix} \,. \tag{3.12}$$

Equation (3.10) can be viewed as an operator equation in the normed space

$$BC^0(\mathbb{R}, \mathbb{R}^2) = \{ \, U \ : \ \mathbb{R} \to \mathbb{R}^2 \,, \ \text{bounded} \,, \ \text{continuous} \, \} \tag{3.13}$$

with norm $\|U\| = \sup_{\xi\in\mathbb{R}}|U(\xi)|$. Let

$$U(\xi,\varepsilon) = U^0(\xi) + \varepsilon^2 V(\xi,\varepsilon)\,, \tag{3.14}$$

where $U^0(\xi)$ is a heteroclinic connection of the KPP system (3.9). The perturbation function $V(\xi,\varepsilon)$ satisfies

$$V_\xi = \mathbf{A}(\xi)V + G(U^0,0) + \mathcal{O}(\varepsilon^2)\,, \quad \text{with} \quad \mathbf{A}(\xi) = Df(U^0(\xi))\,. \tag{3.15}$$

An explicit expression for $G(U^0,0)$ can be obtained by using the leading-order expression for the invariant manifold $\mathcal{M}_\varepsilon$, to second order in ε. A straightforward calculation yields

$$\begin{aligned} w &= h(u,v,\varepsilon) = u + \varepsilon^2(u^2-u) + \mathcal{O}(\varepsilon^3) \\ y &= g(u,v,\varepsilon) = \varepsilon v + \mathcal{O}(\varepsilon^3)\,. \end{aligned} \tag{3.16}$$

and hence

$$G(U^0,0) = \begin{pmatrix} 0 \\ u_0^2(u_0-1) \end{pmatrix}\,. \tag{3.17}$$

The function $u_0(\xi)$ is bounded for all $\xi \in \mathbb{R}$ and therefore $G(U^0,0) \in BC^0(\mathbb{R},\mathbb{R}^2)$.

Define the linear operator $\mathbf{L} : BC^1(\mathbb{R},\mathbb{R}^2) \to BC^0(\mathbb{R},\mathbb{R}^2)$ by

$$\mathbf{L} = \frac{d}{d\xi} - \mathbf{A}(\xi)\,, \tag{3.18}$$

with $\mathbf{A}(\xi)$ defined in (3.15). Then (3.15) can be written

$$\mathbf{L}V = G(U^0,0) + \mathcal{O}(\varepsilon^2)\,. \tag{3.19}$$

The persistence question reduces to solvability of this equation in the function space $BC^0(\mathbb{R},\mathbb{R}^2)$. In fact we will prove that solutions persist – for ε sufficiently small – independent of the precise form of $G(U^0,0)$ and independent of the precise value of c (as long as $c \neq 0$). This anomaly is a consequences of the fact that $\mathbf{L}$ is a Fredholm operator of non-zero index. Recall, an operator is Fredholm if the Ker($\mathbf{L}$) and Ker($\mathbf{L}^*$) are finite, and the index of a Fredholm operator is equal to dimKer($\mathbf{L}$) minus dimKer($\mathbf{L}^*$).

It follows from standard theory (cf. Chow & Hale [1982, §11.3]) that (3.19) has a solution in $BC^0(\mathbb{R},\mathbb{R}^2)$, for ε sufficiently small, if and only if $G(U^0,0)$ is in the range of the operator $\mathbf{L}$; that is, for *every* solution $\eta \in BC^1(\mathbb{R},\mathbb{R}^2)$ in the kernel of the adjoint of $\mathbf{L}$ it is required that

$$\int_{-\infty}^{+\infty} (\eta, G(U^0,0))\,d\xi = 0\,, \tag{3.20}$$

where $(\cdot,\cdot)$ is an inner product on $\mathbb{R}^2$. The adjoint of $\mathbf{L}$, denoted $\mathbf{L}^*$, is

$$\mathbf{L}^* = -\frac{d}{d\xi} + \mathbf{A}(\xi)^T\,. \tag{3.21}$$

A curious feature of the operator $\mathbf{L}^*$ is that

$$\mathrm{Ker}(\mathbf{L}^*) \cap BC^1(\mathbb{R}, \mathbb{R}^2) = \emptyset \,. \tag{3.22}$$

Before proving (3.22) we note that a consequence of this result is that (3.20) is satisfied for *any* $G(U^0, 0) \in BC^0(\mathbb{R}, \mathbb{R}^2)$ and therefore, for the particular $G(U^0, 0)$ in (3.17), the heteroclinic connection trivially persists.

The fact that $\mathrm{Ker}(\mathbf{L}^*)$ is empty is curious because the $\mathrm{Ker}(\mathbf{L})$ is not empty. The homogeneous equation, $z_\xi = \mathbf{A}(\xi)z$, has a solution in $BC^1(\mathbb{R}, \mathbb{R}^2)$, namely

$$z = \frac{d}{d\xi} U^0(\xi) \,. \tag{3.23}$$

Now, if z is any solution of $z_\xi = \mathbf{A}(\xi)z$ then

$$\eta(\xi) = e^{-\int_0^\xi \mathrm{Tr}(\mathbf{A}(s))ds}\, \mathbf{J} z(\xi) \,, \quad \mathbf{J} = \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix} , \tag{3.24}$$

is a solution of $\mathbf{L}^*\eta = 0$ or

$$\eta_\xi = -\mathbf{A}(\xi)^T \eta \,. \tag{3.25}$$

This follows by direct substitution and the fact that any 2×2 matrix $\mathbf{A}$ satisfies

$$\mathbf{J}\,\mathbf{A} + \mathbf{A}^T \mathbf{J} = \mathrm{Tr}(\mathbf{A})\,\mathbf{J} \,. \tag{3.26}$$

Therefore it is clear that

$$\eta(\xi) = e^{c\xi} \mathbf{J} \frac{d}{d\xi} U^0(\xi) \,, \tag{3.27}$$

satisfies (3.25). But this function is not bounded. The function $\frac{d}{d\xi}U^0(\xi)$ is bounded for all $\xi \in \mathbb{R}$ but after multiplication by $e^{c\xi}$ it grows exponentially as $\xi \to \infty$, and so $\eta \notin BC^1(\mathbb{R}, \mathbb{R}^2)$.

To show that (3.25) has no bounded solutions and to see the connection with the Fredholm index, define

$$\mathbf{A}_\pm = \lim_{\xi \to \pm\infty} \mathbf{A}(\xi) = \begin{pmatrix} -\frac{1}{2}c & 1 \\ \frac{1}{4}c^2 \mp 1 & -\frac{1}{2}c \end{pmatrix} . \tag{3.28}$$

Let $s_\pm$ be the number of eigenvalues of $\mathbf{A}_\pm$ with negative real part. A direct calculation using (3.28) shows that $s_+ = 2$ and $s_- = 1$, for all $c > 0$. It follows from a result of Sacker [1979] that the Fredholm index of the operator $\mathbf{L}$ is $s_+ - s_-$: the operator $\mathbf{L}$ is a Fredholm operator of index 1.

To complete the verification of (3.22), note that *both eigenvalues of* $-\mathbf{A}_+^T$ *have strictly positive real part for all* $c > 0$. Since

$$\lim_{\xi \to +\infty} -\mathbf{A}(\xi)^T = -\mathbf{A}_+^T \,,$$

it follows that every solution of (3.25) grows exponentially as $\xi \to +\infty$: (3.25) has no solutions which are bounded for all $\xi \in \mathbb{R}$.

This completes the proof that on $\mathcal{M}_\varepsilon$ for ε sufficiently small, the heteroclinic connection, and hence the front solution of the delayed KPP equation, persists for any $c > 0$.

This persistence result is abstract – it does not require an explicit expression for the KPP front (u_0, v_0, c). In fact, even though an explicit expression is known for a particular value ($c = 5/\sqrt{6}$) no further information is gained. Because of the nature of this persistence result, it suggests that KPP fronts are extraordinarily robust and will likely persist under an even larger class of perturbations.

4. Persistence of travelling fronts for large delays

We now numerically investigate persistence of travelling fronts in (3.2) for much larger values of the parameter $\varepsilon = 1/\sqrt{b}$. To this end, we look for solutions $Z(\xi)$ of equation (3.2) subject to boundary conditions

$$\begin{array}{ll} Z(\xi) \to Z^1 & \text{as } \xi \to -\infty; \\ Z(\xi) \to Z^0 & \text{as } \xi \to \infty. \end{array} \tag{4.1}$$

Truncating this equation to a finite (but long) interval, $\xi \in [-X, X]$ we apply techniques of de Hoog and Weiss (1980), Lentini and Keller (1980) and Beyn (1990) to compute approximations that converge to the correct solution as $X \to \infty$. To this end, assume that we have bases for the following linear subspaces of $\mathbb{R}^4$:

$$\begin{array}{ll} \text{span}\{e_i \ : \ i = 1, \cdots, n_u\} & = E^u(\mathbf{A}_0) \\ \text{span}\{e_i^* \ : \ i = 1, \cdots, n_u\} & = E^u(\mathbf{A}_0^*) \\ \text{span}\{f_i \ : \ i = 1, \cdots, n_s\} & = E^s(\mathbf{A}_1) \\ \text{span}\{f_i^* \ : \ i = 1, \cdots, n_s\} & = E^s(\mathbf{A}_1^*) \end{array}$$

We truncate the boundary conditions (4.1) to

$$\Pi^0(Z(X) - Z^0) = 0, \quad \Pi^1(Z(-X) - Z^1) = 0 \tag{4.2}$$

where

$$\Pi^0(Z) = \sum_{i=0}^{n_u} (e_i^*, Z) e_i \,.$$

The operator $\Pi^0 : \mathbb{R}^4 \to E^u(Z^0)$ is a projection operator with kernel equal to the stable eigenspace and $(\cdot, \cdot)$ is the standard inner product on $\mathbb{R}^4$. Similarly the operator $\Pi^1 : \mathbb{R}^4 \to E^s(Z^1)$ defined by

$$\Pi^1(Z) = \sum_{i=0}^{n_s} (f_i^*, Z) f_i$$

is a projection with kernel equal to the unstable eigenspace at Z^1.

In the parameter region of interest $n_u = \dim(E^u(Z^0)) = 1$ and $n_s = \dim(E^s(Z^1)) = 2$. Therefore the system (3.2,4.2) consists of four first order ODEs and three boundary conditions. For a unique solution, one additional condition is required. Since the ODE is autonomous any translate, $Z(\xi+\theta)$ $\theta \in \mathbb{R}$, is also a solution. To overcome this natural degeneracy, we add a *phase condition*: $\Phi(Z) = 0$. For definiteness we fix this condition at

$$\Phi(Z) = (\mathbf{e}_1, Z)|_{\xi=0} - \tfrac{1}{4} = u(0) - \tfrac{1}{4} = 0\,. \tag{4.3}$$

This condition is based on the observation that first component of Z decays from 1 at Z^1 to 0 at Z^0. Note that there need not necessarily be a unique solution to the nonlinear problem (3.2,4.2,4.3), but if there is then it is (generically) locally unique.

Solutions of this truncated problem can be shown to converge exponentially to the exact problem as $X \to \infty$, using properties of the exponential dichotomies induced by the hyperbolicity of the matrices $\mathbf{A}_{0,1}$; see e.g. Beyn (1990). Note that because we are computing structurally stable connecting orbits, we do not have to consider parameter perturbations that are typically necessary for other solutions such as homoclinic orbits.

For solution of the system (3.2,4.2,4.3) we have used the NAG finite difference boundary value problem solver *D02RAF* successively solving on the interval $\xi \in [-30, 30]$ until a global error tolerance was below 10^{-6}. This typically needed 60 collocation points at unevenly spaced intervals.

Figure 4.1 shows results of a number of computations with $c = 5/\sqrt{6} = 2.04124$ where the singular limit $b = \infty$ has an exact solution

$$u(\xi) = \frac{1}{(\exp(\xi/\sqrt{6})+1)^2} = \frac{1}{(\exp(0.408348\xi)+1)^2} \tag{4.4}$$

satisfying (3.2) and the phase condition (4.3). Observe that (i) the numerical solutions converge to the exact solution as $b \to \infty$, as proven in the previous section and (ii) for b small enough ($b < 4$) the stable eigenvalues of $\mathbf{A}_1$ become a complex pair and the front can be seen to lose monotonicity for $b < 4$ due to the onset of oscillations as $\xi \to -\infty$.

It was found possible to reduce the value of b and find approximations of connecting heteroclinic orbits for values of b as low as $b = 0.1$, although for $b < 0.5$ the fact that the unstable eigenvalues of $\mathbf{A}_1$ are close to the imaginary axis means that a solution on the $\xi-$interval $[-30, 30]$ is insufficiently resolved to get reasonable convergence (as a rule of thumb, one needs to have a time interval considerably longer than $1/|\lambda|$ where λ is the real part of the *leading eigenvalue* for the connections, i.e. the eigenvalue of $\mathbf{A}_{0,1}$ that is closest to the imaginary axis; for example with $b = 0.1$ and $c = 5/\sqrt{6}$, the leading eigenvalues have real part $\lambda = 0.0346$ implying a decay rate of 28.9). Figure 4.2 shows a result on a longer $\xi-$interval of the computed connecting orbit for $b = 0.2$.

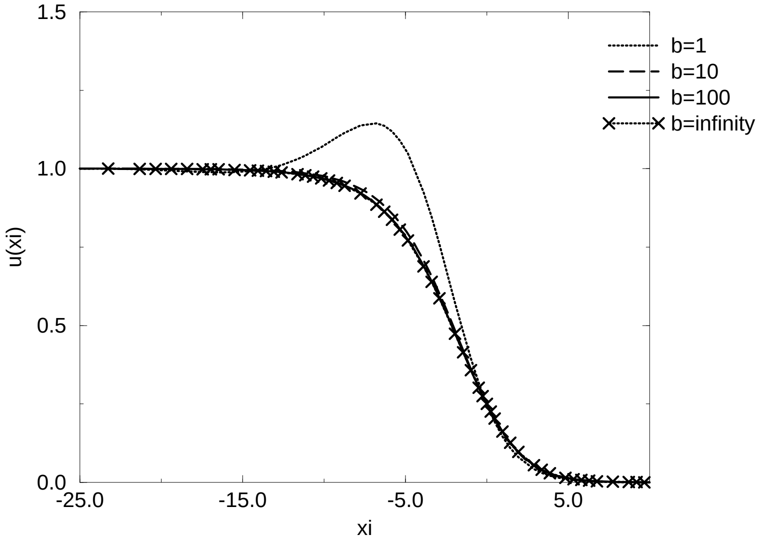

Figure 4.1: Connecting orbits shown in the u, ξ plane for $c = 5/\sqrt{6}$; note that the phase condition ensures that all orbits satisfy $u(0) = \frac{1}{4}$. The cases $b = 1, 10$ and 100 were computed numerically while the case $b = \infty$ is known analytically for this case ($c = 5/\sqrt{6}$). The oscillations as $\xi \to -\infty$ correspond to the presence of a complex pair of unstable eigenvalues in the linearisation about Z^1 at $\xi = -\infty$.

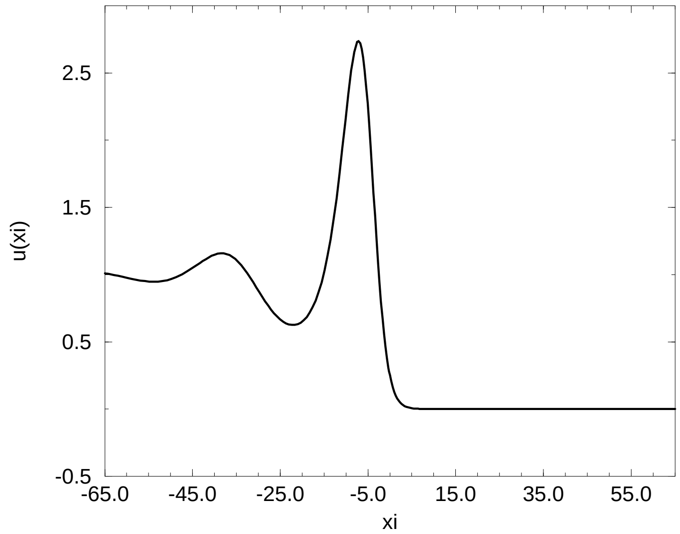

Figure 4.2: Connecting orbit in the u, ξ plane for $b = 0.2$ and $c = 5/\sqrt{6}$ computed in a range $[-65, 65]$. There are large oscillations for $\xi < 0$, although they do not enter into the region $u < 0$.

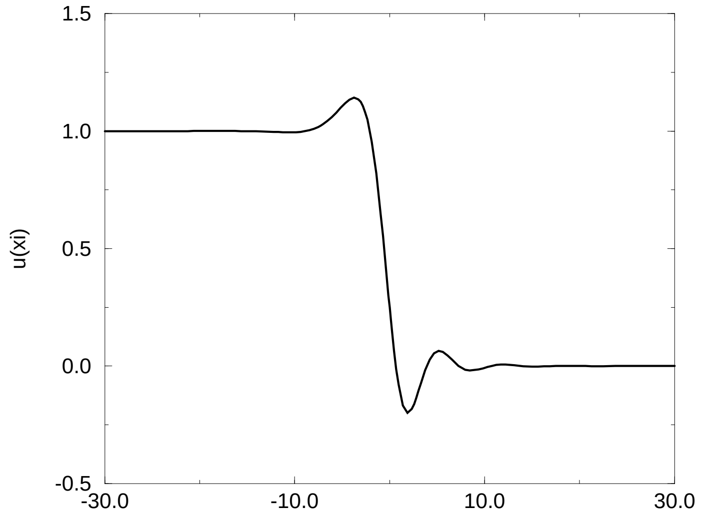

Figure 4.3: Connecting orbit in the u, ξ plane for $b = c = 0.7$ showing oscillatory approach to the fixed points for both $\xi \to -\infty$ and $\xi \to \infty$. In this case the oscillations with $u < 0$ preclude this solution from having physical relevance if u is to represent a population.

In Figure 4.3 we show an example computation of a connecting orbit with $b = c = 0.7$ where both asymptotic tails are oscillatory due to the presence of complex unstable eigenvalues at Z^1 and complex stable eigenvalues at Z^0.

5. The numerical initial-value problem for travelling fronts

In the previous section, the travelling fronts were found by solving a boundary-value problem associated with the ODE obtained by restricting to a moving frame. In this section we compute travelling fronts by numerically integrating the initial value problem for the PDE (1.6). The purpose is three-fold: firstly, it acts as a check on the computation in §4; secondly it gives an indication of the stability of the fronts, and thirdly, we are able to extend the analysis to include a larger class of delays.

Figure 5.1 shows the result of a numerical integration using the NAG routine *D03PCF* of the PDE (1.6) with $b = 1$. The initial data in the simulation was taken to be a step function, the form of which is given in the figure caption. The discontinuity is smoothed out immediately by the parabolic form of the PDE. The simulation clearly shows rapid convergence to a permanent-form travelling wave, with the qualitative form obtained in §4 (cf. Figure 4.1). The speed of this wave is deduced to be approximately 2, which is the minimum speed at which a front can have a non-oscillatory approach to the zero state (see Figure 2.1), and is known to be the critical speed in the temporal stability analyis of fronts (cf. Fife & McLeod [1977], Kirchgässner [1992] and references therein). The numerical integration does indicate that the travelling front with b finite is temporally stable. However it is not clear that there is a critical front – corresponding to a particular $b-$dependent value of c – which is temporally stable, as in the KPP equation, or whether the stability properties change dramatically due to the delay.

One of the advantages of numerical integration is that we can enlarge the class of delay kernels. A particular form of delay of interest is a discrete delay. By taking $g(x,t) = \delta(x)\delta(t-T)$ with $T > 0$, where $\delta(\cdot)$ is the Dirac delta function, the integro-differential equation (1.2) reduces to

$$\frac{\partial}{\partial t}u(x,t) = \frac{\partial^2}{\partial x^2}u(x,t) + [1-u(x,t-T)]u(x,t), \qquad x \in \mathbb{R}, \quad t \geq 0\,. \tag{5.1}$$

Here we call $T \geq 0$ the delay. When $T = 0$, this equation reduces to the KPP equation with its well-known travelling front connecting $u = 0$ with $u = 1$. An intriguing feature of the model (5.1) is that – unlike the KPP with delay (1.5) – it is possible for the uniform state $u = 1$ to become unstable, which leads to qualitatively new behaviour of the travelling front.

It is known that the steady state $u = 1$ of the time-delayed ODE $u_t = u(t)(1-u(t-T))$ loses stability through a Hopf bifurcation at $T = \pi/2$ (for a detailed discussion of Hopf bifurcations in delay equations see Wu [1996]). When T exceeds this value

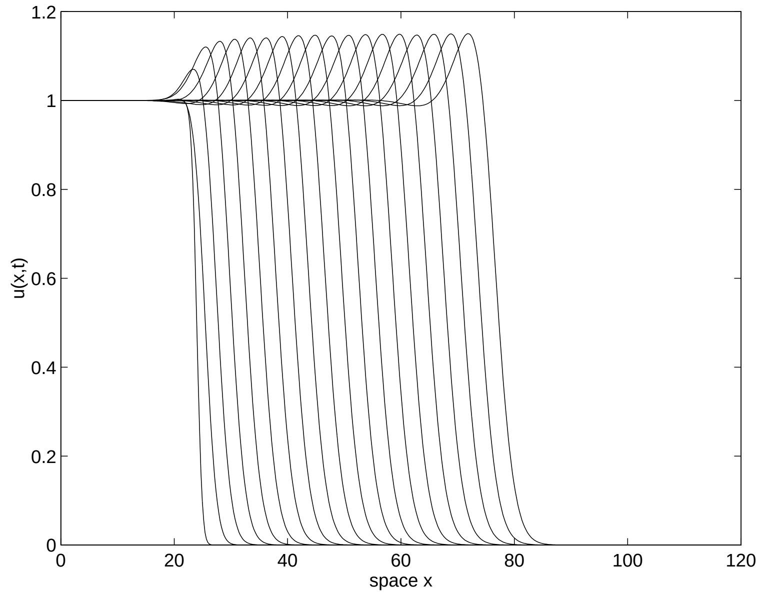

Figure 5.1: Numerical simulation of system (1.6) for $b = 1$. The initial condition was $u(x,0) = 1$ for $0 \leq x \leq 20$, $u(x,0) = 0$ for $20 < x \leq 120$ with similar initial conditions for $w(x,0)$. The following boundary conditions were used: $u_x = w_x = 0$ at $x = 0$ and $u = w = 0$ at $x = 120$. The profiles are plots of the solution at equally-spaced times from $t = 0$ to $t = 30$.

the solution will evolve to a stable limit cycle for all but special initial conditions. For *non-delay* reaction-diffusion systems in one space dimension, periodic travelling waves (wavetrains) are the generic solution form when the kinetics are oscillatory. Note that at least two coupled scalar equations are necessary for a non-delay system to show locally oscillatory dynamics.

These periodic wavetrains are particularly easy to investigate for the class of reaction-diffusion systems known as $\lambda - \omega$ systems, and for these systems their stability can be computed exactly (Kopell & Howard [1973]) – waves with large amplitude are stable while those with small amplitude are unstable.

Periodic wavetrains also exist for equation (5.1); they arise via Hopf bifurcation from the uniform state $u = 1$. To see this, we first convert (5.1) into travelling wave form, by writing $u(x,t) = \tilde{u}(x - ct) = \tilde{u}(\xi)$, to obtain

$$\tilde{u}_{\xi\xi}(\xi) + c\tilde{u}_{\xi}(\xi) + \tilde{u}(\xi)\left(1 - \tilde{u}(\xi + cT)\right) = 0. \tag{5.2}$$

Linearising about the $\tilde{u} = 1$ state by setting $\tilde{u} = 1 + \tilde{v}$ and ignoring higher order terms gives

$$\tilde{v}_{\xi\xi}(\xi) + c\tilde{v}_{\xi}(\xi) - \tilde{v}(\xi + cT) = 0.$$

To seek a periodic solution we set $\tilde{v} = e^{i\omega\xi}$. This gives

$$\omega^2 + \cos\omega cT = 0 \quad \text{and} \quad \omega c = \sin\omega cT.$$

Solving these equations (and noting carefully that they imply ωcT is a second quadrant angle) gives

$$T = \frac{\pi - \sin^{-1}\sqrt{1-\omega^4}}{\sqrt{1-\omega^4}}, \qquad c = \frac{1}{\omega}\sqrt{1-\omega^4}\,. \tag{5.3}$$

These equations define a curve (the bifurcation curve) in the (T, c) parameter plane, parametrised by $\omega \in [0, 1]$. Fig. 5.2 shows the qualitative form of this curve.

Thus for any $c > 0$ a family of periodic travelling waves with speed c will bifurcate from the uniform state $u = 1$ at a critical value of the delay T which increases as c decreases. Close to this bifurcation the wavetrain will have small amplitude and this means it must be unstable, by a result of Gourley & Britton [1993] for a more general class of systems. Further from bifurcation the waves will have larger amplitude and thus may be stable, and some numerical simulations we have carried out confirm this, as we discuss below.

We have carried out numerous numerical simulations of the initial value problem for (5.1) to discover what happens in the wake of an invading wavefront, focussing attention particularly on the case $T > \pi/2$ when the uniform state is unstable and, as we have just shown, periodic wavetrains can exist. All simulations were carried out using the NAG routine *D03PCF*. This NAG routine is not actually intended for delay equations but it is possible to use the routine by storing past solution

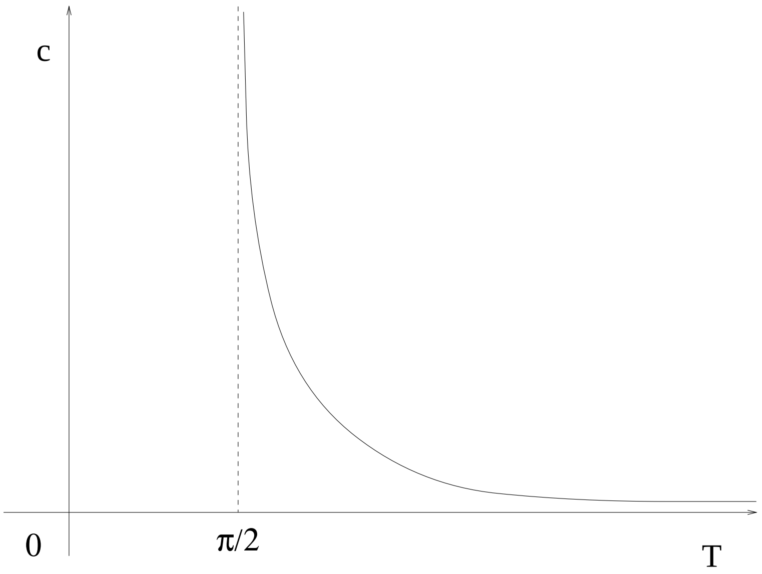

Figure 5.2: Hopf bifurcation curve in the (T, c) parameter plane for equation (5.1). As this curve is crossed a periodic travelling wave solution (wavetrain) will bifurcate from the uniform solution $u = 1$ of (5.1).

values and supplying the $u(x, t - T)$ term to the routine as a forcing function. This approach seems to work well provided the temporal stepsizes are small compared to the delay.

We use a large spatial domain $x \in [0, 2000]$. Since the equation (5.1) involves a discrete time delay the initial data has to be prescribed for all values of $t \in [-T, 0]$ and not just at $t = 0$. The initial data was taken as zero throughout the domain except for a small positive perturbation at the far left (corresponding to the introduction of a small number of the species at one end), and the data was identically prescribed this way for all $t \in [-T, 0]$. The boundary conditions are taken as $u_x = 0$ (i.e. zero flux) at the left hand boundary and $u = 0$ at the right hand boundary. The simulations of (5.1) were carried out for various values of the delay T. The simulations are always stopped before the travelling front reaches the right hand end of the boundary since our main interest here is in the behaviour behind an invading wavefront. We have found a moderately rich variety of dynamical behaviour which depends fundamentally on the particular value of the delay parameter T.

In Fig. 5.3 we take $T = 1.2$; for this value of the delay the uniform steady state $u = 1$ is stable. Thus one can see the solution has evolved to a travelling wave which differs from the KPP wave only in that at the rear the convergence to $u = 1$ is oscillatory rather than monotonic, similar to the fronts in §4 (cf. Figure 4.2). Behind the front (in the so-called wake) the dynamics converges to a steady state as expected for small T. The travelling front solutions of (5.1) are only non-monotone

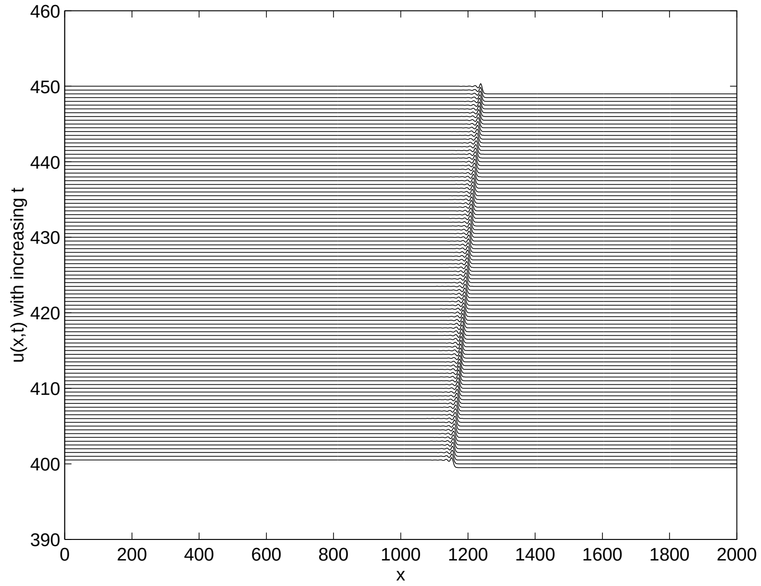

Figure 5.3: Numerical simulation of (5.1) for $T = 1.2$. Boundary and initial conditions are described in the text.

for T exceeding a certain critical value which can be computed analytically in a manner following the calculations described in Gopalsamy et al [1988]. Such loss of monotonicity is associated with a total loss of all relevant real eigenvalues of the travelling wave equation (5.2) linearised about the $\tilde{u} = 1$ state. What it amounts to, after some algebra, is an investigation of the roots λ of the equation

$$F(\lambda; T) := \lambda^2 + c\lambda - e^{\lambda c T} = 0. \tag{5.4}$$

When the delay T is zero the above equation has two real roots of opposite sign and of course in this case the travelling wave equation for (5.1) (i.e. equation (5.2)) can be analysed in the $(\tilde{u}, \tilde{u}_\xi)$ phase plane. The travelling wave in this phase plane is a heteroclinic connection from the fixed point $(1, 0)$ into the origin, and it leaves the fixed point $(1, 0)$ along the unstable manifold thereof, which is associated with the positive root of $F(\lambda; 0) = 0$. For $T > 0$ as far as monotonicity is concerned it is a question of what happens to this positive root. Graphical arguments show that as T is increased from 0 the positive root of (5.4) becomes *two* positive roots which get closer together, eventually coalesce and then go complex. Loss of monotonicity of the front happens at the critical value, which we call $T_{\rm cr}$, at which this coalescence occurs. Using elementary calculus one finds that $T_{\rm cr}$ is found by solving the equation

$$cT_{\rm cr} \exp\left(1 - \frac{1}{2}c^2 T_{\rm cr} + \sqrt{1 + \frac{c^4 T_{\rm cr}^2}{4}}\right) = \frac{2}{cT_{\rm cr}} + \sqrt{\frac{4}{c^2 T_{\rm cr}^2} + c^2}$$

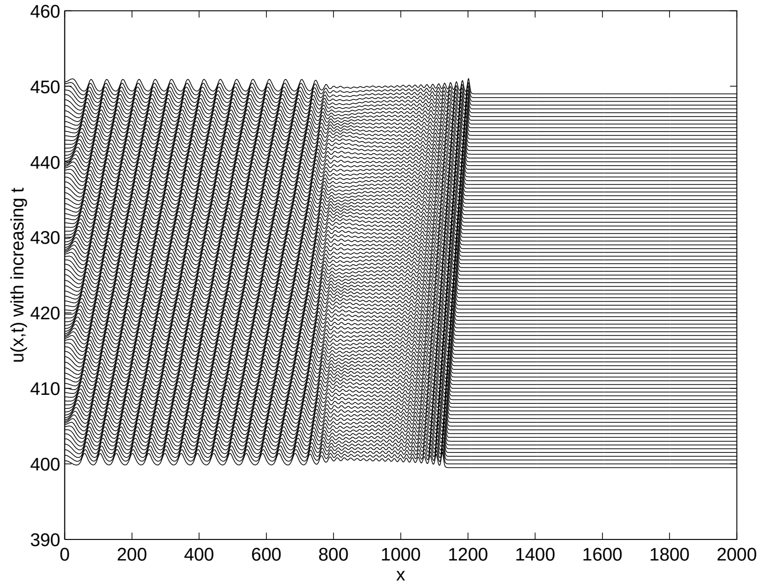

Figure 5.4: Numerical simulation of (5.1) for $T = 1.7$. Boundary and initial conditions are described in the text.

and so loss of monotonicity is predicted for $T > T_{\mathrm{cr}}$. When $c = 2$, which is the minimum speed and the speed observed in the numerical simulations, one finds that $T_{\mathrm{cr}} = 0.56077$. Fig. 5.3 is for a value of T well in excess of this.

In Fig. 5.4 we have chosen $T = 1.7$; at this value of T the uniform state $u = 1$ is unstable. Immediately behind the front there are periodic spatio-temporal oscillations moving parallel to the front and the amplitude of these oscillations decreases as we move away from the front (the solution in this region actually gets very close to the unstable uniform state). Further back we see a band of large amplitude stable periodic travelling waves whose speed is slightly faster than that of the invading front. As far as we are aware these are the first observations of interactions between a travelling front and trains of periodic waves in a scalar integro-differential equation.

In systems of reaction diffusion equations without delay terms and other coupled models such as coupled map lattices and integro-difference equations, this phenomenon has been reported by Sherratt et al [1997]. In fact in many of their simulations they found bands of periodic travelling waves moving in the opposite direction to invasion, although we have not observed this in simulations of our scalar-delayed KPP equation.

Increasing further the delay parameter to $T = 1.9$ we observe in Fig. 5.5 that, again, there are decaying spatio-temporal oscillations immediately behind the front and moving in parallel with it, but further back there is a region in which the solution develops irregular spatial fluctuations whilst apparently being periodic in

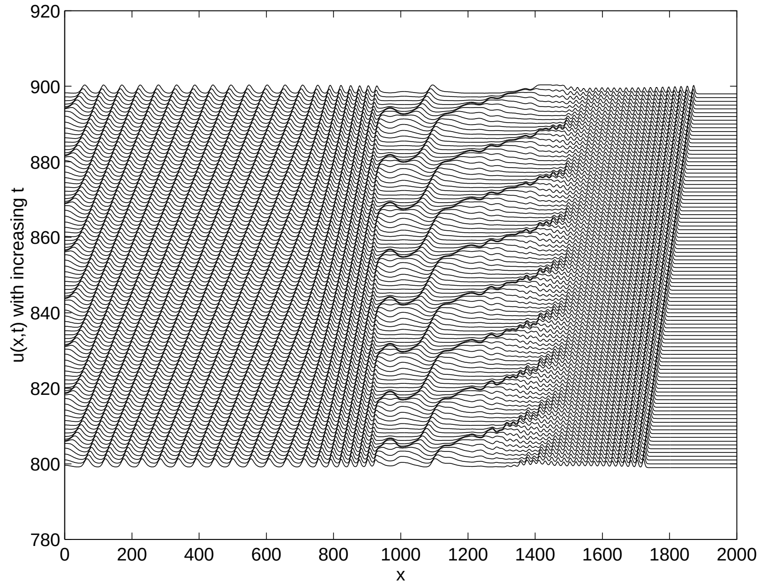

Figure 5.5: Numerical simulation of (5.1) for $T = 1.9$. Boundary and initial conditions are described in the text.

time. Behind this region we once again see a band of periodic travelling waves as in Fig. 5.4. For $T = 2.0$ the dynamical behaviour behind the front stabilises and Fig. 5.6 shows a region of large amplitude waves moving parallel to the front, behind which is another region containing another band of waves moving with a faster speed. We have carried out further numerical simulations for larger values of T but found no new behaviour.

6. Discussion

Travelling fronts are of fundamental importance in mathematical biology and a basic model for travelling fronts is the KPP or Fisher equation. In this paper we have considered an integro-differential equation based on the KPP equation with time-delay and spatial averaging acting on the nonlinearity. Using dynamical systems techniques and numerics, we have shown that travelling fronts are robust and persist for a large class of time-delay and spatial-averaging kernels.

Using invariant manifold theory and geometric singular perturbation theory, a proof of persistence of the KPP front for small delay was given. This approach is a dynamical systems view of travelling fronts, modelled as heteroclinic orbits, and is an alternative to the method of matched asymptotic expansions for singular perturbation problems. Geometric singular perturbation theory is abstract, rigorous

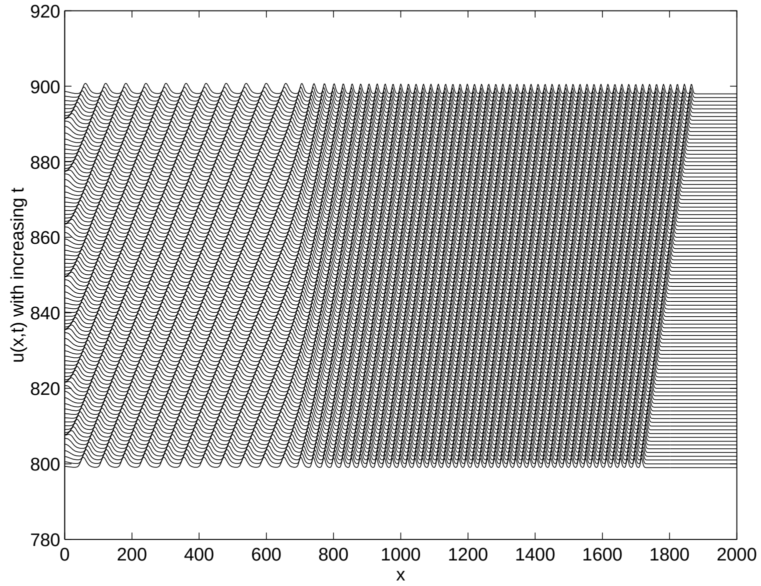

Figure 5.6: Numerical simulation of (5.1) for $T = 2$. Boundary and initial conditions are described in the text.

and does not require an explicit expression for the basic KPP wave. Therefore this technique should have wide applicability to persistence questions for travelling fronts of KPP subjected to perturbations such as spatio-temporal or temporal delay kernels and KPP coupled with reaction-diffusion equations having small diffusion.

The paper applied two numerical approaches to the analysis of fronts: numerical calculation of heteroclinic orbits of the reduced dynamical system by treating it as a boundary-value problem, and direct simulation of the initial-value problem. These two approaches are complementary. Computing heteroclinic orbits of the boundary-value problem is computationally less intensive and both stable and unstable fronts can be calculated. However the class of kernels is limited. On the other hand, numerical simulation of the initial-value problem, while computationally more intensive, is applicable to a larger class of delay kernels and provides important information about the stability and time-evolution of fronts, and, as shown in §5, interaction between travelling fronts and periodic wavetrains can be simulated.

Acknowledgements

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