International Journal of Bifurcation and Chaos, Vol. 3, No. 5 (1993) 1269–1279

TRANSITION WAVES THAT LEAVE BEHIND REGULAR OR IRREGULAR SPATIOTEMPORAL OSCILLATIONS IN A SYSTEM OF THREE REACTION–DIFFUSION EQUATIONS

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Received February 22, 1993; Revised April 12, 1993

Transition waves are widespread in the biological and chemical sciences, and have often been successfully modelled using reaction–diffusion systems. I consider a particular system of three reaction–diffusion equations, and I show that transition waves can destabilise as the kinetic ordinary differential equations pass through a Hopf bifurcation, giving rise to either regular or irregular spatiotemporal oscillations behind the advancing transition wave front. In the case of regular oscillations, I show that these are periodic plane waves that are induced by the way in which the transition wave front approaches its terminal steady state. Further, I show that irregular oscillations arise when these periodic plane waves are unstable as reaction–diffusion solutions. The resulting behavior is not related to any chaos in the kinetic ordinary differential equations.

1. Introduction

A transition wave is a wave that moves through a domain, converting the system concerned from one homogeneous steady state to another. Such waves are widespread in biology and chemistry, and some of the most popular models for their theoretical investigation are systems of reaction–diffusion equations. Specific transition wave phenomena to which reaction–diffusion models have been applied include waves of pursuit and evasion in predator–prey systems [Okubo, 1980], the spatial spread of epidemics [Murray *et al.*, 1986], advancing cell fronts in wound healing [Sherratt & Murray, 1991], calcium waves during development [Lane *et al.*, 1987], and travelling chemical fronts in the Belousov–Zhabotinskii reaction [Kopell & Howard, 1973a]. In this paper I investigate transition waves in a particular system of three coupled reaction–diffusion equations. I consider changing the parameter values so that the steady state behind the wave front undergoes a Hopf bifurcation in the kinetic ordinary differential equations governing the local dynamics. I ask a simple question: how does the transition wave change when this Hopf bifurcation occurs in the local dynamics. One intuitively appealing possibility is that rather than remaining in a homogeneous steady state behind the front, the system will execute spatially homogeneous oscillations, corresponding to the periodic solution of the local dynamics. However, I will show that this does not happen, and that rather the behavior behind the front is spatiotemporal oscillations, which can be

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either regular or irregular. In the case of regular oscillations, I will show that their form is determined by the particular way in which the rear of the transition front perturbs the terminal steady state. Moreover, I will show that when the behavior is irregular, it arises from the destabilisation of regular spatiotemporal oscillations, and that it is not related to chaos in the local dynamics, even when these local ordinary differential equations have a strange attractor rather than a simple stable limit cycle.

2. The Equations

The reaction–diffusion system I consider arises from a model for early tumour growth, developed by Sherratt & Nowak [1992]. The equations address the way in which cells that have undergone a genetic mutation compete with the normal cells around them. Such mutant cells will typically have a proliferative advantage, conferred by the mutation. The division rate of normal cells is self-regulated by a number of biochemicals. These are secreted by the cells into the extracellular domain, and then bind to the cell surface; the amount of surface–bound chemical controls cell division. Genetic mutations can cause cells to alter either the rate at which they secrete chemical regulators into the external environment, or their response to a given level of bound chemical on the cell surface [Weinberg, 1989]. I consider here the case of a cell population whose growth is regulated by a single biochemical, which is produced by the cells, and which inhibits the rate of cell division when it binds to the cell surface. After appropriate nondimensionalisation, the model of Sherratt & Nowak [1992] then has the following form:

$$\partial n/\partial t = \overbrace{D\,\partial^2 n/\partial x^2}^{\text{Cell movement}} + \overbrace{nf(n+m)g(c)}^{\text{Cell division}} - \overbrace{n}^{\text{Cell death}} \tag{1a}$$

$$\partial m/\partial t = D\,\partial^2 m/\partial x^2 + mf(n+m)g(\xi c) - \gamma m \tag{1b}$$

$$\partial c/\partial t = \underbrace{D_c\,\partial^2 c/\partial x^2}_{\text{Chemical diffusion}} + \underbrace{hn + Phm}_{\text{Chemical production}} - \underbrace{hc}_{\text{Chemical decay}}. \tag{1c}$$

Here $n(x, t)$ and $m(x, t)$ are the local densities of normal and mutant cells respectively, and $c(x, t)$ is the local concentration of extracellular chemical; x and t denote space and time, and for simplicity I restrict attention to the case of one space dimension. I represent cell movement by simple linear diffusion, with diffusion coefficient D, which I assume to be unaffected by the mutation; $D_c(\gg D)$ is the chemical diffusion coefficient. The function $f(\cdot)$ represents the effect of crowding on cell division, and $g(\cdot)$ represents the inhibitory effect of the chemical; f and g are both decreasing functions. The parameter h is the (constant) rate at which the normal cells secrete the chemical into the extracellular domain. The mutation is characterised by the parameters ξ and P, which are both < 1 and reflect the decreased response to, and production of the inhibitor, respectively. Finally, the constant γ is > 1, and corresponds to the increased death rate of mutant cells due to an immune response. The nondimensionalisation means that in normal tissue $n = c = 1$, $m = 0$, and to ensure that this is a steady state I require that $f(1) = g(1) = 1$. To be specific, in numerical simulations I will take the following simple functional forms satisfying these criteria: $f(\theta) = (N-\theta)/(N-1)$ and $g(\theta) = k/[1+(k-1)\theta]$. Here N and k are constants > 1, and in all the numerical solutions in the figures, I take $k = 15$ and $N = 10$. However very similar results are obtained for other values of these parameters.

I consider the solution of (1) following a small, localised perturbation to the steady state $n = c = 1$, $m = 0$. Sherratt & Nowak [1992] and Sherratt [1993a] have previously shown that such a perturbation rapidly decays if the immune response is sufficiently strong that $\gamma > g(\xi)$. However, if $\gamma < g(\xi)$, the perturbation induces a transition wave, which moves outwards from the site of the perturbation with speed given approximately by $2\sqrt{D[g(\xi)-\gamma]}$. The passage of the transition wave leaves the system in a new steady state, which corresponds to an early tumour precursor. The form of this steady state depends on the parameter P. For $1 > P > P_{\text{crit}}$, the system is left in the steady state $n = 0$, $m = M$, $c = PM$, where M is the unique root on $(1, \infty)$ of $f(M)g(\xi PM) = \gamma$. However, the system bifurcates at $P = P_{\text{crit}}$, and for $P < P_{\text{crit}}$, the steady state behind the transition wave changes, and has a nonzero value of n, corresponding to a tumour precursor containing a mixture of normal and mutant cells. I denote this new steady state by $n = n_s$, $m = m_s$, $c = c_s$. It is straightforward to determine n_s, m_s, c_s and P_{crit} analytically [Sherratt, 1993a]. Typical solutions for $P > P_{\text{crit}}$ and $0 < P < P_{\text{crit}}$

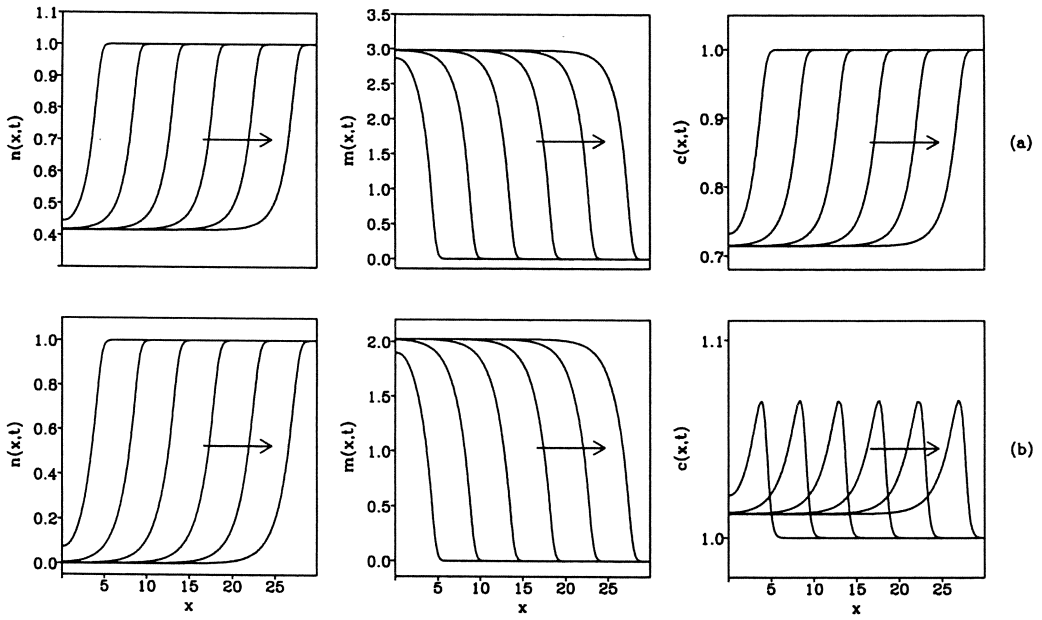

Fig. 1. A typical solution of the system (1) when the parameter P lies in the interval (a) $0 < P < P_{\text{crit}}$, (b) $P > P_{\text{crit}}$ following a small perturbation to the steady state $n = c = 1$, $m = 0$ near $x = 0$ at $t = 0$. This solution has the form of an advancing wave of mutant cells and a receding wave of normal cells, with an associated wave of chemical regulator. Behind this transition wave front, the system is left in an equilibrium in which m and c are nonzero, and (a) $n > 0$, (b) $n = 0$. The solutions are plotted as a function of space at equal time intervals of $t = 20$, and the parameter values are $\xi = 0.1$, $\gamma = 5.5$, $h = 10$, $D = 0.01$, $D_c = 1$, and (a) $P = 0.1$, (b) $P = 0.5$. (For these values of the other parameters, $P_{\text{crit}} \approx 0.21$). Here and in other figures, the partial differential equations were solved numerically using the method of lines and Gears' method.

are illustrated in Fig. 1. Here and throughout the paper I solve (1) on $[0, \infty)$ subject to $\partial n/\partial x = \partial m/\partial x = \partial c/\partial x = 0$ at $x = 0$ and $n, c \to 1$, $m \to 0$ as $x \to \infty$. This use of a semi-infinite domain with a symmetric boundary condition reduces the time taken for numerical solution, and the solutions are essentially the same as those given by solving on $(-\infty, \infty)$ subject to $n, c \to 1$, $m \to 0$ as $x \to \pm\infty$.

Numerical calculation shows that for some values of the other parameters, as P is decreased below zero, the steady state (n_s, m_s, c_s) undergoes a Hopf bifurcation in the kinetic ordinary differential equations corresponding to (1), giving rise to a limit cycle; these kinetic equations are simply

$$dn/dt = nf(n+m)g(c) - n\,, \tag{2a}$$

$$dm/dt = mf(n+m)g(\xi c) - \gamma m\,, \tag{2b}$$

$$dc/dt = h \cdot (n + Pm - c)\,. \tag{2c}$$

It is important to stress that $P < 0$ is not a biologically realistic parameter regime, and thus the corresponding behavior is of mathematical interest only. The destabilisation of the steady state (n_s, m_s, c_s) of (1) through a Hopf bifurcation in the kinetics is quite different from the much studied Turing bifurcation (reviewed by Murray [1989]), since in the case of a Hopf bifurcation, the system becomes unstable to perturbations of all wave numbers. I consider here the change that occurs in the behavior behind the transition wave when this Hopf bifurcation occurs in the kinetics. In a previous publication [Sherratt, 1993b] I have considered this question for the simpler case of the system of two reaction–diffusion equations given by putting $h = \infty$ in (1). Here, I demonstrate very similar behavior in the full system (1), and I investigate the way in which the value of the parameter ratio D_c/D affects the solution. In this full system there is the additional complication that the kinetic ordinary differential equations are third order, and may thus have chaotic behavior themselves. I consider the effects of this in Sec. 6.

3. Regular and Irregular Spatiotemporal Oscillations

I have solved the reaction–diffusion system (1) numerically for a wide range of parameter sets for which the kinetic equations (2) have a limit

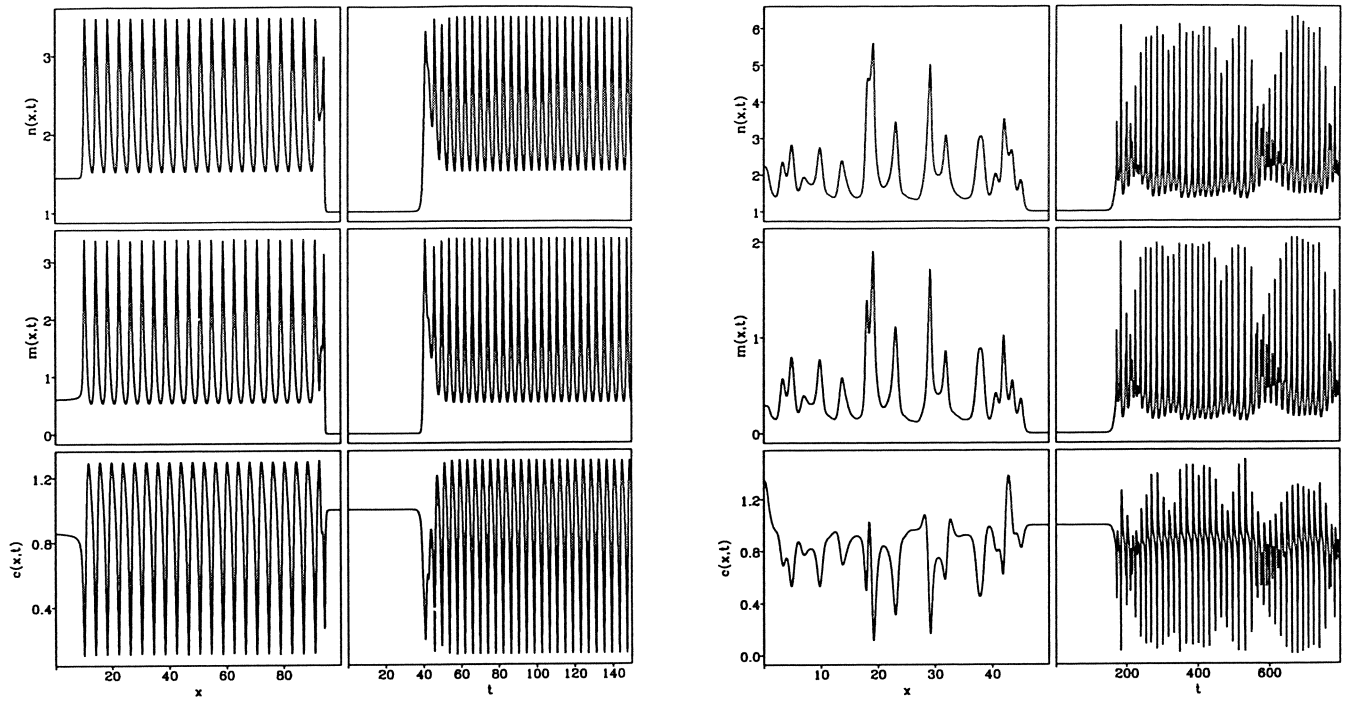

Fig. 2. Solutions of (1) for parameter values such that there is a limit cycle in the kinetic ordinary differential equations. In both cases, a front moves out in the positive x direction; it leaves behind regular spatiotemporal oscillations in (a), and irregular spatiotemporal oscillations in (b). The parameter values are (a) $\xi = 0.15$, $\gamma = 4$, $P = -1$, $h = 20$, $D = 0.01$, $D_c = 1$; (b) $\xi = 0.45$, $\gamma = 2$, $P = -3$, $h = 20$, $D = 0.01$, $D_c = 1$, and the solutions are plotted as a function of x at (a) $t = 400$, (b) $t = 800$, and as a function of t at (a) $x = 10$, (b) $x = 5$. For all of the wide range of other parameter sets I have tried, the solution falls into one or other of these two categories, although in some cases both types of behavior are observed [see Figs. 6 and 7(a)].

cycle. As previously, I am considering the behavior following a small, localised perturbation to the steady state $n = c = 1$, $m = 0$. For all parameter sets, a wave moves outwards from the site of the perturbation. However, the wave no longer connects two steady states; rather, the behavior behind the wave front is of one of two types, either regular or irregular spatiotemporal oscillations. Examples of these two types of solution are illustrated in Fig. 2.

As in the solutions for $P > 0$, the wave front moves with constant shape and constant speed, given approximately by $2\sqrt{D(g(\xi) - \gamma)} \equiv a$, say. I therefore expect the front to be well approximated by a solution of (1) that is a function of the similarity variable $z = x/a + t$. Such solutions satisfy the ordinary differential equations

$$n' = (D/a^2)n'' + nf(n+m)g(c) - n, \tag{3a}$$

$$m' = (D/a^2)m'' + mf(n+m)g(\xi c) - \gamma m, \tag{3b}$$

$$c' = (D_c/a^2)c'' + h \cdot (n + Pm - c), \tag{3c}$$

where prime denotes d/dz. When the kinetics have not passed through Hopf bifurcation, so that the solution of partial differential equations has the form of a simple transition wave such as that illustrated in Fig. 1, this transition wave corresponds to a heteroclinic connection in the ordinary differential equation system (3). (However, I have only numerical evidence for the existence of such a connection). An obvious first step in understanding the spatiotemporal oscillations shown in Fig. 2 is therefore to consider whether the system (3) undergoes any bifurcation at the same parameter values as Hopf bifurcation in the kinetics (2). Linear analysis near the steady states of (3) suggests that this is not so, and this is confirmed by numerical solutions. I concluded that the transition wave continues to exist as a connection between two steady states. It is for this reason that it is reasonable to continue to refer to the initial wave front as a transition wave. However, as the kinetics pass through Hopf bifurcation, the steady state behind the transition wave becomes unstable in the full system (1).

4. Periodic Plane Waves Behind the Transition Wave

For parameter values giving regular spatiotemporal oscillations behind the transition wave front, careful numerical investigation suggests that the spatial oscillations appear to move away from the front with a speed considerably greater than that of the front (Fig. 3). This raises the possibility that the regular spatiotemporal oscillations may in fact be periodic plane waves. These are travelling wave solutions of constant shape and speed that oscillate in both space and time. For a system of reaction–diffusion equations with a stable limit cycle in the kinetics, Kopell & Howard [1973b] showed that periodic plane wave solutions exist for wave speeds greater than a critical value, and arise via a Hopf bifurcation in the travelling wave ordinary differential equations. For the system (1), the equations are

$$n' = (D/s^2)n'' + nf(n+m)g(c) - n\,, \tag{4a}$$

$$m' = (D/s^2)m'' + mf(n+m)g(\xi c) - \gamma m\,, \tag{4b}$$

$$c' = (D_c/s^2)c'' + h\cdot(n + Pm - c)\,, \tag{4c}$$

where s is the wave speed, $\zeta = t + x/s$ is the travelling wave variable, and prime denotes $d/d\zeta$. Periodic plane waves correspond to a limit cycle solution of (4).

If the regular spatiotemporal oscillations behind the transition wave are periodic plane waves, then their speed must be given by the ratio of the spatial to temporal periods of these oscillations. For a number of different parameter sets, I therefore calculated these two periods from the numerical solution of the reaction–diffusion system (1), and determined the prospective periodic plane wave speed as the period ratio. I then determined numerically the form of the periodic solution of (4) for this value of the speed s. This is in fact a nontrivial numerical calculation, since the limit cycle of the sixth order system (4) is unstable as an ordinary differential equation solution, and I used the computer package AUTO [Doedel, 1981; Doedel & Kernevez, 1986] to track the limit cycle with increasing s from its birth at Hopf bifurcation. In all cases, the comparison is very good between the periodic plane wave calculated in this way and the spatiotemporal oscillations in the partial differential equation solutions (Fig. 4).

An important question is why the passage of the transition wave induces a periodic plane wave moving in the opposite direction. A partial answer to this question can be found by considering the way in which the rear of the transition wave front approaches the steady state (n_s, m_s, c_s). This approach has the form of exponentially decaying oscillations, whose form can be determined from the eigenvalues of (3) at this steady state. This suggested a simple numerical experiment. I calculated these eigenvalues and solved the equations (1) numerically with initial conditions given by applying the corresponding decaying oscillations as a small perturbation to the steady state (n_s, m_s, c_s). For a wide range of parameter values, this initial perturbation grew to give exactly the same behavior as was observed behind the transition wave front. That is, when regular spatiotemporal oscillations (in the form of a periodic plane wave) were observed

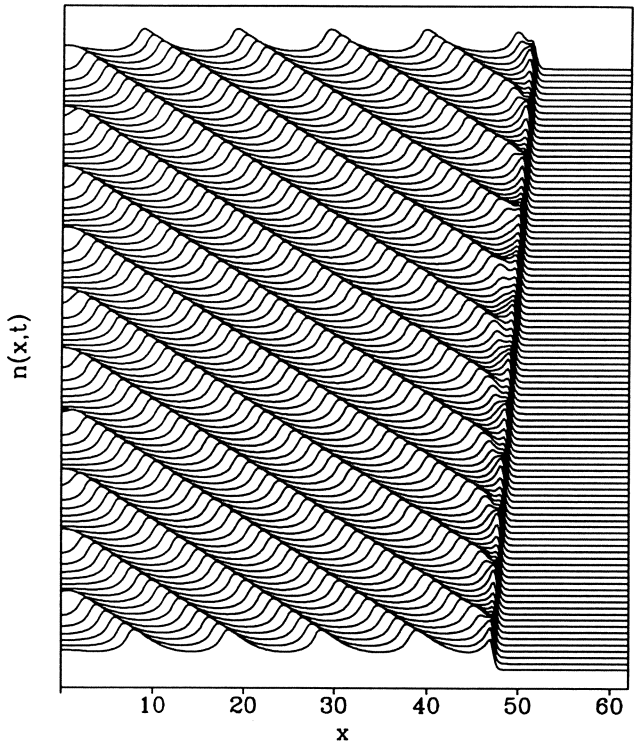

Fig. 3. A different visualisation of the solution of (1) for parameters giving regular oscillations behind the advancing front. The solution for $n(x, t)$ is plotted as a function of space x at successive times, with the vertical separation of any two solutions proportional to the time interval between them. This presentation of the solutions shows that the regular oscillations move in the negative x direction, apparently with constant shape and speed. The solutions for $m(x, t)$ and $c(x, t)$ are qualitatively very similar. The parameter values are $\xi = 0.6$, $\gamma = 1.5$, $P = -2$, $h = 10$, $D = 0.01$, $D_c = 1$, and $550 \leq t \leq 600$.

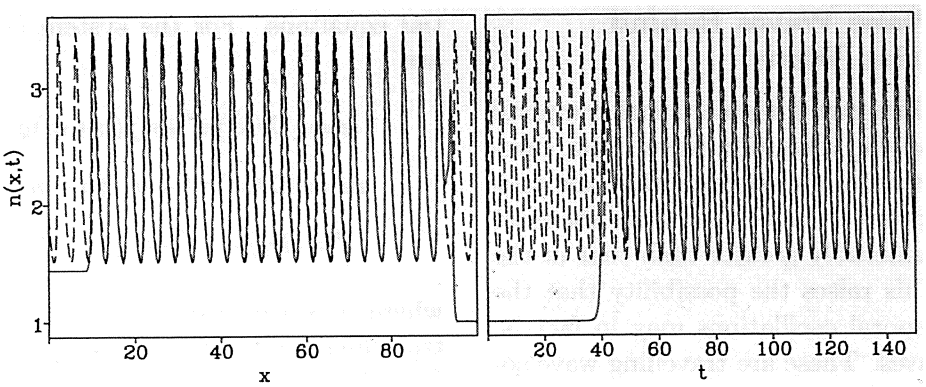

Fig. 4. A comparison of the solution of (1) (full red curve) with the corresponding periodic plane wave (broken black curve). The periodic plane wave is the limit cycle solution of (4) with $s \approx 0.989$. This value of the wave speed s was calculated as the ratio of the average space and time periods of the regular oscillations in the solution of the partial differential equations (1), and the phase of the periodic plane waves is chosen to match the partial differential equation solutions (this represents an appropriate choice of the origin of $\zeta = t + x/s$). The parameter values are as in Fig. 2(a), and the solution for $n(x, t)$ is plotted as a function of x at $t = 150$ and as a function of t at $x = 10$. The comparison between the periodic plane wave and partial differential equation solutions for $m(x, t)$ and $c(x, t)$ is also extremely good, and is omitted for brevity.

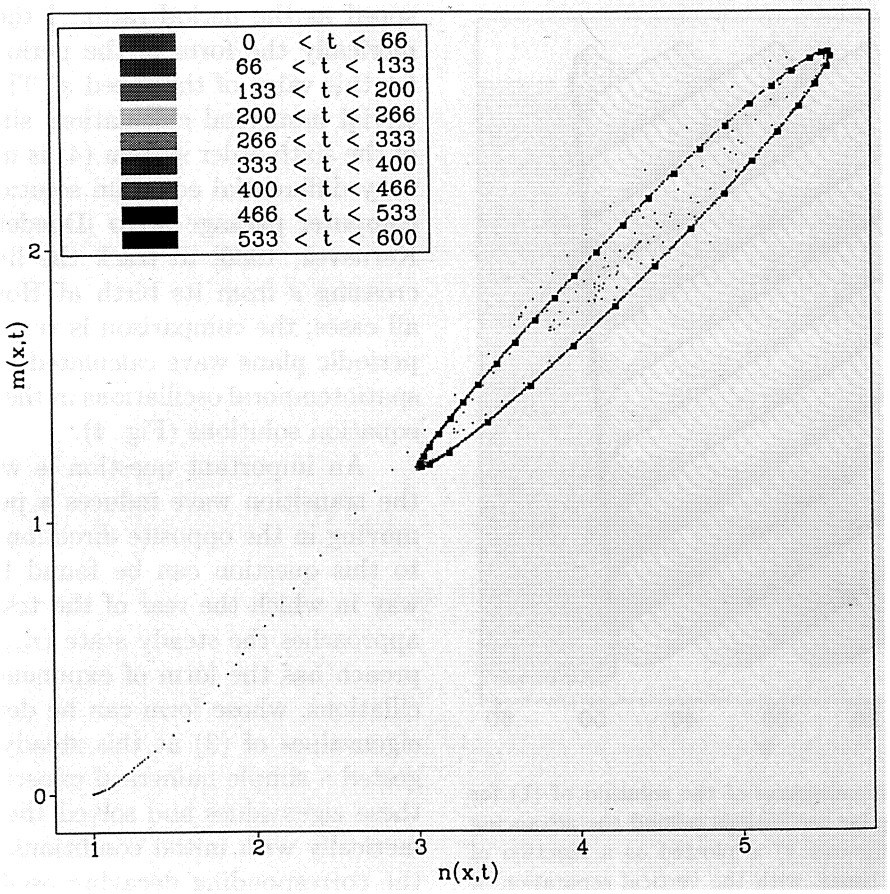

Fig. 5. An illustration of the temporal evolution in the n–m plane of a solution exhibiting regular oscillations behind the transition wave. The parameters are as in Fig. 2(a), and the solution is illustrated as t varies at $x = 10$; the color coding shows the temporal evolution. The solution starts at the far field steady state (1, 0, 1), and evolves to (n_s, m_s, c_s). It then spirals out to the orbit corresponding to the regular oscillations. This orbit compares very well with the projection onto the n–m plane of the limit cycle solution of (4) with $s = 2.1$, which is indicated by black squares. This wave speed s was calculated as the ratio of the average space and time periods of the regular oscillations.

behind the transition wave, the small perturbation grew to give a periodic plane wave of the same speed, moving in the direction in which the perturbation decayed, which corresponds to the direction opposite to that of the movement of the transition wave front. Moreover, when irregular oscillations were observed behind the transition front, similar oscillations arose from the decaying oscillatory perturbation in the numerical experiment. These results strongly suggest that the behavior behind the transition wave front is determined in large part by the way in which the rear of this wave front approaches the terminal steady state (n_s, m_s, c_s). Figure 5 illustrates the temporal evolution of the periodic plane waves from this terminal steady state in the case of regular oscillations.

5. Unstable Periodic Plane Wave Give Rise to Irregular Oscillations

It remains to consider the relationship between the periodic plane waves that constitute the regular oscillations behind the transition wave for some parameter values, and the irregular oscillations that are observed for other parameters. In some cases, there is a mixture of these behaviors, with regular oscillations immediately behind the front, and irregular oscillations further back [Figs. 6 and 7(a)]. This suggested to me that the irregular oscillations may arise because although the passage of the front does induce periodic plane waves, these waves are unstable as solutions of the full system (1). The stability of periodic plane waves has been considered by a number of authors, for example Kopell & Howard [1973b], Othmer [1977], Cope [1980], Maginu [1979, 1981]. These papers all discuss partial answers to the question of when a periodic plane wave is stable as a partial differential equation solution and when it is unstable, but a full answer is far from clear. However, it is relatively straightforward to investigate stability numerically: one just calculates the form of the plane wave limit cycle, and then uses this, with small random perturbations, as an initial condition in the numerical solution of the reaction–diffusion equations. This enabled me to test the hypothesis that the regularity of oscillations behind the transition wave front depends on the stability of the periodic plane wave induced by

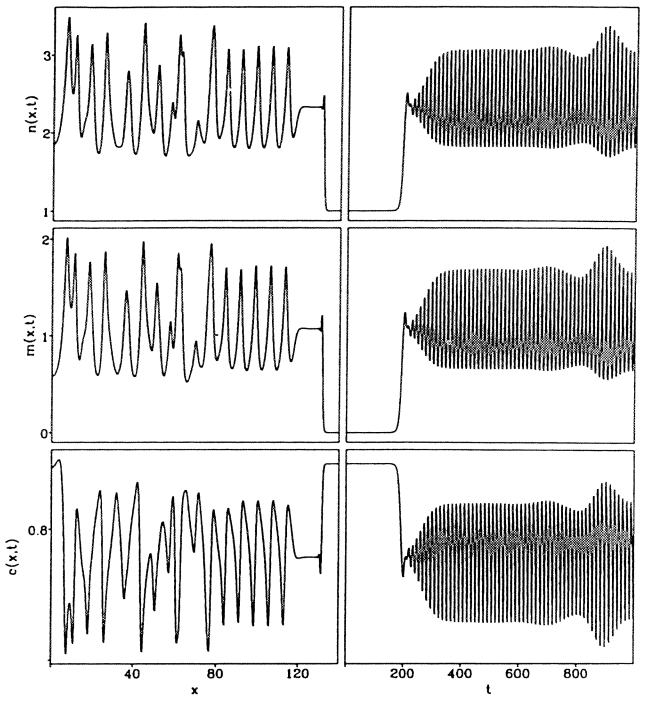

Fig. 6. A solution of (1) exhibiting both regular and irregular oscillations behind the transition wave. This behavior occurs because the passage of the transition front induces periodic plane waves that are just unstable as reaction–diffusion solutions. Therefore the regular oscillations are visible close to the front, but further back they have destabilised to give more irregular behavior. The parameter values are $\xi = 0.45$, $\gamma = 2$, $P = -1.5$, $h = 20$, $D = 0.01$, $D_c = 0.5$, and the solution is plotted as a function of x at $t = 2500$, and as a function of t at $x = 14$.

this front. I considered a wide range of parameter values falling into two classes, in which the behavior behind the transition front is either regular spatiotemporal oscillations, or regular oscillations immediately behind the front, with irregular oscillations further back. For each set of parameters falling into the latter class, the periodic plane wave corresponding to the regular oscillations proved to be unstable in a numerical test, whereas for each parameter set in the former class, the corresponding periodic plane wave was stable. This is consistent with the hypothesis, and suggests that when the oscillations are irregular even immediately behind the front (as in Fig. 2), this occurs because the front again induces a periodic plane wave, but with a speed such that the wave is very unstable as a reaction–diffusion solution. Examples of the strange attractors on which the irregular oscillations lie are illustrated in Figs. 7(a) and 7(b).

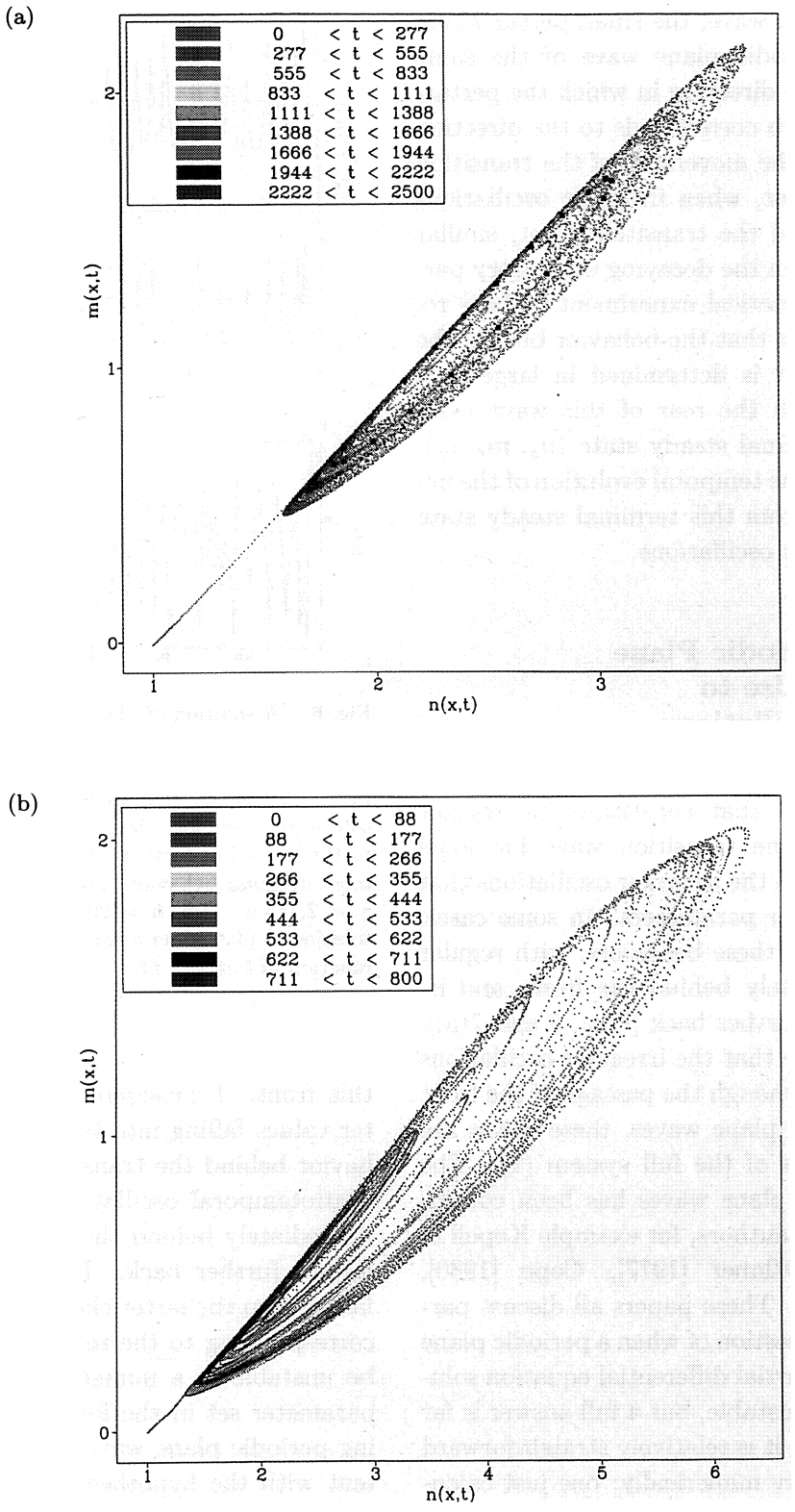

Fig. 7. Illustrations of the temporal evolution in the n–m plane of solutions of (1) exhibiting irregular oscillations behind the transition front. The parameter values are (a) as in Fig. 6, (b) as in Fig. 2(b), and the solution is illustrated as t varies at (a) $x = 14$, (b) $x = 5$; the color coding shows the temporal evolution. In both cases the solution starts at the far field steady state (1, 0, 1), and evolves to irregular oscillations on what appears to be a strange attractor. In (a), regular oscillations are visible immediately behind the transition front (see Fig. 6), and correspondingly in this figure the solution remains close to the orbit corresponding to these regular oscillation (denoted by black squares) throughout the time phase in which the solution is shown in pink. The orbit corresponding to the regular oscillations is simply the projection onto the n–m plane of the limit cycle solution of (4) with $s = 0.64$.

6. The Roles of D_c and Period Doubling

An important omission in the discussion thus far has been the role of the parameter D_c. Multiplying both D and D_c by any given factor corresponds simply to a change in the spatial scale, but the ratio D_c/D is an important determinant of the behavior of the equations. This ratio corresponds to the relative dispersal rates of the biochemical regulator of cell division compared to that of the cells themselves; intuitively one expects $D_c/D \gg 1$. Detailed numerical investigation suggests that as the ratio is increased, the qualitative form of the solution remains the same, but both the spatial scale of the oscillations behind the advancing front and the duration of the regular oscillation phase increase (Fig. 8). This is as expected intuitively: a rapidly diffusing regulator tends to both stabilise and homogenise a reaction–diffusion solution.

Another outstanding issue is the possibility of chaotic behavior in the kinetic ordinary differential equations (2), which is a third order system. Numerical investigation reveals that such behavior does exist for some parameter values, arising via a period doubling cascade, as illustrated in Fig. 9. I have solved the reaction–diffusion system (1) for sets of parameter values corresponding to successive period doublings in the kinetic ordinary differential equations, and these reaction–diffusion solutions do not exhibit any corresponding bifurcation (Fig. 10). This is consistent with my hypothesis in the previous section, that irregular oscillations in the reaction–diffusion system arises from destabilization of periodic plane waves and is unrelated to whether or not there is chaos in the kinetic ordinary differential equations.

Intuitively, one can think of the reaction–diffusion system (1) as the limiting form of a series of identical coupled oscillators. On this basis, a number of previous authors have studied such coupled oscillator systems as charicatures of reaction–diffusion systems [for example, Wang & Nicolis, 1987; Aaronson *et al.*, 1987]. In one such study, Fujisaka & Yamada [1983] showed that when two identical chaotic oscillators are coupled by a discrete representation of diffusion, the system exhibits nonuniform chaos when the coupling is sufficiently strong. The present study shows quite different results in a full reaction–diffusion system — the introduction of diffusive coupling can induce regular spatiotemporal behavior, albeit transiently, in chaotic oscillators (Figs. 9 and 10). This

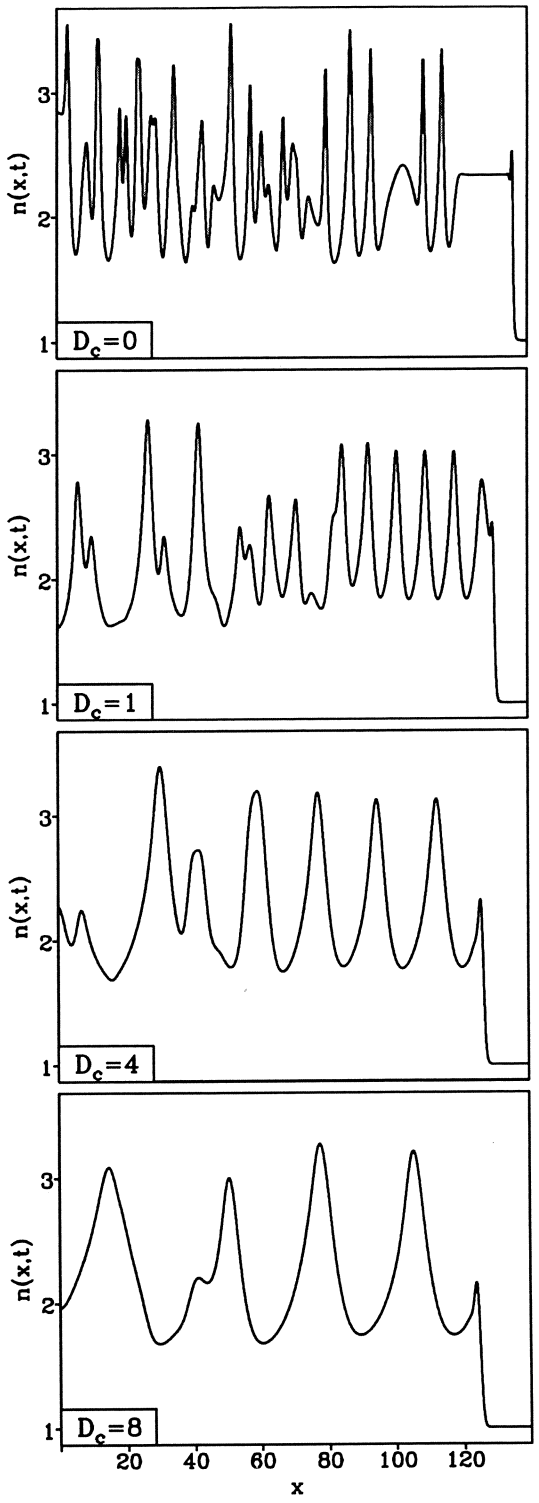

Fig. 8. An illustration of the effect of varying the parameter D_c on the solution of (1). As D_c increases, the spatial scale of the oscillations behind the wave front increases, and regular oscillations persist for a longer time before destabilising. For brevity, I show the solution for n as a function of x at time $t = 2500$ only; the solutions for m and c are qualitatively very similar. The other parameter values are $\xi = 0.45$, $\gamma = 2$, $P = -1.5$, $h = 20$, $D = 0.01$. The solution for $D_c = 0.5$ is illustrated in Fig. 6.

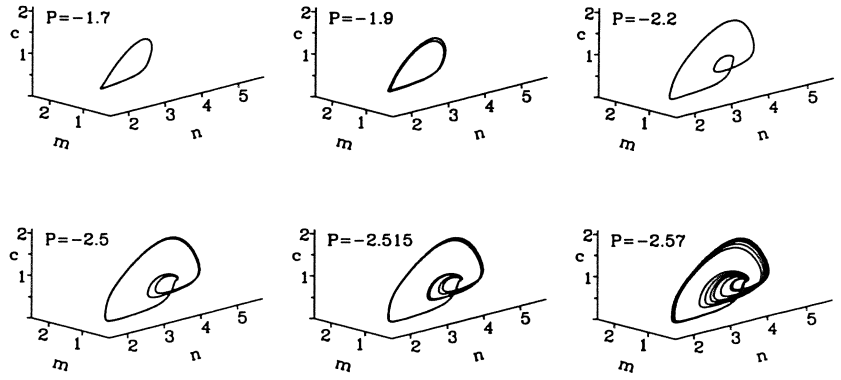

Fig. 9. An example of a period-doubling cascade giving rise to a strange attractor in the kinetic ordinary differential equations (2). The solutions are shown for 6 values of the parameter P; the other parameter values are $\xi = 0.2$, $\gamma = 3$, $h = 10$. The system (2) was solved numerically using a Runge–Kutta–Merson method, and the solution was plotted after allowing sufficient time for transients to dissipate. Numerical evidence suggests that in each case, the illustrated attractors are global attractors within the first quadrant.

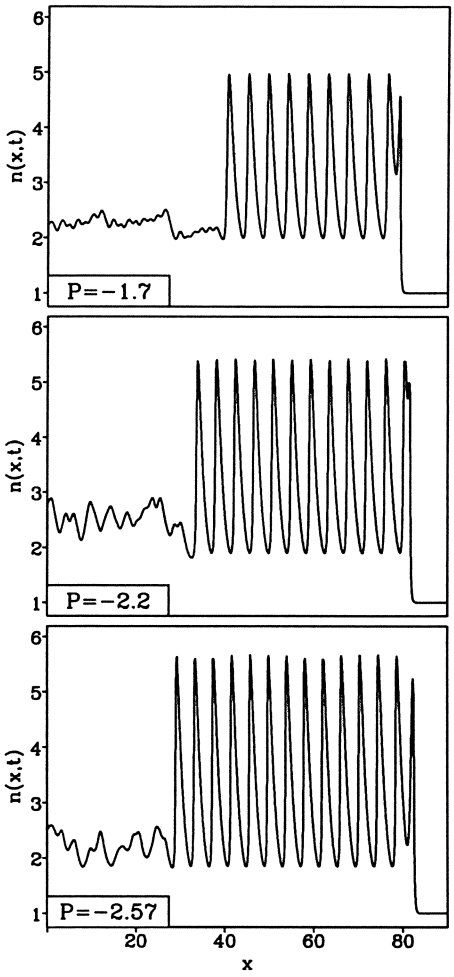

Fig. 10. An illustration of the continuity of solutions of (1) as the kinetic ordinary differential equations (2) pass through a period doubling cascade. The solutions are shown for three values of the parameter P; the other parameters are as in Fig. 9, and the corresponding attractors in the kinetics are shown in that figure. I plot $n(x, t)$ as a function of x at $t = 270$ only; the solutions for m and c are qualitatively very similar.

result is reminiscent of the phenomenon of chaotic synchronisation in ordinary differential equation systems [Pecora & Carroll, 1990].

7. Conclusions

Reaction–diffusion equations are a highly successful class of models with a wide range of applications throughout the biological and chemical sciences. One important phenomenon that has been modelled using reaction–diffusion systems is that of transition waves. Here I have considered a way in which transition waves can be destabilized, so that the system exhibits spatiotemporal oscillations behind the transition wave front, rather than remaining at a steady state. I have shown that such a change in behavior occurs as the kinetics pass through a Hopf bifurcation, and that the resulting spatiotemporal oscillations are periodic plane waves, moving away from the transition wave front. If these periodic plane waves are stable as solutions of the reaction–diffusion equations, they persist, but if they are unstable they degenerate into irregular spatiotemporal oscillations. This behavior is unrelated to any chaos in the kinetic ordinary differential equations, and is a novel way in which spatiotemporal irregularities can arise naturally in reaction–diffusion systems.

Acknowledgments

I am extremely grateful to Dr Alan Champneys (School of Mathematics, University of Bath) for help with the AUTO package. Thanks also to Dr Philip Maini (Mathematical Institute, Oxford) for advice and support.

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