Stripes or spots? Nonlinear effects in bifurcation of reaction–diffusion equations on the square

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Bifurcation to spatial patterns in a two-dimensional reaction–diffusion medium is considered. The selection of stripes versus spots is shown to depend on the nonlinear terms and cannot be discerned from the linearized model. The absence of quadratic terms leads to stripes but in most common models quadratic terms will lead to spot patterns. Examples that include neural nets and more general pattern formation equations are considered.

1. Introduction

Reaction–diffusion models are commonly used as mechanisms for pattern formation in development and other biological phenomena (Murray 1989). Analogous models are used in modelling neural pattern formation (Ermentrout & Cowan 1979). These depend on lateral inhibition and the so-called Turing instability. The Turing instability can be loosely defined as a mechanism by which spatially inhomogeneous perturbations of a steady state grow exponentially, while constant perturbations decay. Bifurcation theory can be used to prove the existence of small-amplitude spatial patterns for these systems (Fife 1979). In his recent book, Murray (1989) comments that in two-dimensional spatial domains, stripes are difficult to obtain for reaction–diffusion models whereas they arise quite naturally in many 'neural' models. In this note, we demonstrate a selection mechanism for 'stripes' versus 'spots' in systems of reaction–diffusion and other Turing instability-driven systems. We restrict ourselves to a square with periodic boundary conditions, thus eliminating any intrinsic anisotropy. By keeping on a finite domain, we also remove the problems of infinitely many wave modes intrinsic to problems on the whole plane. The 'dispersion' relation for the linearized problem will be typical ('vanilla' in Murray's parlance, which means that there is a single maximum at the critical wavenumber) and will have a maximum at some non-zero wave mode. As the bifurcation parameter varies, the maximum will be pushed across the zero and result in instability. This mode will grow until the nonlinear terms become important. It is these oft ignored nonlinear terms that determine the selection of stripes versus spots. Indeed, we show that both stripes and spots cannot simultaneously be stable and one and only one will be selected. This selection mechanism was first described by Sattinger using symmetry arguments for general equations in a Banach space (Sattinger 1978). Busse (1978) noted the importance of quadratic terms in his analysis of symmetry breaking in the Benard convection models and how they can lead to selection of 'spots' or stripes. We applied Sattinger's techniques in

Ermentrout & Cowan (1979) to show the selection in a model for hallucinations. Here, we are more concrete in that we provide a general algorithm for determining the selected pattern for arbitrary reaction–diffusion equations of two variables. The source code for the algorithm is available by request.

In §2, we derive the nonlinear equations and analyse them to determine the keys to selection. We apply the general results of this section to a one-variable planar lateral-inhibitory neural network. In §3, we numerically solve a simple planar activator–inhibitor model and show how as the quadratic parameter varies, a transition from spots to stripes is made. No change in the linearized equations occurs; this is a purely nonlinear effect.

2. Derivation of nonlinear equations

We start abstractly with the following equation:

$$\mathscr{L}u = \mathscr{Q}(u,u) + \mathscr{C}(u,u,u) + \tilde{\lambda}\mathscr{B}u + \text{h.o.t.}, \tag{2.1}$$

where $\mathscr{L}$ represents the linear terms, $\tilde{\lambda}$ is the bifurcation parameter, $\mathscr{Q}$ is quadratic terms, $\mathscr{C}$ is cubic terms, and 'h.o.t.' denotes higher-order nonlinear terms and terms depending on the bifurcation parameter in a nonlinear fashion. The domain is the unit torus (the square with periodic boundary conditions). For example in a typical reaction diffusion system,

$$\mathscr{L} = -A - D\nabla^2, \mathscr{Q}(u,u) = q(u,u), \mathscr{B} = B \quad \text{and} \quad \mathscr{C}(u,u,u) = c(u,u,u), \tag{2.2}$$

where A, B, and D are matrices, q is a quadratic form, and c is a cubic form. We assume without loss of generality that we are on the square with side 2π and that the first unstable mode occurs at the wavenumber $k = 1$ (If the first unstable wavenumber is some other value, then we shrink the domain size by the appropriate factor.) Thus we assume that $\mathscr{L}(\boldsymbol{e}\cos x) = (L_1\boldsymbol{e})\cos x$, where L_1 is a matrix with a simple zero eigenvalue and $\boldsymbol{e}$ is the eigenvector. We also assume that there is an adjoint eigenvector $\boldsymbol{f}$ satisfying $\mathscr{L}^*(\boldsymbol{f}\cos x) = (L_1^{\mathrm{T}}\boldsymbol{f})\cos x$ and such that $\boldsymbol{f}\cdot\boldsymbol{e} = 1$. For the reaction–diffusion system, $L_1 = -A + D$ and the determinant of L_1 is zero. We assume that for all other wavenumbers k the corresponding matrix L has all eigenvalues in the left half-plane. Due to isotropy of the medium, $\boldsymbol{e}\cos y$ is also an eigenfunction for $\mathscr{L}$. Thus the solution to the linearized equation of (2.1) is $\boldsymbol{e}(r\cos x + s\cos y)$, where r and s are arbitrary scalars. Note that if $r = 0$ and $s \neq 0$, we have a 'stripe' while if both r and s are non-zero and in particular, equal, we have a 'spot'. Thus our goal is to see if r and s are determined from the nonlinear terms.

We let $\tilde{\lambda} = \epsilon^2\lambda$ and seek a perturbation expansion in $u(x,y)$:

$$u(x,y) = \epsilon\boldsymbol{e}(r\cos x + s\cos y) + \epsilon^2 u_1 + \epsilon^3 u_2 + \dots \tag{2.3}$$

Substitution into (2.1) reveals that u_1 satisfies:

$$\mathscr{L}u_1 = \tfrac{1}{2}(r^2+s^2)\,Q_0(\boldsymbol{e},\boldsymbol{e}) + \tfrac{1}{2}Q_4(\boldsymbol{e},\boldsymbol{e})\,(s^2\cos 2y + r^2\cos 2x) + 2rs\cos x\cos y\,Q_2(\boldsymbol{e},\boldsymbol{e}). \tag{2.4}$$

$Q_j(\boldsymbol{e},\boldsymbol{e})$ are the vectors defined by:

$$Q_0(\boldsymbol{e},\boldsymbol{e}) = \mathscr{Q}(\boldsymbol{e},\boldsymbol{e}), \quad Q_4(\boldsymbol{e},\boldsymbol{e})\cos 2x = \mathscr{Q}(\boldsymbol{e},\boldsymbol{e}\cos 2x),$$
$$Q_2(\boldsymbol{e},\boldsymbol{e})\cos x\cos y = \mathscr{Q}(\boldsymbol{e}\cos x,\boldsymbol{e}\cos y).$$

Let L_0, L_2, and L_4 be defined by:

$$\mathscr{L}\boldsymbol{v} = L_0\,\boldsymbol{v}, \tag{2.5}$$

$$\mathscr{L}(\boldsymbol{v}\cos x\cos y) = (L_2\,\boldsymbol{v})\cos x\cos y, \tag{2.6}$$

$$\mathscr{L}(\boldsymbol{v}\cos 2x) = (L_4\,\boldsymbol{v})\cos 2x, \tag{2.7}$$

where $\boldsymbol{v}$ is an arbitrary vector. For the reaction diffusion model, these are respectively, $-A$, $-A+2D$, and $-A+4D$. Each of these matrices is invertible since we assumed all wave modes other than $k\equiv 1$ were stable (and so had no zero eigenvalues). Thus we can solve for u_1:

$$u_1(x,y) = \tfrac{1}{2}L_0^{-1}Q_0(\boldsymbol{e},\boldsymbol{e})\,(r^2+s^2)+\tfrac{1}{2}L_4^{-1}Q_4(\boldsymbol{e},\boldsymbol{e})\,(r^2\cos 2x+s^2\cos 2y) + 2L_2^{-1}Q_2(\boldsymbol{e},\boldsymbol{e})\,rs\cos x\cos y). \tag{2.8}$$

$u_2(x,y)$ satisfies:

$$\mathscr{L}u_2 = 2\mathscr{Q}(u_1,\boldsymbol{e}(r\cos x+s\cos y)) +\mathscr{C}(\boldsymbol{e}(r\cos x+s\cos y),\cdot,\cdot)+\lambda B\boldsymbol{e}\,(r\cos x+s\cos y). \tag{2.9}$$

Here B is the analogue of L_j above. Equation (2.9) has a solution if and only if the right-hand side is orthogonal to the nullspace of $\mathscr{L}^*$ which is spanned by the two functions $\boldsymbol{f}\cos x$ and $\boldsymbol{f}\cos y$. We define the following quantities:

$$\alpha_0 = \boldsymbol{f}Q_1(\boldsymbol{e},L_0^{-1}Q_0(\boldsymbol{e},\boldsymbol{e})),\quad \alpha_4 = \boldsymbol{f}Q_1(\boldsymbol{e},L_4^{-1}Q_4(\boldsymbol{e},\boldsymbol{e})),$$
$$\alpha_2 = 4\boldsymbol{f}Q_1(\boldsymbol{e},L_2^{-1}Q_2(\boldsymbol{e},\boldsymbol{e})),\quad \beta = \boldsymbol{f}C_1(\boldsymbol{e},\boldsymbol{e},\boldsymbol{e}). \tag{2.10}$$

This leads to the following equations for r and s:

$$0 = r(\mu\lambda+ar^2+bs^2),\quad 0 = s(\mu\lambda+as^2+br^2), \tag{2.11}$$

where

$$\mu = \boldsymbol{f}\cdot B\boldsymbol{e}, \tag{2.12}$$

$$a = \alpha_0+\tfrac{1}{2}\alpha_4+\tfrac{3}{4}\beta, \tag{2.13}$$

and

$$b = \alpha_0+\tfrac{1}{2}\alpha_2+\tfrac{3}{2}\beta. \tag{2.14}$$

We have the following stability theorem.

Theorem. (i) *The solution* $s=0$, $r=\surd(-\mu\lambda/a)$ (*or vice versa*) *is stable if and only if*

$$b<a<0.$$

(ii) *The solution* $r=s=\surd[-\mu\lambda/(a+b)]$ *is stable if and only if*

$$a<-|b|<0.$$

This result shows that stripes ($r=0$ or $s=0$) and spots ($r=s\neq 0$) are mutually exclusive as stable patterns. In a symmetric system with no quadratic terms, stripes are always selected over spots as long as $\beta<0$. If $\beta>0$, no patterns are selected. The key to the appearance of spots is the existence of quadratic terms in the nonlinear functions; without these terms spots can never stably exist.

The algorithm for selection is clear; we need only evaluate the above algebraic quantities and apply the selection mechanism. Any model that has symmetry or is nearly symmetric will yield stripes rather than spots. The calculation is particularly easy for the scalar case. For example, Murray (1989), considers several equations of the form:

$$u_t = -\mathscr{L}u + Qu^2 + Cu^3 + \lambda\mathscr{B}u + \ldots, \tag{2.15}$$

where $\mathscr{L}$ is a scalar lateral-inhibition type of operator (e.g. negative diffusion with a biharmonic component). We let L_k denote the Fourier transform of $\mathscr{L}$ to wavenumbers whose squares add to k. Then, $L_k > 0, k \neq 1, L_1 = 0$, and the determining coefficients a and b are:

$$a = Q^2(1/L_0 + \tfrac{1}{2}L_4) + \tfrac{3}{4}C, \quad b = Q^2(1/L_0 + 2/L_2) + \tfrac{3}{2}C. \tag{2.16}$$

For the 'vanilla' dispersion relation, the Q^2 coefficient for b is always greater than that of a thus for $C < 0$, as $|Q|$ increases, we expect to see a transition from stripes to spots. If $C > 0$, neither pattern bifurcates stably. A similar calculation for the one-dimensional neural net (Maxwell & Renninger 1980):

$$u_t(\boldsymbol{x}, t) = -u(\boldsymbol{x}, t) + \int_\Omega \mathrm{d}yK(\|\boldsymbol{x}-\boldsymbol{y}\|)\,(Mu(\boldsymbol{y}, t) + Qu(\boldsymbol{y}, t)^2 + Cu(\boldsymbol{y}, t)^3) + \ldots, \tag{2.17}$$

where $K(r)$ is a lateral-inhibition kernel and $M > 0$, Q and C are scalars, shows that,

$$Ma = Q^2[K_0/(1-MK_0) + K_4/2(1-MK_4)] + \tfrac{3}{4}C, \tag{2.18a}$$

$$Mb = Q^2[K_0/(1-MK_0) + 2K_2/(1-MK_2)] + \tfrac{3}{2}C. \tag{2.18b)}$$

Here, K_j is the Fourier transform of K evaluated at wavenumbers whose squares sum to j $(1-MK_1 \equiv 0)$. Since $K_2 > K_4$, the quadratic term of b is again larger than that of a so as $|Q|$ increases, spots will arise instead of stripes. We finally note that for the scalar problem, cubic terms are required for any stable pattern to bifurcate.

3. A numerical example

We consider the following activator–inhibitor type of reaction–diffusion equation. We have no particular mechanism in mind, rather, our goal is to illustrate how by altering the quadratic terms, we can obtain stripes or spots. The system is:

$$\left.\begin{aligned} \partial u/\partial t &= (a_{11}+\lambda)\,u - a_{21}\,v + Cu^3 + Qu^2 + d_1\,\Delta u, \\ \partial v/\partial t &= a_{12}\,u - a_{22}\,v + d_2\,\Delta v. \end{aligned}\right\} \tag{3.1}$$

On the periodic domain of size $2\pi \times 2\pi$ we choose the parameters as shown in the figure legend. Figure 1a shows a stripe that forms after letting the system settle down from an initially random configuration. Here, $Q \equiv 0$ and as we expect, stripes form spontaneously. The magnitude of the stripe is 0.38. The nonlinear theory shows that the magnitude should be 0.39877 which is close since the theory is only an asymptotic approximation. In figure 1b, we set $Q = 0.08$ which according to the calculations above should lead to spots. As in figure 1a, the initial data are random and the resulting pattern is a spot. The numerical magnitude is 0.38 and the predicted magnitude is 0.44. The calculation of the parameter a and b is done by applying the theory in §2 and doing the required algebra numerically. The numerical solutions shown in figure 1 were done on a 25×25 grid with an Euler integration scheme with $\Delta t = 0.01$ for the 20000 time steps.

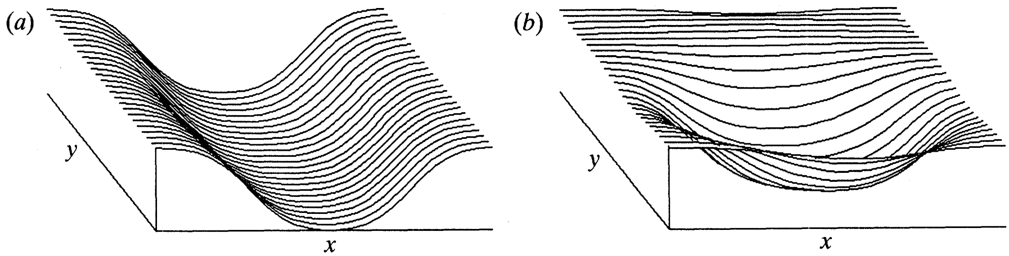

Figure 1. Numerical integration of (3.1) with $a_{11}+\lambda = 0.6$, $a_{21} = 1$, $a_{12} = 2$, $a_{22} = 4$, $d_1 = 0.08$, $d_2 = 1$, $C = -1$. (*a*) $Q = 0.0$. Height above axis depicts deviation from equilibrium. (*b*) $Q = 0.08$.

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Received 7 November 1990; accepted 30 April 1991