M3A21 Mathematical Biology: Handout 1 October 1998 A.J. Mestel

Pattern Formation: The Turing reaction-diffusion mechanism

There is an enormous variety of patterns in nature, for example in animal coat colourings. Sometimes, but not always, the evolutionary advantage of specific colourings is clear. Here we shall concern ourselves with how, rather than why, such patterns form. Frequently, an embryo is monochrome when small, but when it reaches a given size a pattern spontaneously appears. This suggests a size-dependent spatial instability may be the cause. In 1952 Turing suggested **differential diffusion** was a plausible mechanism.

Suppose $u(\mathbf{x}, t)$ and $v(\mathbf{x}, t)$ represent concentrations of two interacting chemicals (morphagens or pigments) in a domain Ω, bounded by $\partial\Omega$ to which the unit normal is $\widehat{\mathbf{n}}$. We assume there is a steady, uniform state $u = u_0$, $v = v_0$ which is stable in the absence of spatial variation, and we will investigate whether it can nevertheless be unstable to an $\mathbf{x}$-dependent perturbation. If it is, then differing concentrations of u and v will develop locally and colour patterns may appear. For example, areas where $u > u_0$ might appear white and $u < u_0$ black.

We consider the non-dimensional reaction-diffusion system

$$\left.\begin{aligned} u_t &= f(u,\, v) + \nabla^2 u \\ v_t &= g(u,\, v) + d\nabla^2 v \end{aligned}\right\} \quad \text{in} \quad \Omega\,, \tag{3.7}$$

with the no-flux boundary conditions

$$\widehat{\mathbf{n}}\cdot\nabla u = \widehat{\mathbf{n}}\cdot\nabla v = 0 \qquad \text{on} \quad \partial\Omega\,.$$

In (3.7) d is a given positive constant, and for $d \neq 1$ the chemicals diffuse at different rates. As we shall see, this is vital for any instability to occur.
The state $(u_0,\, v_0)$ is temporally stable if, from (3.2),

$$f(u_0,\, v_0) = g(u_0,\, v_0) = 0\,, \qquad f_u + g_v < 0 \qquad \text{and} \qquad \det A \equiv f_u g_v - f_v g_u > 0\,. \tag{3.2}$$

Here and henceforth, the partial derivatives f_u *etc.* are evaluated at $(u,\, v) = (u_0,\, v_0)$. We now investigate small perturbations to the uniform state, writing $u = u_0 + \varepsilon u_1(\mathbf{x}, t)$, $v = v_0 + \varepsilon v_1(\mathbf{x}, t)$ for $1 \gg \varepsilon > 0$. Neglecting terms of $O(\varepsilon^2)$, we have

$$\begin{pmatrix} u_1 \\ v_1 \end{pmatrix}_t = A\begin{pmatrix} u_1 \\ v_1 \end{pmatrix} + \begin{pmatrix} 1 & 0 \\ 0 & d \end{pmatrix}\nabla^2\begin{pmatrix} u_1 \\ v_1 \end{pmatrix} \qquad \text{where} \quad A = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}\,, \tag{3.8}$$

where A is the matrix of first derivatives of f and g evaluated at $(u_0,\, v_0)$. We now seek separable solutions to (3.8), with $(u_1,\, v_1) \propto \exp(\lambda t)\phi(\mathbf{x})$, so that λ is the *growth rate* of the disturbance. If $\Re e(\lambda) > 0$, then the uniform state is unstable. A solution of this kind is possible provided $\phi(\mathbf{x})$ satisfies the Helmholz equation for some k:

$$\left.\begin{aligned} \nabla^2\phi + k^2\phi &= 0 \qquad \text{in} \quad \Omega \\ \widehat{\mathbf{n}}\cdot\nabla\phi &= 0 \qquad \text{on} \quad \partial\Omega \end{aligned}\right\}\,. \tag{3.9}$$

This is a differential eigenvalue problem. It has the trivial solution $k = 0$, with ϕ constant, which corresponds to the stable, spatially uniform state. There are also infinitely many eigenvalues (see M2M2) $0 < k_0 < k_1 < k_2 \dots$ For such a k, (3.8) reduces to the matrix eigenvalue problem for λ:

$$\left(A - \begin{pmatrix} 1 & 0 \\ 0 & d \end{pmatrix} k^2 - \lambda I\right) \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} = 0 \ ,$$

where I is the identity matrix. This has non-trivial solutions for (u_1, v_1) provided

$$\begin{vmatrix} f_u - k^2 - \lambda & f_v \\ g_u & g_v - dk^2 - \lambda \end{vmatrix} = 0 \ , \qquad \text{or}$$

$$\lambda^2 - \lambda\big[(f_u + g_v) - (d+1)k^2\big] + (f_u - k^2)(g_v - dk^2) - f_v g_u \equiv \lambda^2 + B\lambda + C = 0 \ . \quad (3.10)$$

The perturbation will grow if at least one root of the quadratic is such that $\Re e(\lambda) > 0$. As by hypothesis $f_u + g_v < 0$ (see (3.2)), the coefficient $B > 0$, and the sum of the two roots is negative. Instability therefore occurs if and only if $C < 0$. Now

$$C = dk^4 - k^2(df_u + g_v) + (f_u g_v - f_v g_u) \equiv dk^4 - k^2(df_u + g_v) + \det A \ ,$$

another quadratic, this time in k^2. Can C be negative? We recall that $d > 0$ and $\det A > 0$ from (3.2). Thus C can only be negative if $df_u + g_v > 0$ and

$$(df_u + g_v)^2 > 4d \det A \qquad \text{or} \quad df_u + g_v > 2\sqrt{d \det A} \ . \qquad (3.11)$$

Suppose $f_u > 0$, so that $g_v < 0$ and $f_u + g_v < 0$. Then it is clear that for large enough values of d, both (3.2) and (3.11) can hold. If this is the case we conclude that $C < 0$, and hence that there is a positive root for λ, if k^2 lies in the range $k_-^2 < k^2 < k_+^2$, where

$$k_\pm^2 = \frac{(df_u + g_v) \pm \sqrt{(df_u + g_v)^2 - 4d \det A}}{2d} \ .$$

We return now to the Helmholz equation (3.9). Only some discrete values of k^2 are possible for a given domain Ω. If one of these eigenvalues lies between k_- and k_+, an instability in the spatially uniform structure will manifest itself. If more than one eigenvalue lies in this range, then the one with the greatest λ will grow fastest and will presumably be seen.

Note: (i) As the size of the domain Ω increases, the eigenvalues get closer together (e.g. in one dimension $k^2 = n^2\pi^2/L^2$; consider varying L.)

(ii) The most unstable mode can have quite complex structure. It may very well not be the lowest eigenvalue (with usually the simplest spatial eigenfunction) which lies between k_- and k_+. Thus as the embryo grows, a complex pattern may suddenly appear.

(iii) As the amplitude of the perturbation grows, the linearisation will cease to be valid, and non-linear effects will limit the growth. Nevertheless, the final pattern which forms will probably resemble the linearly unstable eigenfunction.