

Note: this section will use ideas from linear algebra and Fourier analysis of the diffusion equation to solve a pair of coupled partial differential equations. If any of that sounds like gibberish, don't worry. You can omit reading this part of the article without missing out on anything crucial. I will also use the notation $\dot{x} = \partial x / \partial t$.

Here, we will follow the specific examples given by Turing himself. First consider the case of two cells on a ring, labeled a and b . Cell a has a concentration of the two morphogens X_a and Y_a , and similar for cell b . The morphogens can diffuse between the two cells proportionally to the difference in their concentrations. We can then write:

$$\begin{aligned}\dot{X}_a &= \alpha X_a + \beta Y_a - 2D_X(X_a - X_b) \\ \dot{Y}_a &= \gamma X_a + \delta Y_a - 2D_Y(X_a - X_b)\end{aligned}\tag{1}$$

And similar for cell b by switching all the a 's and b 's in the above equations. The last term is the diffusion term and the factor of 2 comes from the fact that we are considering these cells to live on a ring. Imagining the cells as squares connected edge to edge, cell a is actually connected to cell b on both its right and its left, giving two sources of diffusion. In a more simple case of 1D diffusion, a particle can diffuse to right or left, so there are two degrees of freedom.

Let's take the specific example. Looking at Eq. (1), we will use $\alpha = 5$, $\beta = -6$, $\gamma = 6$, $\delta = -7$, $D_X = 0.5$, and $D_Y = 4.5$. We will make a change of variables:

$$\begin{aligned}\bar{X} &= \frac{X_a + X_b}{2} & \Delta_X &= \frac{X_b - X_a}{2} \\ \bar{Y} &= \frac{Y_a + Y_b}{2} & \Delta_Y &= \frac{Y_b - Y_a}{2}\end{aligned}$$

Taking the time derivative of each of the new variables and plugging everything in, we find the four resulting equations:

$$\begin{aligned}\dot{\bar{X}} &= 5\bar{X} - 6\bar{Y} & \dot{\Delta}_X &= 4\Delta_X - 6\Delta_Y \\ \dot{\bar{Y}} &= 6\bar{X} - 7\bar{Y} & \dot{\Delta}_Y &= 6\Delta_X - 16\Delta_Y\end{aligned}$$

Writing the first two equations in matrix form, $\dot{\vec{z}} = A\vec{z}$, with $\vec{z} = (\bar{X}, \bar{Y})$, we see that

$$A = \begin{pmatrix} 5 & -6 \\ 6 & -7 \end{pmatrix}$$

The eigenvalues of any 2×2 matrix satisfy the characteristic equation $\lambda^2 - Tr(A)\lambda + det(A) = 0$. Here, $Tr(A) = -2$ and $det(A) = 1$. One can then check that λ is a negative real number, indicating a stable fixed point.

Now, looking at the second two equations, we see

$$A = \begin{pmatrix} 4 & -6 \\ 6 & -16 \end{pmatrix}$$

This time, $Tr(A) = -12$ and $det(A) = -28$, and we find that one eigenvalue is a positive number, indicating an exponentially growing concentration! This

is the basis of how patterns can form from a reaction-diffusion equation. The incredible part is that diffusion is usually known to “smooth” out functions, not lead to sharp instabilities as it does here.

We can instead consider the case of a continuous ring of cells, where all morphogens can diffuse freely along the ring. The coupled reaction-diffusion equations are then:

$$\begin{aligned}\dot{X}(s, t) &= -D_X \partial^2 X / \partial x^2 + \alpha_X X + \beta_X Y + c_X \\ \dot{Y}(s, t) &= -D_Y \partial^2 Y / \partial x^2 + \alpha_Y X + \beta_Y Y + c_Y\end{aligned}\tag{2}$$

Where s is the coordinate going around the ring, $s \in [0, 2\pi]$. We can look for solutions of the form $X(s, t) = A(t)e^{\lambda s}$, and same for $Y(s, t)$, we will find the same type of solution (within the right parameters) as we found for the set of ordinary differential equations above. This will be left as an exercise for the reader (see section 7 of Turing’s original paper).