# TURING MECHANISM

KAIBO HU

## 1. General mechanism

Pattern formation is an important topic in biology and other fields. Positional information is a phenomenological concept of pattern formation and differentiation, which suggests that calls are preprogrammed to react to a chemical (morphogen) concentration and differentiate accordingly. Turing used reaction-diffusion equations to describe the concentration of chemicals, and investigated the mechanism governed by these equations. We consider a simple case where two chemicals interact with each other. The equations are

$$\frac{\partial A}{\partial t} = F(A, B) + D_A \Delta A, \tag{1.1a}$$

$$\frac{\partial B}{\partial t} = G(A, B) + D_B \Delta B, \tag{1.1b}$$

where $A(\boldsymbol{x}, t)$ and $B(\boldsymbol{x}, t)$ are two chemical species, $F$ and $G$ are reaction terms which are in general nonlinear, and $\Delta A$ and $\Delta B$ are diffusion terms. Turing's idea was that under certain conditions, chemicals can react and diffuse to produce steady state heterogeneous spatial patterns. In the absence of diffusion ($D_A = D_B = 0$), $A$ and $B$ tend to a steady state solution ($A_t = B_t = 0$) which is linearly stable. Such solutions are usually uniform, i.e., $A$ and $B$ are constant, meaning that the chemicals uniformly distribute in space. A profound idea is that with proper parameters (in particular, $d_A \neq d_B$) the diffusion terms lead to linear instability of the stead state solution and non-uniform solutions (Turing patterns) emerge. With this idea, linear analysis provides information on the range of parameters that lead to linear instability and the patterns in the linear region.

We have the dimensionless form of the equations

$$\frac{\partial u}{\partial t} = \gamma f(u, v) + \Delta u, \tag{1.2a}$$

$$\frac{\partial v}{\partial t} = \gamma g(u, v) + d\Delta v. \tag{1.2b}$$

Here $\gamma$ has the dimension of $L^2$, where $L$ is the characteristic length. Before carrying out detailed analysis of (1.2), we given an example of $f$ and $g$:

$$f(u, v) = a - bu + \frac{u^2}{v}, \quad g(u, v) = u^2 - v.$$

In the absence of diffusion, the steady state solution is obtained from $f(u, v) = g(u, v) = 0$, which gives the uniform stead state $u = (a + 1)/b$, $v = [(a + 1)/b]^2$. This constant solution is considered as a trivial pattern.

Assume that $(u_0, v_0)$ is a steady state solution for the system without diffusion (i.e., $f(u_0, v_0) = 0,\ g(u_0, v_0) = 0$). The *linear stability analysis of Turing mechanism* consists of the following steps:

(1) Find conditions such that the linearised solution is stable in the absence of diffusion.

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(2) In the presence of diffusion, we are interested in the parameters $d, \gamma$, geometry of domain etc. such that the linearised solution is linearly unstable.

The linearised equation is

$$\boldsymbol{w}_t = \gamma A \boldsymbol{w} + D\Delta \boldsymbol{w}, \tag{1.3}$$

where

$$\boldsymbol{w} = \begin{pmatrix} u - u_0 \\ v - v_0 \end{pmatrix}, \quad A = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}, \quad D = \begin{pmatrix} 1 & 0 \\ 0 & d \end{pmatrix}.$$

Here the linearisation is around $(u_0, v_0)$. Therefore $f_u$ should be understood as $f_u(u_0, v_0)$, and other terms are similar.

With some assumptions on $f$ and $g$, from Step (1) we get the following conditions:

$$f_u + g_v < 0, \quad f_u g_v - f_v g_u > 0. \tag{1.4}$$

For Step (2), we get the following necessary (not sufficient) conditions:

$$df_u + g_v > 0, \quad (df_u + g_v)^2 - 4d(f_u g_v - f_v g_u) > 0. \tag{1.5}$$

To further analyse the linear instability, we transform the partial differential equations (1.2) to algebraic equations. To this end, consider a Fourier decomposition of $\boldsymbol{w}$ using eigenfunctions of the Laplacian:

$$\boldsymbol{w}(\boldsymbol{x}, t) = \sum_k c_k e^{\lambda t} \boldsymbol{W}_k(\boldsymbol{x}), \tag{1.6}$$

where $\boldsymbol{W}_k$ is obtained from the eigen-equations

$$-\Delta \boldsymbol{W}_k = k^2 \boldsymbol{W}_k, \tag{1.7}$$

with the boundary condition

$$(\boldsymbol{n} \cdot \nabla)\boldsymbol{W}_k = 0, \quad \text{on } \partial\Omega,$$

where $\boldsymbol{n}$ is the unit normal vector of the boundary. This is a coupled eigenvalue problem (the coupling of $w_1 := u - u_0$ and $w_2 := v - v_0$ is through the boundary condition). There are infinitely many eigenpairs $(k^2, \boldsymbol{W}_k)$. For simple domains (and only for these cases), one may obtain all the eigenpairs analytically. Here we use $k^2$ to denote the eigenvalue (rather than $k$), because $-\Delta$ has a positive spectrum. As we shall see below, $k$, i.e., the square root of the eigenvalue, corresponds to the wave number. In fact, consider a finite domain in one dimension. The eigenfunction is a trigonometric function with the form $\sin(kx)$ or $\cos(kx)$. Thus the eigenvalues are proportional to $k^2$, reflecting the fact that $-\Delta$ is a second order operator. Another remark is that the eigenpairs only depend on the domain. On bounded domains, Laplacian has a discrete spectrum, meaning that only certain discrete values of $k^2$ can solve (1.7).

Substituting the Fourier mode (1.6) into (1.3), we get

$$\lambda \boldsymbol{W}_k = \gamma A \boldsymbol{W}_k - Dk^2 \boldsymbol{W}_k,$$

and therefore

$$|\lambda I - \gamma A + Dk^2| = 0. \tag{1.8}$$

Given any $k^2 > 0$, we can solve two values of $\lambda$ from (1.8). The function $\lambda = \lambda(k^2)$ is called the dispersion relation.

Step (2) requires the linearly instability. This means that $\mathrm{Re}(\lambda) > 0$ for at least one of the two roots (therefore $\boldsymbol{w}$ in (1.6) has an exponential growth in time [a]

With some analysis, we can determine a critical value of $d$, denoted by $d_c$, from the following equation:

$$d_c^2 f_u^2 + 2(2f_v g_u - f_u g_v)d_c + g_v^2 = 0.$$

When $d \leq d_c$, the maximal real part of $\lambda$ is less than or equal to zero for all $k^2 \geq 0$, and when $d > d_c$, *there exists* $k^2 \geq 0$ such that at least one $\lambda$ (solved from (1.8)) has a positive real part, and thus the steady state is linearly unstable. For $d > d_c$, we can in turn determine the range of $k^2$ for which the linear instability occurs:

$$\alpha := \frac{\gamma}{2d}[(df_u+g_v)-[(df_u+g_v)^2-4d|A|]^{1/2}] < k^2 < \frac{\gamma}{2d}[(df_u+g_v)+[(df_u+g_v)^2-4d|A|]^{1/2}] := \beta. \tag{1.9}$$

We should keep in mind that for bounded domains, $k^2$ can only achieve some discrete values. Therefore even if (1.9) holds for some real number $k^2 > 0$, it cannot guarantee the existence of linearly unstable modes. To further analyse this, we should consider specific examples.

The above argument provides conditions for the uniform steady state solution to become unstable, and thus evolve to non-homogeneous patterns. It is also a basic assumption that the eigenfunction $\boldsymbol{W}_k$ such that $\mathrm{Re}(\lambda(k^2))$ achieves the largest positive value will be selected in the evolution. Therefore such $\boldsymbol{W}_k$ is the chemical distribution predicted by the linear analysis. Nevertheless, the linear stability analysis becomes invalid as the solutions leave from $(u_0, v_0)$. Therefore, although $\boldsymbol{W}_k$ contains useful information and one can explain the formation of strips and spots using $\boldsymbol{W}_k$, the linear analysis deviate from solutions to the full nonlinear system (1.2) and conclusions can only be drawn in a certain region.

## 2. Detailed analysis for examples

We consider examples by specifying $f$, $g$ and the domain, which in turn determines possible values of $k^2$. For example, we may consider $f = a - u + u^2 v$ and $g = b - u^2 v$, and a rectangular domain. Eigenfunctions (trigonometric functions) and eigenvalues on these domains can be determined explicitly. Then one can discuss how the Turing space (the set of parameters $(a, b, d)$ such that (1.4) and (1.5) hold), scaling ($\gamma$) and geometry (length and width of the rectangular domain) affect the emergence of different Turing patterns, e.g., strips and spots.

## 3. The project

The project has the following concrete goals:

(1) Learn about the Turing mechanism. For specific examples, analyse the effect of parameters (e.g., $(a, b, d)$), scaling ($\gamma$) and geometry in 1D and 2D rectangular domains. Explain the emergence of strips/spots etc.
(2) Investigate how the linear analysis fails when the solutions leave the steady state, i.e., how solutions to the nonlinear problem (1.2) deviate from $\boldsymbol{W}_k$ in 1D and possibly in 2D. The nonlinear equations can be solved by numerical computation.
(3) Investigate the effect of other factors, e.g., growing domains where the domain is a function of $t$, and effects of curvature (in this case, the Laplacian $-\Delta$ should be replaced by the Laplace-Beltrami operator).

[a]This does not mean that the solution to the nonlinear problem (1.2) exponential grows. Because the linear stability analysis here is essentially for small perturbation around $(u_0, v_0)$. As the perturbation grows, the ansatz does not hold anymore. Therefore we should be careful when we draw conclusions for the nonlinear problems. ).

## References

[1] J. D. Murray, *Mathematical biology II: spatial models and biomedical applications*, vol. 3, Springer New York, 2001.

Mathematical Institute, University of Oxford, Oxford, UK
*E-mail address*: kaibo.hu@maths.ox.ac.uk