

# AP3162: Lecture - Turing mechanism for spatial patterning

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## I. MAIN IDEA OF THE TURING MECHANISM

The Turing mechanism for spatial-pattern formation describes a uniformly spread-out molecules suddenly self-organizing into spatial-patterns (usually periodic stripes and dots). Specifically, the Turing mechanism states a seemingly uniform sea of molecules can have a small ripple at some location (i.e, slightly higher concentrations of the molecules at some location) and that this ripple could grow over space, causing the entire sea of molecules to reorganize their concentration profiles to form highly ordered patterns, including waves, stripes, and dots. Thus a uniform field of molecules is unstable. Turing had three surprising insights that enabled the Turing mechanism to have a lasting impact. First, Turing showed that at least two chemicals are necessary for pattern-formations to occur from an initially uniform state. Secondly - and the one that is perhaps the most surprising - is that diffusion can actually be destabilizing factor that causes the system to be unstable. This latter point is counter-intuitive since diffusion has the role of homogenizing a field of chemicals, by smoothing out spatial variations in the chemical concentrations, which is the opposite of pattern formations. Finally, Turing's third major insight was that the diffusion-caused instability can induce growth of a structure (i.e., local inhomogeneity in chemical concentration) to grow at a particular wavelength, which would ensure patterns such as stripes with regular spacings.

## II. THE TURING MECHANISM

As we will see, these patterns arise when the diffusion constants of at least two chemicals substantially differ. To generate such instability, the diffusion constants of the molecules and the interactions between them must satisfy a single condition. To derive this condition, we start with the reaction-diffusion equation that is always used for describing Turing mechanism. We will, as usual, use a reaction-diffusion equation with two types of molecules:

$$\frac{\partial u}{\partial t} = D_1 \nabla^2 u + R_1(u, v) \quad (1a)$$

$$\frac{\partial v}{\partial t} = D_2 \nabla^2 v + R_2(u, v) \quad (1b)$$

where  $u$  and  $v$  are concentrations of molecules,  $A$  and  $I$ ,  $D_1$  and  $D_2$  are diffusion coefficients of  $A$  and  $I$ , and  $R_1$  and  $R_2$  are reaction rates for  $A$  and  $I$  (i.e., net creation rates for  $A$  and  $I$ ). The form of the reaction-rate functions,  $R_i$ , depends on the specific chemical system under consideration. Some of the functional forms for  $R_i$  are given special names such as the **Gierer-Meinhardt model**, **Schnakenberg model**, and **Thomas model**.

To obtain the Turing mechanism, we assume that when the concentration is uniform - that is,  $u(x, y) = U$  and  $v(x, y) = V$ , where  $U$  and  $V$  are the steady-state constant profiles) - then  $R_1 = 0$  and  $R_2 = 0$ . That is,

$$0 = R_1(U, V) \quad (2a)$$

$$0 = R_2(U, V) \quad (2b)$$

But now suppose that there are small spatial inhomogeneities,  $\delta u$  and  $\delta v$  - that is,  $u(x, y) = U + \delta u(x, y)$  and  $v(x, y) = V + \delta v(x, y)$ . Then we can Taylor expand  $R_1$  and  $R_2$  near their values about the uniform concentrations  $U$  and  $V$ :

$$R_1(u, v) = r_{11} \delta u + r_{12} \delta v \quad (3a)$$

$$R_2(u, v) = r_{21} \delta u + r_{22} \delta v, \quad (3b)$$

where  $r_{ij}$ 's are the following Jacobian elements of  $R_i$ :

$$r_{i1} \equiv \left. \frac{\partial R_i}{\partial u} \right|_U \quad (4a)$$

$$r_{i2} \equiv \left. \frac{\partial R_i}{\partial v} \right|_V \quad (4b)$$

By defining matrices,

$$\vec{D} \equiv \begin{bmatrix} D_1 & 0 \\ 0 & D_2 \end{bmatrix}, \quad \vec{r} \equiv \begin{bmatrix} r_{11} & r_{12} \\ r_{21} & r_{22} \end{bmatrix}, \quad (5)$$

and

$$\vec{c} \equiv \begin{bmatrix} u \\ v \end{bmatrix} \quad (6)$$

we can rewrite the reaction-diffusion equations in terms of matrix multiplications as

$$\frac{\partial \vec{c}}{\partial t} = \vec{D} \nabla^2 \vec{c} + \vec{r} \vec{c} \quad (7)$$

To solve Eq. 7, we must first impose boundary conditions (and also state where our boundaries are). Typically, studies of the Turing mechanism impose either a periodic boundary condition (thus still keeping the system finite) or assume an infinite space without boundaries. In either case, we can consider solutions that are spatially periodic, since a periodic boundary condition and an infinite space both mean that there is a translational symmetry in the solution to Eq. 7. We will confine ourselves one-dimension as a three-dimensional system with periodic or infinite boundaries proceed in the same way. We consider spatial perturbations of the form  $e^{iqx}$  and temporal perturbations of the form  $e^{k_q t}$ , where  $k_q$  is a complex number and  $q$  is a real number. Since we can represent more general, non-periodic perturbations in space as a sum of these periodic perturbations (i.e., Taylor series) - this is because Eq. 7 is linear - it is sufficient to analyze the periodic perturbations. Specifically, we seek solutions of the form:

$$\vec{c} \equiv \begin{bmatrix} u_o \\ v_o \end{bmatrix} e^{iqx} e^{k_q t}, \quad (8)$$

where  $u_o$  and  $v_o$  are constant amplitudes of perturbation.

The real component of  $k_q$  (i.e.,  $\text{Re}(k_q)$ ) is the rate of growth or shrinkage of the spatial perturbation. Specifically, if  $\text{Re}(k_q) < 0$ , then the initial perturbation decays over time - such system is called "linearly stable" because Eq. 3b used a linear approximation - whereas  $\text{Re}(k_q) > 0$  leads to the initial perturbation growing over time, at least for a time when the linear approximation (Eq. 3b) is valid. Thus the problem of finding if uniform concentrations of  $A$  and  $I$  are unstable reduces to determining the sign of  $k_q$  for each  $q$ . Plugging the perturbation (Eq. 8) into the reaction-diffusion equation (Eq. 7), we obtain

$$k_q \vec{c} = (\vec{r} - \vec{D} q^2) \vec{c} \quad (9)$$

Then by defining  $\vec{P}_q = \vec{r} - \vec{D} q^2$ , we obtain the following eigenvalue-eigenvector equation:

$$k_q \vec{c} = \vec{P}_q \vec{c}, \quad (10)$$

where  $k_q$  is an eigenvalue and  $\vec{c}$  is an eigenvector. Thus solving the reaction-diffusion equation with a small perturbation has reduced to finding the eigenvalue and an eigenvector for each  $q$ . For  $c$  to be non-zero, Eq. 10 tells us that

$$0 = \det(\vec{P}_q - k_q \vec{I}) \quad (11a)$$

$$= k_q^2 - \text{tr}(\vec{P}_q) k_q + \det(\vec{P}_q) \quad (11b)$$

where  $\vec{I}$  is the 2 x 2 identity matrix. Solving this quadratic equation, we obtain the eigenvalue,  $k_q$

$$k_q = \frac{1}{2}tr(\vec{P}_q) \pm \frac{1}{2}\sqrt{(tr(\vec{P}_q))^2 - 4det(\vec{P}_q)} \quad (12)$$

Eq. 12 is perhaps the most important equation related to the Turing mechanism because it tells us everything that we need to know about when a uniform concentration field becomes unstable and what the spatial length (defined by  $q$ ) associated with the instability is. We can diagrammatically summarize our finding (Fig. 1):

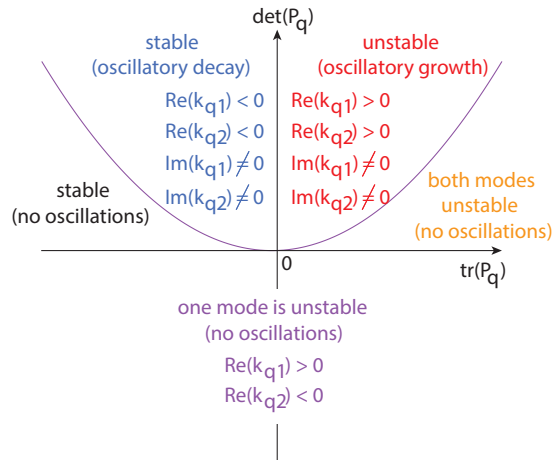


Figure 1. Graphical summary of conditions for generating Turing instability (graphical representation of Eq. 12). The parabola represents  $tr(\vec{P}_q)^2 = 4det(\vec{P}_q)$ .

Thus, for a uniformly mixed  $A$  and  $I$  (i.e.,  $u = U, v = V$ ) to be **stable**, we need *both* of the following conditions to be satisfied:

$$tr(\vec{P}_q) = r_{11} + r_{22} - (D_1 + D_2)q^2 < 0 \quad (\text{Stability condition 1}) \quad (13a)$$

$$det(\vec{P}_q) = (r_{11} - D_1q^2)(r_{22} - D_2q^2) - r_{12}r_{21} > 0 \quad (\text{Stability condition 2}) \quad (13b)$$

If one of the two conditions (Eqs. 13a and 13b) is violated for a non-zero wave number (i.e.,  $q > 0$ ), then we say that the chemical system exhibits a **Turing instability** (aka. **Turing bifurcation**). If the system consists of  $N$  chemicals, then our  $P_q$  would be a  $N \times N$  matrix and our problem would be to solve for  $N$  eigenvalues (if any one of them is negative, then again, the system would exhibit Turing instability). Turing's insight was that he focused on a two-chemical system, which simplified analysis while exhibiting non-trivial behaviours.

Turing's main physical insight was that diffusion could drive the instability. To see this, suppose we start with a uniform mixture of  $A$  and  $I$  by, for example, constantly stirring the beaker that contains both chemicals. Given that the stirring is vigorous enough, the diffusion constants,  $D_1$  and  $D_2$ , are set to zero. Then Eqs. 13a and 13b become

$$tr(\vec{P}_q) = r_{11} + r_{22} < 0 \quad (14a)$$

$$det(\vec{P}_q) = r_{11}r_{22} - r_{12}r_{21} > 0 \quad (14b)$$

Eq. 14a and the fact that the diffusion constants and  $q^2$  are non-negative mean that when we turn on the diffusion constants, we have

$$tr(\vec{P}_q) = r_{11} + r_{22} - (D_1 + D_2)q^2 \quad (15a)$$

$$< r_{11} + r_{22} \quad (15b)$$

$$< 0 \quad (15c)$$

Thus, Eq. 13a is automatically satisfied, after we turn on the diffusion constants (i.e., after we stop stirring), if a well-mixed condition is stable in the absence of diffusion. Hence, the only way that the uniformly mixed chemicals become unstable is if Eq. 13b is violated (i.e., if the system resides in the lower left quadrant in Fig. 1). Note that the determinant of  $\vec{P}_q$  is quadratic in  $q^2$  with a positive factor in front of it (Eq. 13b). This means that the graph of  $\det(\vec{P}_q)$ , as a function of  $q^2$ , is a parabola with its opening facing upwards (in positive direction). Thus we only need to know if the minimum of this parabola is below zero. If not, then there is no Turing instability. If there is and this minimum value occurs at a non-zero  $q$ , then there is Turing instability. The minimum value occurs at  $q = q_o$ , where

$$0 = \left. \frac{d(\det(\vec{P}_q))}{d(q^2)} \right|_{(q_o)^2}, \quad (16)$$

Solving above equation, we find

$$(q_o)^2 = \frac{D_1 r_{22} + D_2 r_{11}}{2D_1 D_2} \quad (17)$$

and that the minimum value of the determinant is

$$\det(\vec{P}_{q_m}) = r_{11}r_{22} - r_{12}r_{21} - \frac{(D_1 r_{22} + D_2 r_{11})^2}{4D_1 D_2} \quad (18)$$

From Eq. 18, we see that the stability condition 2 (Eq. 13b) is violated (i.e., there exists a value of  $q$  for which  $\det(\vec{P}_q) < 0$ ) when,

$$D_1 r_{22} + D_2 r_{11} > 2\sqrt{D_1 D_2 (r_{11} r_{22} - r_{12} r_{21})} \quad (\text{Condition for linear instability of uniform mixture}) \quad (19)$$

Eq. 19 is the **sole condition that is necessary and sufficient for Turing instability** - this is the condition that must be satisfied for uniformly mixed chemicals,  $A$  and  $I$ , become unstable due to diffusion.

Let us now analyze some consequences of Eq. 19. First, we note that Eq. 14b and Eq. 19 together imply

$$D_1 r_{22} + D_2 r_{11} > 0 \quad (20a)$$

$$\implies \frac{D_1}{D_2} > \frac{-r_{11}}{r_{22}} \quad (20b)$$

Since the diffusion coefficients are always positive,  $r_{11}$  and  $r_{22}$  must have opposite signs. Without loss of generality, let us say that  $r_{11} > 0$  and  $r_{22} < 0$ . Then  $A$ , with diffusion coefficient  $D_1$ , is called an **activator** and  $I$ , with diffusion coefficient  $D_2$ , is called an **inhibitor**. They are called as such because  $A$  promotes its own instability while  $I$  inhibits its own growth.

A second consequence of Eq. 19 is that **the activator must have a lower diffusion coefficient than the inhibitor for the Turing instability**. To see this, we must rewrite the stability condition (Eq. 19) in terms of the diffusion lengths of  $A$  and  $I$ , which are  $L_1$  and  $L_2$  respectively:

$$L_1 \equiv \sqrt{\frac{D_1}{r_{11}}} \quad L_2 \equiv \sqrt{\frac{-D_2}{r_{22}}} \quad (21)$$

In terms of  $L_1$  and  $L_2$ , the instability condition (Eq. 19) becomes

$$\frac{1}{2} \left( \frac{1}{L_1^2} - \frac{1}{L_2^2} \right) > \sqrt{\frac{r_{11} r_{22} - r_{12} r_{21}}{D_1 D_2}} > 0 \quad (\text{equivalent to the Turing-instability condition (Eq. 19)}) \quad (22)$$

Thus it follows that for a uniform mixture of chemicals to be unstable to diffusion, a necessary but not sufficient condition is that the activator must diffuse slower than the inhibitor (i.e.  $L_1 > L_2$ ). This alone is insufficient for

having instability because the right side of the inequality in Eq. 22 must still be satisfied - this is not guaranteed by having the activator diffuse slower than the inhibitor. The condition that  $L_1 > L_2$  is why we often say "**local activation and long-range inhibition**" for Turing instability. Finding real chemical systems that satisfy Eq. 22 has been difficult. For one, Eq. 20b sets an upper bound on how much larger the inhibitor's diffusion constant must be. In real systems, the ratio  $-r_{22}/r_{11}$  can be as large as 10 (thus so must the corresponding diffusion coefficients). This is a large number.