

III. Turing Patterns

1. Biological background: patterns in development
2. Turing instability

Recall $N=2$ dynamical system

$$\begin{cases} \dot{u} = f(u, v) \\ \dot{v} = g(u, v) \end{cases} \quad \begin{matrix} u = \bar{u} + \delta u \\ v = \bar{v} + \delta v \end{matrix} \quad \begin{pmatrix} \delta \dot{u} \\ \delta \dot{v} \end{pmatrix} = M \begin{pmatrix} \delta u \\ \delta v \end{pmatrix}$$

Community matrix M :

$$M = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix};$$

$$\det(M - \lambda I) = 0$$

$$\rightarrow (f_u - \lambda)(g_v - \lambda) - f_v g_u = 0$$

$$\lambda^2 - \lambda \underbrace{(f_u + g_v)}_{\text{Tr } M} + \underbrace{f_u g_v - f_v g_u}_{\det M} = 0$$

(Note derivatives evaluated at \bar{u}, \bar{v})

$$\lambda = \frac{1}{2} \text{Tr } M \pm \sqrt{\underbrace{\left(\frac{1}{2} \text{Tr } M\right)^2 - \det M}_{\Delta}}$$

→ Condition for stability:

$$\left. \begin{matrix} \text{Tr } M < 0 \\ \det M > 0 \end{matrix} \right\}$$

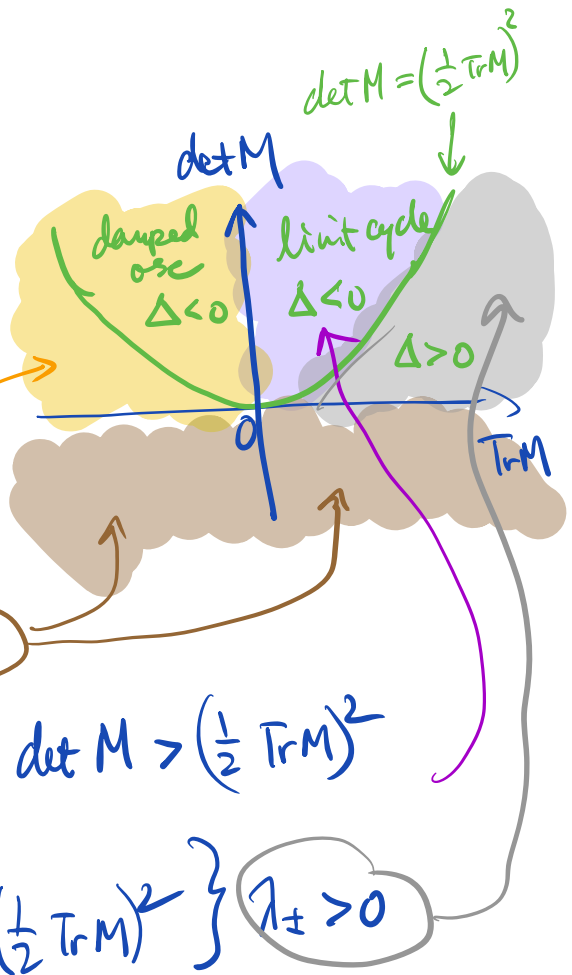
$$\lambda_{\pm} < 0$$

→ bistability (saddle pt)

$$\det M < 0: \lambda_+ > 0, \lambda_- < 0$$

→ unstable spiral: $\text{Tr } M > 0, \det M > \left(\frac{1}{2} \text{Tr } M\right)^2$

→ unstable node: $\left. \begin{matrix} \text{Tr } M > 0 \\ \det M < \left(\frac{1}{2} \text{Tr } M\right)^2 \end{matrix} \right\} \lambda_{\pm} > 0$



from the stable state ($\text{Tr} M < 0$, $\det M > 0$) (135)

= transition across $\text{Tr} M = 0$: Hopf bifurcation

- transition across $\det M = 0$ (for finite k):

Turing instability (1952)

* Consider diffusive spatial coupling:

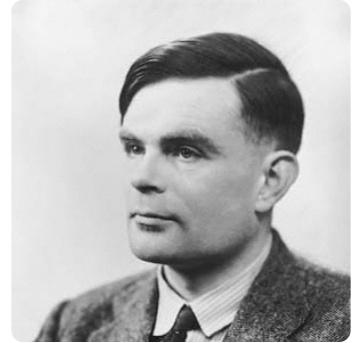
$$\partial_t u = f(u, v) + D_u \partial_x^2 u$$

$$\partial_t v = g(u, v) + D_v \partial_x^2 v.$$

Finite wavelength perturbation ($k = \text{wave}^\#$)

$$\text{let } u(x,t) = \bar{u} + S_u(t) e^{ikx}$$

$$v(x,t) = \bar{v} + S_v(t) e^{ikx}$$



(1912 - 1954)

$$\frac{d}{dt} \begin{pmatrix} S_u \\ S_v \end{pmatrix} = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix} \begin{pmatrix} S_u \\ S_v \end{pmatrix} + \begin{pmatrix} -D_u k^2 S_u \\ -D_v k^2 S_v \end{pmatrix}$$

$$\Rightarrow \underbrace{\begin{pmatrix} f_u - D_u k^2 & f_v \\ g_u & g_v - D_v k^2 \end{pmatrix}}_{M(k)} - \lambda I = 0$$

Stability at k : $\det [M(k) - \lambda I] = 0$

$$\rightarrow \lambda^2 - \lambda \underbrace{\text{Tr}(M(k))}_{T(k)} + \underbrace{\text{Det}(M(k))}_{D(k)} = 0$$

$$\lambda(k) = \frac{\tau(k)}{2} \pm \sqrt{\left(\frac{\tau(k)}{2}\right)^2 - D(k)} \quad (\text{dispersion relation}) \quad (136)$$

* Express $\tau(k)$ and $D(k)$ in terms of $\tau(0)$, $D(0)$

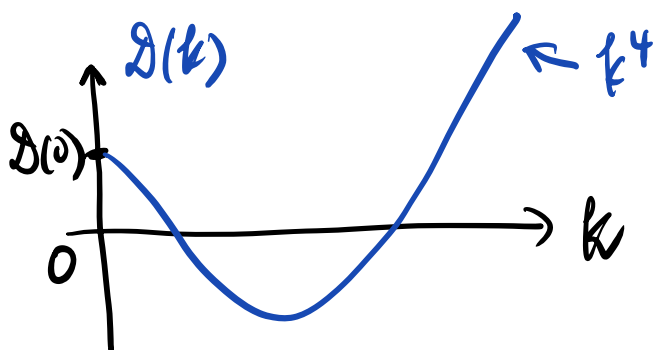
$$\begin{aligned} \tau(k) &= f_u - D_u k^2 + g_v - D_v k^2 \\ &= \tau(0) - D_u k^2 - D_v k^2 \end{aligned}$$

→ since $k=0$ state stable, $\tau(0) < 0$, → $\tau(k) < 0 \forall k$.

$$\begin{aligned} D(k) &= f_u g_v - f_v g_u + D_u D_v k^4 \\ &\quad - (g_v D_u k^2 + f_u D_v k^2) \\ &= D(0) - (g_v D_u + f_u D_v) k^2 + D_u D_v k^4 \end{aligned}$$

Since $k=0$ state stable, then $D(0) > 0$.

→ possible for $D(k)$ to be -ve for some k .



- requires $g_v D_u + f_u D_v > 0$

but since $f_u + g_v = \tau(0) < 0$,

→ must have $D_u \neq D_v$

and f_u, g_v have opposite sign.

Without loss of generality, take $f_u > 0 > g_v$

(137)

i.e., v is auto-inhibiting,
 u is auto-activating

Since $f_u + g_v < 0 \rightarrow |g_v| > |f_u|$

$f_u f_u D_v + g_v D_u > 0$,

must have $D_v > D_u$

\Rightarrow Inhibitor diffuses more rapidly than activator!

Note: Since $D(0) = f_u g_v - f_v g_u > 0$.

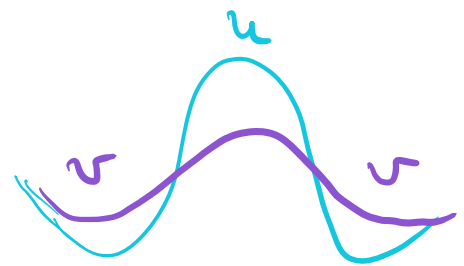
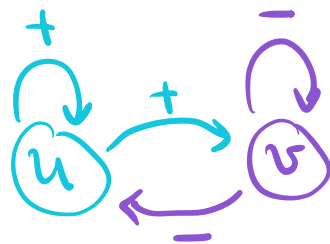
and $f_u g_v < 0$

we must also have $f_v g_u < 0$

two scenarios:

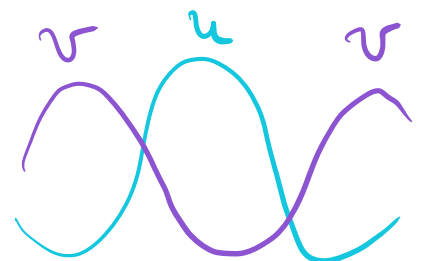
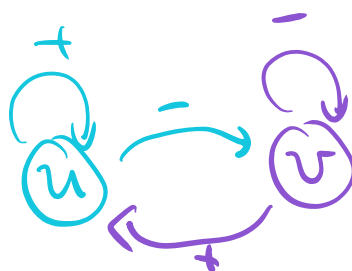
i) $f_v < 0, g_u > 0$.

$$M = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$$



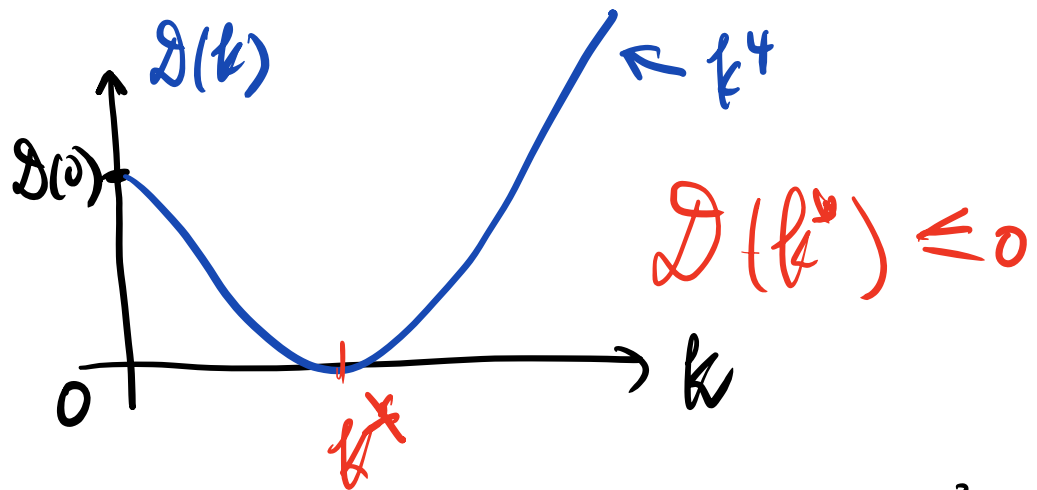
ii) $f_v > 0, g_u < 0$

$$M = \begin{pmatrix} + & + \\ - & - \end{pmatrix}$$



* Quantitative criterion for Turing instability: (138)

$$D(k) = D(0) - (g_v D_u + f_u D_v) k^2 + D_u D_v k^4$$



Minimum: $\left. \frac{d}{dk} D(k) \right|_{k^*} = 0 = -2k^* (g_v D_u + f_u D_v) + 4(k^*)^3 D_u D_v$

$$(k^*)^2 = \frac{g_v D_u + f_u D_v}{2 D_u D_v}$$

$$\begin{aligned} D(k^*) &= D(0) - \frac{(g_v D_u + f_u D_v)^2}{2 D_u D_v} + \cancel{D_u D_v} \frac{(g_v D_u + f_u D_v)^2}{4 D_u D_v} \\ &= D(0) - \frac{(g_v D_u + f_u D_v)^2}{4 D_u D_v} \end{aligned}$$

\Rightarrow Quantitative criterion for Turing instability:

$$D(k^*) \leq 0: \quad g_v D_u + f_u D_v \geq 2 \sqrt{D(0) D_u D_v}$$

at threshold, unstable mode is

$$(k^*)^2 = \frac{g_v D_u + f_u D_v}{2 D_u D_v} = \frac{2 \sqrt{D(0) D_u D_v}}{2 D_u D_v} = \sqrt{\frac{D(0)}{D_u D_v}}$$

3. Turing space:

parameter space where Turing instability occurs

$$\begin{cases} \partial_t u = f(u, v) + D_u \partial_x^2 u \\ \partial_t v = g(u, v) + D_v \partial_x^2 v \end{cases}$$

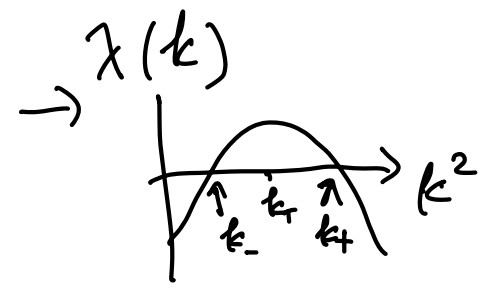
work on specific examples: requires $f_u > 0 > g_v$

- predator-prey: $g_v = 0$.
- Meinhardt's activator-inhibitor model: math too cumbersome
- Brusselator: $\begin{cases} A \rightarrow B \\ 2A + B \rightarrow 3A \end{cases}$

$$\begin{aligned} f(u, v) &= a - (1+b)u + u^2v \\ g(u, v) &= bu - u^2v \end{aligned}$$

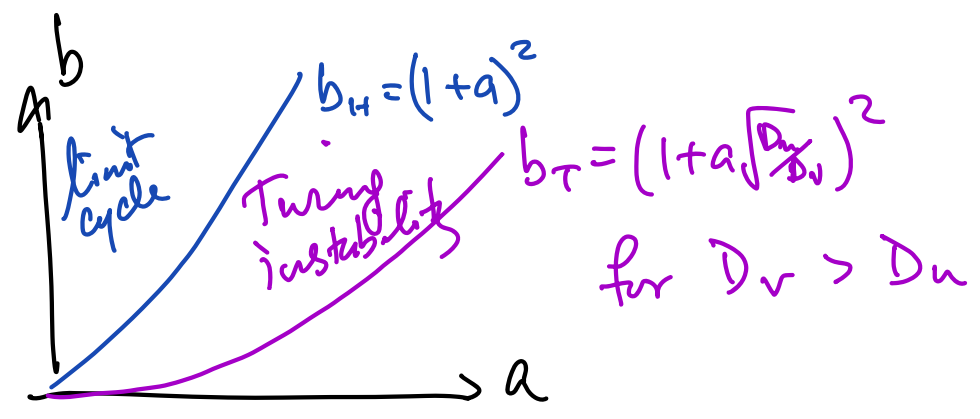
Solve for Turing space: ($\text{Tr} M < 0$, and $f_u > 0 > g_v$)

$$\begin{aligned} \text{try } u(x, t) &= u^0 + \delta u e^{\lambda t} \cdot e^{ikx} \\ v(x, t) &= v^0 + \delta v e^{\lambda t} \cdot e^{ikx} \end{aligned}$$



max λ at $k = k_T = \dots$

$$\lambda_{\max} = \lambda(k_T) = 0 \text{ for } b = b_T = \left(1 + a \sqrt{\frac{D_u}{D_v}}\right)^2$$

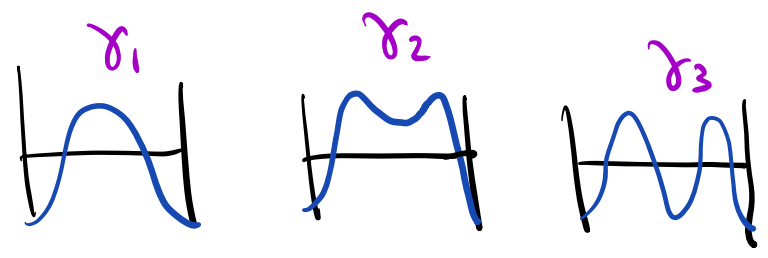
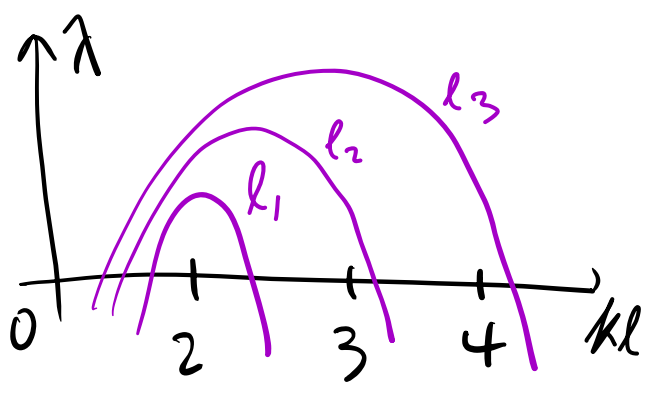
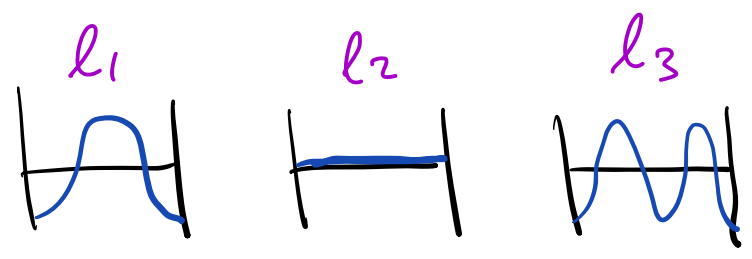
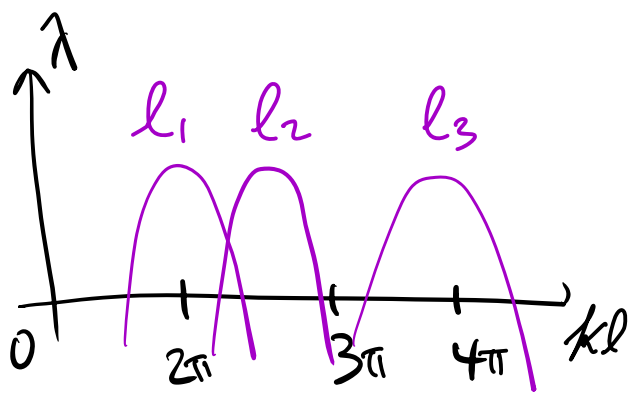
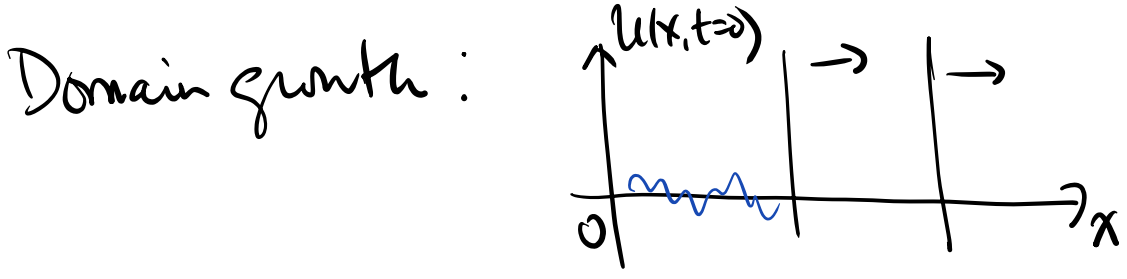


4. Mode Selection

only discrete wavelength allowed

for system size l , $kl = n\pi$, $n = \text{integers}$

→ for small systems, unstable modes appear only if $k-l < n\pi < k+l$.



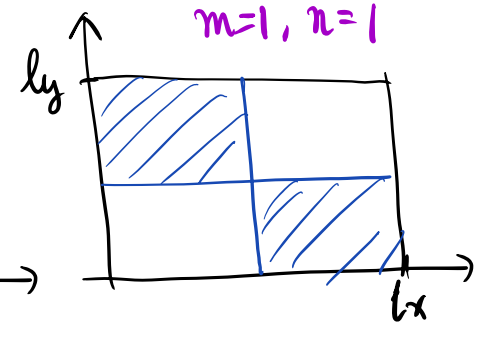
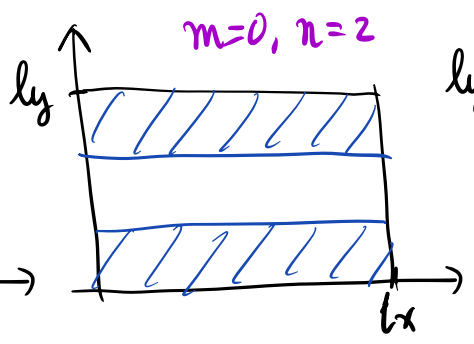
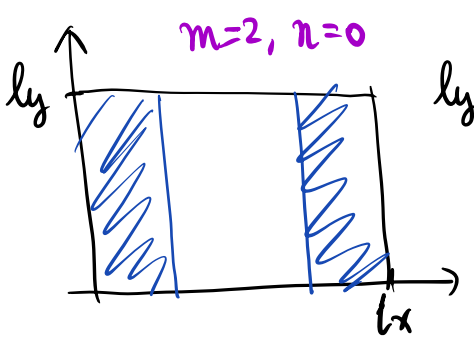
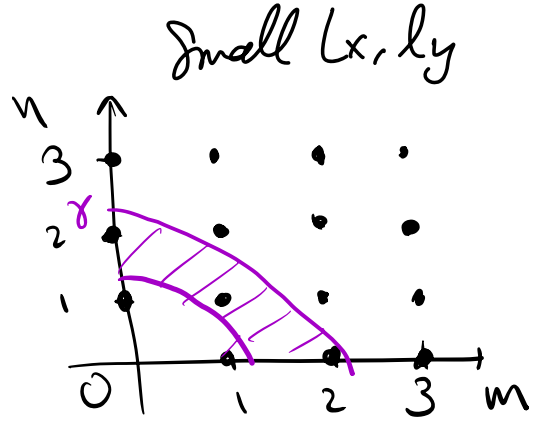
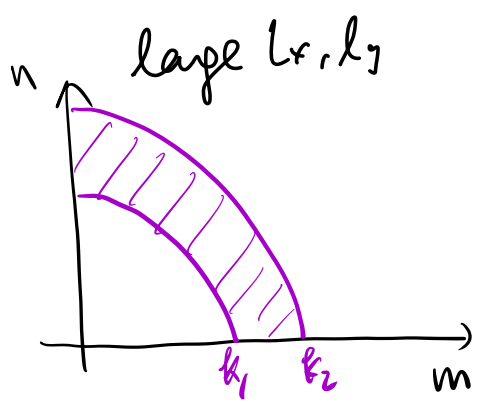
Many biological applications

* 2d patterns:

Same condition for instability: $k_-^2 < k^2 < k_+^2$

but for $u(x,y) \sim \cos \frac{m\pi x}{l_x} \cdot \cos \frac{n\pi y}{l_y}$

$$k^2 = \left(\frac{m\pi}{l_x}\right)^2 + \left(\frac{n\pi}{l_y}\right)^2$$



Other tessellation pattern, e.g. hexagonal.

$$u(x,y) \sim \cos kx + \cos k\left(\frac{x}{2} + \frac{\sqrt{3}}{2}y\right) + \cos k\left(\frac{\sqrt{3}}{2}y - \frac{x}{2}\right)$$

\Rightarrow regular array of spots

(e.g. hair follicles, spot coating, ...)

or combinations of stripes and spots.

