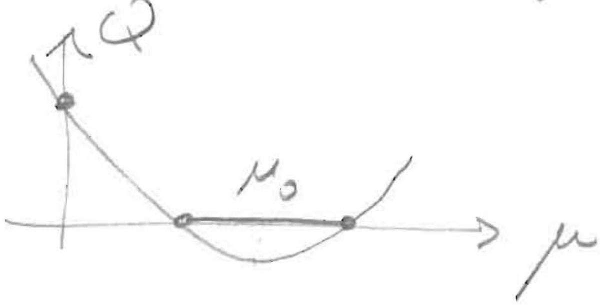
D. GURARIE

Lect. 25: Turing analysis of linearized RD

Op-tor: $\mathcal{L} = \begin{bmatrix} D_1 & \\ & D_2 \end{bmatrix} \nabla^2 + \underbrace{\begin{bmatrix} a & -b \\ c & -d \end{bmatrix}}_{J}$ with B.C

Dispersion f-n of Laplace BVP eigen μ

$$Q(\mu) = \det\left(J - \mu \begin{bmatrix} D_1 & \\ & D_2 \end{bmatrix}\right) = D_1 D_2 \mu^2 + a_1 \mu + a_2$$



$$\begin{cases} a_1 = dD_1 - aD_2 \\ a_2 = \det J \end{cases}$$

$$\Delta = a_1^2 - 4a_0 a_2$$

Turing Cond.

T1: $\boxed{a_1 < 0} \Rightarrow \boxed{aD_2 \geq dD_1}$

T2: $\boxed{\Delta > 0} \Rightarrow \boxed{(aD_2 + dD_1)^2 \geq 4D_1 D_2 bc}$

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1. Ranges / length-scales

u-activation: $r_1 = \sqrt{\frac{2D_1}{a}}$ $\left(a \approx \frac{1}{\text{act. time}}\right)$

V-inhibition: $r_2 = \sqrt{2D_2/d}$ $\left(d \approx \frac{1}{\text{inh.}}\right)$

$\boxed{T1}$: $\boxed{r_1^2 = \frac{2D_1}{a} < \frac{2D_2}{d_2} = r_2^2}$ ← short activ. long inhib.

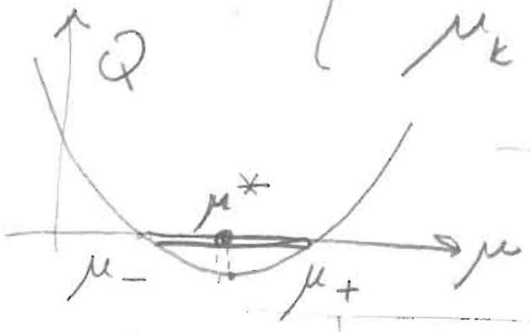
$\boxed{T2}$: $\frac{1}{r_1^2} + \frac{1}{r_2^2} \geq \sqrt{\frac{bc}{}}$

2. Domain size & bifurcations

Laplace BVP eigen $\begin{cases} \mu = \mu_k = \left(\frac{\pi k}{l}\right)^2 \text{ - Neum} \\ \mu_k = \left(\frac{2\pi k}{l}\right)^2 \text{ - Periodic} \end{cases}$

$k \geq 1$

Turing instab. range



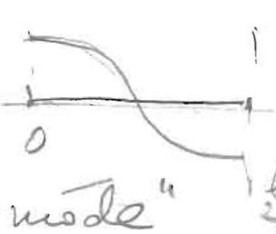
$$\mu^* = \frac{aD_1 - dD_2}{2D_1D_2} = \frac{1}{r_1^2} - \frac{1}{r_2^2} \qquad \boxed{\mu_\pm = \mu^* \pm \frac{\sqrt{\Delta}}{2D_1D_2}}$$

Domain size: $\boxed{\mu_k = \left(\frac{\pi k}{l}\right)^2 \approx \mu^*}$

(or $\mu_- < \mu_k < \mu_+$)

$$\boxed{l = l_k \approx \frac{\pi k r_1}{\sqrt{1-(r_1/r_2)^2}}} \qquad k = 1, 2, \ldots$$

Min size: $l_1 = \frac{\pi r_1}{\sqrt{1-(\,)^2}}$: "1-mode"



$$\boxed{\frac{\pi}{\sqrt{\mu_+}} k \leq l_k < \frac{\pi}{\sqrt{\mu_-}} k}$$

$l_2 = \frac{\pi r_1 2}{\sqrt{1}}$: "2-mode"

patterns in 1D

4. **Q.:** Is "Turing" realistic
for diff.-driven chemistry / biochemistry

Ans: Unlikely!

Need: $\boxed{\xi=\sqrt{D_1/D_2} \le \frac{a}{\sqrt{bc}+\sqrt{bc-ad}}}$ ←

or $\frac{r_1}{r_2} \le \frac{\alpha}{1+\sqrt{1-\alpha^2}}$; $\boxed{\alpha=\sqrt{\frac{ad}{bc}}<1}$

- unrealistic (in water $D_1 \approx D_2 \propto \sqrt{\text{molec. size}}$)

⊕ Activ. / inhib. / immobilizer

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5. **Color patterns:**

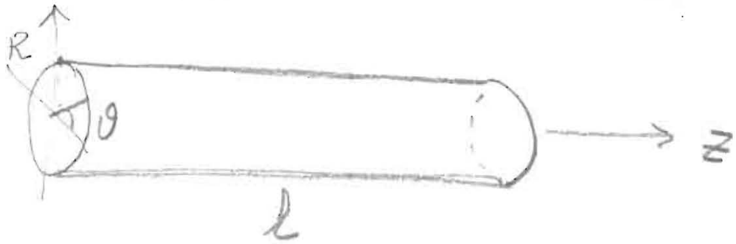
$\boxed{\text{melanoblast (precursor)} \rightarrow \text{melanocyte (color cell)}}$

- Genetic switch "on" melanoblast
- Migration of melanoblasts ← (diff)
- "blast" - "cyte" conversion
- "cyte" respond to $\boxed{\text{environ. chem.}}$ }

Chem: { Mb → Mc conversion
Mc-activation by "environ. chem."

Diffusion: "slow diff." of Mb → skin
"Fast diff" of env. chem.

model of coat pattern



cylinder: $0 < \theta < 2\pi$

$0 < z < l$

radius $R \ll l$

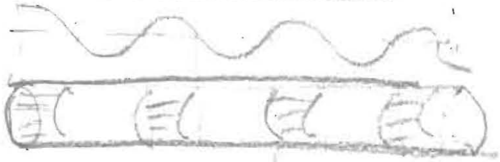
Linearized eigenmodes:

$$\boxed{\psi_{k,m}(z,\theta) = \cos\frac{\pi k z}{l}\, e^{\pm i m \theta}} \quad k = 1, 2 \ldots \quad m = 0, 1, \ldots$$

$$\boxed{\mu_- \le \mu_{k,m} = \left(\frac{\pi k}{l}\right)^2 + \left(\frac{m}{R}\right)^2 \le \mu_+} \quad (1)$$

For fixed RD - param. $J = \begin{bmatrix} a & -b \\ c & -d \end{bmatrix}$ $\boxed{l, R}$ ask for (k, m) that satisfy (1)

$\boxed{m = 0}$ ⇒ stripes
$k = 1, 2, \ldots$



$\boxed{m > 1}$ ⇒ spots

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Eigen mode expansion for linearized Turing instability

Solution of linear RD can be expanded in eigen f-ns of Diff. operator $\mathcal{L}$

$$\mathcal{L} = D\nabla^2 + a \quad \text{— scalar / single spp}$$

$$\mathcal{L} = \begin{bmatrix} D_1 & \\ & D_2 \end{bmatrix}\nabla^2 + J \quad \text{— matrix / interact spp}$$

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1. Scalar case: $\begin{cases} u_t = D u_{xx} + a u; & 0 < x < \ell \\ \text{BC: } u|_{x=0,\ell} = 0 \\ \text{IC: } u|_{t=0} = u_0(x) \end{cases}$

Laplace eigens	F-modes	$\mathcal{L}$ - eigens
$\mu_k = \left(\frac{\pi k}{\ell}\right)^2$	$\psi_k = \cos\frac{\pi k x}{\ell}$	$\lambda_k = -D\mu_k + a$

$k = 0, 1, \ldots$

$$u(x,t) = \sum_0^\infty f_k e^{\lambda_k t} \psi_k(x) = \underbrace{\sum_{\lambda_k \geq 0} f_k e^{\lambda_k t} \psi_k}_{\text{unstable}} + \ldots$$

F. coeff: $\boxed{f_k = \frac{\langle u_0 | \psi_k \rangle}{\|\psi_k\|^2} = \frac{2}{\ell}\int u_0(x)\psi_k(x) \quad \text{or} \quad \frac{1}{\ell}\int u_0\,dx}$ $k=0$

2. Matrix case (Turing)

k	0	1	- -	– wave #/vect. of $\psi_k(x)$
μ	μ_0	μ_1	- -	– eigenvalue of ∇^2
$\lambda_k^\pm$	$\lambda_0^\pm$	$\lambda_1^\pm$		– eigenvalue of L or $B(\mu)$
$X_k^\pm$	$X_0^\pm$			– (2D) eigen vector of $B(\mu)$

Matrix: $B(\mu) = -\mu\begin{bmatrix}D_1 & \\ & D_2\end{bmatrix} + J$

has eigendata $\mu_k \longrightarrow \begin{Bmatrix}\lambda_k^\pm \\ X_k^\pm\end{Bmatrix}$ – real or complex

Solution: $U(x,t) = \begin{pmatrix}u(x,t)\\ v(x,t)\end{pmatrix}$ of IVP $\begin{pmatrix}p(x)\\ q(x)\end{pmatrix}$

$$U(x,t) = \sum_{k=0}^{\infty}\Big(f_k^+ \underbrace{X_k^+ e^{\lambda_k^+ t} + f_k^- X_k^- e^{\lambda_k^- t}}_{U_k(t)}\Big)\psi_k(x)$$

$$= \underbrace{\sum_{Re\,\lambda_k \geq 0} \cdots}_{\text{unstable}} + \cdots$$

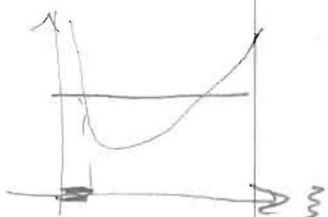
Coefficients: $f_k^\pm$ solve linear algebraic

$(t=0)$ $$\boxed{f_k^+ X_k^+ + f_k^- X_k^- = \frac{1}{\|\psi_k\|^2}\langle U_0|\psi_k\rangle = \frac{1}{\|\psi_k\|^2}\begin{pmatrix}\langle p|\psi_k\rangle \\ \langle q|\psi_k\rangle\end{pmatrix}}$$

If $M_k = [X_k^+ \;\; X_k^-]$ – eigen matrix

then $\begin{pmatrix} f_k^+ \\ f_k^- \end{pmatrix} = M_k^{-1} \cdot \begin{pmatrix} p_k \\ q_k \end{pmatrix} \leftarrow$ F. coeff. of $\begin{pmatrix} p(x) \\ q(x) \end{pmatrix}$

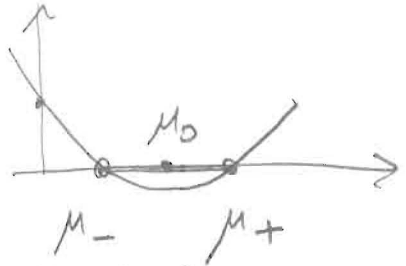
Example: $L = \begin{bmatrix} D_1 & \\ & 1 \end{bmatrix} \partial_x^2 + \begin{bmatrix} 3 & 13 \\ -1 & -3 \end{bmatrix}$



with $D_1 = .9 \max(D_1) = \dfrac{.9a}{\sqrt{bc} + \sqrt{bc-ad}}$

$B(\mu) = -\mu \begin{bmatrix} D_1 & \\ & 1 \end{bmatrix} + J \Rightarrow$ instability range

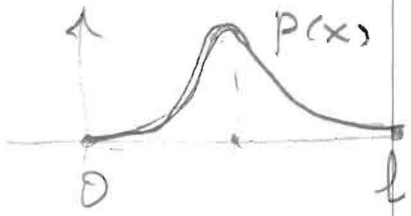
$(\det B(\mu) < 0)$



μ_0	μ_-	μ_+
4.32	2.55	6.09

Take IV: $\begin{cases} p(x) = e^{-(x-l/2)^2/\varepsilon} = p_0 + p_2\psi_2 + p_4\psi_k + \dots \\ q(x) = 0 \end{cases}$

Choose: $l = l_4 = \dfrac{4\varpi}{\sqrt{\mu_0}}$ – length



k	0		2		4	
μ	0		1.07973		4.31893	
λ	2 i	-2 i	-0.679032 + 1.19802 i	-0.679032 - 1.19802 i	-5.5772	0.144946
x₁	-3 - 2 i	-3 + 2 i	0.963624 + 0. i	0.963624 + 0. i	-0.867227	0.991144
x₂	1	1	-0.252077 + 0.0888029 i	-0.252077 - 0.0888029 i	0.497913	-0.132792

Solution: $U(x,t) = \overbrace{\left(f_0^\pm X_0^\pm e^{\pm 2it}\right)}^{\text{oscill}} + \overbrace{\left(f_2^\pm X_2^\pm e^{\lambda_2^\pm t}\right)}^{\text{decay}} \psi_2$

$+ \underbrace{\left(f_4^+ X_4^+ e^{\lambda_4^+ t}\right)}_{\text{Growth}} \psi_4(x) + \dots$

The oscillating patterns observed in numeric experiments come from marginally stable k=0 - mode (with complex eigens = 2i,-2i)