Random and chemotactic motion (1D first)

$B(t,x)$ microorganism density

$$\frac{\partial B}{\partial t} = -\frac{\partial}{\partial x}(J_{ch} + J_{rd}) \qquad \text{(sem. 19)}$$

J_{ch} = chemotactic flux, motion due to environmental causes (nutrition, light, temperature, ...), attraction

J_{rd} = random flux, modeled as diffusion, repulsion:

$$J_{rd} = -\mu \frac{\partial B}{\partial x} \quad \text{(Fick's law)}, \quad \mu = \text{motility/dispersal rate (diffusion constant)}$$

Model for J_{ch}: $J_{ch} = \chi \cdot B \frac{\partial s}{\partial x}$, $s(t,x)$ = substrate/nutrient concentration, χ = chemotactic constant

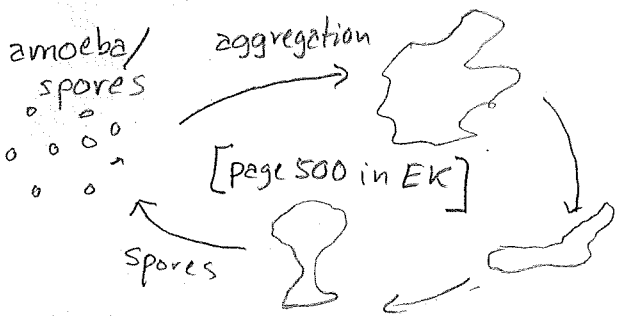
$$\Rightarrow \frac{\partial B}{\partial t} = -\chi\left(\frac{\partial B}{\partial x}\cdot\frac{\partial s}{\partial x} + B\frac{\partial^2 s}{\partial x^2}\right) + \mu\frac{\partial^2 B}{\partial x^2}, \text{ to be used!}$$

Pattern formation, morphogenesis

morpho = shape/form, genesis = formation

We study two models 1. aggregation of cellular slime molds
2. Turing's chemical morphogenesis

Slime molds



How can we describe the aggregation phase?
Amoeba secrete cAMP to attract others (when too little bacteria for feeding)

Keller-Segel model

1. Cells have random motion and chemotactic motion towards cAMP
2. No cells dying or dividing
3. cAMP produced at constant rate by each cell
4. Rate of degradation of cAMP is linear in its concentration

} simplifications

5. cAMP spreads by diffusion

Model for 1D (2D later)

$a(t,x)$ = density of cellular slime mold amoeba
$c(t,x)$ = concentration of cAMP

$$\begin{cases} \dfrac{\partial a}{\partial t} = -\dfrac{\partial}{\partial x}(J_{rd} + J_{ch}) = \mu \dfrac{\partial^2 a}{\partial x^2} - \chi \underbrace{\left(\dfrac{\partial a}{\partial x}\dfrac{\partial c}{\partial x} + a \dfrac{\partial^2 c}{\partial x^2} \right)}_{(*)} & , \mu > 0, \chi > 0 \\ \dfrac{\partial c}{\partial t} = D \dfrac{\partial^2 c}{\partial x^2} + \underbrace{fa - kc}_{\text{sources}} & , D > 0 \end{cases}$$

(diffusion with sources)

fa: $f > 0$ rate of cAMP secretion, linear in a by 3.
$-kc$: $k > 0$ rate of cAMP degradation, linear in c by 4.

Non-linear system because of term (*) (products) ⇒ difficult (impossible?) to find general or global solution.

Homogeneous steady states

- constant in time and space $\begin{cases} a(t,x) = \bar{a} \\ c(t,x) = \bar{c} \end{cases}$

Easy to find, all derivatives $= 0$ ⇒ $f\bar{a} - k\bar{c} = 0$ only condition
Stable? Or, more interestingly, unstable? So that something (aggregation) can happen.

Perturbations, linearization near $\bar{a}, \bar{c}$

$$\begin{cases} a(t,x) = \bar{a} + \hat{a}(t,x) \\ c(t,x) = \underbrace{\bar{c}}_{\text{constants}} + \underbrace{\tilde{c}(t,x)}_{\text{small}} \end{cases}$$

Into the system ⇒

$$\begin{cases} \dfrac{\partial \hat{a}}{\partial t} = \mu \dfrac{\partial^2 \hat{a}}{\partial x^2} - \chi \overbrace{\dfrac{\partial \hat{a}}{\partial x}\dfrac{\partial \tilde{c}}{\partial x}}^{\text{neglect}} - \chi(\bar{a} + \hat{a}) \dfrac{\partial^2 \tilde{c}}{\partial x^2} \\ \dfrac{\partial \tilde{c}}{\partial t} = D \dfrac{\partial^2 \tilde{c}}{\partial x^2} + \underbrace{f(\bar{a} + \hat{a}) - k(\bar{c} + \tilde{c})}_{=0} \end{cases}$$

Neglect 2nd-order terms in $\hat{a}$ and $\tilde{c}$

⇒ Linearized system

$$\begin{cases} \dfrac{\partial \hat{a}}{\partial t} = \mu \dfrac{\partial^2 \hat{a}}{\partial x^2} - \chi \bar{a} \dfrac{\partial^2 \tilde{c}}{\partial x^2} \\ \dfrac{\partial \tilde{c}}{\partial t} = D \dfrac{\partial^2 \tilde{c}}{\partial x^2} + f\hat{a} - k\tilde{c} \end{cases}$$

Linear system of PDE's of diffusion type for $\hat{a}$ and $\tilde{c}$

We could start from "scratch" with separation of variables, but using our previous studies of diffusion equations (with no flux boundary conditions), we look for solutions

$$\begin{cases} \hat{a}(t,x) = A e^{\sigma t} \cos qx \\ \tilde{c}(t,x) = C e^{\sigma t} \cos qx \end{cases} \quad (**)$$

that are exponential in t and cos in x;

Find relations σ and q (single eq. $\sigma \sim \lambda \le 0$, $q \sim \sqrt{|\lambda|}$).

Substitute (**) into linear system $\Rightarrow$

$$\begin{cases} \sigma A e^{\sigma t}\cos qx = -\mu q^2 A e^{\sigma t}\cos qx + \chi\bar{a} q^2 C e^{\sigma t}\cos qx \\ \sigma C e^{\sigma t}\cos qx = -Dq^2 C e^{\sigma t}\cos qx + (fA - kC) e^{\sigma t}\cos qx \end{cases}$$

Divide by $e^{\sigma t}\cos qx$ $\Rightarrow$

$$\begin{cases} (\sigma + \mu q^2)A - \chi\bar{a} q^2 C = 0 \\ -fA + (\sigma + Dq^2 + k)C = 0 \end{cases}$$

Linear system in A, C, $A = C = 0$ is the unique (uninteresting) solution if the determinant of the system $\neq 0$.

We want

$$0 = \begin{vmatrix} \sigma + \mu q^2 & -\chi\bar{a} q^2 \\ -f & \sigma + Dq^2 + k \end{vmatrix} = \sigma^2 + \underbrace{((\mu + D)q^2 + k)}_{=\beta > 0}\sigma + \underbrace{\mu q^2(Dq^2 + k) - f\chi\bar{a} q^2}_{=\gamma}$$

$$\Rightarrow \sigma_{1,2} = \underbrace{-\frac{\beta}{2}}_{<0} \pm \frac{1}{2}\sqrt{\beta^2 - 4\gamma}$$

Solutions with $\sigma < 0$ will $\to 0$ as $t \to \infty$ $\Rightarrow$ will not cause aggregation

We want unstable perturbations, i.e., $\sigma > 0$ (or $Re\,\sigma > 0$). If $4\gamma > \beta^2$, $Re\,\sigma_{1,2} < 0$. If $\beta^2 \ge 4\gamma > 0$, $\sigma_{1,2} < 0$. If $\gamma < 0$, $\sqrt{\beta^2 - 4\gamma} > \beta$ and $\sigma_1 > 0$ (and $\sigma_2 < 0$) $\Rightarrow$

The condition for aggregation is

$$\gamma < 0 \iff \mu(Dq^2 + k) < f\chi\bar{a}$$

Interpretations

If amoeba restricted to $0 < x < L$ and we have no-flux conditions

$$\frac{\partial a}{\partial x}(t,0) = \frac{\partial a}{\partial x}(t,L) = \frac{\partial c}{\partial x}(t,0) = \frac{\partial c}{\partial x}(t,L) = 0$$ at the ends, the same holds for $\hat{a}$ and $\hat{c}$. Check $\frac{\partial \hat{a}}{\partial x} = -qAe^{\sigma t}\sin qx$

at $x = 0$: $-qAe^{\sigma t}\sin(q\cdot 0) = 0$ O.K.

at $x = L$: $-qAe^{\sigma t}\sin(qL) = 0 \Rightarrow qL = n\pi \Rightarrow q = \frac{n\pi}{L}$, $n = 0, 1, 2, \ldots$

($q = 0 \Rightarrow \hat{a}, \hat{c}$ constants, neither increasing nor decreasing)

Conditions on $\frac{\partial \hat{c}}{\partial x}$ are also ok with $q = \frac{n\pi}{L}$

$\Rightarrow$ the aggregation condition becomes

$$\mu\left(\frac{Dn^2\pi^2}{L^2} + k\right) < f\chi\bar{a} \qquad (= k\chi\bar{c})$$

To satisfy this, one should have

$\left\{ \begin{array}{l} \mu, k, D \text{ small} \\ \chi, \bar{a}, f \text{ large} \end{array} \right.$

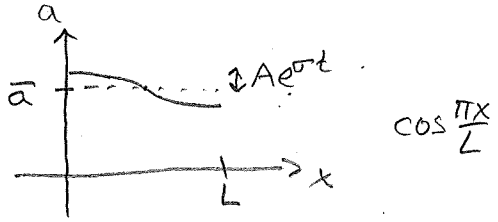
Means:

Low random motility μ of amoeba/cells, low rate k of degradation of cAMP, low diffusion D of cAMP, large chemotactic constant χ, high secretion rate f, high density $\bar{a}$ of amoeba ($f\bar{a} = k\bar{c}$ means also $\bar{c}$ higher).

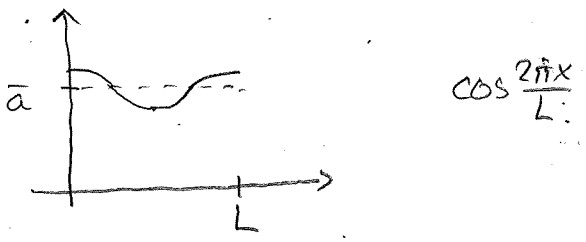
The term $\frac{n^2}{L^2}$ means larger L better (and $\bar{a}$ is density, not L-dependent), and that smaller n appear easier.

For $f\chi\bar{a} < \mu k$, the homog. steady state $\bar{a}, \bar{c}$ is stable. If we increase $f\chi\bar{a}$, we get instability for small n (long wavelength),

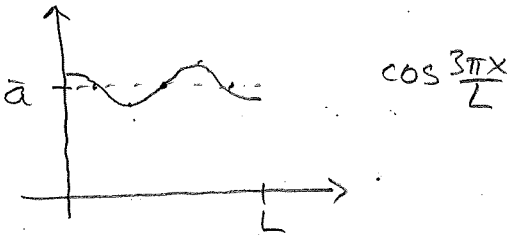
first for $n=1$ if $f\chi\bar{a} > \mu(k + \frac{D\pi^2}{L^2})$



for $n=2$ if $f\chi\bar{a} > \mu(k + \frac{4D\pi^2}{L^2})$



for $n=3$ if $f\chi\bar{a} > \mu(k + \frac{9D\pi^2}{L^2})$



Different combinations of these appear, depending on the shape of the initial perturbation (~ cos-series). The ones with n large, not satisfying the aggregation condition, will vanish.

2D model later.