

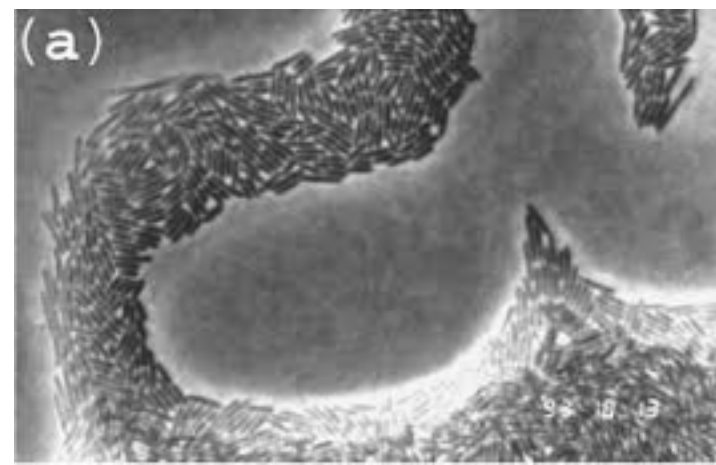
# Active matter - overview

18.354 L23



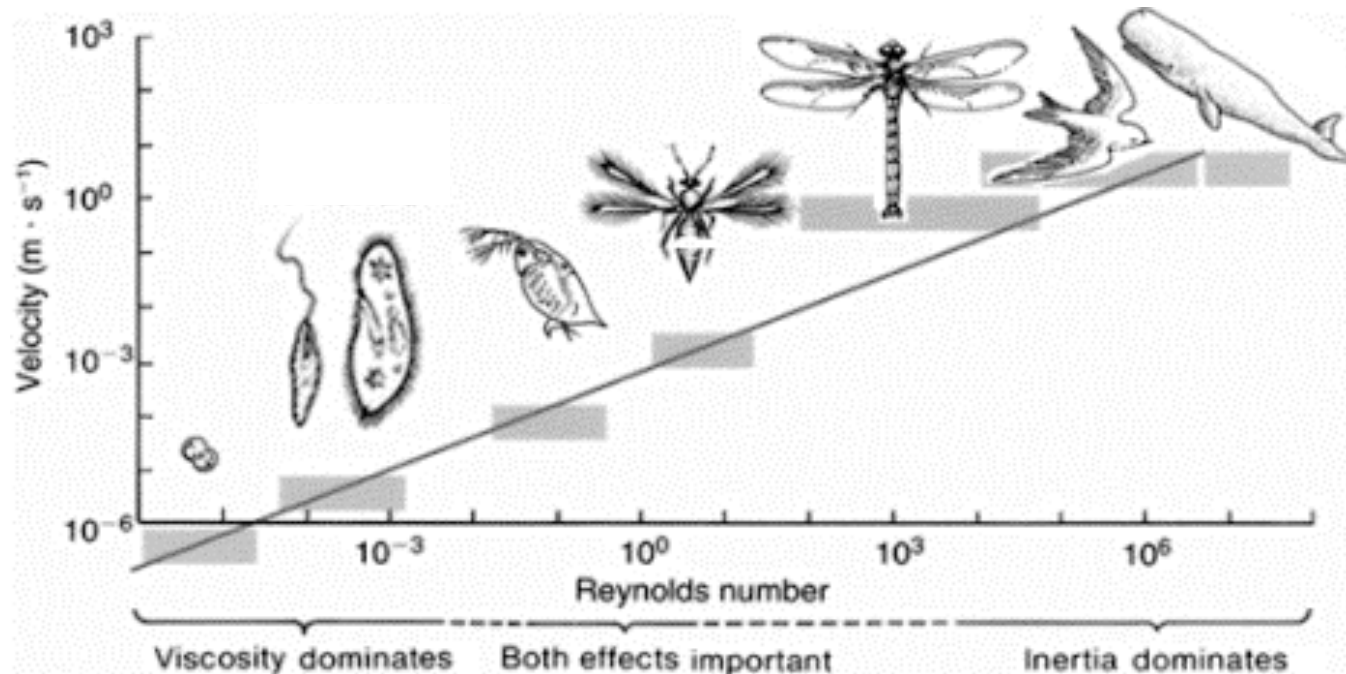
[dunkel@math.mit.edu](mailto:dunkel@math.mit.edu)

# Active matter



# Typical Reynolds numbers

$$Re = \frac{\rho U L}{\mu} = \frac{U L}{\nu}$$



# Birds



# Fish

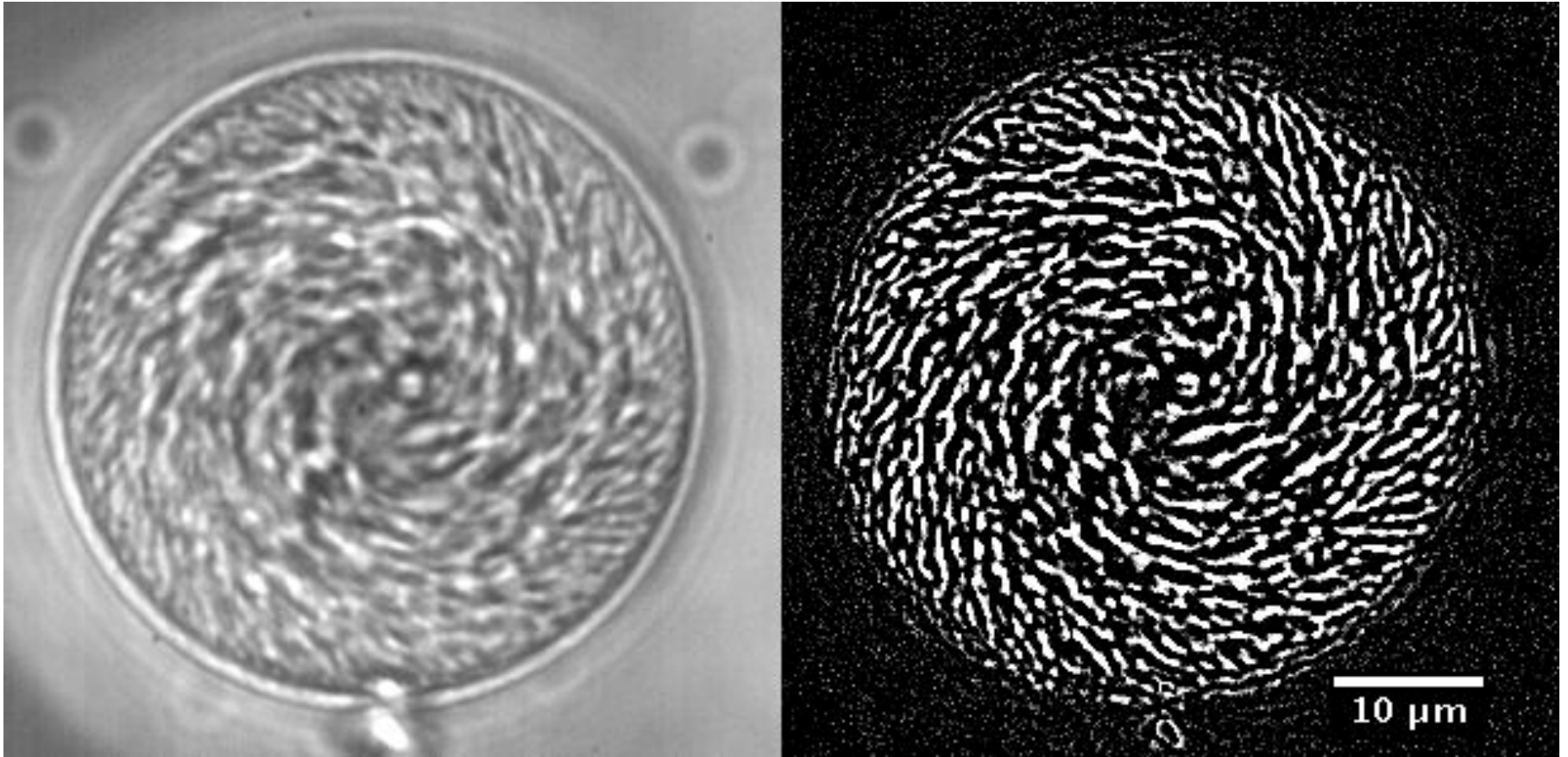


# Bacteria



Berg lab, Harvard

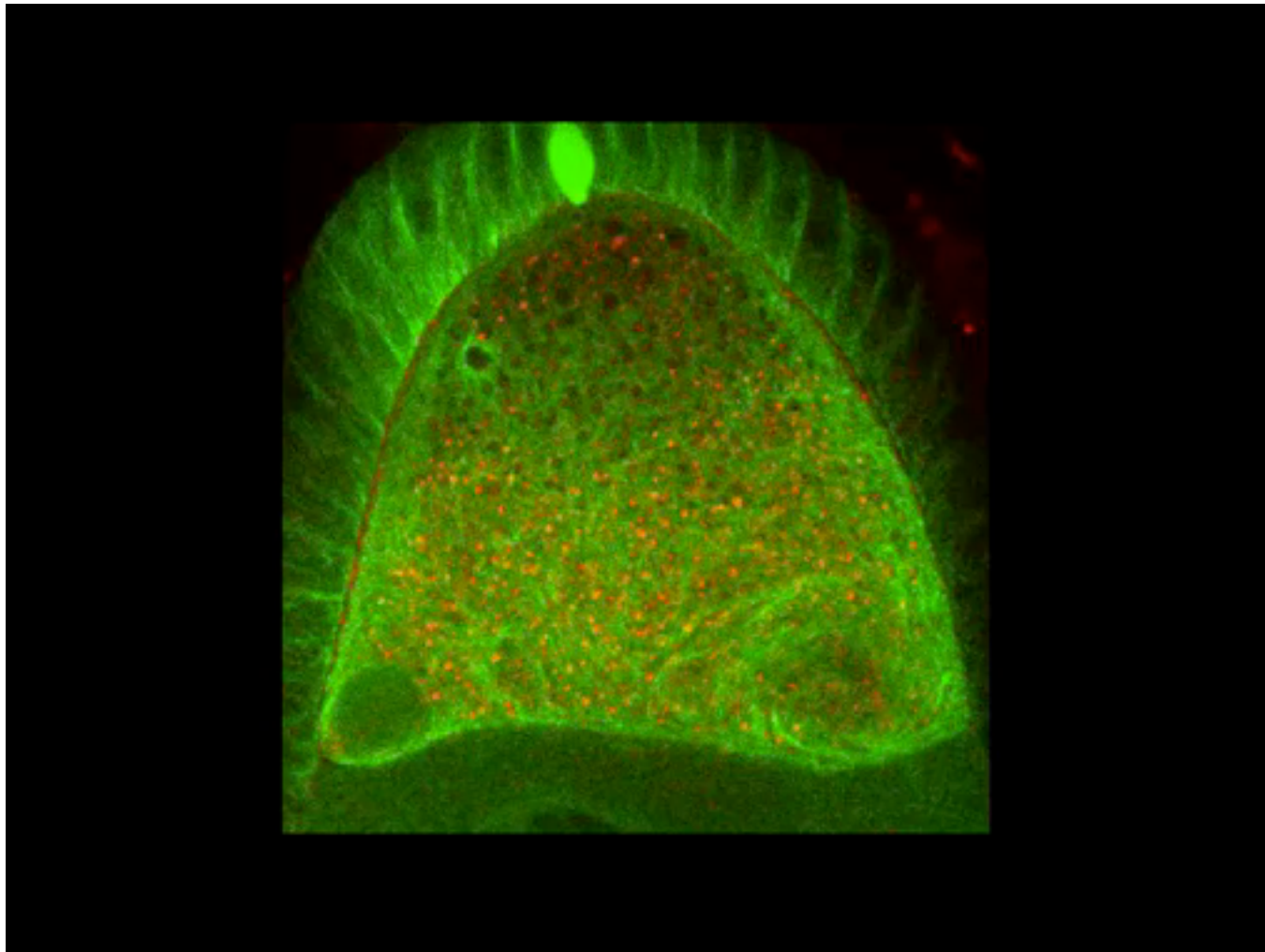
# Bacteria



Wioland et al (2013) PRL

Vortex life time  $\sim$  minutes

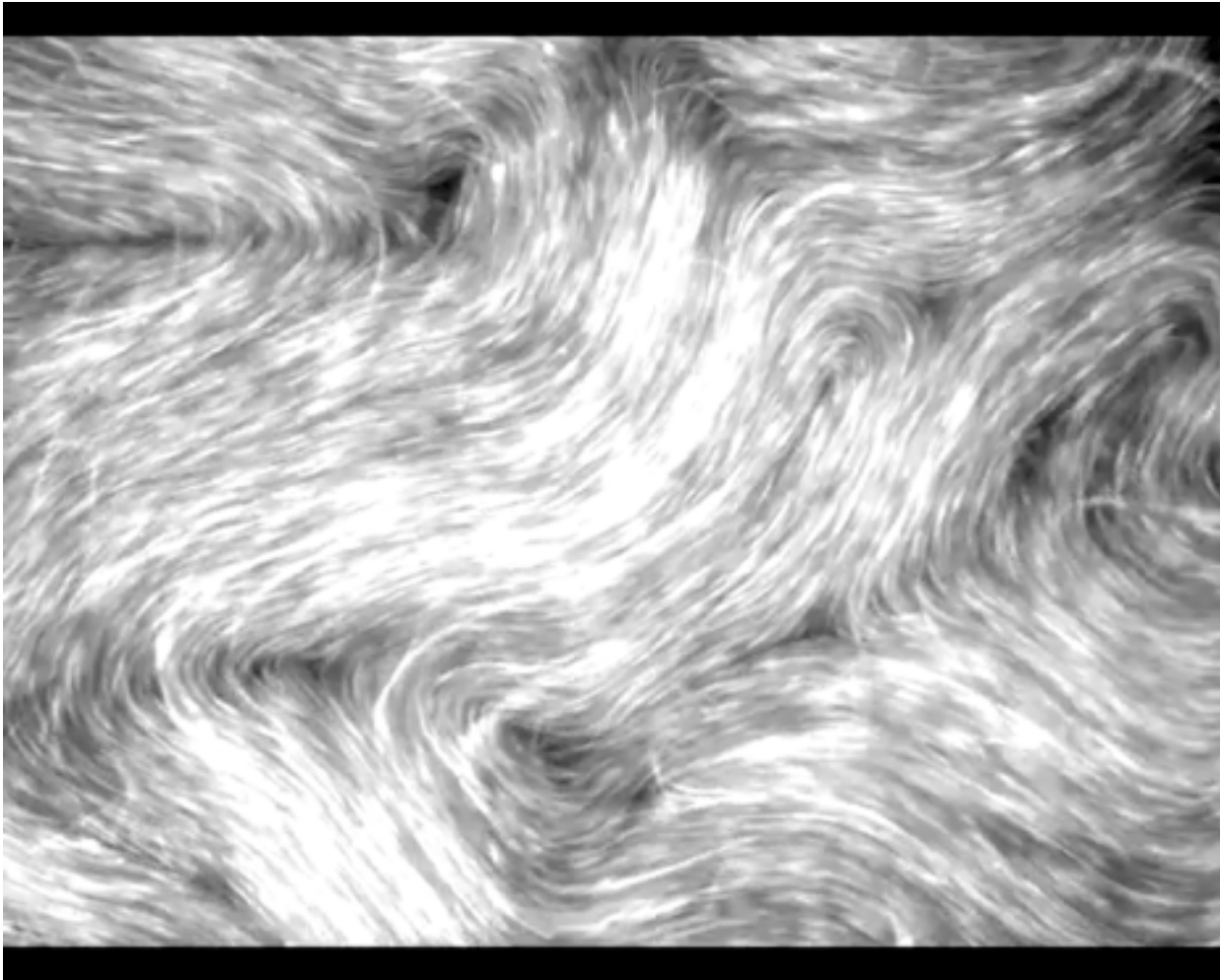
# Motor-driven filaments



Drosophila embryo, Goldstein lab, Cambridge

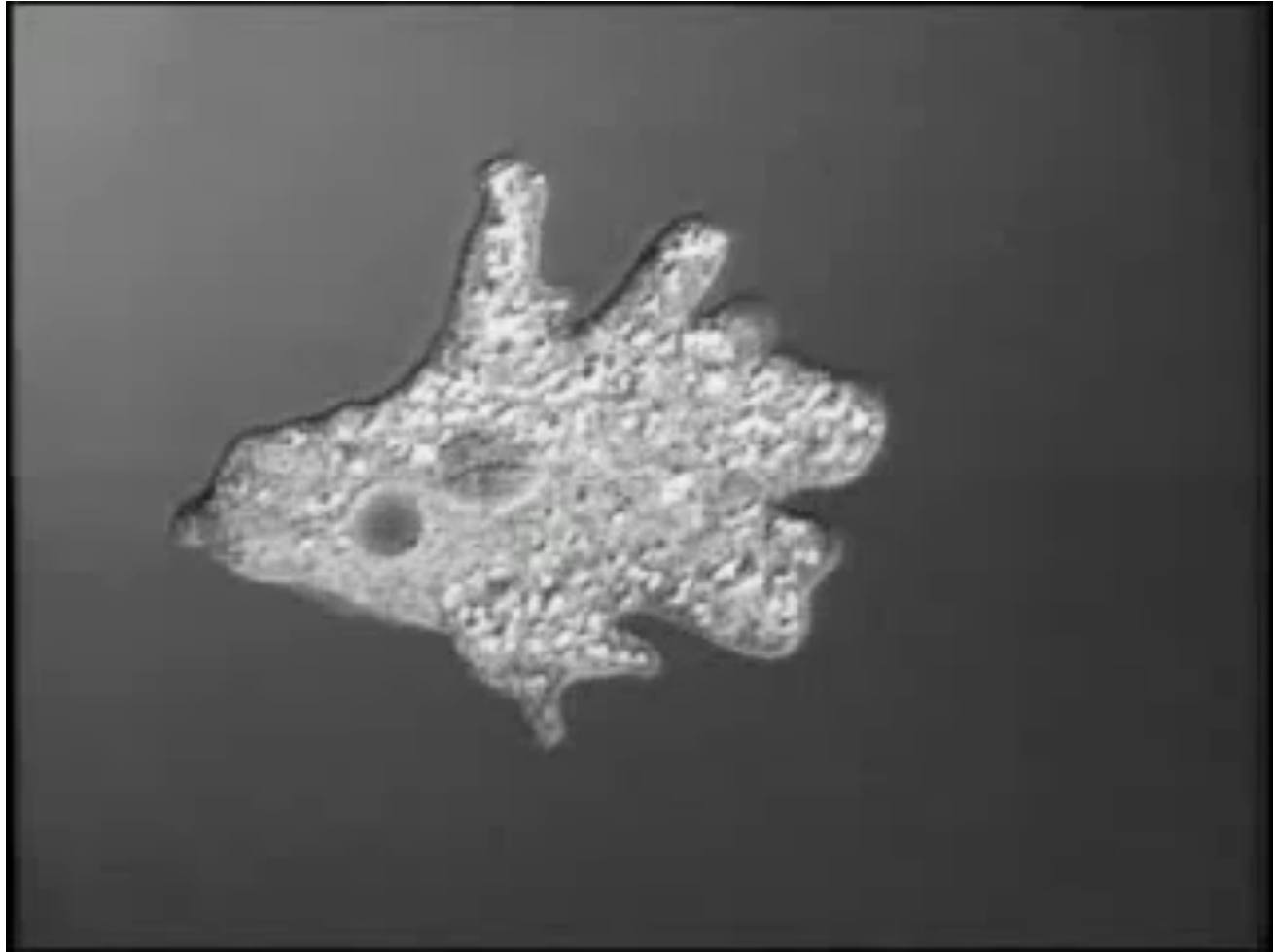


# Motor-driven filaments

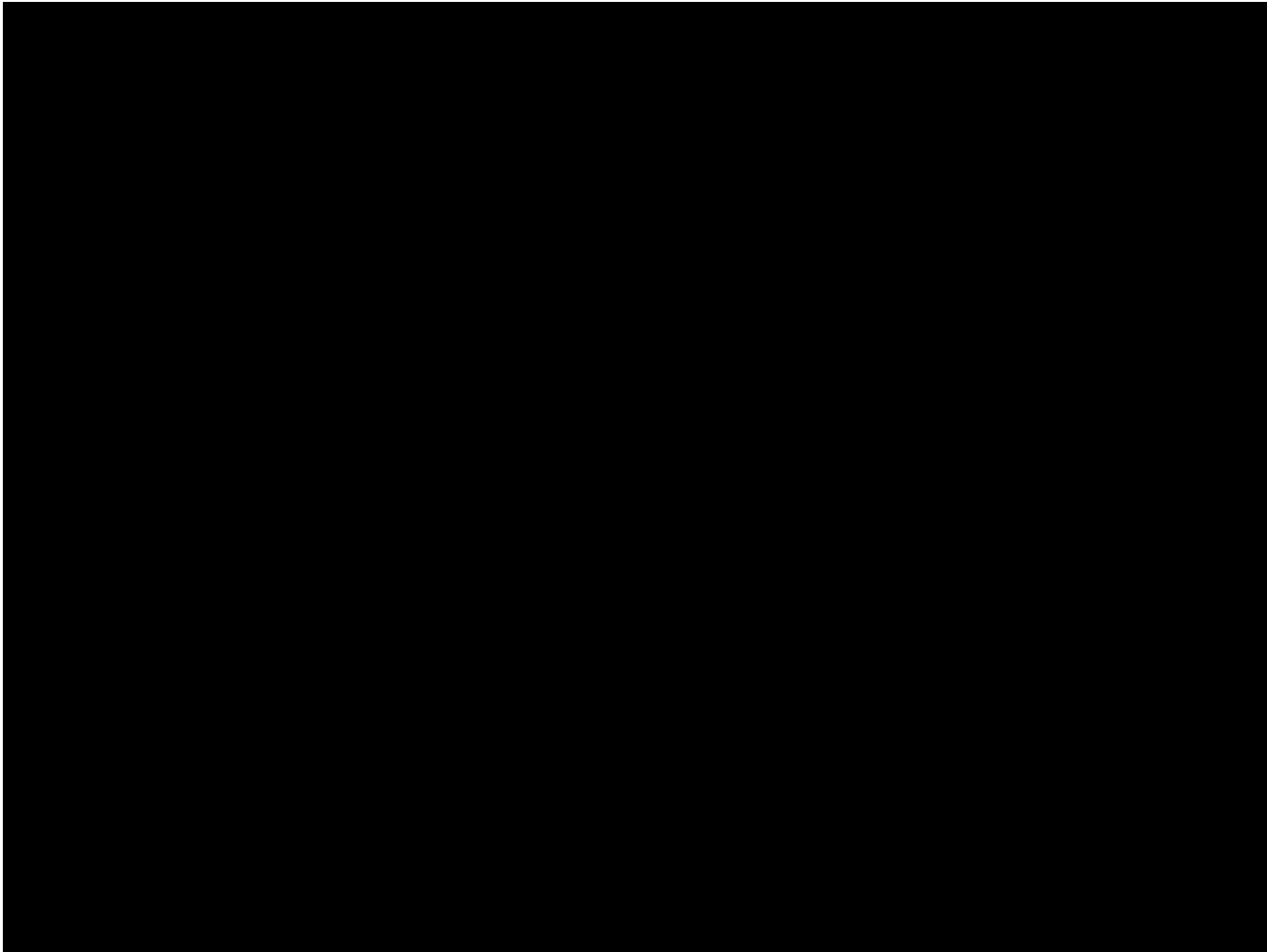


Dogic lab (Brandeis) Nature 2012

# Amoeba

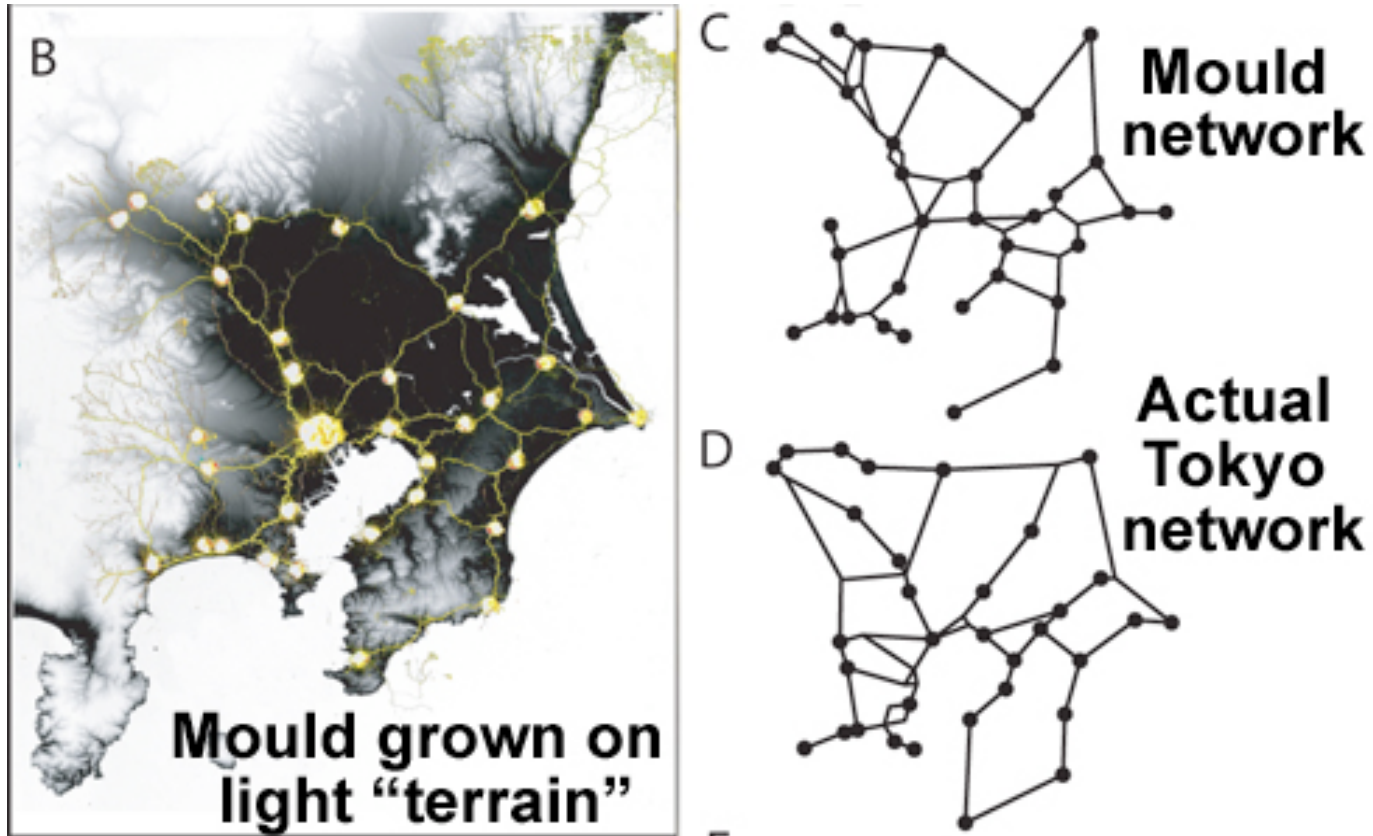


# Physarum



Tero et al, Science 2010

# Physarum



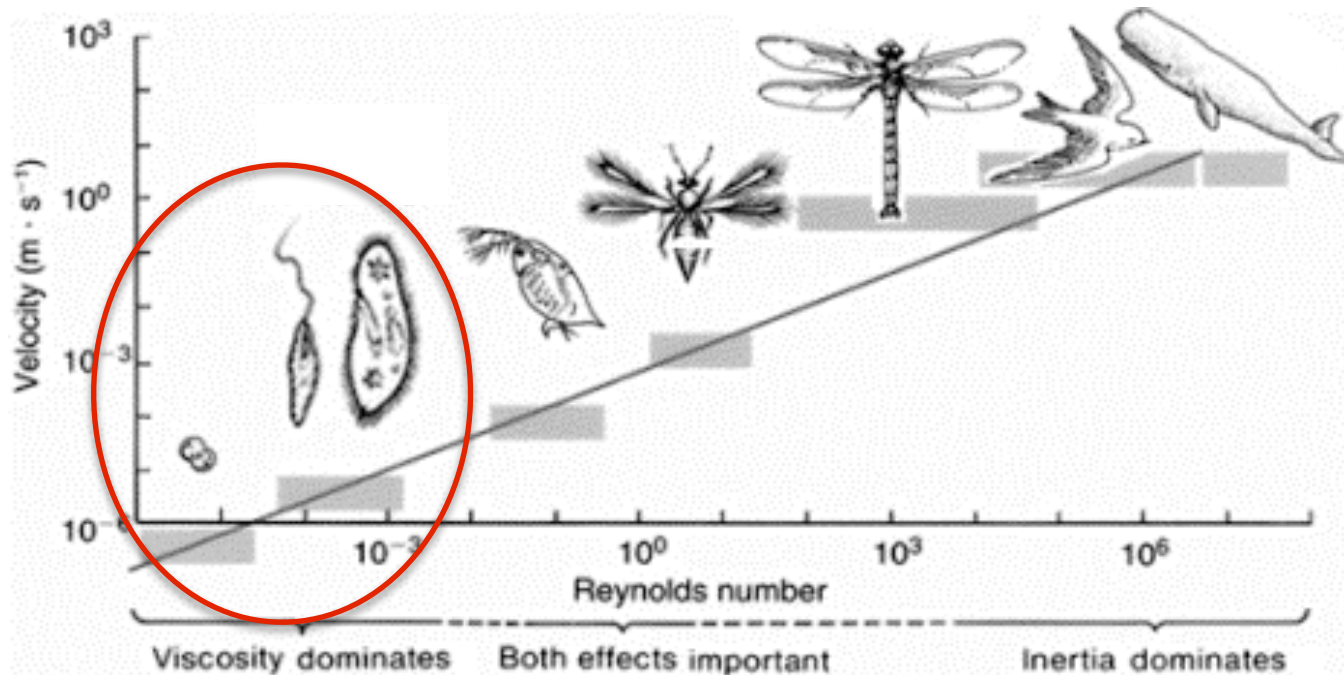
Tero et al, Science 2010

# Questions

- universal aspects of collective motion & self-organization ?
- biological functions ?
- information transport ?
- mathematical description? (microscopically, macroscopically, ...)
- effects of boundary conditions ?

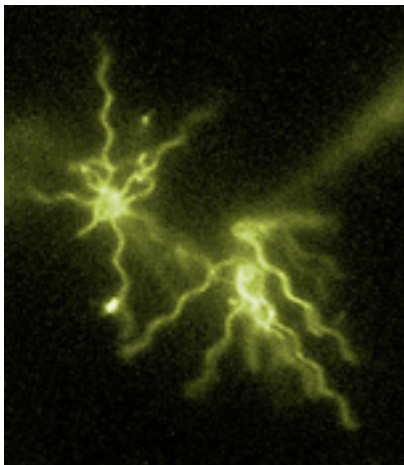
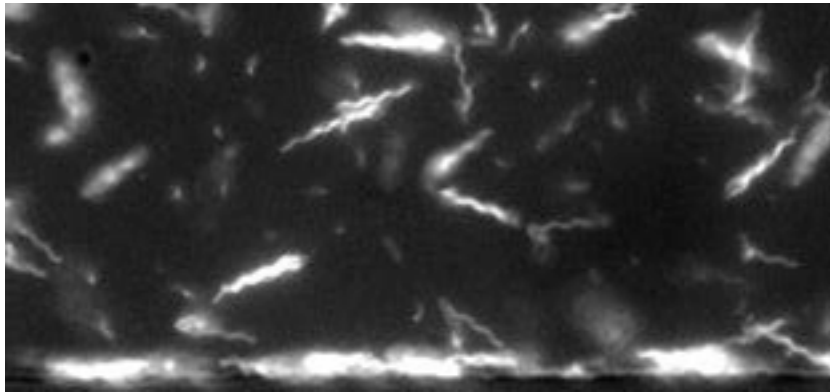
# Typical Reynolds numbers

$$Re = \frac{\rho U L}{\mu} = \frac{U L}{\nu}$$

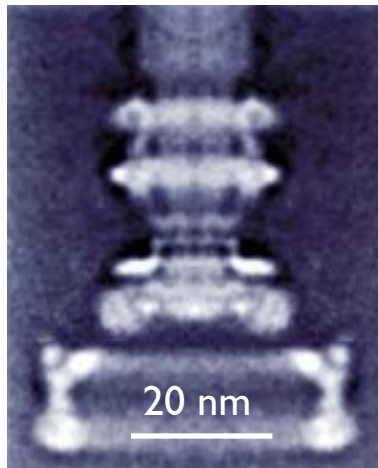


# Bacterial motors

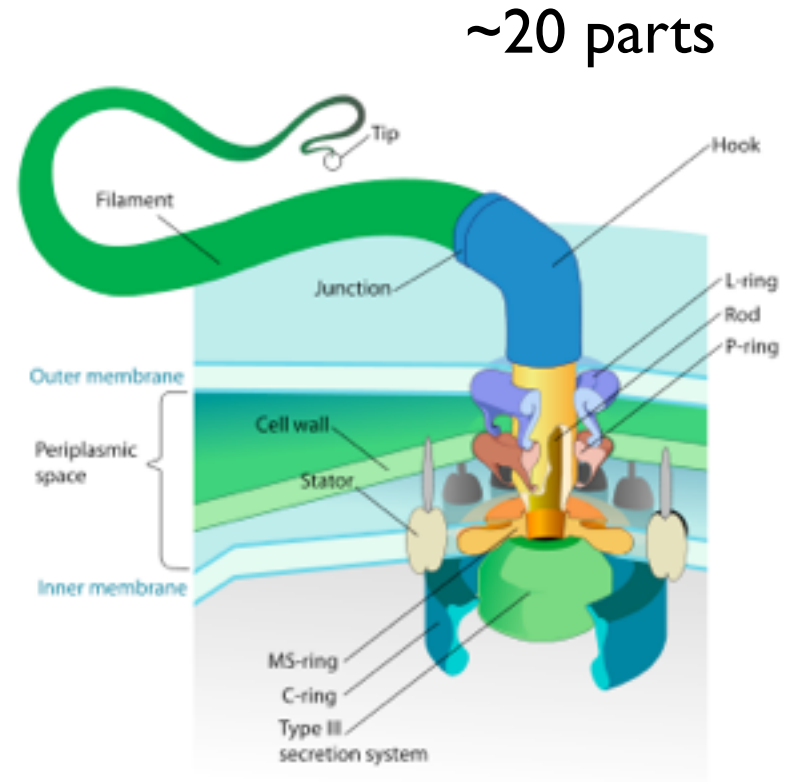
movie: V. Kantsler



Berg (1999) Physics Today

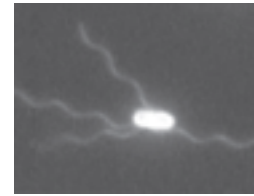


Chen et al (2011) EMBO Journal

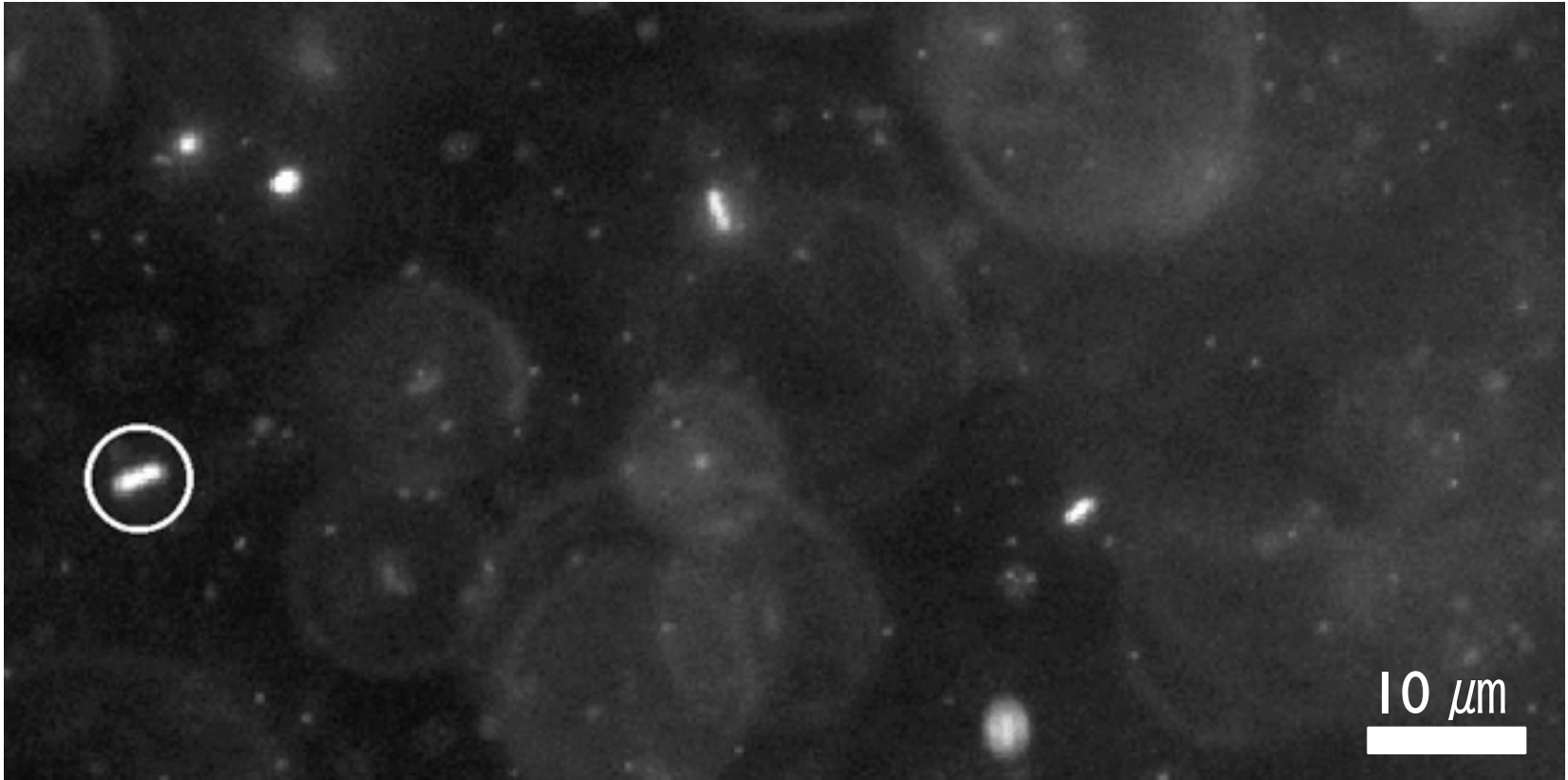


source: wiki

# E. coli (non-tumbling)



non-tumbling HCB 437



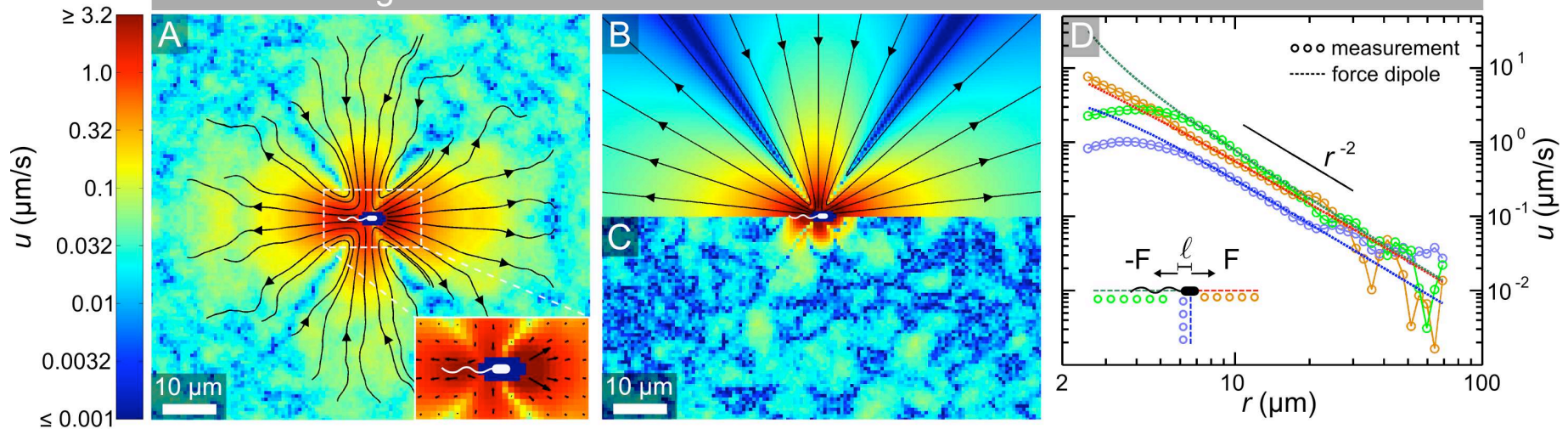
Drescher et al (2011) PNAS



# E.coli (non-tumbling HCB 437)



Free swimming



$$\mathbf{u}(\mathbf{r}) = \frac{A}{|\mathbf{r}|^2} \left[ 3(\hat{\mathbf{r}} \cdot \hat{\mathbf{d}})^2 - 1 \right] \hat{\mathbf{r}}, \quad A = \frac{\ell F}{8\pi\eta}, \quad \hat{\mathbf{r}} = \frac{\mathbf{r}}{|\mathbf{r}|}$$

$$V_0 = 22 \pm 5 \mu\text{m/s}$$

$$\ell = 1.9 \mu\text{m}$$

$$F = 0.42 \text{ pN}$$

‘pusher’ dipole

# Hydrodynamic scattering

dipole flow

$$\mathbf{v} \sim \frac{A}{r^2}$$

vorticity

$$\boldsymbol{\omega} = \nabla \times \mathbf{v} \sim \frac{A}{r^3}$$

encounter time

$$\tau \sim \ell/V$$

HD rotation

$$\langle |\Delta\phi|^2 \rangle \sim (\omega\tau)^2 \sim \left( \frac{A\tau}{r^3} \right)^2$$

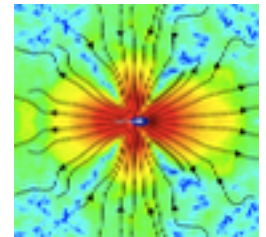
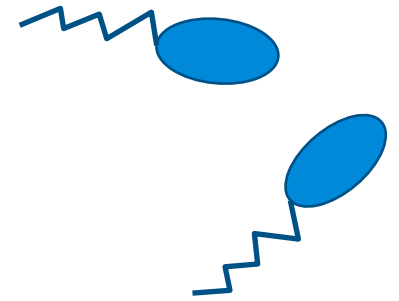
rotational diffusion

$$\langle |\Delta\phi|^2 \rangle \sim D_r\tau$$

balance

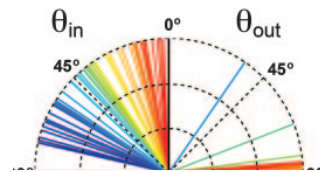
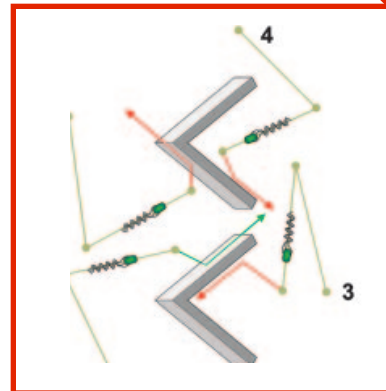
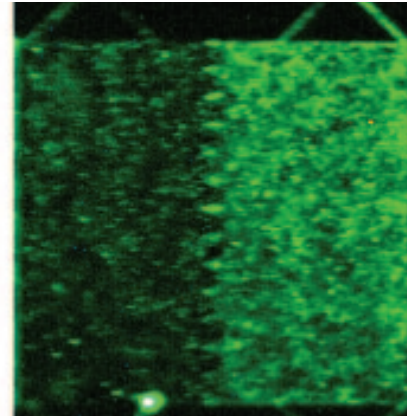
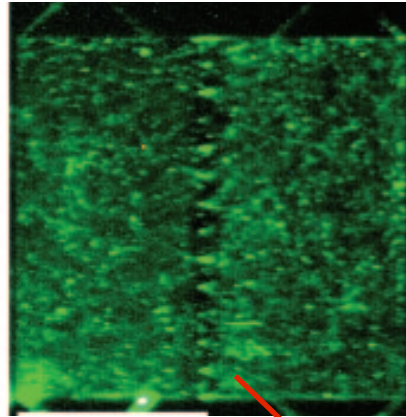
$$r_H \sim \left( \frac{A^2\tau}{D_r} \right)^{1/6}$$

3.3  $\mu\text{m}$  for *E. coli*



$$D_r = 0.057 \text{ rad}^2/\text{s}$$

# Rectification of **prokaryotic** locomotion

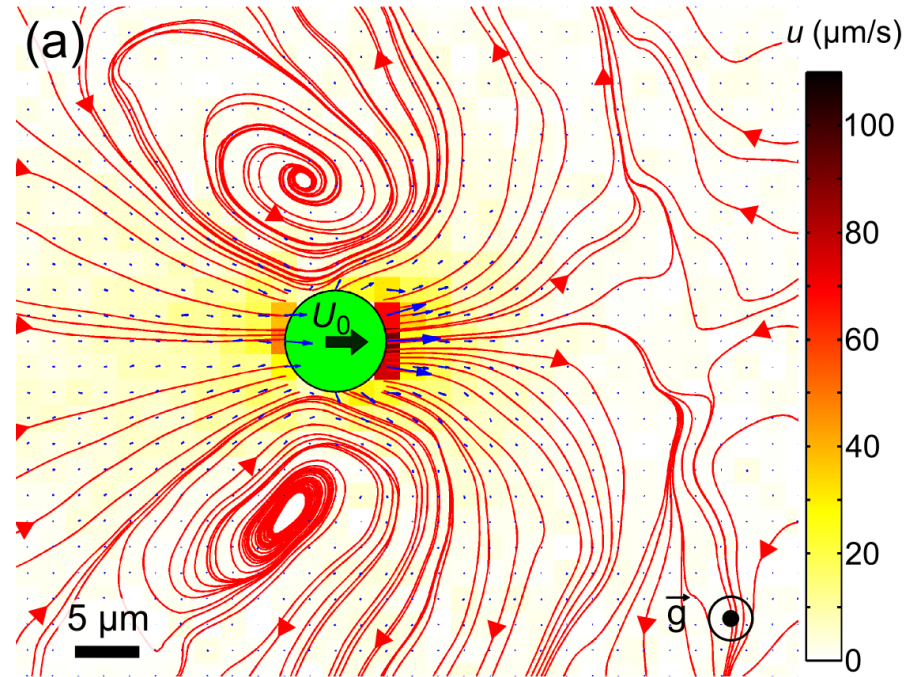
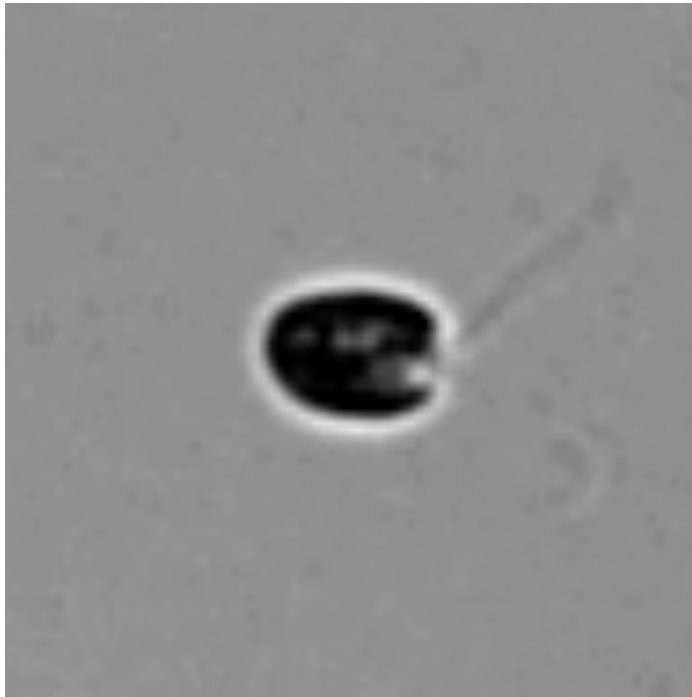


Galadja et al (2009)  
J Bacteriology

Austin lab, Princeton, 2009



# Chlamydomonas

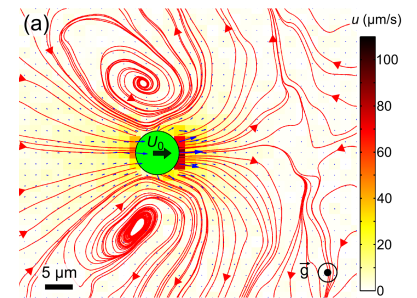
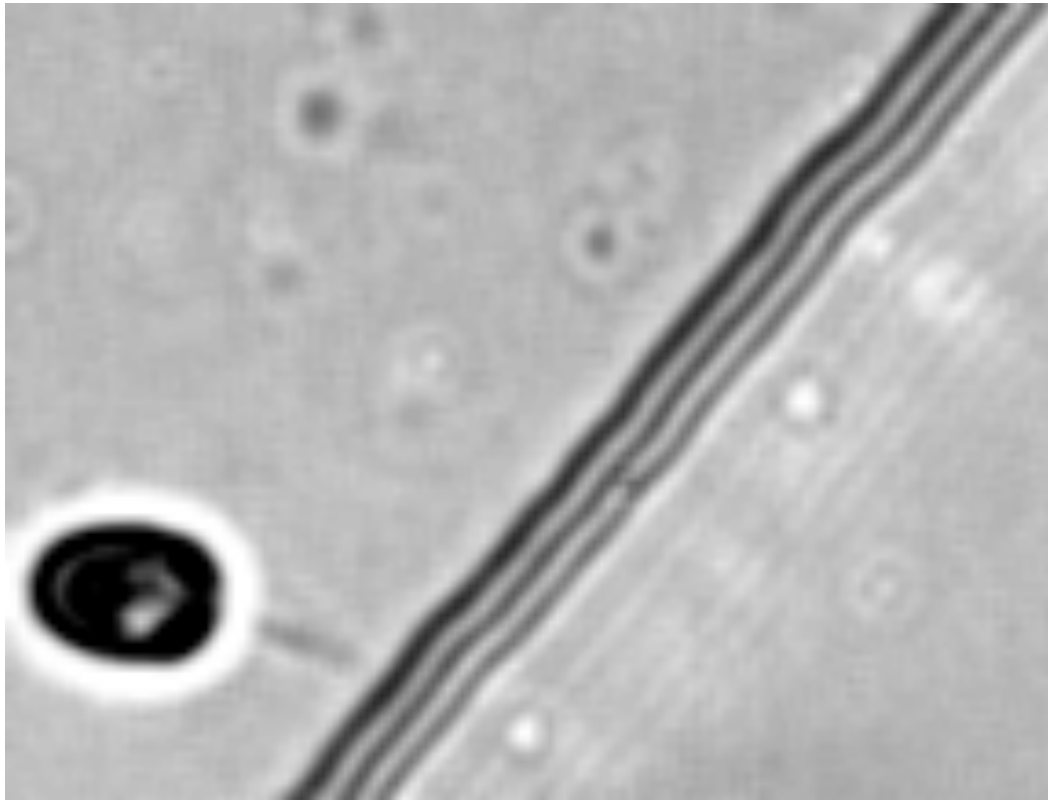


Movie: Jeff Guasto (TUFTS)

Drescher et al PRL 2010  
Guasto et al PRL 2010

size  $\sim 20 \mu\text{m}$   
speed  $\sim 100 \mu\text{m/s}$   
beat frequency  $\sim 30 \text{ Hz}$   
'puller'

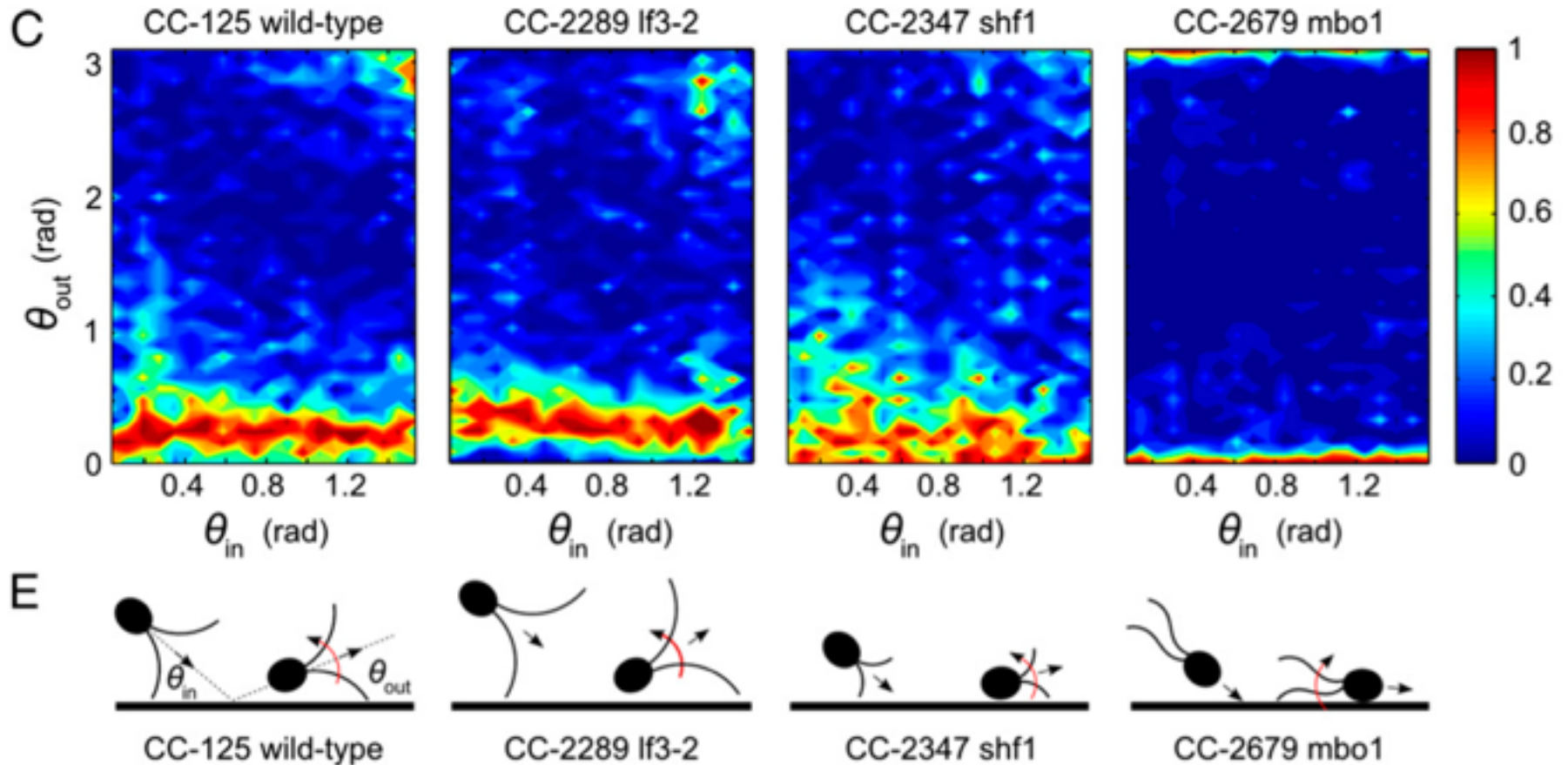
# Mechanical control of algal locomotion



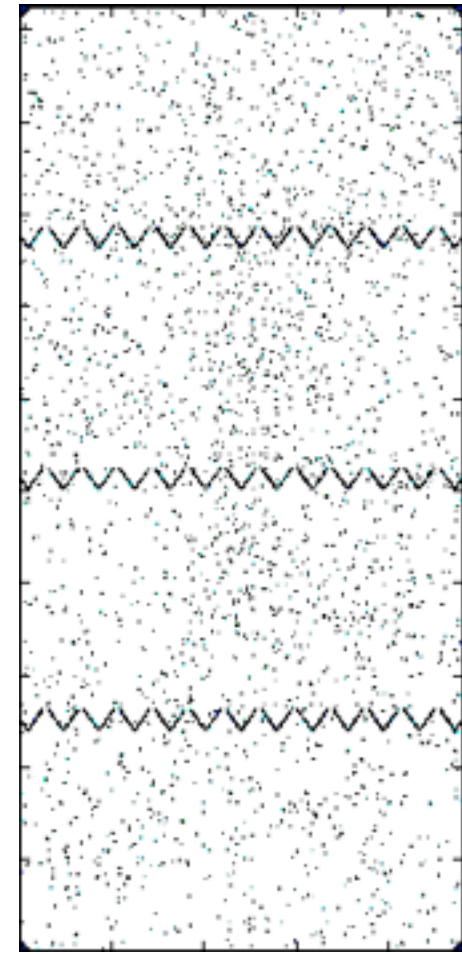
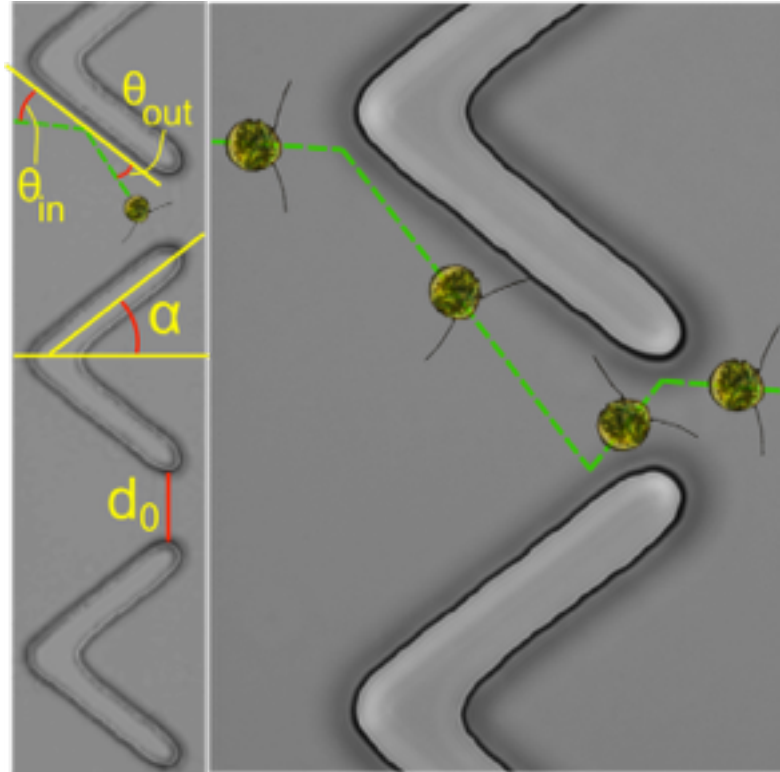
Kantsler, Dunkel, Polin, Goldstein (2012) PNAS



# Surface scattering laws



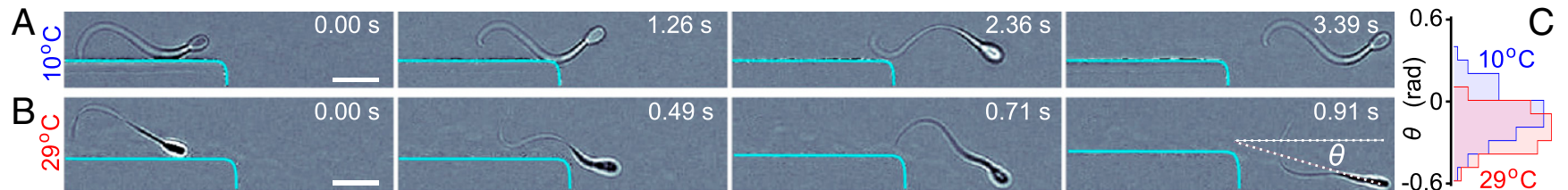
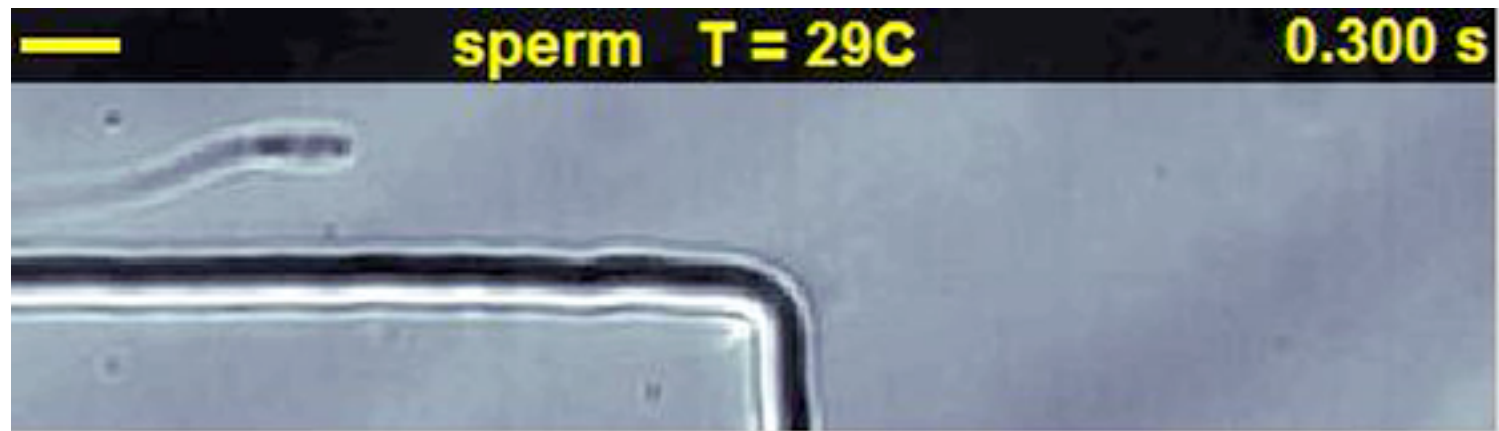
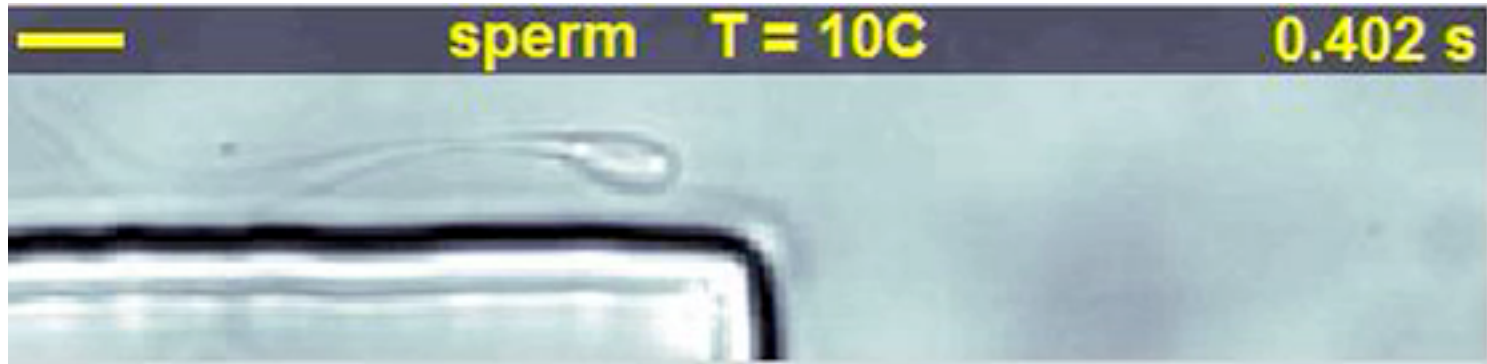
# Control of **algal** locomotion



2h

2 mm

# Sperm near surfaces

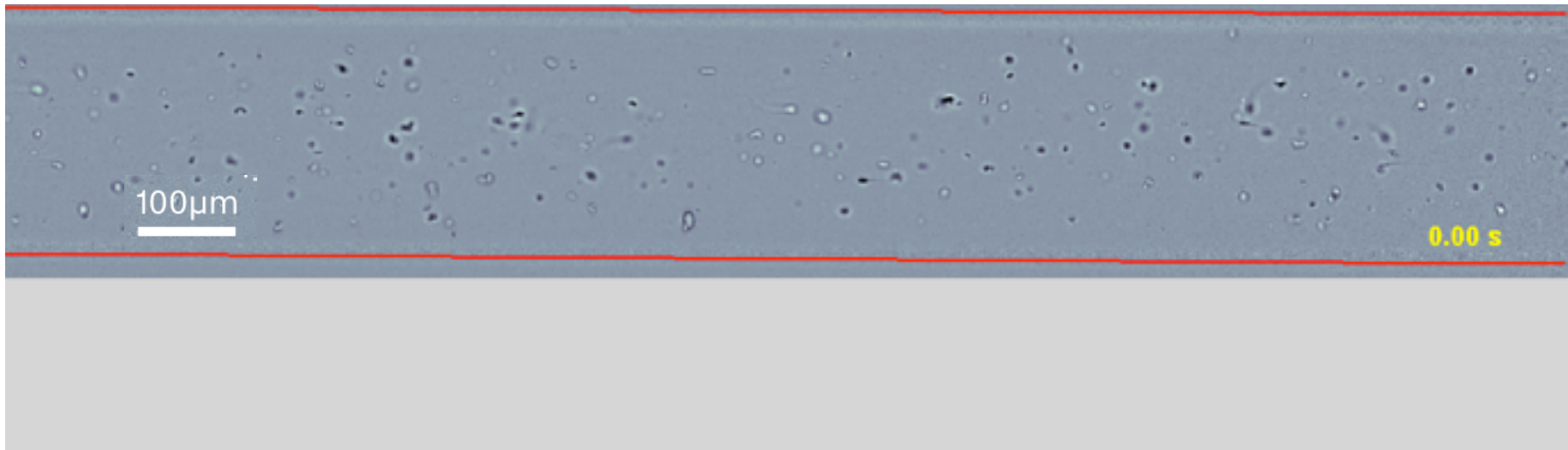




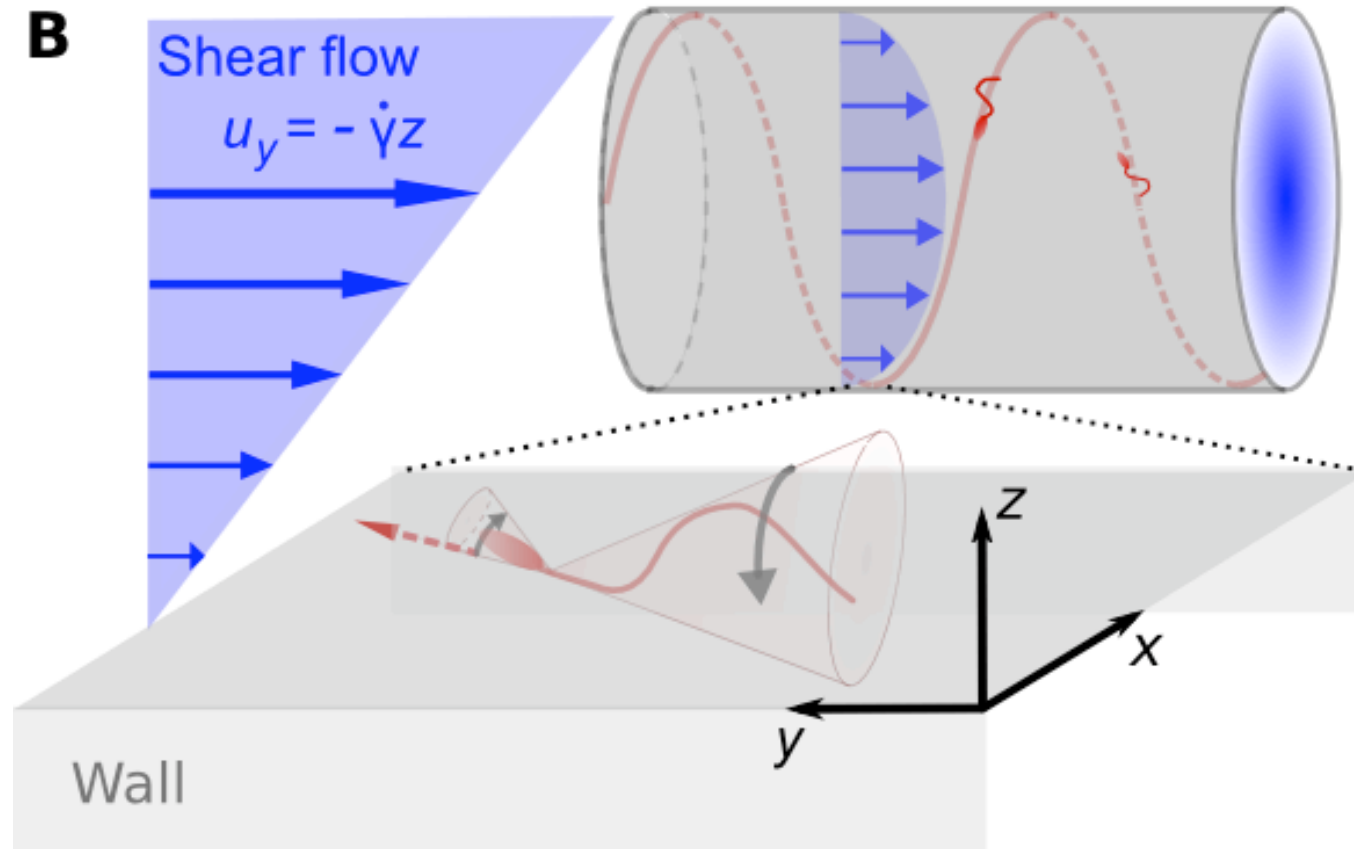
# Sperm



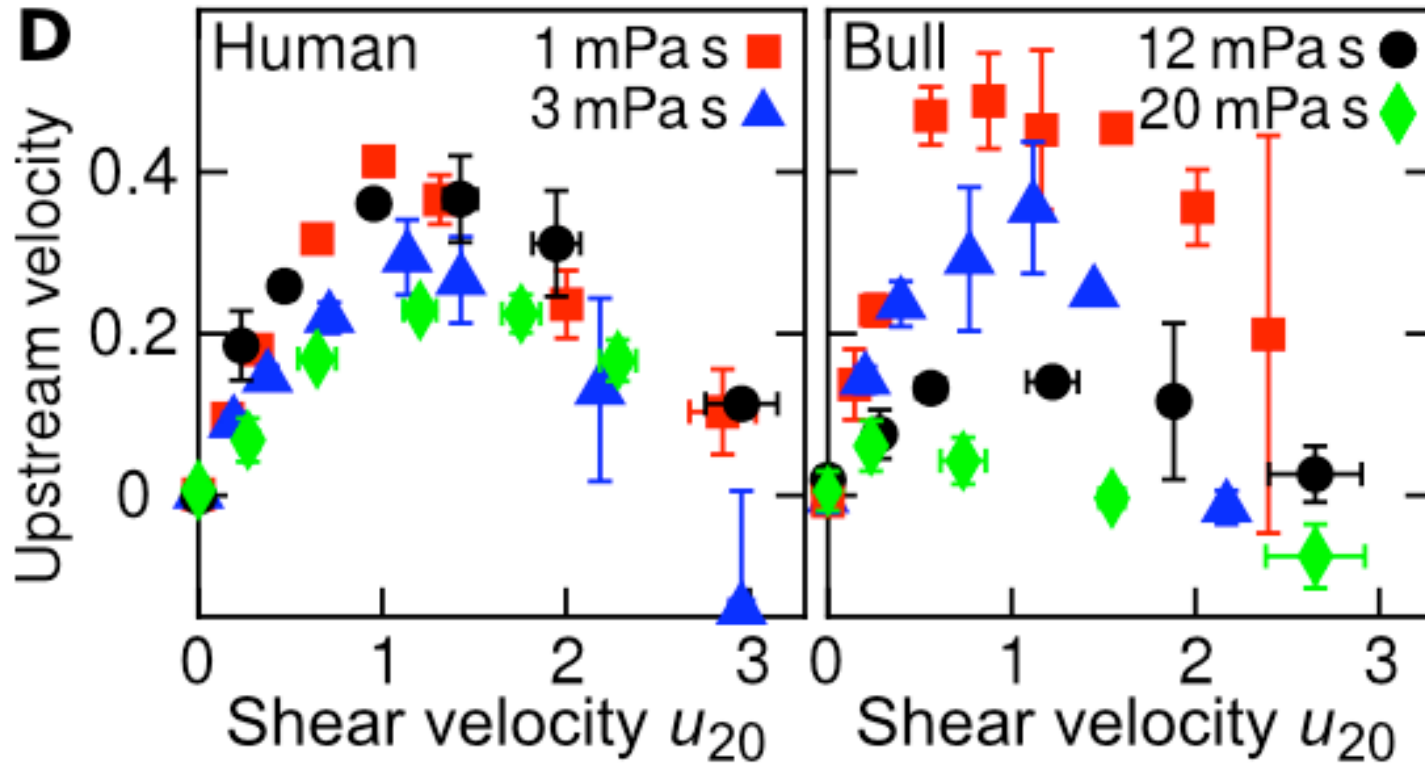
# Surface + shear flow



# Rheotaxis facilitates upstream navigation



# Viscosity & shear dependence



long distance navigation by rheotaxis ?

# 2D minimal model

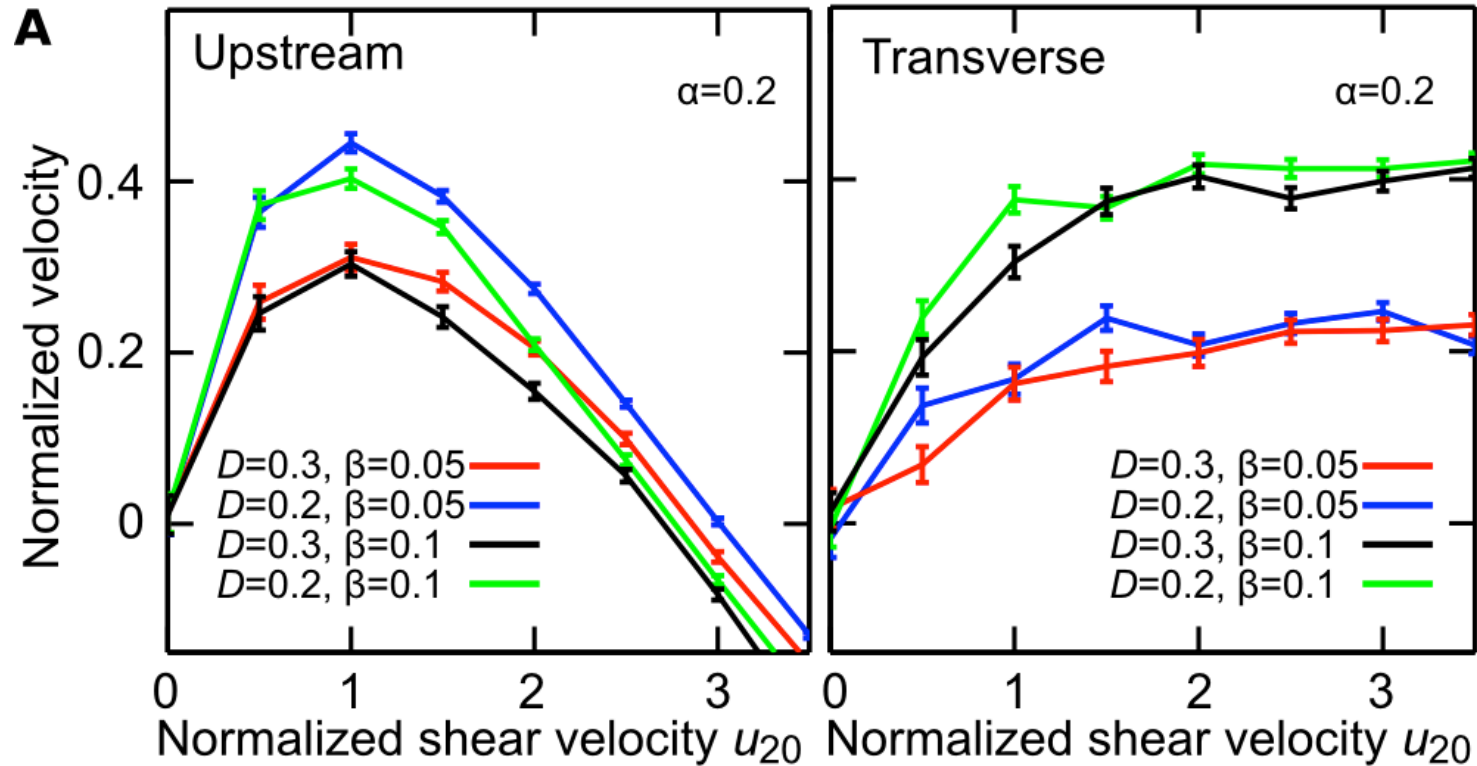
## Resistive force theory

$$0 = F_i = \int_0^S ds \left\| \frac{d\hat{\mathbf{C}}(s)}{ds} \right\| f_i(s),$$
$$0 = \tau_i = \int_0^S ds \left\| \frac{d\hat{\mathbf{C}}(s)}{ds} \right\| \epsilon_{ijk} [C_j(s) - X_j^*] f_k(s)$$
$$\mathbf{f}(s) = \zeta_{\parallel} \left\{ [\mathbf{u}(\mathbf{C}(s)) - \dot{\mathbf{C}}(s)] \cdot \mathbf{t}(s) \right\} \mathbf{t}(s) + \zeta_{\perp} \left\{ [\mathbf{u}(\mathbf{C}(s)) - \dot{\mathbf{C}}(s)] \cdot [\mathbf{I} - \mathbf{t}(s)\mathbf{t}(s)] \right\}$$

+ some approximations + **noise** gives to leading order

$$\dot{\mathbf{R}} = V\mathbf{N} + \sigma\bar{U}\mathbf{e}_y,$$
$$\dot{\mathbf{N}} = \sigma\dot{\gamma}\alpha \begin{pmatrix} N_x N_y \\ N_y^2 - 1 \end{pmatrix} + \sigma\dot{\gamma}\chi\beta \begin{pmatrix} N_x^2 - 1 \\ N_x N_y \end{pmatrix} + (2D)^{1/2}(\mathbf{I} - \mathbf{N}\mathbf{N}) \cdot \boldsymbol{\xi}(t).$$

# 2D minimal model



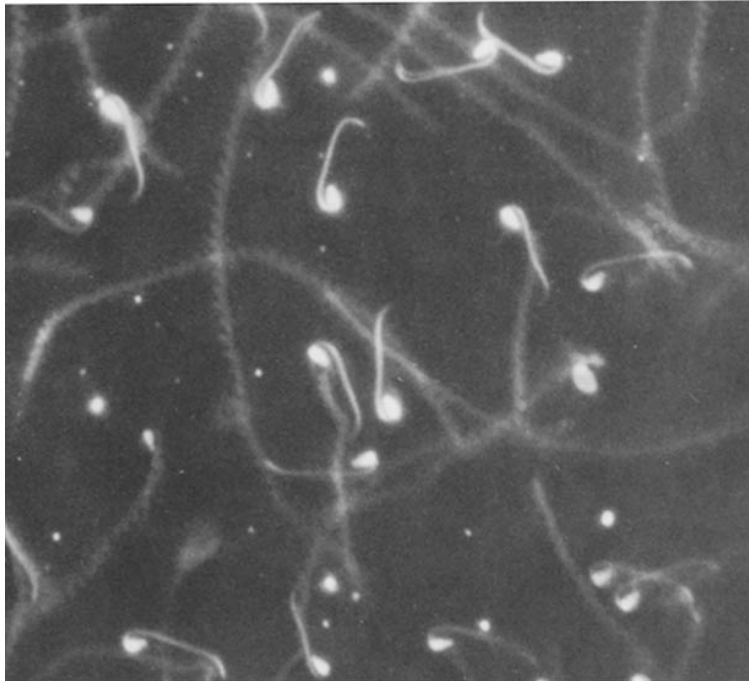
# Collective motion

# Broken reflection-symmetry at surfaces

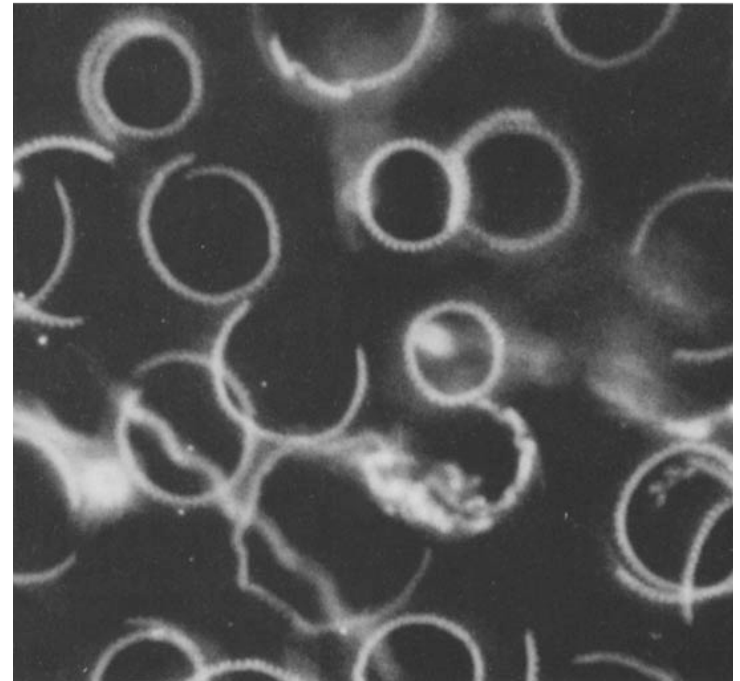
Gibbons (1980) JCB

## Sea urchin sperm

in bulk (dilute)



near surface (dilute)



similar for bacteria (*E. coli*): Di Luzio et al (2005) Nature



# 2d Swift-Hohenberg model

$$\partial_t \psi = -U'(\psi) + \gamma_0 \nabla^2 \psi - \gamma_2 (\nabla^2)^2 \psi$$

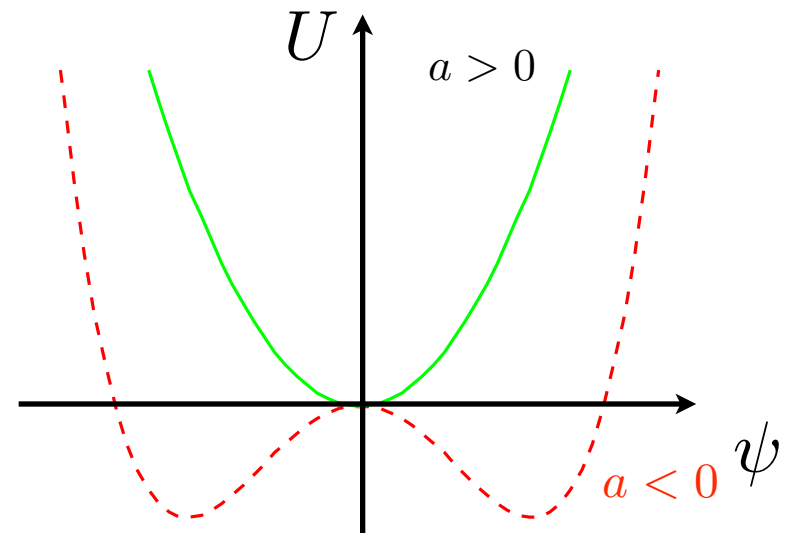
$$U(\psi) = \frac{a}{2} \psi^2 + \cancel{\frac{b}{3} \psi^3} + \frac{c}{4} \psi^4$$

$$\psi(t, \mathbf{x}) = \nabla \times \mathbf{v}$$

reflection-symmetry

$$b = 0$$

$$\psi \mapsto -\psi$$



# 2d Swift-Hohenberg model

$$\partial_t \psi = -U'(\psi) + \gamma_0 \nabla^2 \psi - \gamma_2 (\nabla^2)^2 \psi$$

$$U(\psi) = \frac{a}{2} \psi^2 + \cancel{\frac{b}{3} \psi^3} + \frac{c}{4} \psi^4$$

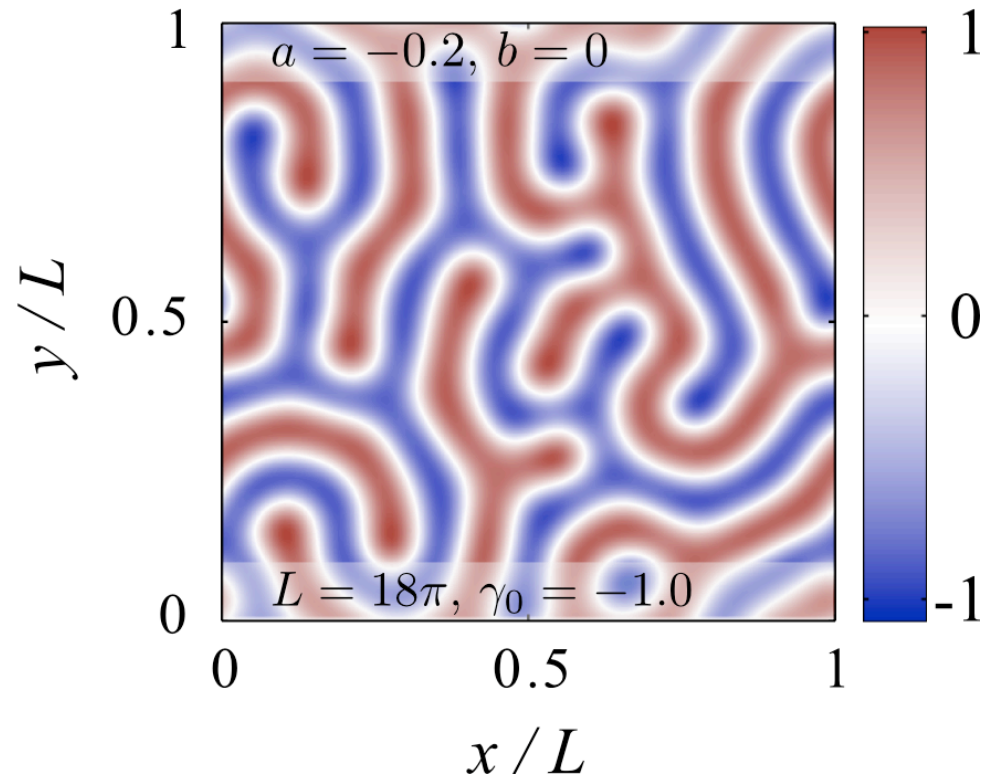
$$\psi(t, \mathbf{x}) = \nabla \times \mathbf{v}$$

reflection-symmetry

$$b = 0$$

$$\psi \mapsto -\psi$$

$$\psi / \psi_m$$



# 2d Swift-Hohenberg model

**broken**  
reflection-symmetry

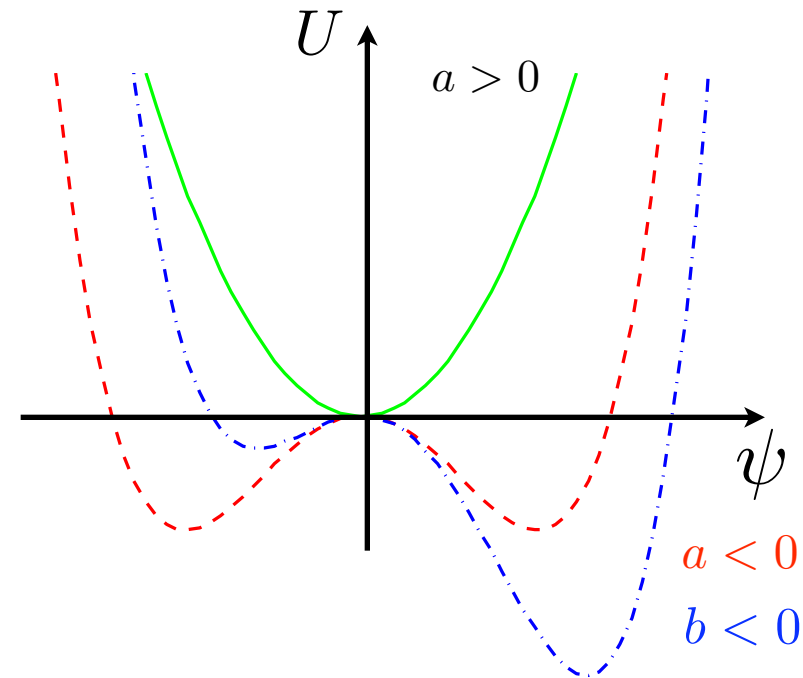
$$\partial_t \psi = -U'(\psi) + \gamma_0 \nabla^2 \psi - \gamma_2 (\nabla^2)^2 \psi$$

$$b \neq 0$$

$$\psi \not\mapsto -\psi$$

$$U(\psi) = \frac{a}{2}\psi^2 + \frac{b}{3}\psi^3 + \frac{c}{4}\psi^4$$

$$\psi(t, \mathbf{x}) = \nabla \times \mathbf{v}$$



# 2d Swift-Hohenberg model

**broken**  
reflection-symmetry

$$\partial_t \psi = -U'(\psi) + \gamma_0 \nabla^2 \psi - \gamma_2 (\nabla^2)^2 \psi$$

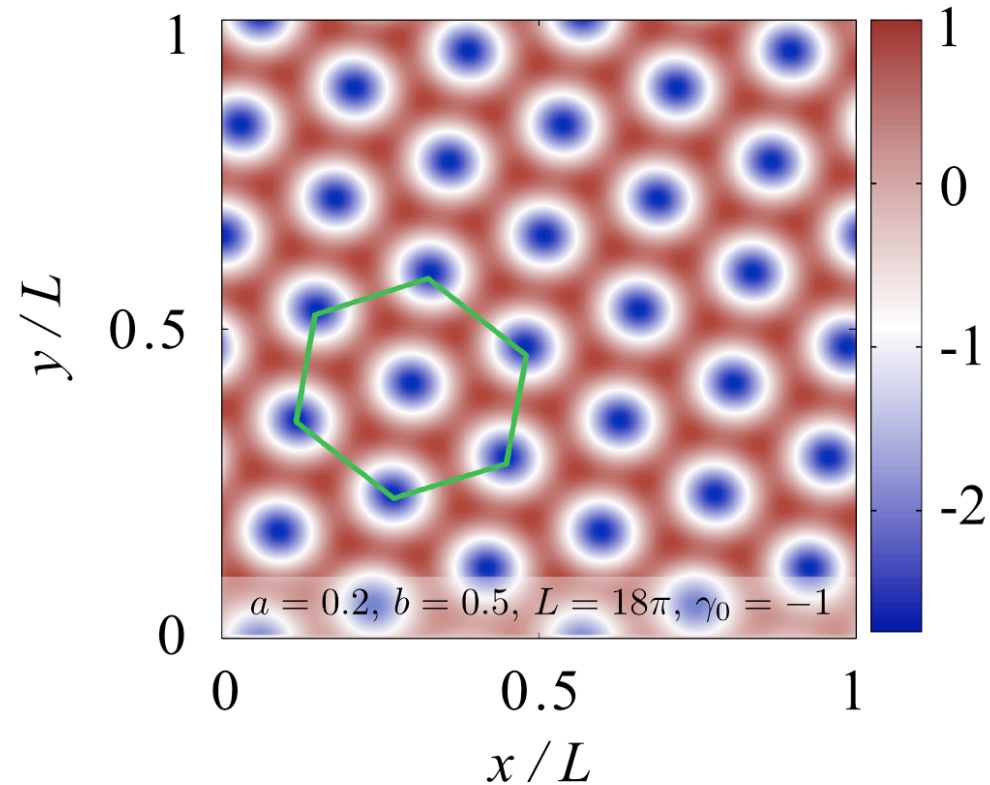
$$b \neq 0$$

$$\psi \not\mapsto -\psi$$

$$\psi / \psi_m$$

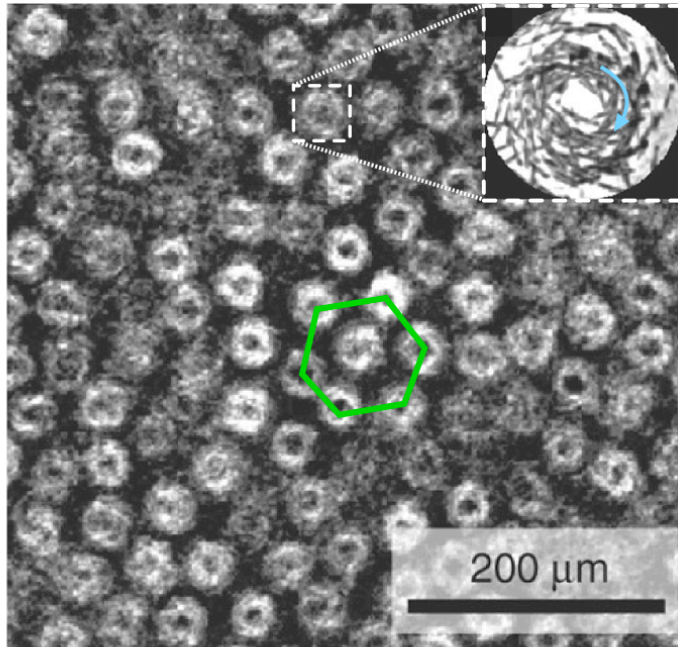
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$$\psi(t, \mathbf{x}) = \nabla \times \mathbf{v}$$



# 2d Swift-Hohenberg model

Sea urchin sperm cells  
near surface  
(high concentration)



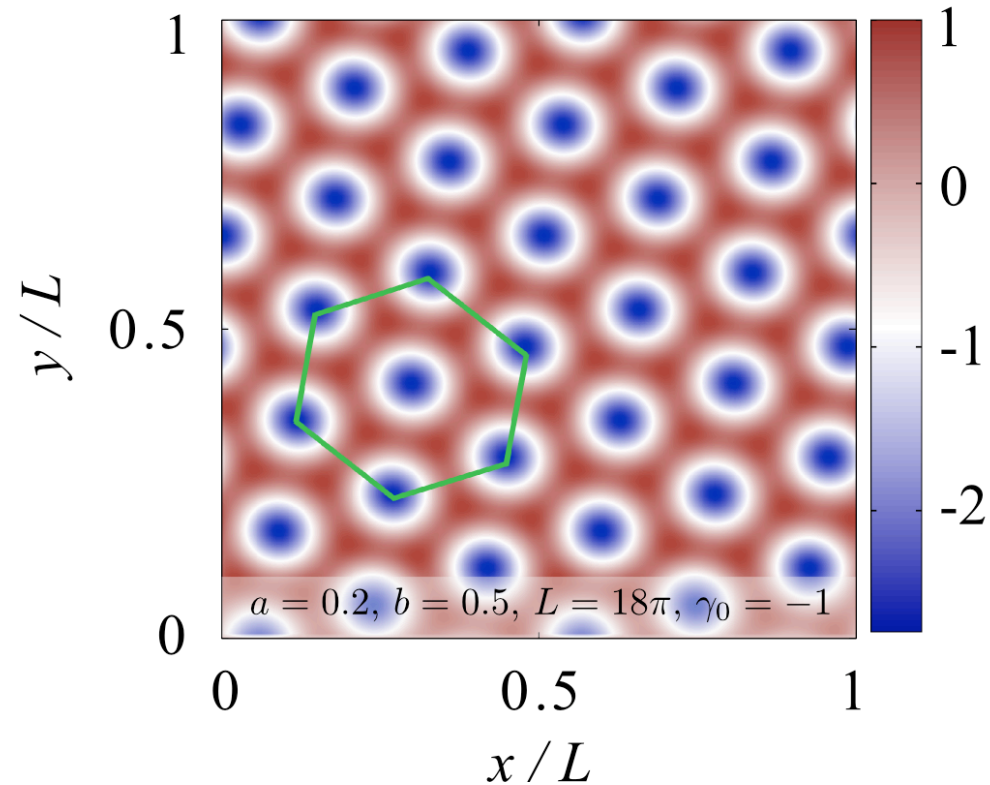
Riedel et al (2007) Science

**broken**  
reflection-symmetry

$$b \neq 0$$

$$\psi \not\leftrightarrow -\psi$$

$$\psi/\psi_m$$



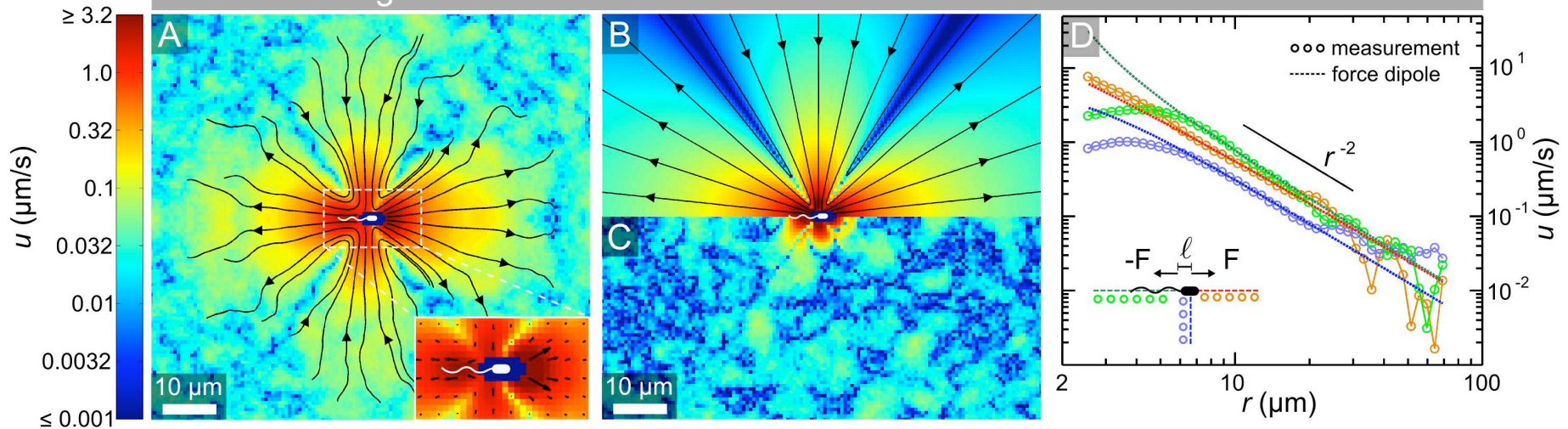
# Active polar fluids

(things with a head and tail)

# E.coli (non-tumbling HCB 437)



Free swimming



$$\mathbf{u}(\mathbf{r}) = \frac{A}{|\mathbf{r}|^2} \left[ 3(\hat{\mathbf{r}} \cdot \hat{\mathbf{d}})^2 - 1 \right] \hat{\mathbf{r}}, \quad A = \frac{\ell F}{8\pi\eta}, \quad \hat{\mathbf{r}} = \frac{\mathbf{r}}{|\mathbf{r}|}$$

$$V_0 = 22 \pm 5 \mu\text{m/s}$$

$$\ell = 1.9 \mu\text{m}$$

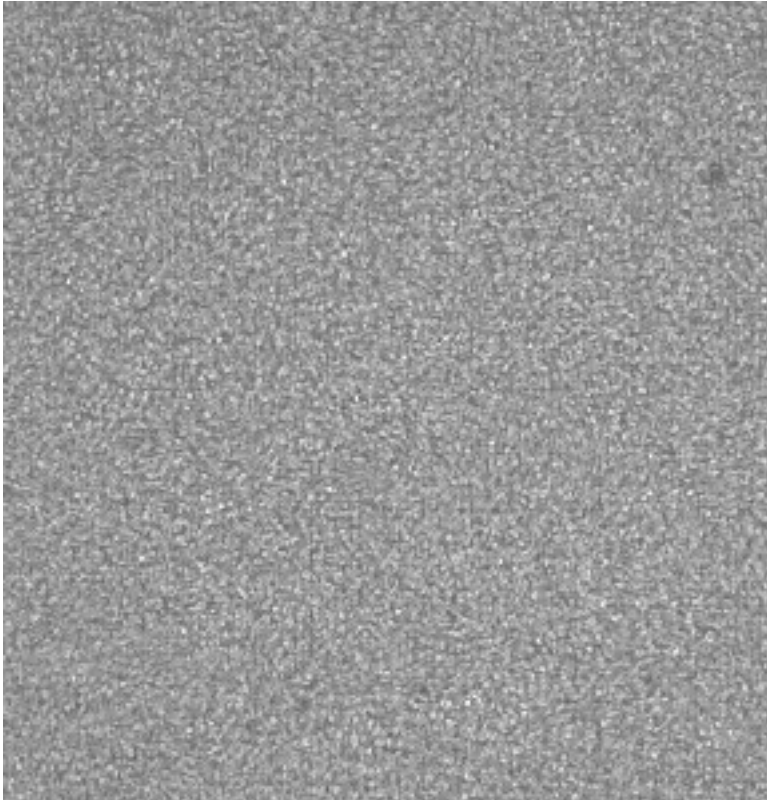
$$F = 0.42 \text{ pN}$$

‘pusher’ dipole

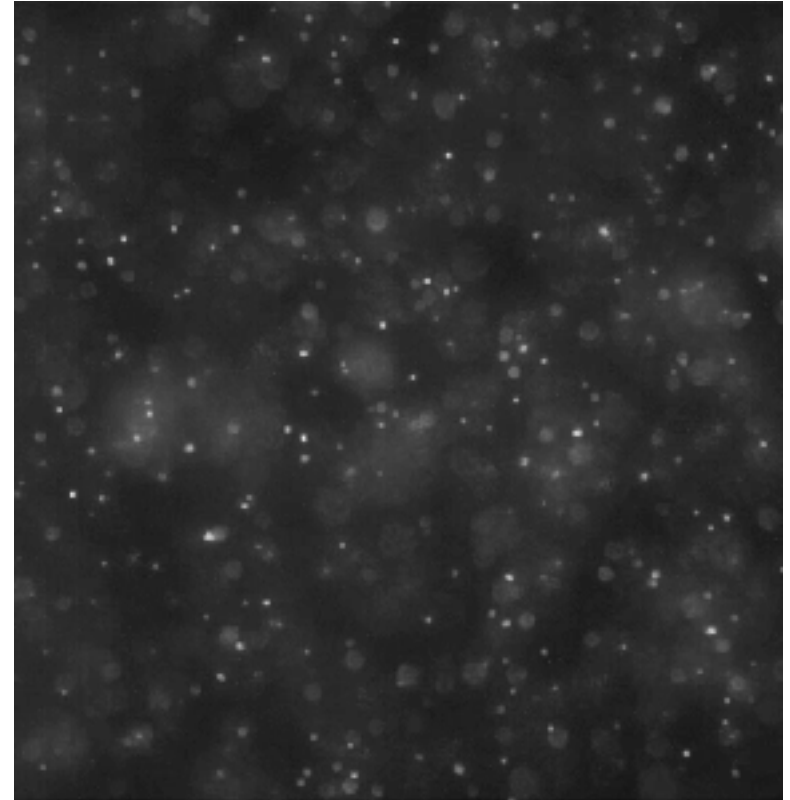
# Active polar fluids

*B. subtilis*

tracers



bright field



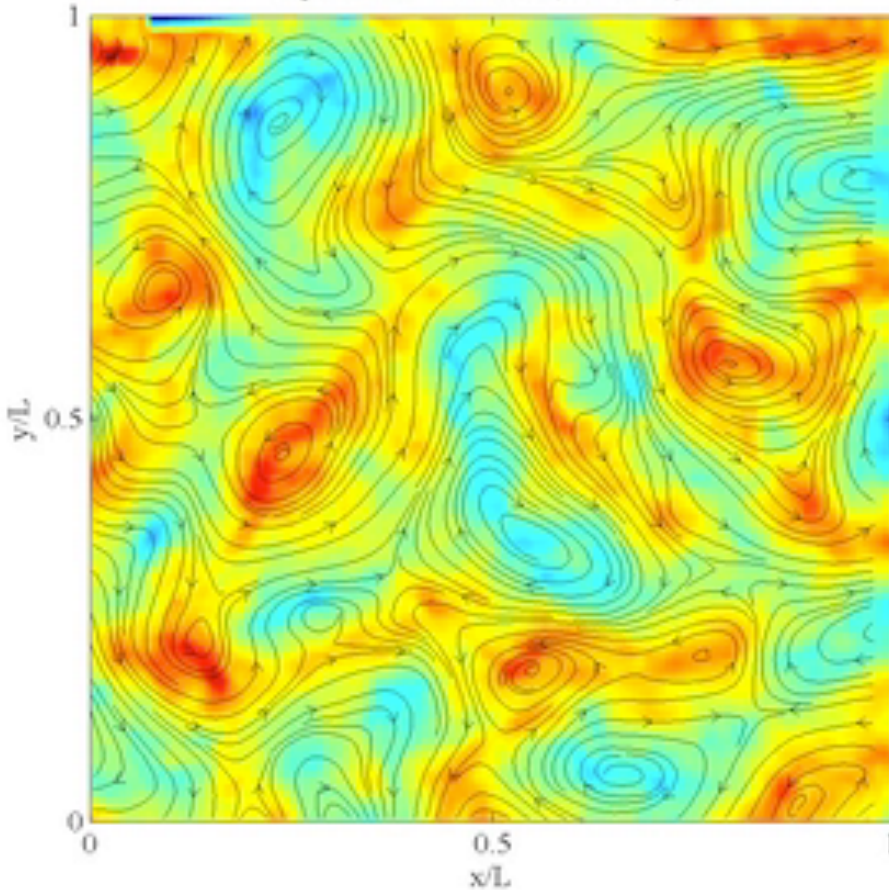
fluorescence



# Bacterial 'turbulence'

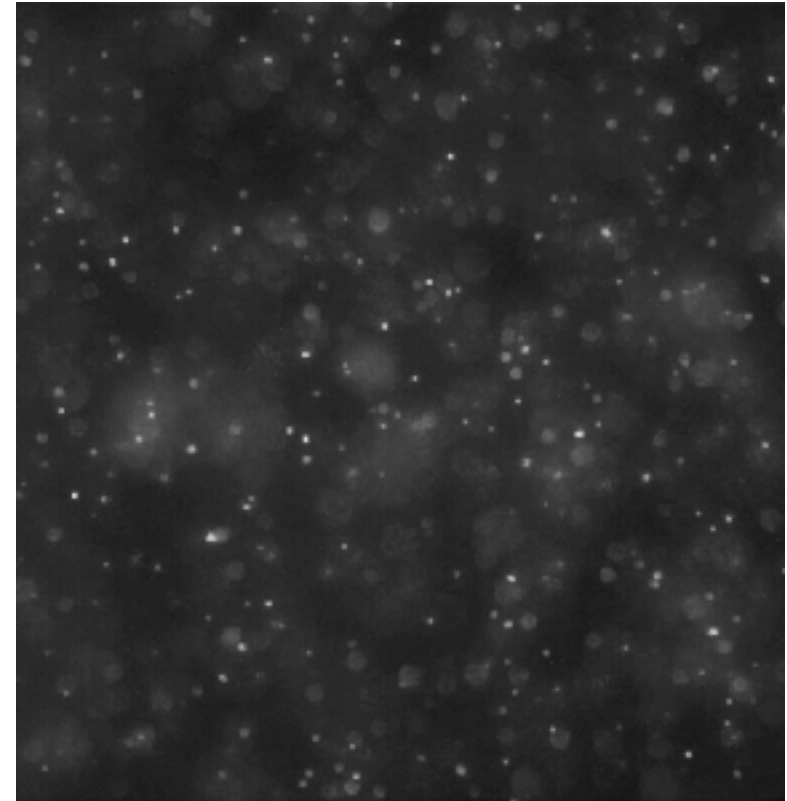
PIV

Experiment:  $t = 0.1 \text{ s}$ ,  $L = 276 \mu\text{m}$



Vortex diameter  $\sim 70 \mu\text{m}$   
Vortex life time  $\sim 1 \text{ sec}$

tracers



fluorescence

Dunkel et al PRL 2013



# Minimal continuum theory for bacterial velocity field

incompressibility

$$\nabla \cdot \mathbf{v} = 0$$

nematic stresses

$\alpha < 0$   
polar alignment

$$(\partial_t + \lambda_0 \mathbf{v} \cdot \nabla) \mathbf{v} = -\nabla(p + \lambda_1 \mathbf{v}^2) - (\beta \mathbf{v}^2 + \alpha) \mathbf{v} + \Gamma_0 \nabla^2 \mathbf{v} - \Gamma_2 (\nabla^2)^2 \mathbf{v}$$

vortices

Isotropic fixed-point  $(p, \mathbf{v}) = (p_0, \mathbf{0})$

$$0 = \mathbf{k} \cdot \boldsymbol{\varepsilon}$$

$$\sigma \boldsymbol{\varepsilon} = -i\mathbf{k}\eta - \alpha \boldsymbol{\varepsilon} - \Gamma_0 k^2 \boldsymbol{\varepsilon} - \Gamma_2 k^4 \boldsymbol{\varepsilon}$$

$$(\eta, \boldsymbol{\varepsilon}) = (\hat{\eta}, \hat{\boldsymbol{\varepsilon}}) e^{i\mathbf{k} \cdot \mathbf{x} + \sigma t}$$

$$\sigma(\mathbf{k}) = -(\alpha + \Gamma_0 k^2 + \Gamma_2 k^4)$$

# Polar fixed-point

$$(p, \mathbf{v}) = (p_0, \mathbf{v}_0)$$

$$\begin{aligned} 0 &= \mathbf{k} \cdot \hat{\mathbf{e}}, & |\mathbf{v}_0| &= \sqrt{|\alpha|/\beta} \\ \sigma \hat{\mathbf{e}} &= -i(\hat{\eta} - 2v_0\lambda_1\hat{\mathbf{e}}_{||})\mathbf{k} + \mathbf{A}\hat{\mathbf{e}}, & \lambda_0 &= 1 - S. \end{aligned}$$

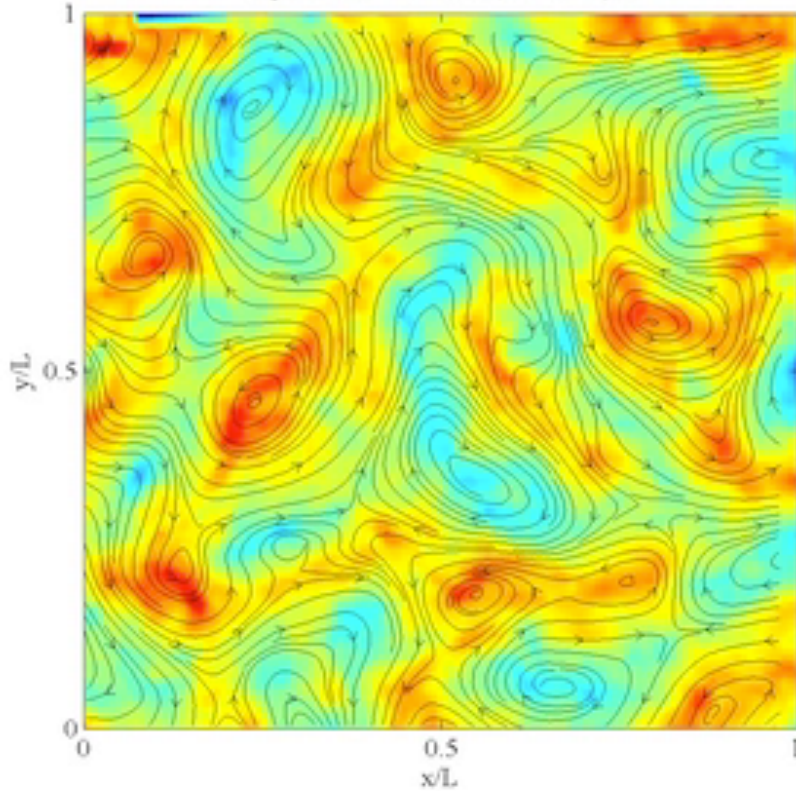
$$\mathbf{A} = \begin{pmatrix} 2\alpha & 0 \\ 0 & 0 \end{pmatrix} - (\Gamma_0 k^2 + \Gamma_2 k^4 + i\lambda_0 k_x v_0) \mathbf{I}$$

Eigenvalues of  $\mathbf{A}_\perp = \Pi(k)\mathbf{A}$  determine stability

$$\sigma(\mathbf{k}) \in \left\{ 0, - \left( \Gamma_0 k^2 + \Gamma_2 k^4 - 2\alpha \frac{k_x^2}{k^2} \right) - i\lambda_0 v_0 k_x \right\}.$$

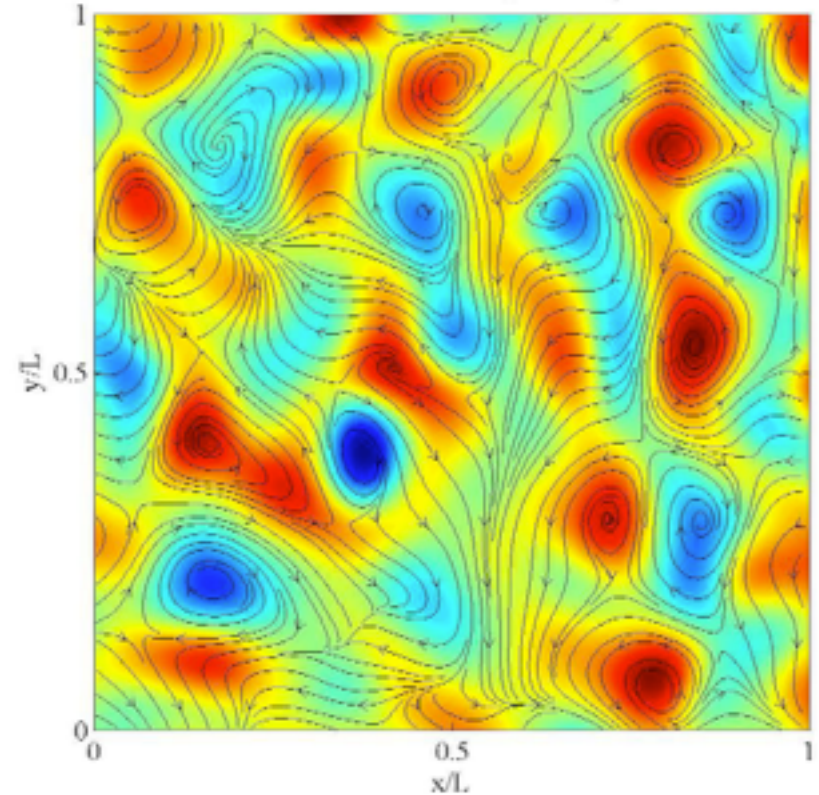
# experiment vs. theory

Experiment:  $t = 0.1 \text{ s}$ ,  $L = 276 \mu\text{m}$



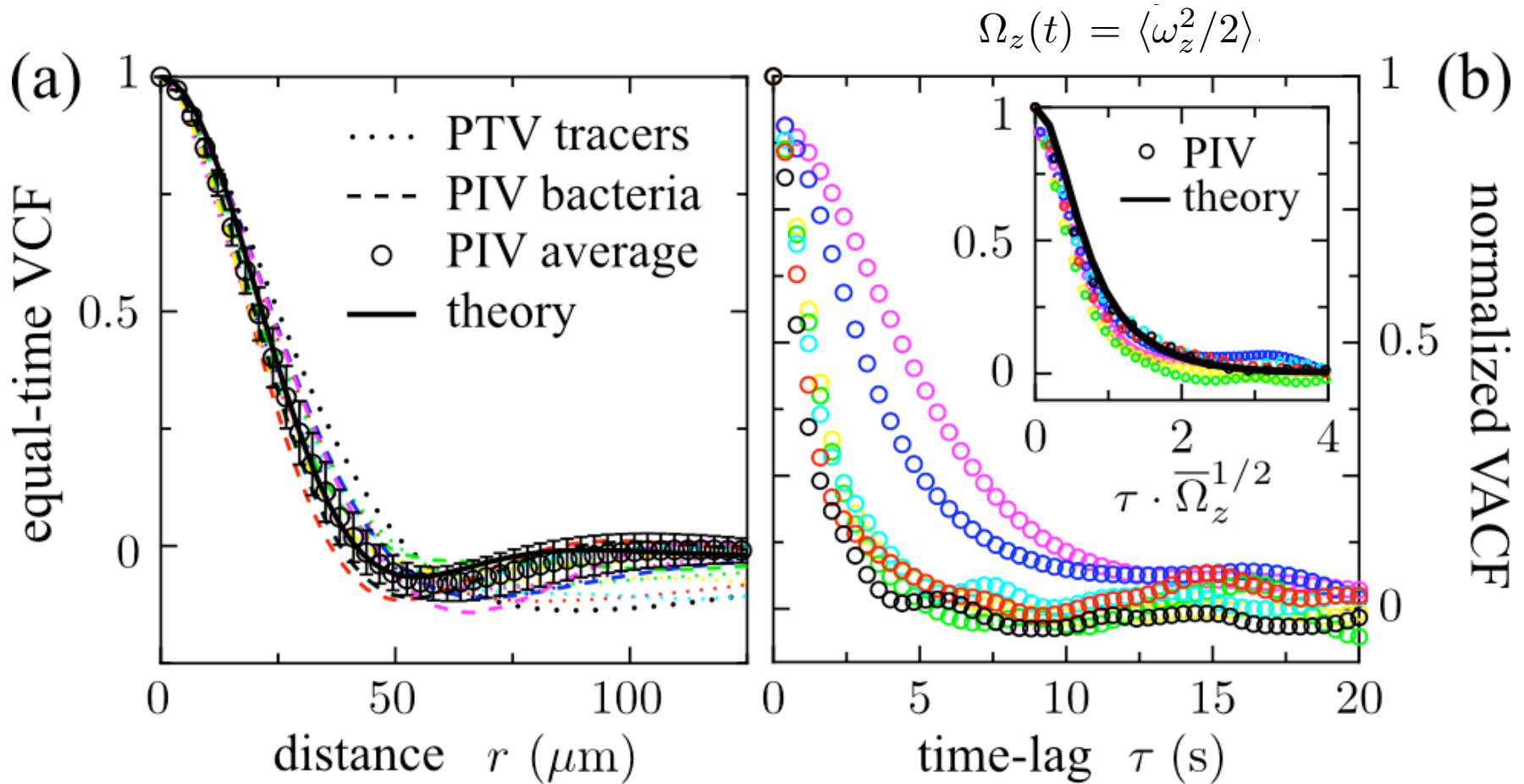
quasi-2D slice

Simulation:  $t = 8.7 \text{ s}$ ,  $L = 300 \mu\text{m}$



2D slice  
from 3D simulation

# Velocity correlations



Vortex diameter  $\sim 70\mu\text{m}$

Vortex life time  $\sim$  seconds

# Continuum theory for bacterial velocity field

incompressibility  $\nabla \cdot \mathbf{v} = 0$

non-conservative



$$(\partial_t + \lambda_0 \mathbf{v} \cdot \nabla) \mathbf{v} = -\nabla(p + \lambda_1 \mathbf{v}^2) - (\beta \mathbf{v}^2 + \alpha) \mathbf{v} + \Gamma_0 \nabla^2 \mathbf{v} - \Gamma_2 (\nabla^2)^2 \mathbf{v}$$

# Conserved dynamics ?

Flow equations

$$\begin{aligned}0 &= \nabla \cdot \mathbf{v} \\ \partial_t \mathbf{v} + (\mathbf{v} \cdot \nabla) \mathbf{v} &= -\nabla p + \nabla \cdot \boldsymbol{\sigma}\end{aligned}$$

with stress tensor

$$\boldsymbol{\sigma} = [\Gamma_0 - \Gamma_2(\nabla^2) + \Gamma_4(\nabla^2)^2](\nabla^\top \mathbf{v} + \nabla \mathbf{v}^\top)$$

Interpretation: effective flow-field for  
**passive solvent + active component**  
that creates non-local stresses



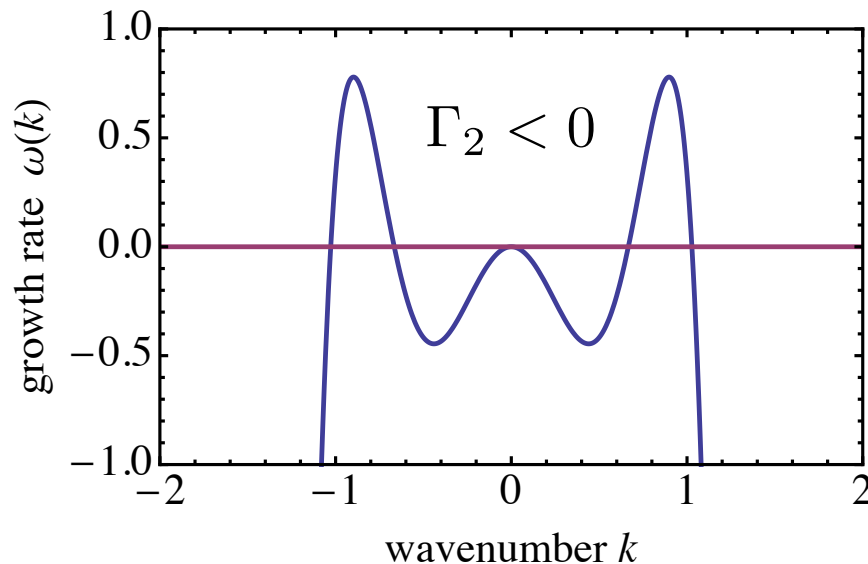
# Conserved dynamics ?

Flow equations

$$0 = \nabla \cdot \mathbf{v}$$
$$\partial_t \mathbf{v} + (\mathbf{v} \cdot \nabla) \mathbf{v} = -\nabla p + \nabla \cdot \boldsymbol{\sigma}$$

with stress tensor

$$\boldsymbol{\sigma} = [\Gamma_0 - \Gamma_2(\nabla^2) + \Gamma_4(\nabla^2)^2](\nabla^\top \mathbf{v} + \nabla \mathbf{v}^\top)$$



linear  
stability

# Conserved dynamics ?

Flow equations

$$\begin{aligned}0 &= \nabla \cdot \mathbf{v} \\ \partial_t \mathbf{v} + (\mathbf{v} \cdot \nabla) \mathbf{v} &= -\nabla p + \nabla \cdot \boldsymbol{\sigma}\end{aligned}$$

with stress tensor

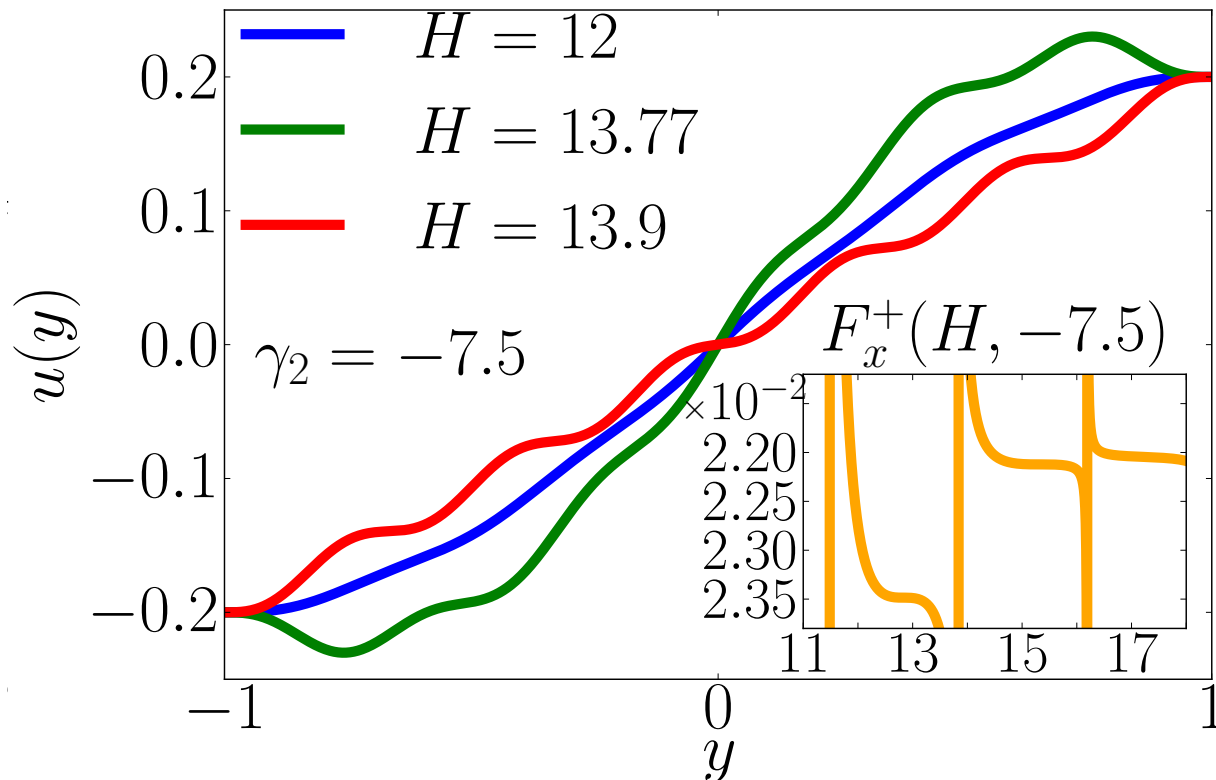
$$\boldsymbol{\sigma} = [\Gamma_0 - \Gamma_2(\nabla^2) + \Gamma_4(\nabla^2)^2](\nabla^\top \mathbf{v} + \nabla \mathbf{v}^\top)$$

## 6th order PDE

*S-type*: First and second-order derivatives vanish.

*W-type*: Second and fourth-order derivatives vanish.

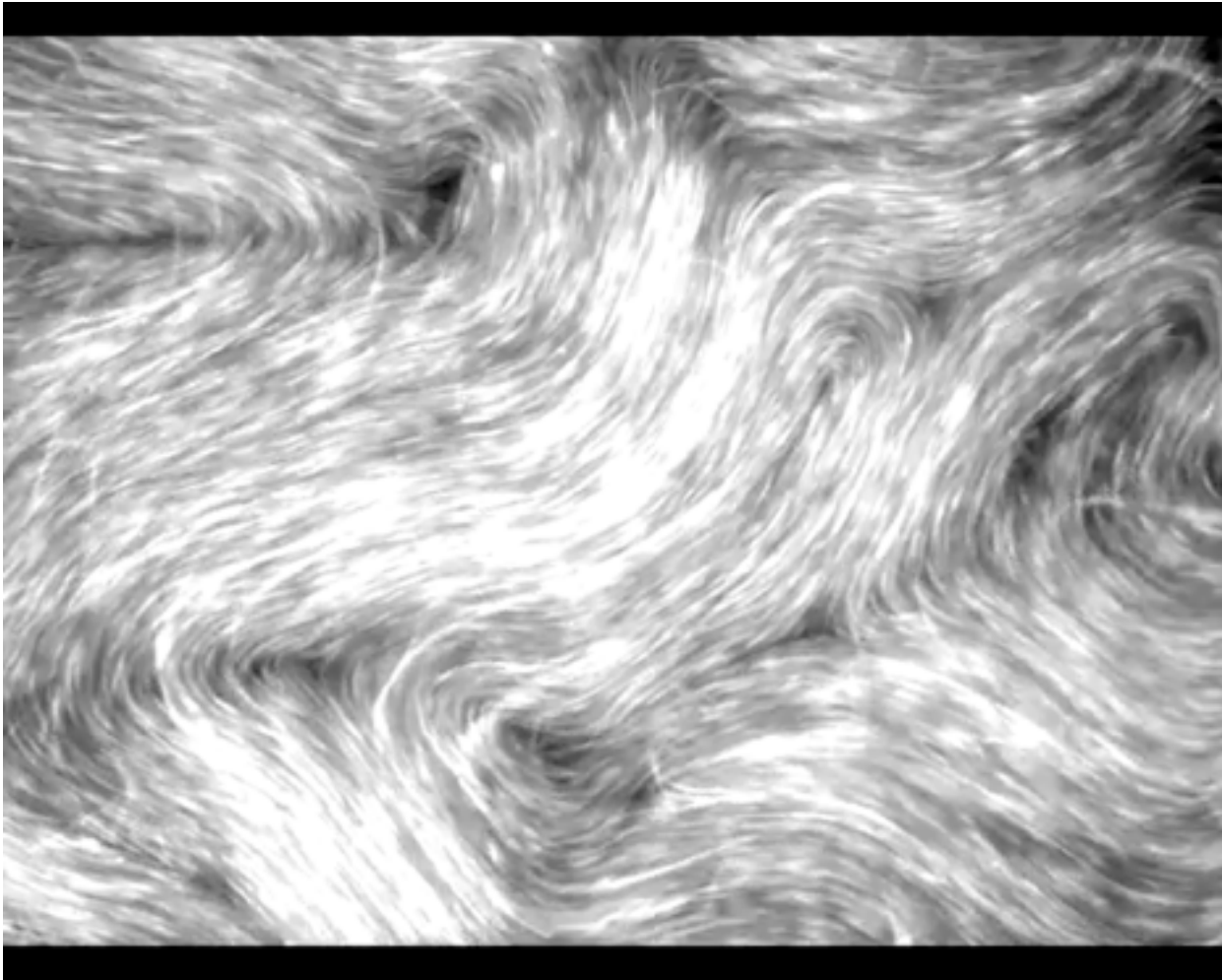
# Mean field prediction for shear flow between two plates



$$u'(\pm H/2) = u''(\pm H/2) = 0$$

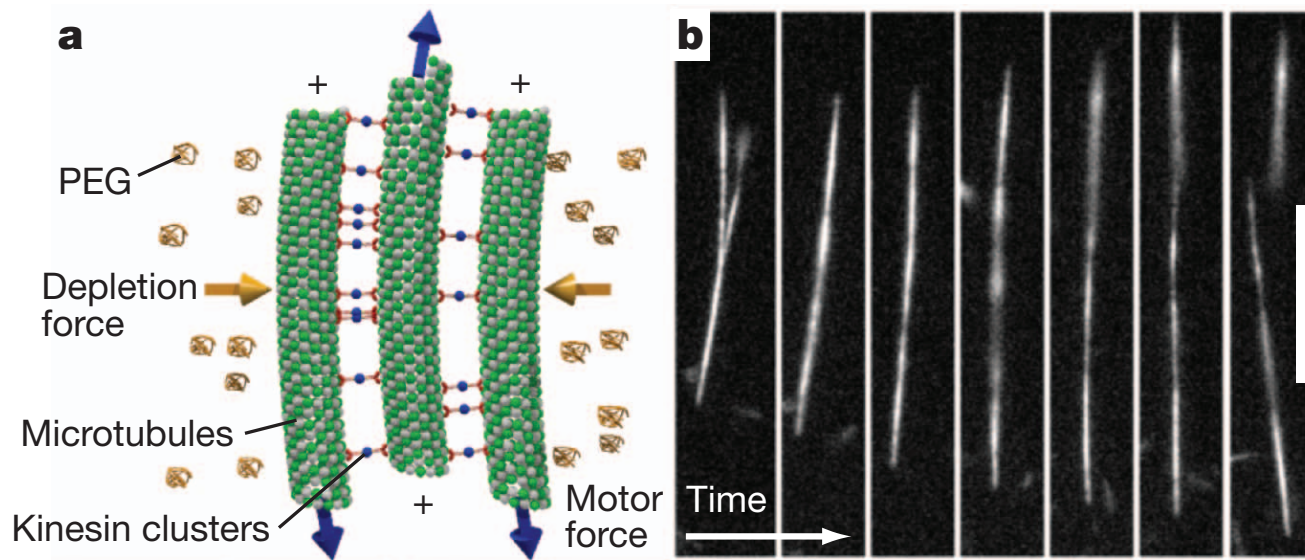
+ periodic BCs in other directions

# Active nematics



Dogic lab (Brandeis) Nature 2012

# Active nematics



Dogic lab (Brandeis) Nature 2012

no head or tail  $\Rightarrow$  Q-tensor order-parameter

$$Q_{ij} = Q_{ji}, \quad \text{Tr } Q = 0, \quad Q = \begin{pmatrix} \lambda & \mu \\ \mu & -\lambda \end{pmatrix}.$$

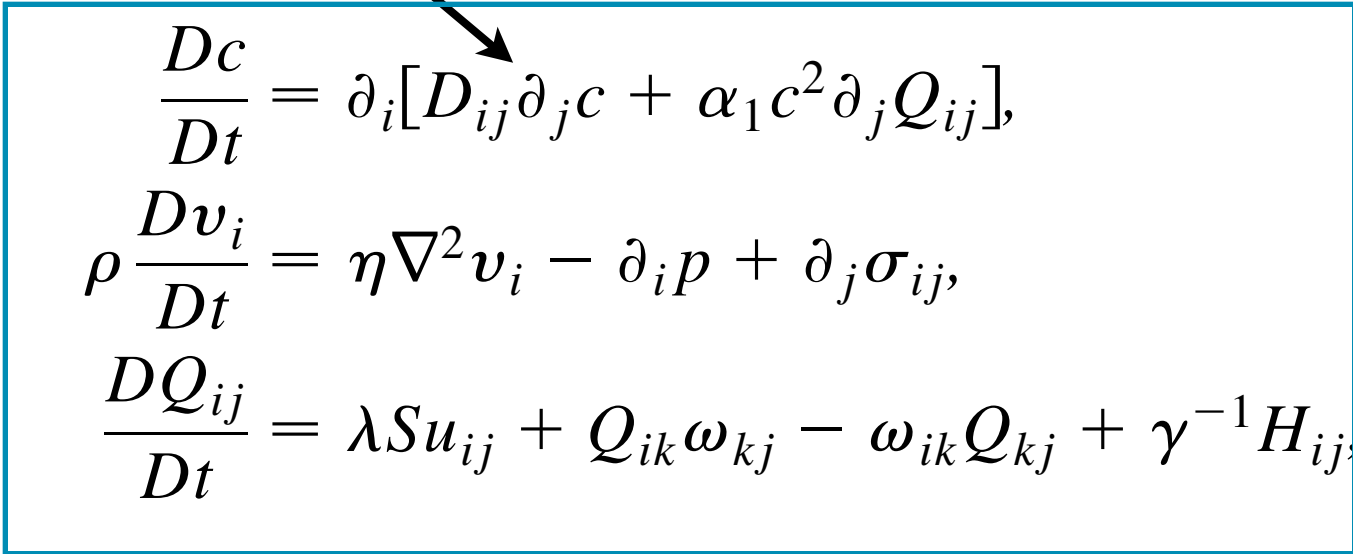
$$\Delta = \sqrt{\lambda^2 + \mu^2}, \quad \Lambda^\pm = \pm \Delta$$

# Active nematics

$$D_{ij} = D_0 \delta_{ij} + D_1 Q_{ij}$$

$$u_{ij} = (\partial_i v_j + \partial_j v_i)/2$$

$$\omega_{ij} = (\partial_i v_j - \partial_j v_i)/2$$

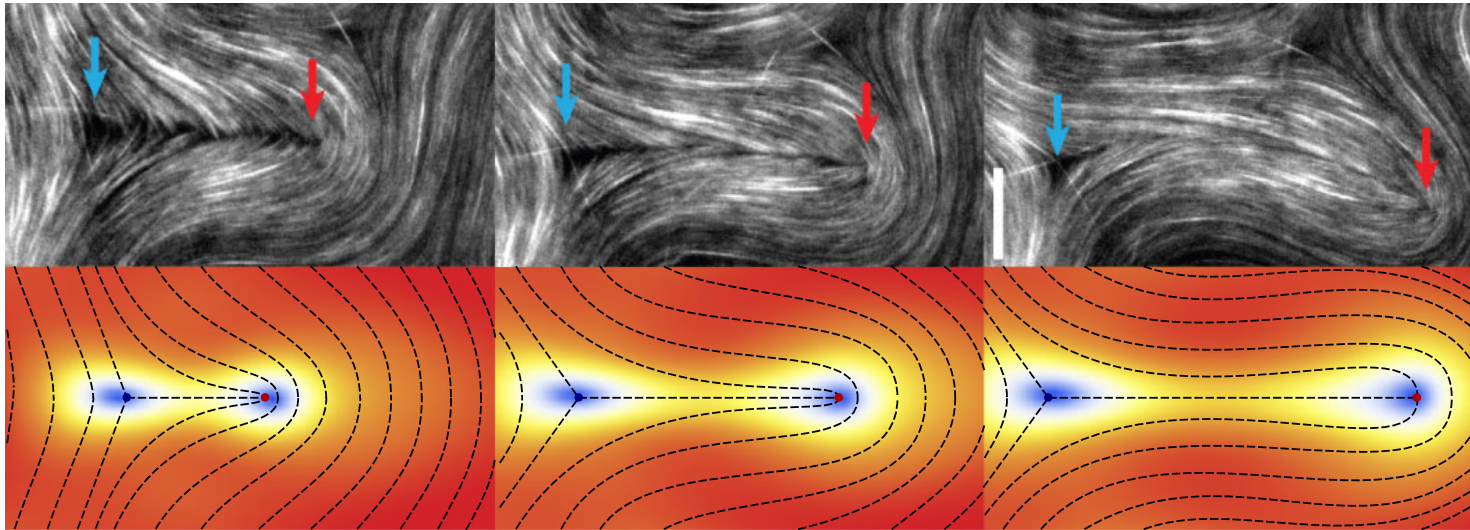

$$\begin{aligned}\frac{Dc}{Dt} &= \partial_i [D_{ij} \partial_j c + \alpha_1 c^2 \partial_j Q_{ij}], \\ \rho \frac{Dv_i}{Dt} &= \eta \nabla^2 v_i - \partial_i p + \partial_j \sigma_{ij}, \\ \frac{DQ_{ij}}{Dt} &= \lambda S u_{ij} + Q_{ik} \omega_{kj} - \omega_{ik} Q_{kj} + \gamma^{-1} H_{ij},\end{aligned}$$

$$\nabla \cdot \mathbf{v} = 0,$$

$$H_{ij} = -\delta F / \delta Q_{ij}, \quad F/K = \int dA \left[ \frac{1}{4} (c - c^*) \text{tr} \mathbf{Q}^2 + \frac{1}{4} c (\text{tr} \mathbf{Q}^2)^2 + \frac{1}{2} |\nabla \mathbf{Q}|^2 \right],$$

Giomi et al PRL 2012

# Active nematics



$$\nabla \cdot \mathbf{v} = 0,$$

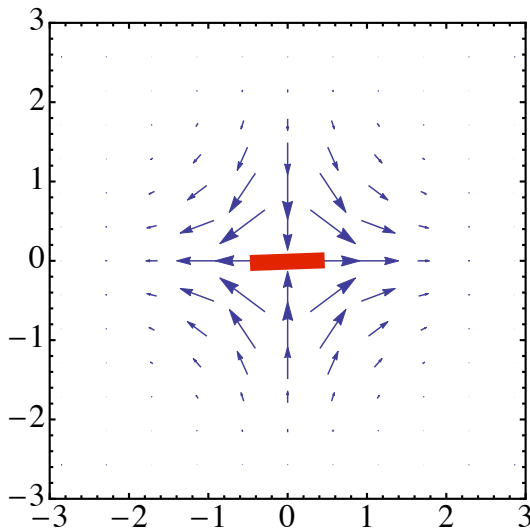
not consistent with  
experimental setup

Giomi et al PRL 2012

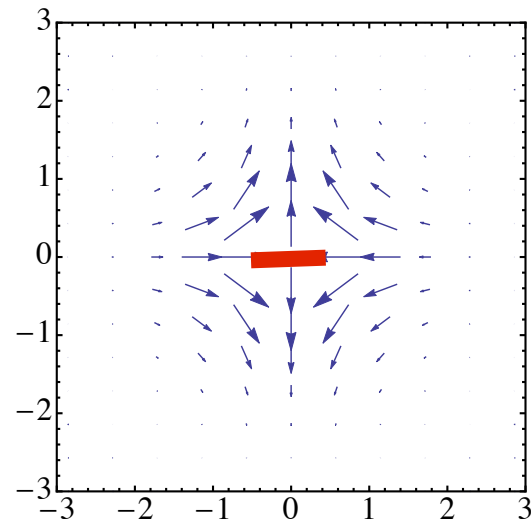
# Alternative approach

$$\partial_t Q_{ij} + v_k \partial_k Q_{ij} = - \frac{\delta \mathcal{F}}{\delta Q_{ij}}$$

$$v_k = D \partial_n Q_{nk}$$



$D < 0$  extensile



$D > 0$  contractile



# Alternative approach

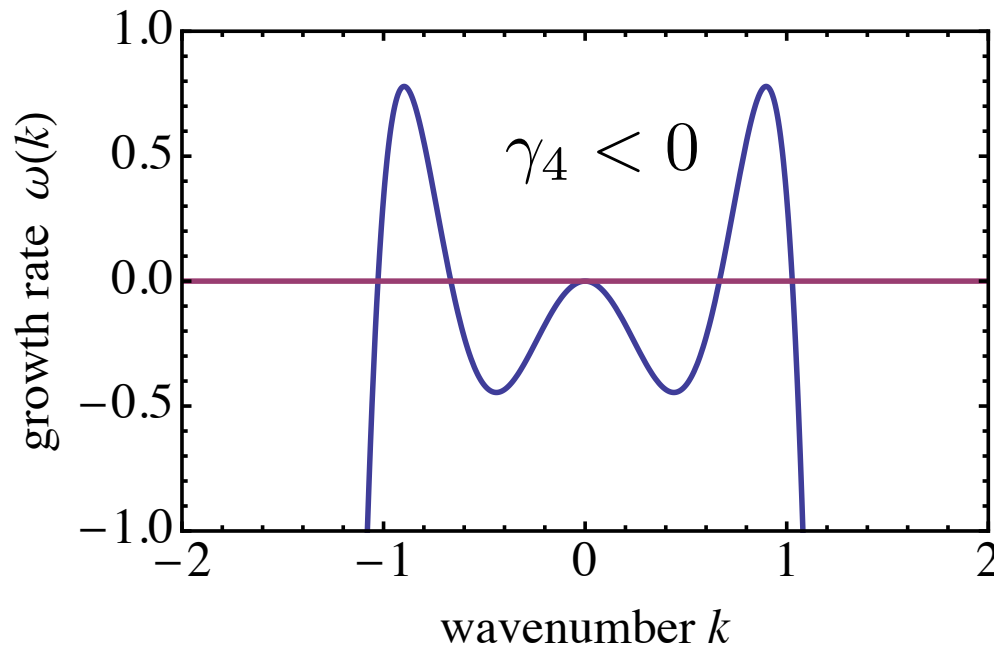
$$\partial_t Q_{ij} + v_k \partial_k Q_{ij} = -\frac{\delta \mathcal{F}}{\delta Q_{ij}}$$

$$v_k = D \partial_n Q_{nk}$$

$$\partial_t Q + D[(\nabla \cdot Q) \cdot \nabla]Q = -aQ - bQ^3 + \gamma_2 \nabla^2 Q - \gamma_4 (\nabla^2)^2 Q + \gamma_6 (\nabla^2)^3 Q$$

# Alternative approach

$$\partial_t Q + D[(\nabla \cdot Q) \cdot \nabla]Q = -aQ - bQ^3 + \gamma_2 \nabla^2 Q - \gamma_4 (\nabla^2)^2 Q + \gamma_6 (\nabla^2)^3 Q$$



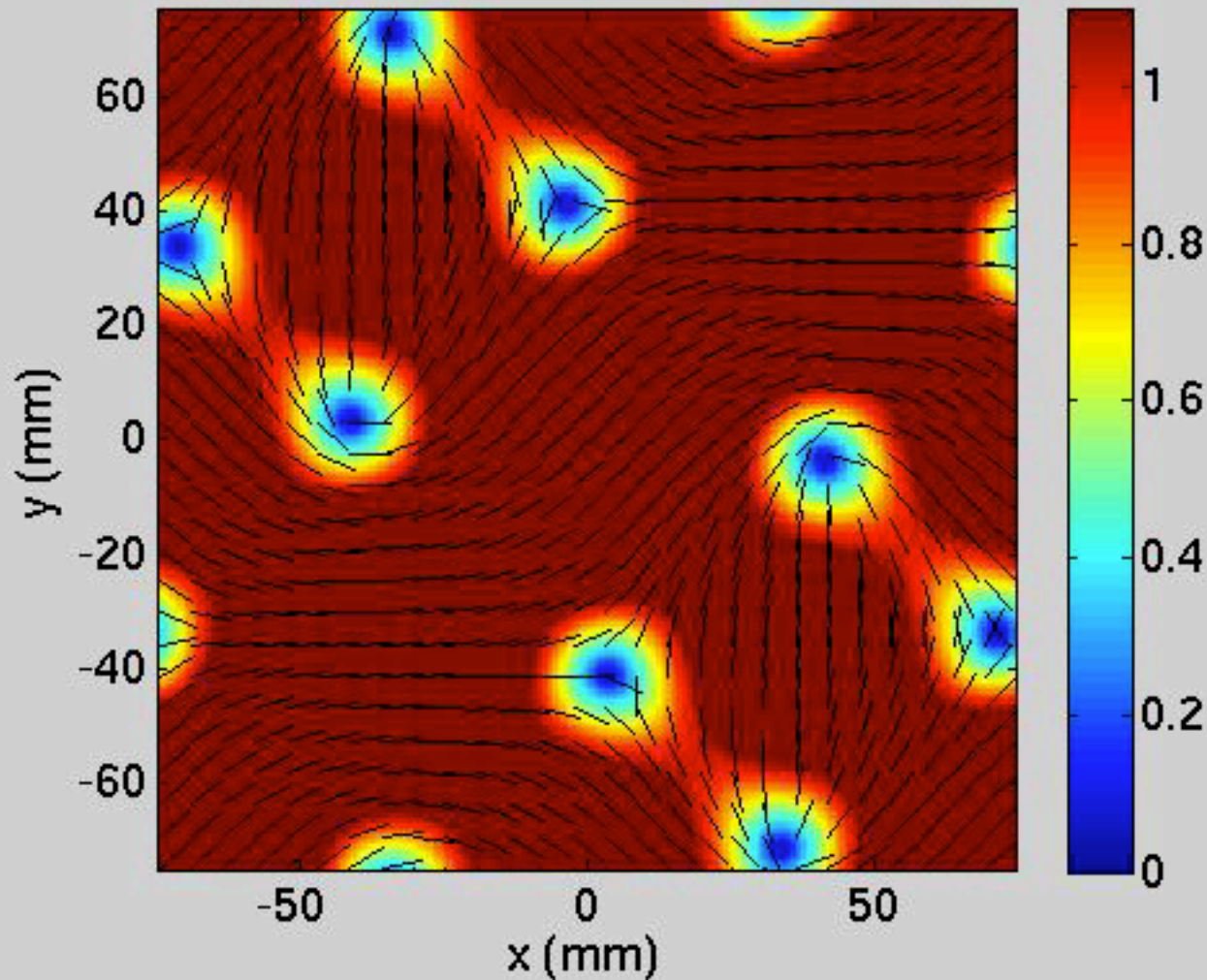
linear  
stability

Chaos possible?

# Prelim. simulation results

$D < 0$  extensile

$t = 0.5$ ;  $Dt = 10$ ;  $N_g = 3$ ;  $N = 243$ ;  $\Delta t = 3.3429e-05$ ;  $t = 0.015043s$



# Prelim. simulation results

$D > 0$  contractile

$\rho t = 0.5$ ;  $Dt = -5$ ;  $N_g = 3$ ;  $N = 243$ ;  $\Delta t = 6.6857e-05$ ;  $t = 0.030086s$

