Bacteria as a fluid: Applying the paradigm of materials theory to biology

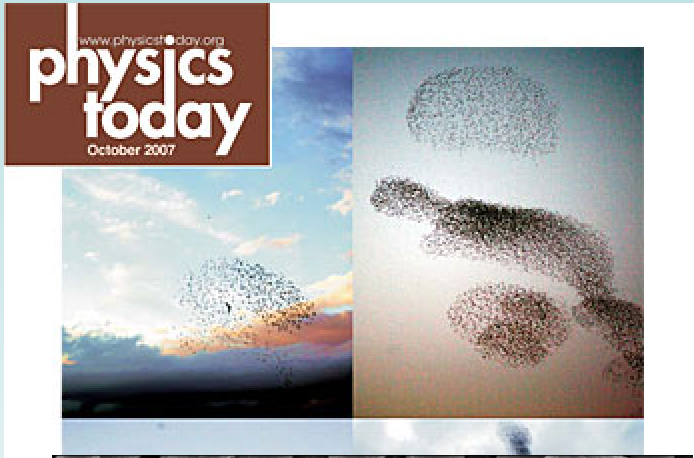
Aparna Baskaran
Syracuse University

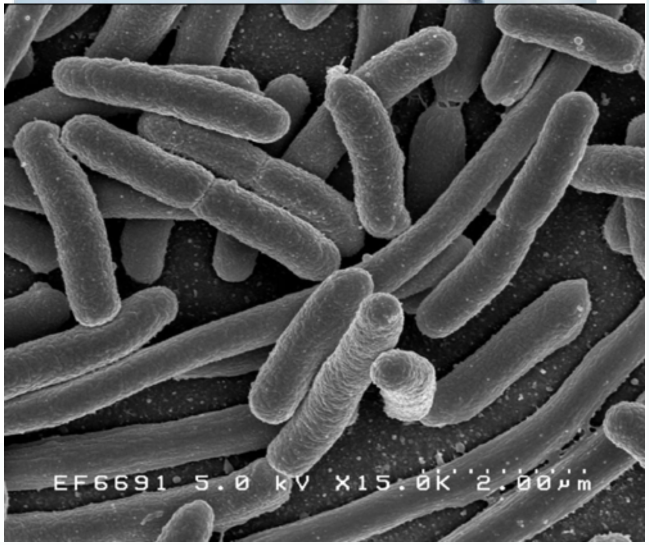
In Collaboration with M. Cristina Marchetti

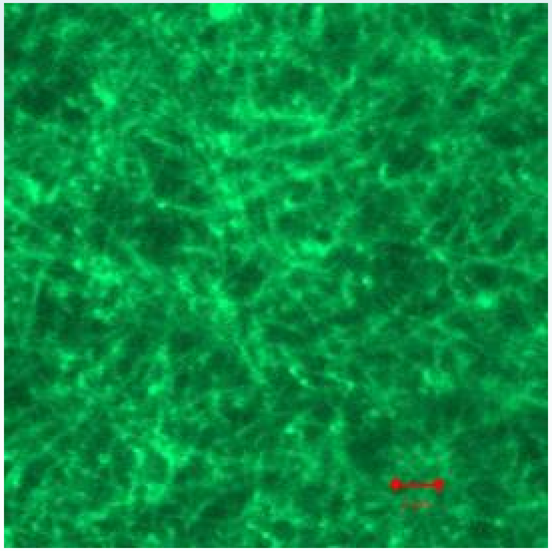
Supported by grants DMR-0705105 and DMR-0806511.

Introduction and Context

Systems of interest

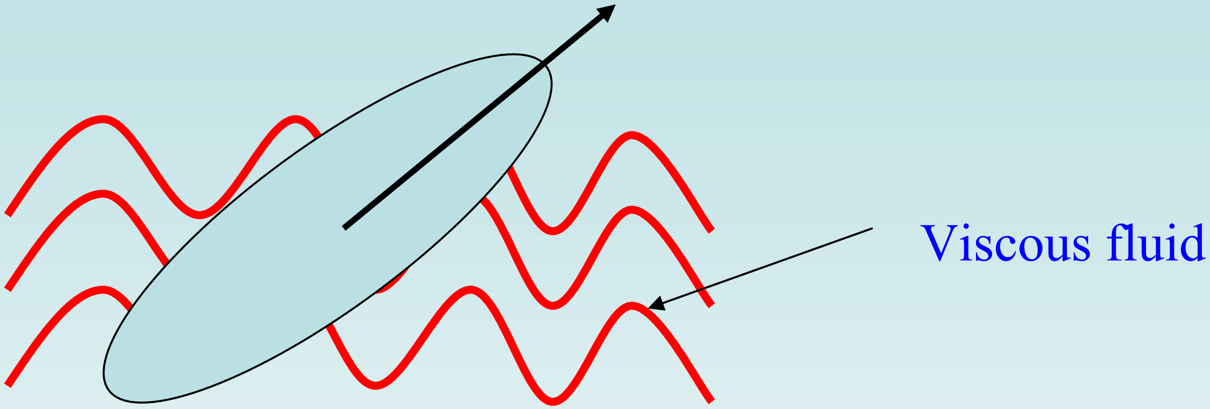






Introduction and Context

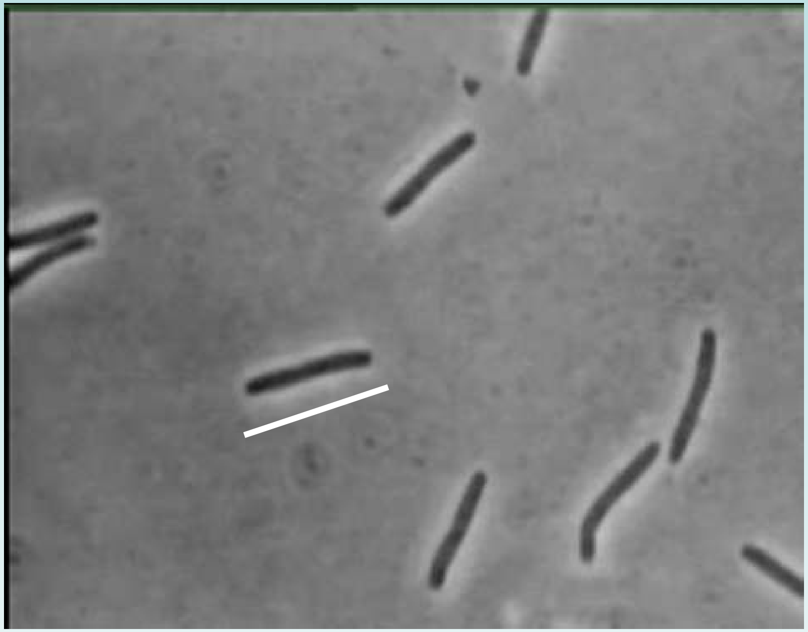
Physically simple unified starting point

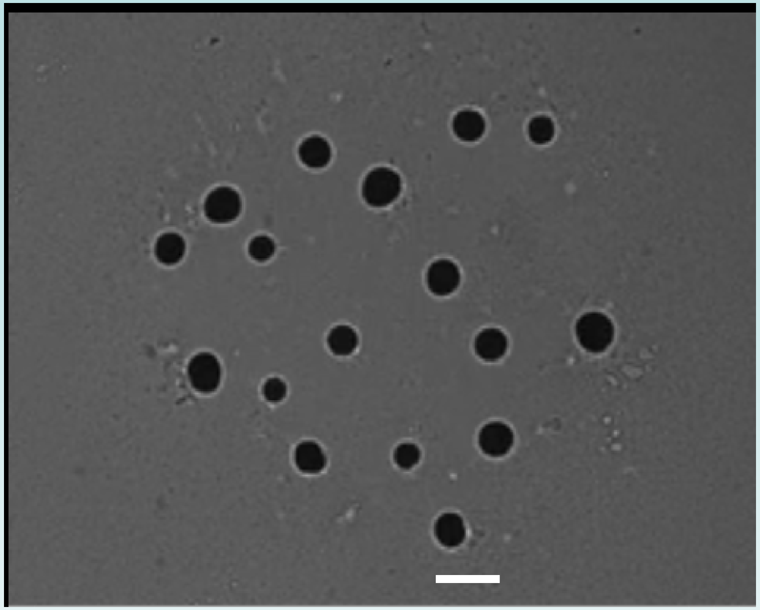


Collectively do exotic things

- Long range ordered states in 2D
- Anomalous fluctuations about these ordered states
- Novel instabilities and pattern formation

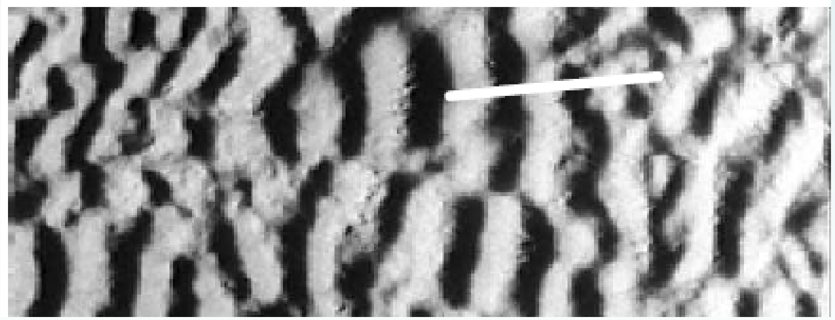
Illustrative example: Myxobacteria





3 D

1 micron



1 mm

100 microns

Objective of this study

Simple
Physical model
swimmers

Statistical mechanics

Symmetry based
Phenomenological
Continuum
equations

Childress, Purcell,
Golestain, Yeomans, Lauga, Powers etc

Ramaswamy, RRI people,
Prost, Joanny etc

Outline of Presentation

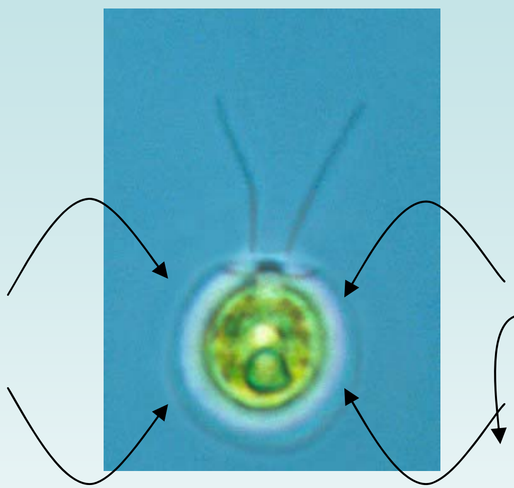
- The context
- The model
- The theory
- The outcomes

The context

- Typical numbers for bacteria: v ~ microns/s, size a ~ microns

$$\frac{\text{Inertial force}}{\text{Viscous force}} = \frac{v\, a\, \rho}{\eta} \quad \text{Reynolds number} = 10^{-3}$$

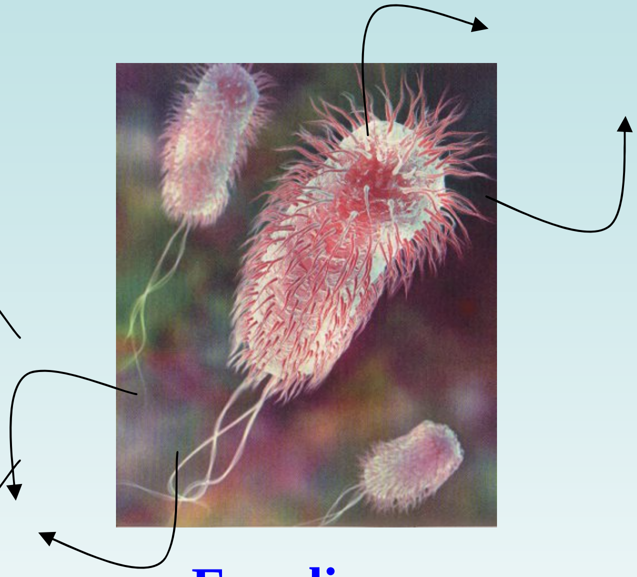
- Mass unimportant – v ~ Force (Aristotle not Newton)
- Extensive studies on propulsion mechanisms in this regime
- Interested in lengthscales >> swimmer, timescales >> stroke period



Chlamydomonas

Puller

Contractile



E- coli

Pusher

Tensile

The context

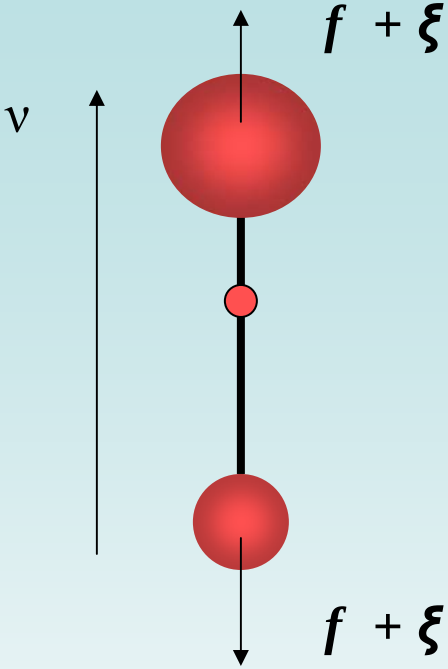
Bacteria as an active suspension

Objective: To develop a theory of collective behavior of many low Reynolds number swimmers on long length and time scales

Outline of Presentation

- ~~The context~~
- The model
- The theory
- The outcomes

The model - I



$$\partial_t \mathbf{r}_h = \mathbf{u}(\mathbf{r}_h)$$
$$\partial_t \mathbf{r}_t = \mathbf{u}(\mathbf{r}_t)$$

$$\eta \nabla^2 \mathbf{u}(\mathbf{r}) - \nabla p + \mathbf{F}_{active} - \mathbf{F}_{random} = 0 \; , \; \nabla \cdot \mathbf{u} = 0$$

$$\mathbf{F}_{active} = f \hat{\nu} \left[\delta(\mathbf{r} - \mathbf{r}_h) - \delta(\mathbf{r} - \mathbf{r}_t) \right]$$

$$\left[\xi^h(t) \delta(\mathbf{r} - \mathbf{r}_h) + \xi^t(t) \delta(\mathbf{r} - \mathbf{r}) \right.$$

Rigid body constraint : $r_h - r_t$ = constant

Hydrodynamic center

$$\mathbf{r}^C = \frac{\zeta_h \mathbf{r}_h + \zeta_t \mathbf{r}_t}{\zeta_h + \zeta_t} = \frac{a_h \mathbf{r}_h + a_t \mathbf{r}_t}{a_h + a_t}$$

The model - I

- Solve for the flow field

- Substitute in the equations of motion

- Go to hydrodynamic center and orientation variables

$$\partial_t \mathbf{r}^C = v_0 \hat{\nu} + \Gamma^T(t)$$

$$v_0 = \frac{f}{4\pi\eta\ell} \frac{a_t - a_h}{(a_h + a_t)}$$

Zero if dumbbell is symmetric

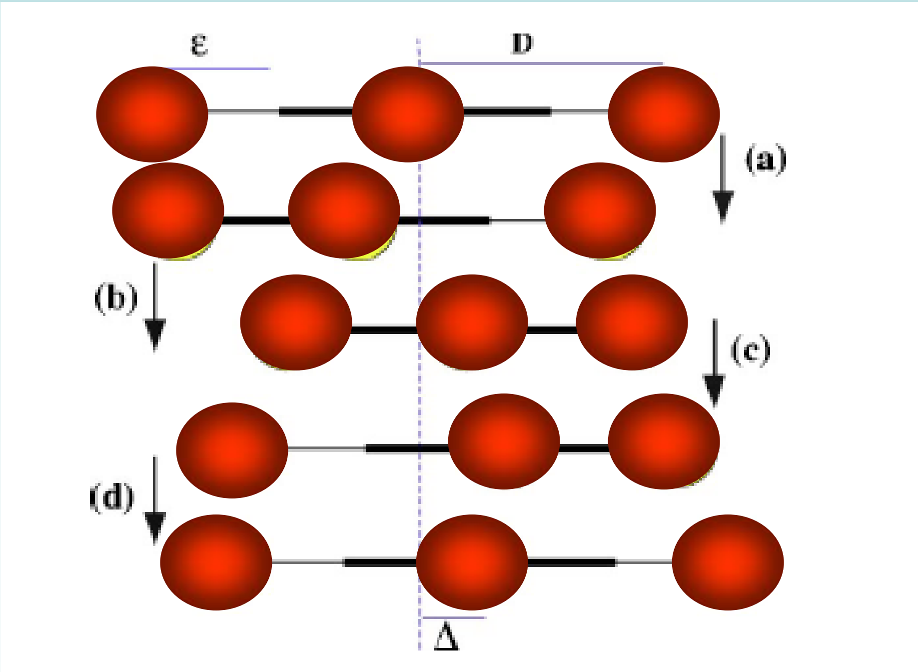
$$\partial_t \hat{\nu} = \omega \times \hat{\nu}$$

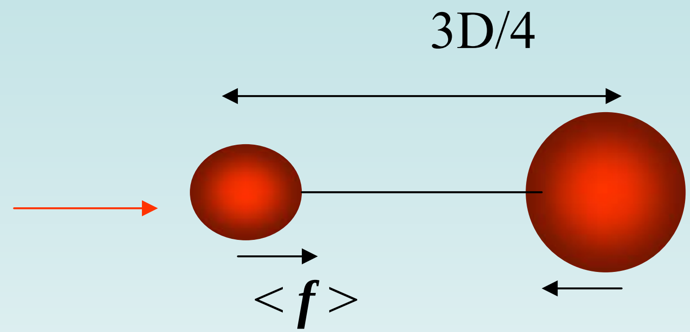
$$\omega = \hat{\nu} \times \Gamma^R(t)$$

Isolated swimmer does not rotate

The model - II

What about the stroke?





$$\langle f \rangle \sim \zeta_R W \frac{\varepsilon}{D} a_R$$

Najafi and Golestanian 2004

$$v_0 \sim \frac{\varepsilon}{D} \frac{f}{\zeta_R}$$

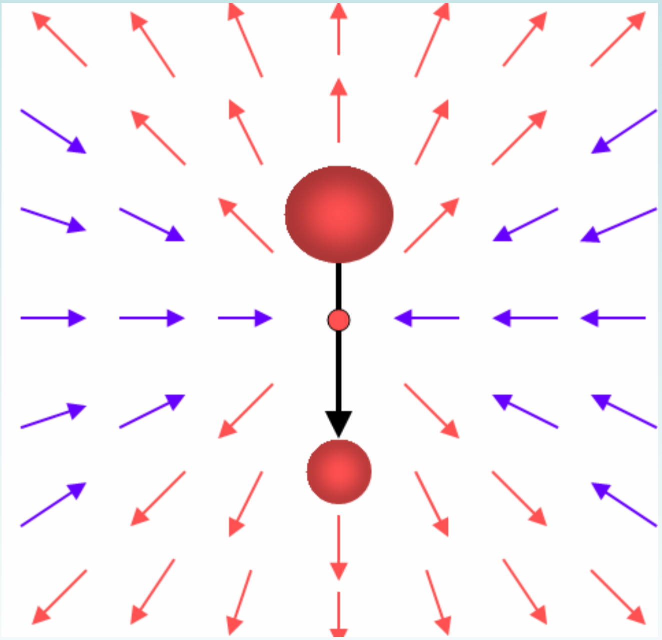
$$v_0 = \frac{f}{4\pi\eta\ell} \frac{a_t - a_h}{(a_h + a_t)}$$

For other real swimmers captures the exact stroke averaged far field flow

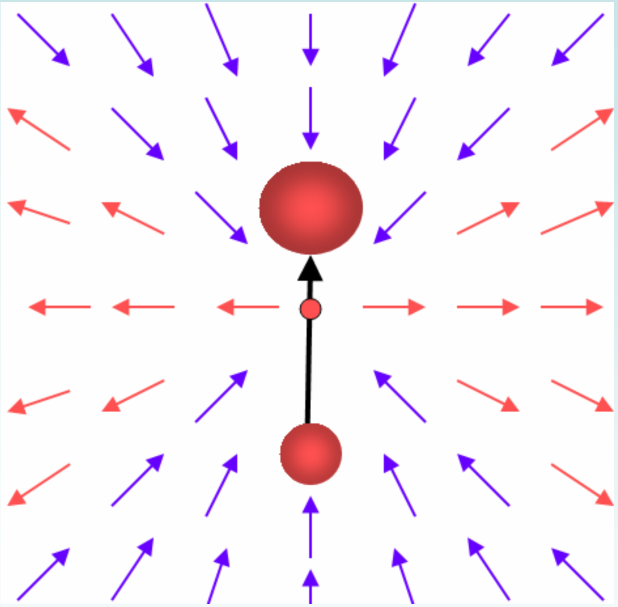
The model - III

Nomenclature in the stroke averaged context

$f > 0$ $f < 0$



Pusher



Puller

Symmetric - Shaker

The model - IV

Swimming with a crowd

$$\partial_t \mathbf{r}_{h\alpha} = \mathbf{u}(\mathbf{r}_{h\alpha})$$
$$\partial_t \mathbf{r}_{t\alpha} = \mathbf{u}(\mathbf{r}_t)_\alpha$$

$$\mathbf{F}_{active} = \sum f \hat{\nu}_\alpha \left[\delta\left(\mathbf{r} - \mathbf{r}_h\right)_\alpha - \delta\left(\mathbf{r} - \mathbf{r}_t\right)_\alpha\right]$$

$$\partial_t \mathbf{r}_\alpha = v_0 \hat{\nu}_\alpha + \frac{1}{\zeta} \sum_{\alpha \neq \beta} \mathbf{F}_{\alpha\beta} + \xi^T_\alpha$$

$$\partial_t \hat{\nu}_\alpha = \omega_\alpha \times \nu_\alpha ; \omega_\alpha = \frac{1}{\zeta \ell^2} \sum_\alpha \tau_{\alpha\beta} + \xi^R_\alpha$$

$$\mathbf{F}_{12} \simeq f(a_h + a_t)\ell \left[3(\hat{\mathbf{r}}_{12} \cdot \hat{\nu}_2)^2 - 1\right] \frac{\hat{\mathbf{r}}_{12}}{r_{12}^2}$$

$$\tau_{12} \simeq f \hat{\nu}_1 \times \left[3\hat{\mathbf{r}}_{12}\hat{\mathbf{r}}_{12} - \delta\right] \cdot \hat{\nu}_2 \left[\frac{(a_h + a_t)^2 \ell^2}{r_{12}^3}(\hat{\nu}_1 \cdot \hat{\nu}_2) - \frac{\ell^5 (a_h - a_t)^2}{(a_h + a_t)\, r_{12}^5}\right]$$

- Force – "nematic" and that of a dipole
- Torque – "nematic" to lowest order and spherically symmetric

The theory - I
Statistical Mechanics

- N overdamped Langevin equations – phase space $\left\{ \mathbf{r}_{\alpha}^{C}, \hat{\nu}_{\alpha} \right\}_{\alpha=1}^{N}$

- "low density"- Smoluchowski Equation

$$\partial_t c\left(\mathbf{r}_1,\hat{\nu}_1,t\right)+\nabla_{\mathbf{r}_1}\cdot\left(v_0\hat{\nu}_1 c\left(\mathbf{r}_1,\hat{\nu}_1,t\right)\right)=-\frac{1}{\zeta}\nabla_{\mathbf{r}_1}\cdot\left(\langle\mathbf{F}_{12}\rangle\, c\left(\mathbf{r}_1,\hat{\nu}_1,t\right)\right)-\frac{1}{\zeta\ell^2}\left(\hat{\nu}_1\times\frac{\partial}{\partial\hat{\nu}_1}\right)\cdot\langle\tau_{12}^{h}\rangle\, c\left(\mathbf{r}_1,\hat{\nu}_1,t\right)$$
$$+D_{ij}^{(1)}\nabla_{\mathbf{r}_{1i}}\nabla_{\mathbf{r}_{1j}}c\left(\mathbf{r}_1,\hat{\nu}_1,t\right)+D_R\left(\hat{\nu}_1\times\frac{\partial}{\partial\hat{\nu}_1}\right)^2 c\left(\mathbf{r}_1,\hat{\nu}_1,t\right)$$

Mean field force and torque

Concentration of swimmers at a point r oriented along ν

Rotational and translational diffusion

The theory - II

Hydrodynamics

Interested in the long wavelength long time physics.

Relevant variables are conserved quantities and broken symmetry variables

Density

$$\rho\left(\mathbf{r},t\right)=\int d\hat{\nu}\,c\left(\mathbf{r},\hat{\nu},t\right)$$

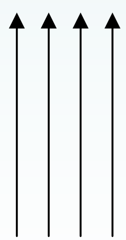
Polarization
(Flow under self propulsion)

$$\mathbf{P}\left(\mathbf{r},t\right)=\int d\hat{\nu}\,\hat{\nu}\,c\left(\mathbf{r},\hat{\nu},t\right)$$

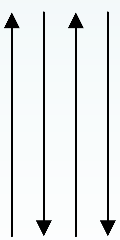
Nematic Order Parameter

$$\overleftrightarrow{Q}\left(\mathbf{r},t\right)=\int d\hat{\nu}\left(\hat{\nu}\hat{\nu}-\frac{1}{3}\mathbf{I}\right)c\left(\mathbf{r},\hat{\nu},t\right)$$

Polar



Nematic



Illustrative outcome - I

Homogeneous States

$$\partial_t \rho = 0$$

$$\partial_t Q_{ij} = -4 D_R Q_{ij}$$

$$\partial_t P = -D_R P$$

- No interaction terms - no ordering, only isotropic state
- Even in mean field, should see an instability
- The hydrodynamic interaction in the Stokes regime is central and pairwise additive – spherical symmetry, no net aligning
- Need other effects to get aligned states – Ex: excluded volume gives nematic alignment

Illustrative outcome - II

Fluctuations in the isotropic state

Linearize the hydrodynamic equations about $\rho = \rho_0 \quad \mathbf{P} = 0 \quad \overleftrightarrow{Q} = 0$

$$\partial_t \delta\widetilde{\rho} = \boxed{ikv_0 P_{\|}} - D\left[1 + \frac{f\,(a_h + a_t)}{k_B T}\right] k^2 \delta\widetilde{\rho}$$

$$\partial_t P_{\|} = -D_R P_{\|} + \boxed{ik\frac{1}{3}v_0\delta\widetilde{\rho}} - \frac{\ell K_1}{\zeta} k^2 P_{\|}$$

$$\partial_t \delta\cancel{\widetilde{Q}}_{\|\|} = -4D_R \delta\widetilde{Q}_{\|\|} - \frac{D}{10} k^2 \delta\widetilde{\rho}$$

For contractile swimmers, $f < 0$ system unstable when

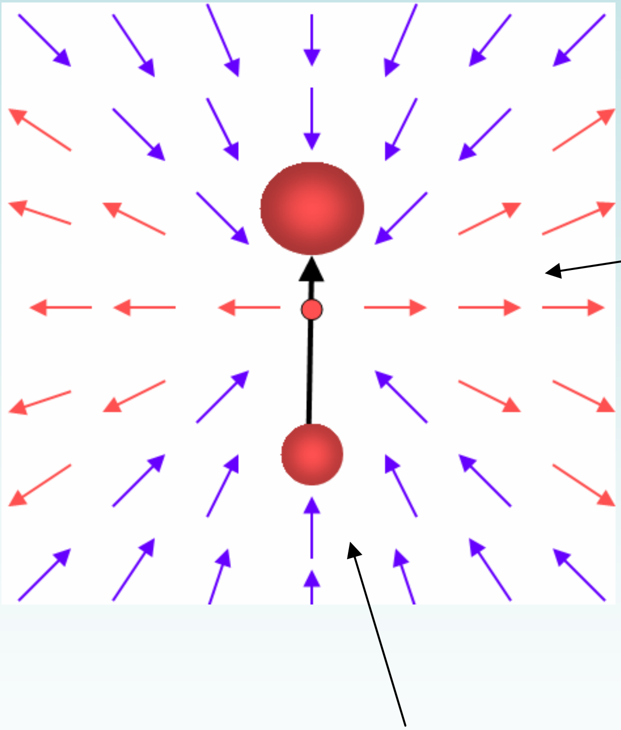
$$|f|\,\frac{(a_h + a_t)}{k_B T} \sim \frac{v_0 \ell}{D} \equiv Pe > 1$$

Convective fluxes lead to propagating modes

$$v_0 > \sqrt{DD_R}$$

Illustrative outcome - II
Fluctuations in the isotropic state

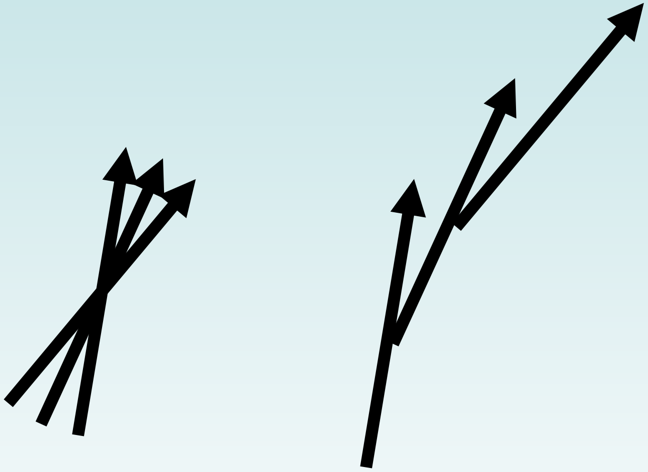
Mechanism?



repulsive

attractive

Suppression of longitudinal diffusion



Polarization fluctuations lead to mass fluxes – relax by diffusion – propagating modes

Illustrative outcome - II

Is everything else decaying at microscopic (D_R or smaller) time scales?

$$\partial_t \delta \widetilde{Q}_{\parallel\perp} = -4 D_R \delta \widetilde{Q}_{\parallel\perp} + \frac{f}{\zeta}\left((a_h + a_t)^2 \rho_0\right) \delta \widetilde{Q}_{\parallel\perp}$$

$$\hat{k}_l \left(\delta_{nm} - \hat{k}_n \hat{k}_m\right) \widetilde{Q}_{lm}$$

Tensile systems go unstable to bend fluctuation,
Density dependent threshold for onset

Theory says no homogeneous isotropic state
Ordered state? – Preliminary evidence says no

Illustrative outcome - III

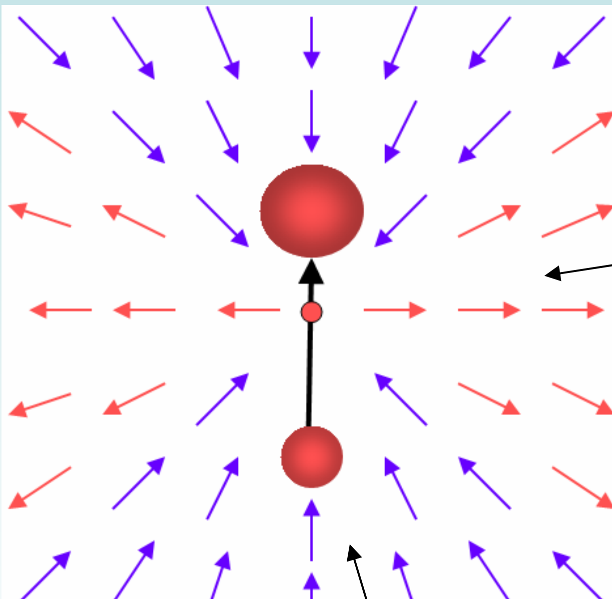
Fluctuations in the Ordered state

- No ordered state with only far field hydrodynamic interactions
- Can get a nematic state by including excluded volume interactions
- Polar state appears to need external symmetry breaking – chemotaxis
- Ordered state always unstable :
    - Contractile / Puller : Splay fluctuations
    - Tensile / Pusher : Bend fluctuations

Illustrative outcome - III

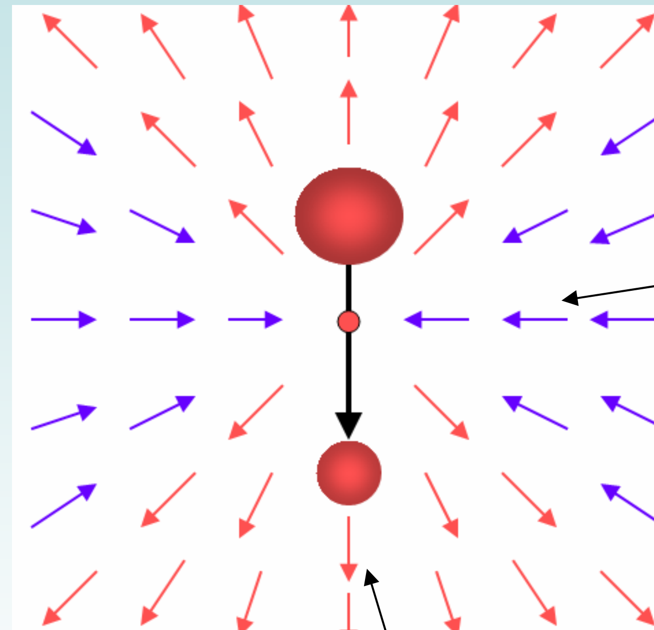
Fluctuations in the Ordered state

Mechanism?



Perpendicular alignment

Parallel alignment



Parallel alignment

Perpendicular alignment

Illustrative outcome - III

When are these instabilities suppressed?

- Crucial point : $1/r^2$ nature of the interactions

- This is suppressed when :

  - The stroke of the swimmer is Time Reversal-Parity invariant – Spirullum Volutans

  - When the medium is visco-elastic – long range interaction is screened

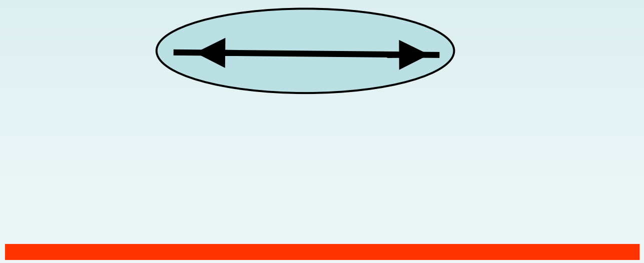
- In confined systems – will lead to pattern formation

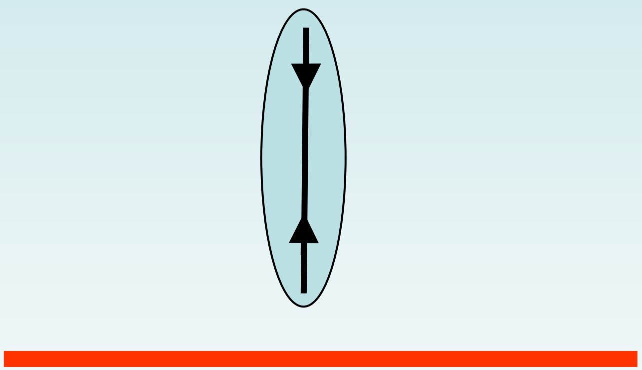
Illustrative outcome - III

Another illustration: Boundaries

Stokes Equation ----> Electrostatics

Walls with no slip ----> Metal walls, method of images





Tensile – parallel anchoring

Contractile – perpendicular anchoring

Together with tendency to be isotropic leads to patterns in confined systems

Conclusions

- Simple yet physical model
- Unified derivation of hydrodynamics of active suspensions
- Integrates lot of previous work

  Kruse/Julicher, Ramaswamy/Simha/Hatwalne/Rao, Marchetti/Liverpool, Santillian/Shelly, Yeomans/Alexander, Prost/Joanny…

- Insights into physical mechanisms at play in emergent behavior
- Many avenues remain to be explored