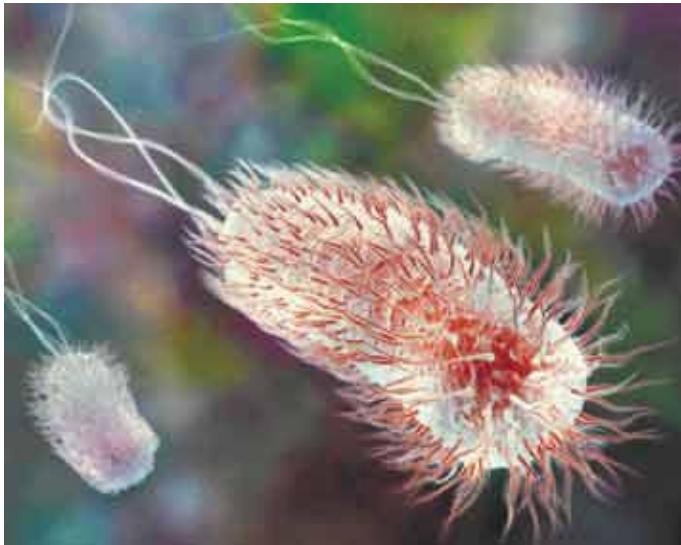
An aerial photograph of the University of Oxford, showing a dense cluster of historic buildings. The architecture is predominantly made of light-colored stone or brick, with numerous gables, dormer windows, and intricate stonework. Notable landmarks include the Radcliffe Camera, the Sheldonian Theatre, and the Divinity School. The city is built on a hillside, with buildings rising from the foreground towards the background. The sky is clear and blue.

Motility in Living Matter

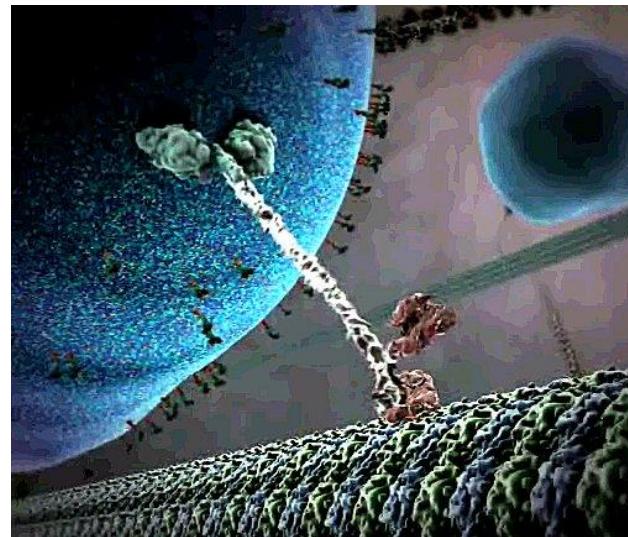
Julia Yeomans
University of Oxford

Active matter



bacteria, self-propelled colloids

active systems operate out of
thermodynamic equilibrium



molecular motors, cells

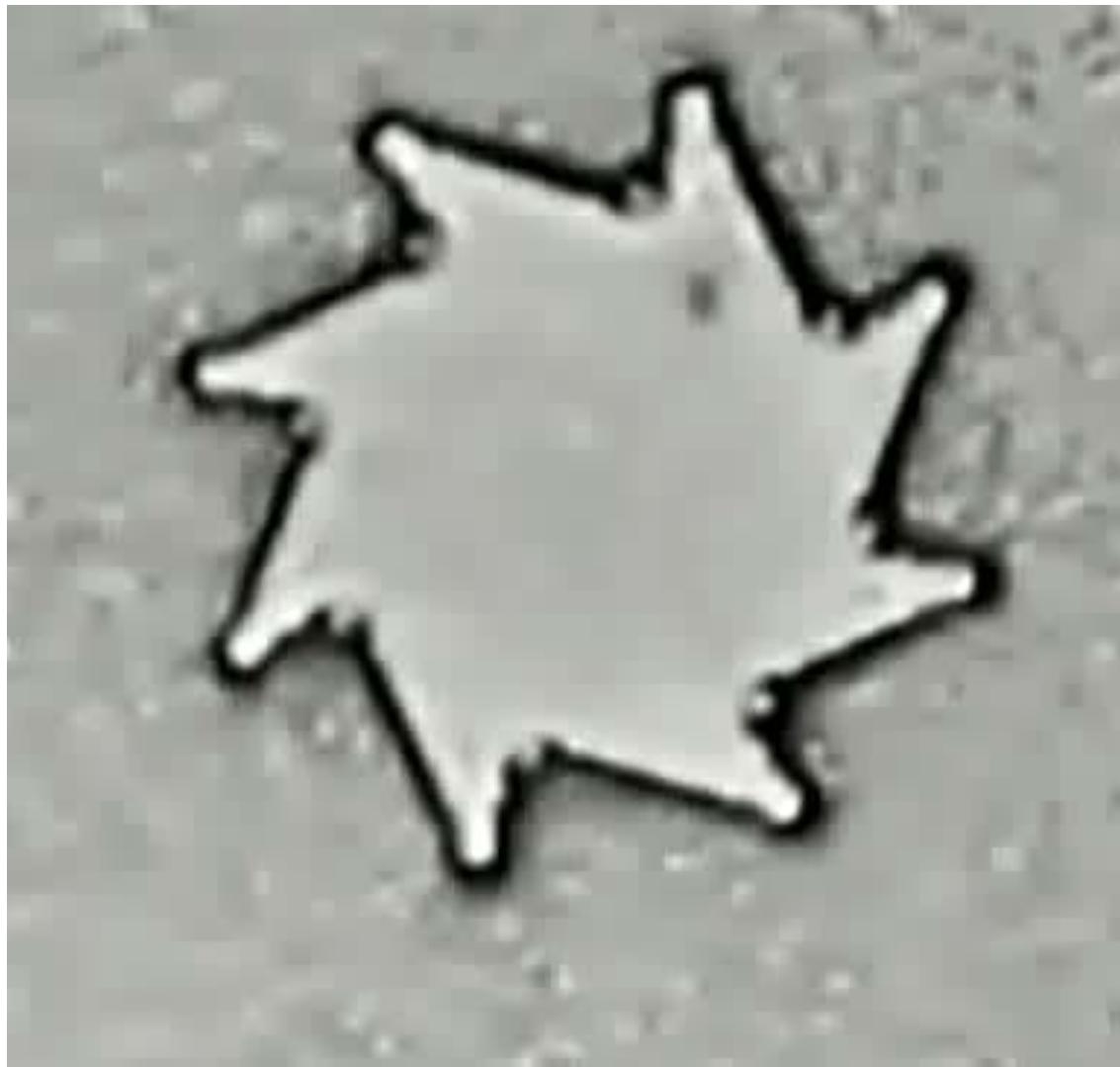


birds, fish

Active matter

Why is active matter interesting?

1. Statistical physics beyond Boltzmann
2. Engineering applications
3. Medical applications



L. Angelani, R. Di Leonardo, Ruocco G.,
Phys. Rev. Lett., 102, 048104, (2009)

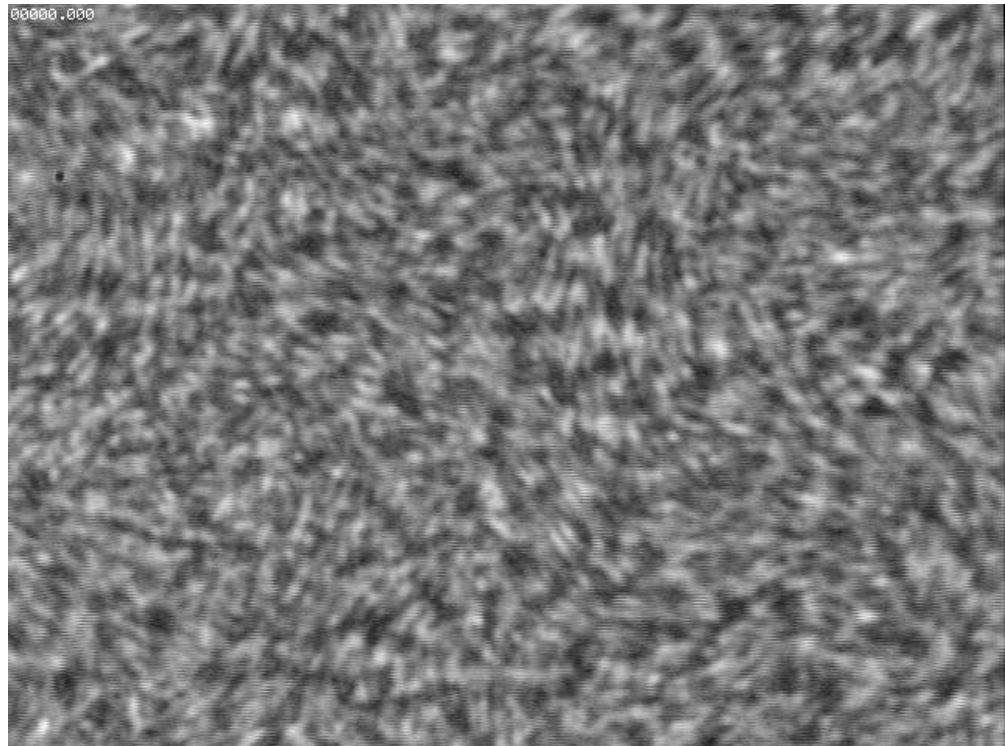
Active matter

Why is active matter interesting?

1. Statistical physics beyond Boltzmann
2. Engineering applications
3. Medical applications

Why is it interesting now?

1. Better microscopy
2. Nanotechnology
3. Faster computers



Swimmers

Swimming without flagella



$$\rho \left\{ \frac{\partial \mathbf{v}}{\partial t} + (\mathbf{v} \cdot \nabla) \mathbf{v} \right\} = -\nabla p + \mu \nabla^2 \mathbf{v} + \mathbf{f}$$

↑ ↑
inertial terms viscous terms

$$\text{Re} = \frac{\text{inertial response}}{\text{viscous response}} \sim \frac{\rho L_0 V_0}{\mu}$$

$$\rho \left\{ \frac{\partial \mathbf{v}}{\partial t} + (\mathbf{v} \cdot \nabla) \mathbf{v} \right\} = -\nabla p + \mu \nabla^2 \mathbf{v} + \mathbf{f}$$


 A diagram illustrating the components of the Navier-Stokes equation. The left side of the equation is enclosed in a large curly brace. Two blue arrows point from labels below the equation to specific terms: one arrow points to the term $\frac{\partial \mathbf{v}}{\partial t} + (\mathbf{v} \cdot \nabla) \mathbf{v}$ with the label "inertial terms", and another arrow points to the term $\mu \nabla^2 \mathbf{v}$ with the label "viscous terms".

$$Re = \frac{\text{inertial response}}{\text{viscous response}} \sim \frac{\rho L_0 V_0}{\mu}$$

Stokes equations

$$\nabla p = \mu \nabla^2 \mathbf{v} + \mathbf{f} \quad \nabla \cdot \mathbf{v} = 0$$



Purcell's Scallop Theorem

$$\nabla p = \mu \nabla^2 \mathbf{v} + \mathbf{f} \quad \nabla \cdot \mathbf{v} = 0$$

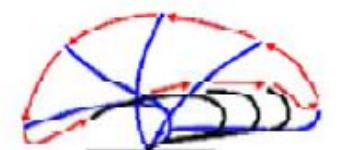
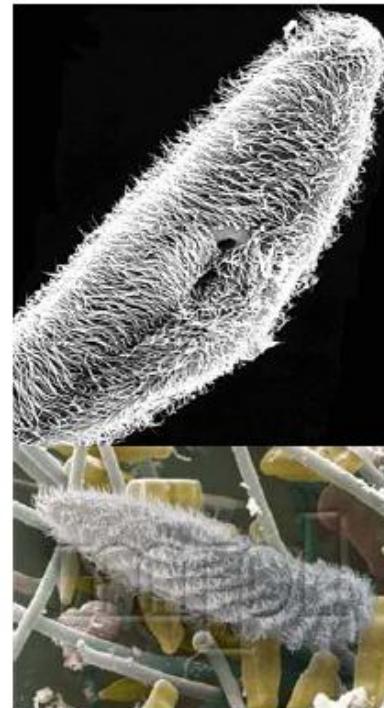
No time dependence implies the Scallop Theorem

A swimming stroke must not be invariant under time reversal



Purcell's Scallop Theorem

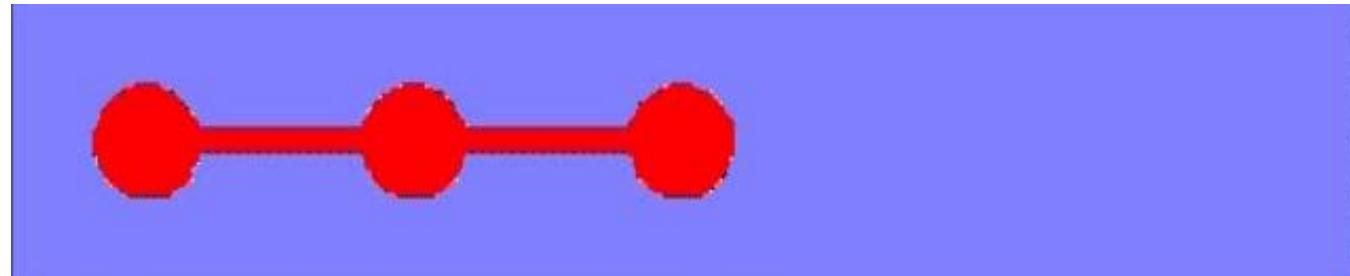
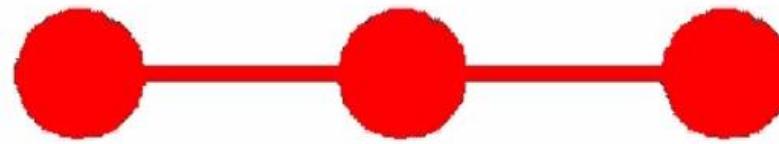
A swimmer strokes must be non-invariant under time reversal



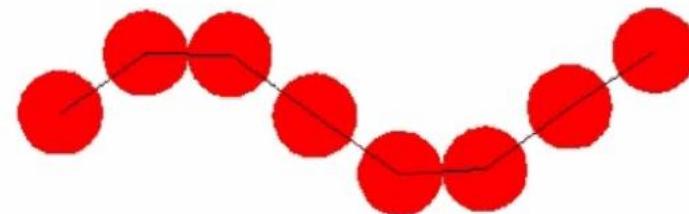
Model swimmers

three sphere swimmer

Najafi and Golestanian,



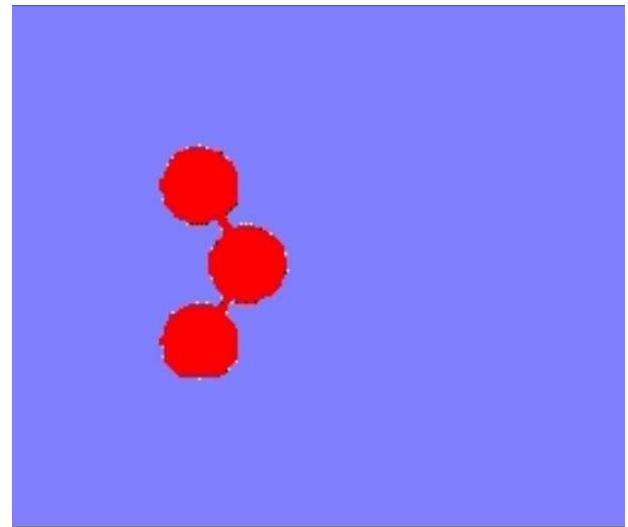
Snake swimmer



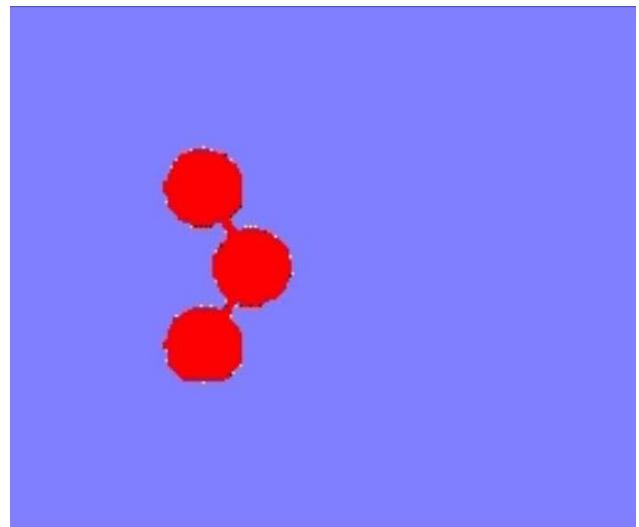
a generalised three sphere swimmer

Radial and tangential motion

forward motion



turning motion



Green function of the Stokes equation

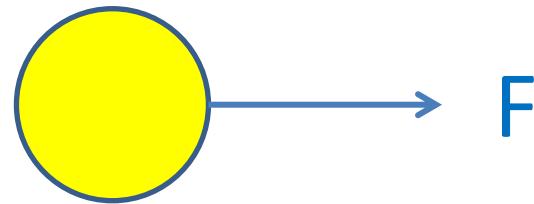
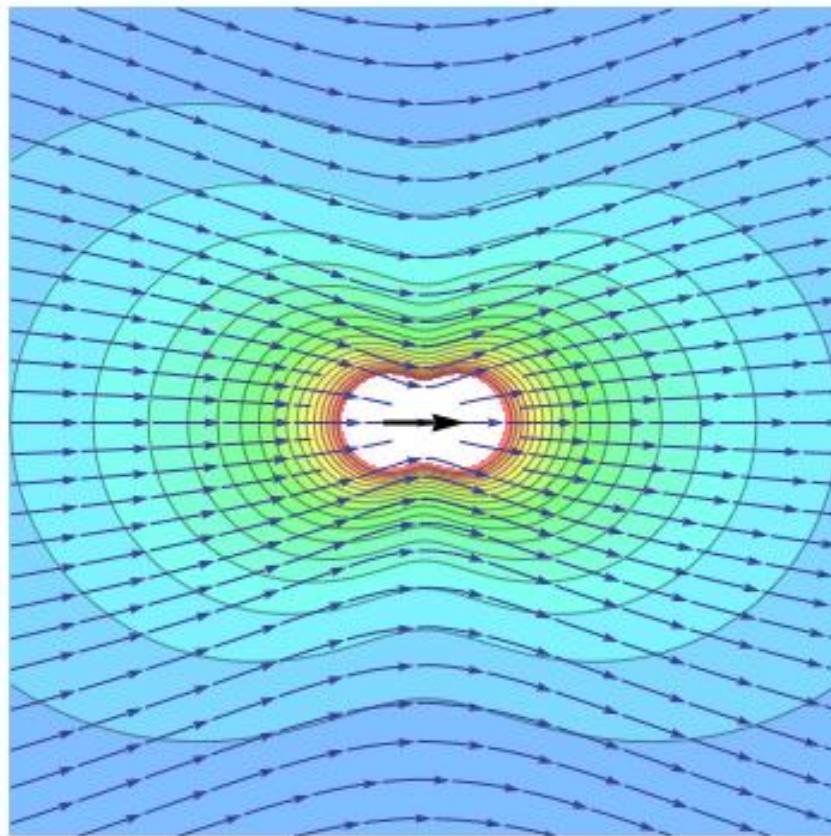
$$\nabla p = \mu \nabla^2 \mathbf{v} + \mathbf{f} \delta(\mathbf{r}) \quad \nabla \cdot \mathbf{v} = 0$$

$$\mathbf{v} = \frac{\mathbf{f}}{8\pi\mu} \cdot \left(\frac{\mathbf{I}}{r} + \frac{\mathbf{r}\mathbf{r}}{r^3} \right) \quad \text{Stokeslet}$$

$$p = p_0 + \frac{\mathbf{f} \cdot \mathbf{r}}{4\pi r^3}$$

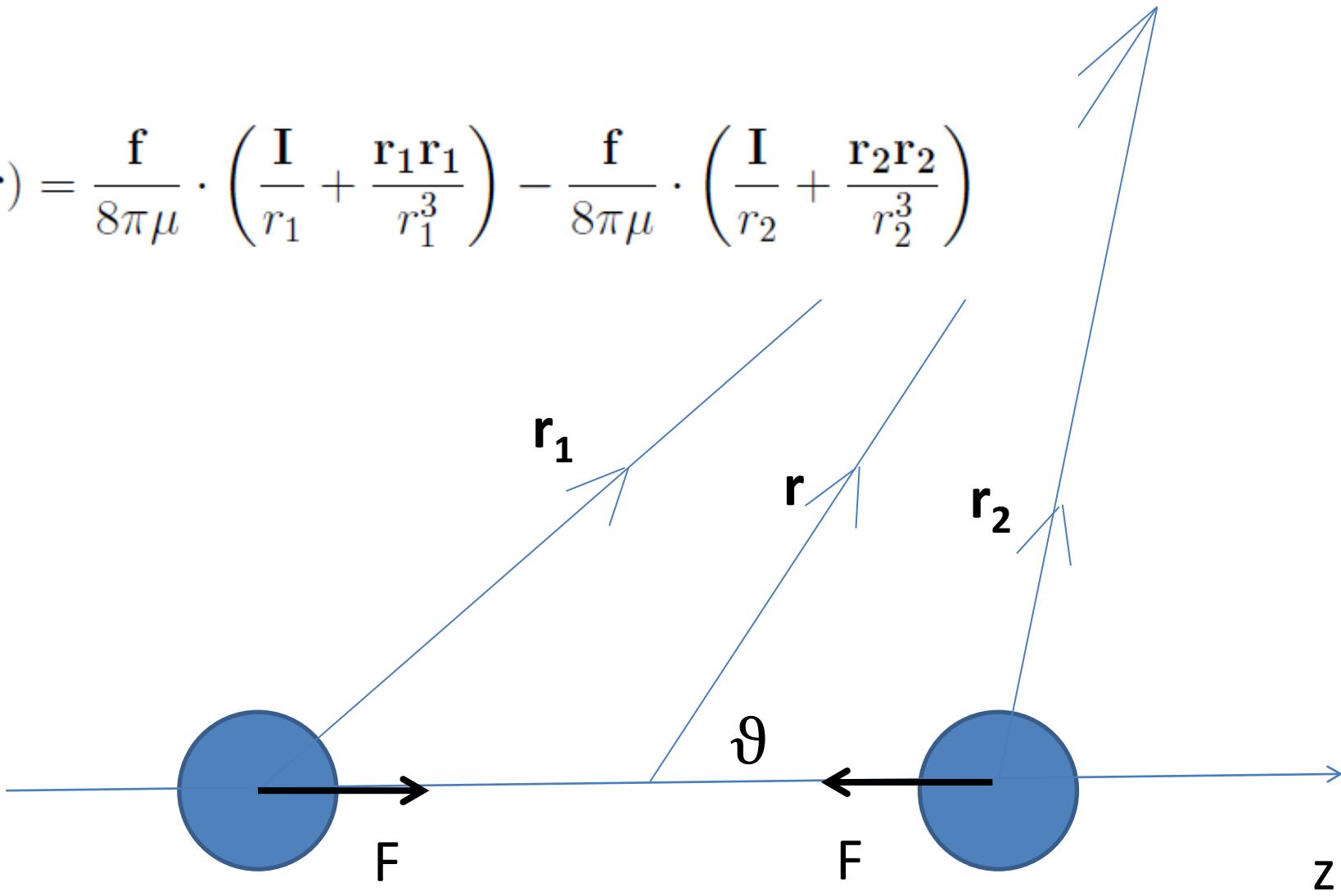
Green function of the Stokes equation

$$\mathbf{v} = \frac{\mathbf{f}}{8\pi\mu} \cdot \left(\frac{\mathbf{I}}{r} + \frac{\mathbf{rr}}{r^3} \right)$$



Dipolar far flow field

$$\mathbf{v}(\mathbf{r}) = \frac{\mathbf{f}}{8\pi\mu} \cdot \left(\frac{\mathbf{I}}{r_1} + \frac{\mathbf{r}_1\mathbf{r}_1}{r_1^3} \right) - \frac{\mathbf{f}}{8\pi\mu} \cdot \left(\frac{\mathbf{I}}{r_2} + \frac{\mathbf{r}_2\mathbf{r}_2}{r_2^3} \right)$$

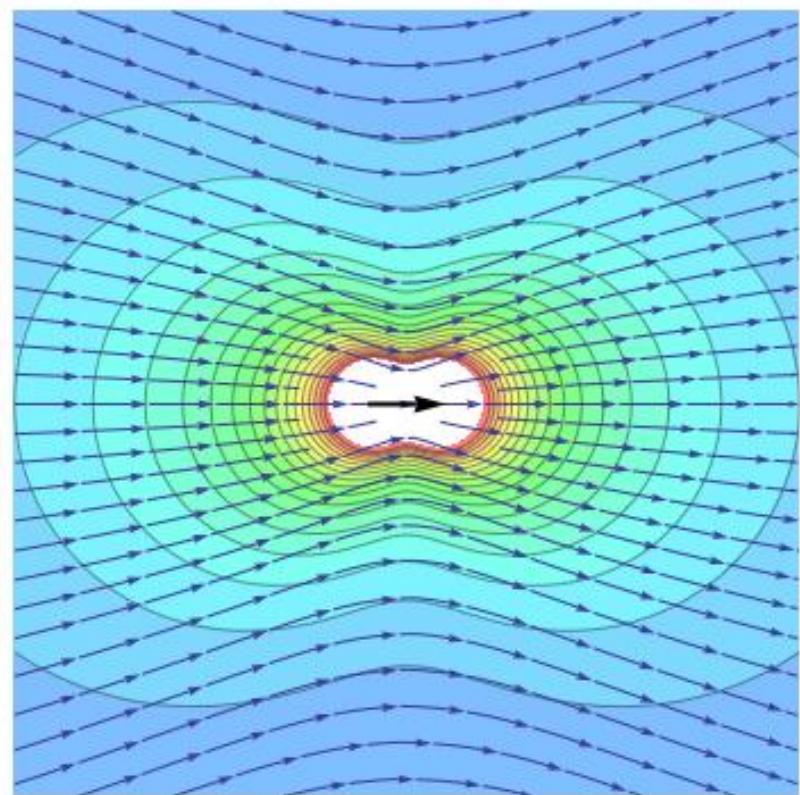
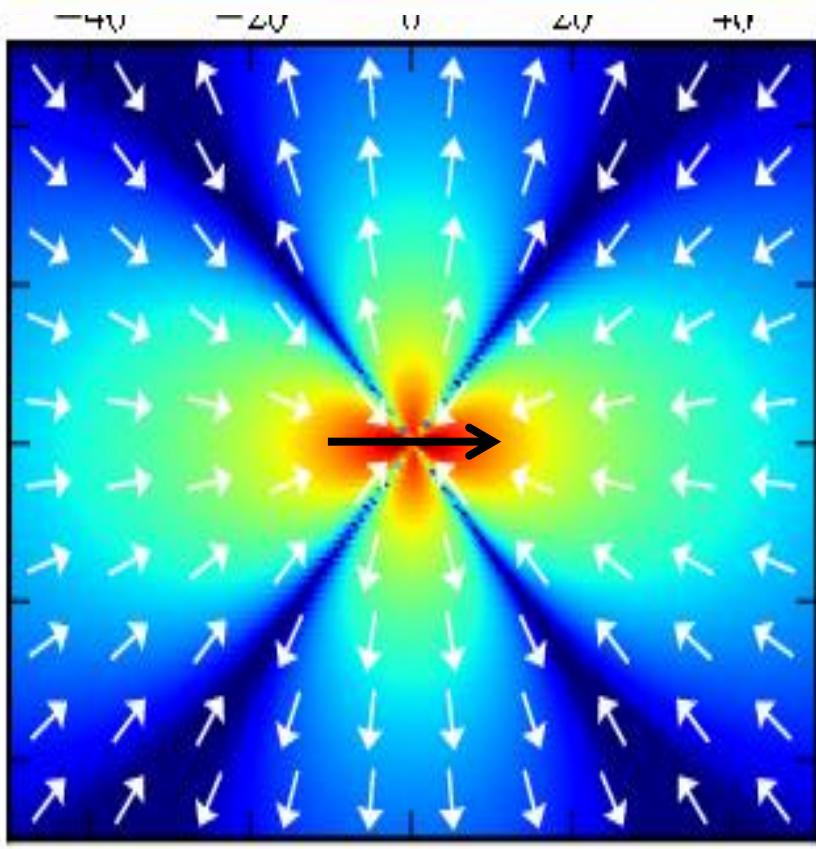


Far flow field of a swimmer

$$v_r = \frac{f}{4\pi\mu} \frac{L}{r^2} (3\cos^2\theta - 1)$$

Swimmers have dipolar far flow fields because they have no net force acting on them

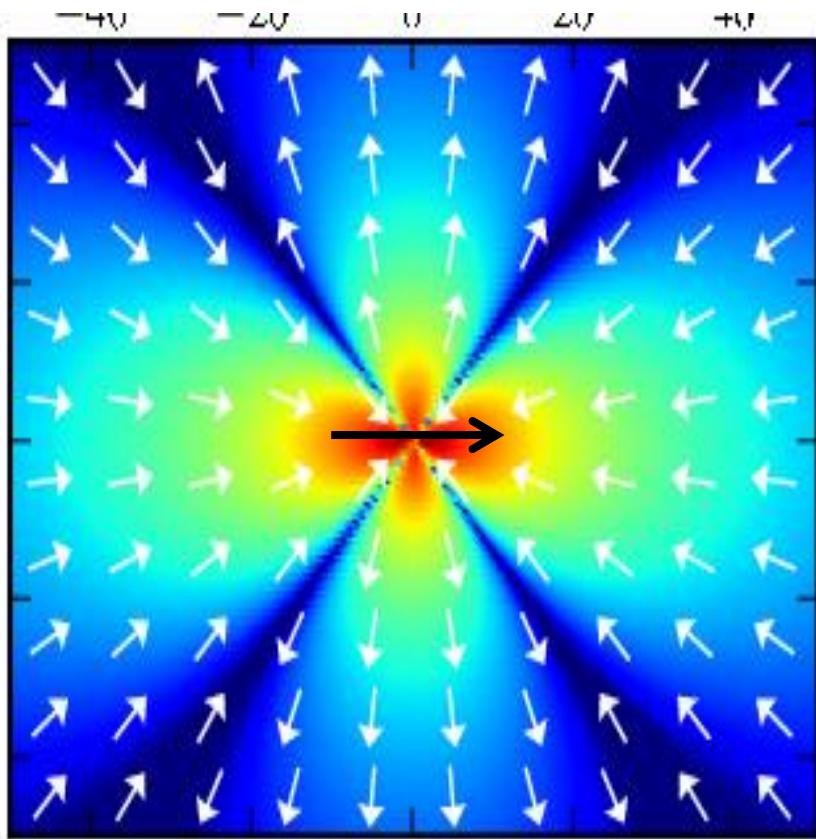
Swimmer and colloidal flow fields



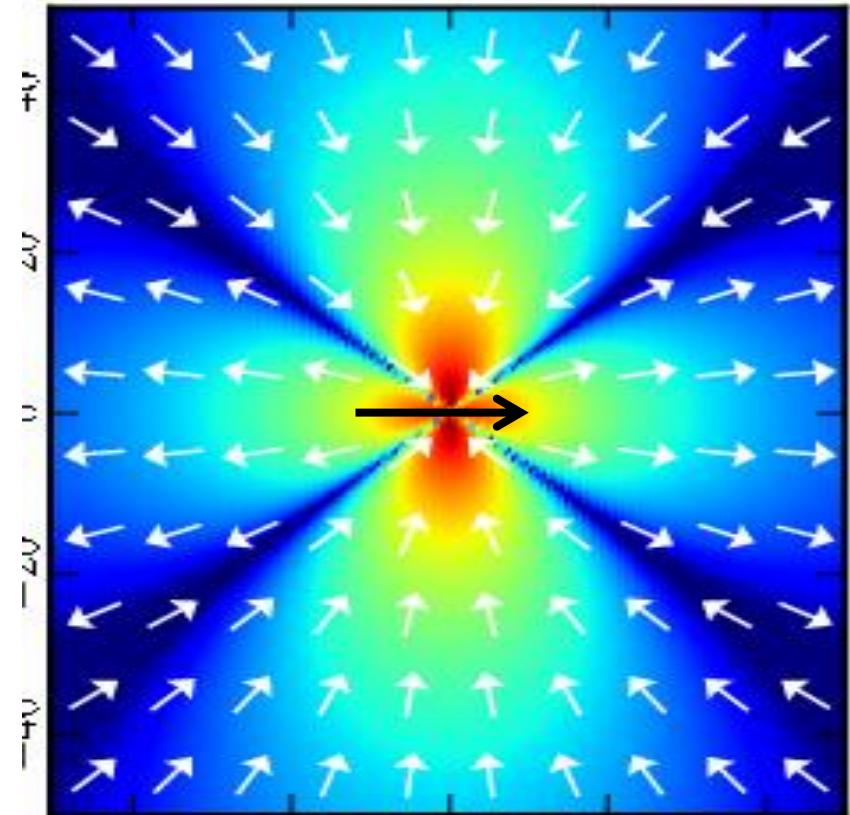
$$v \sim \frac{1}{r^2}$$

$$v \sim \frac{1}{r}$$

Dipolar flow field

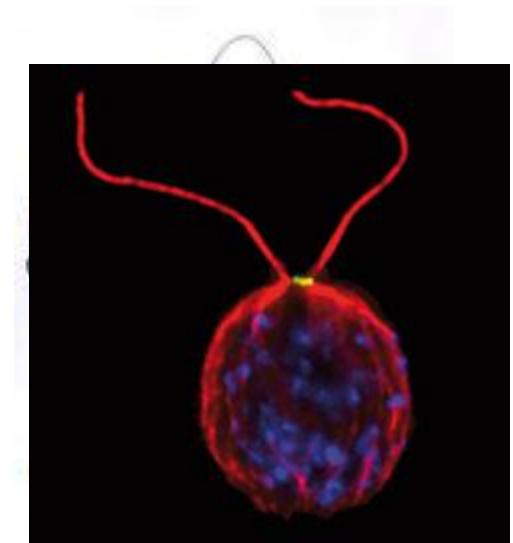
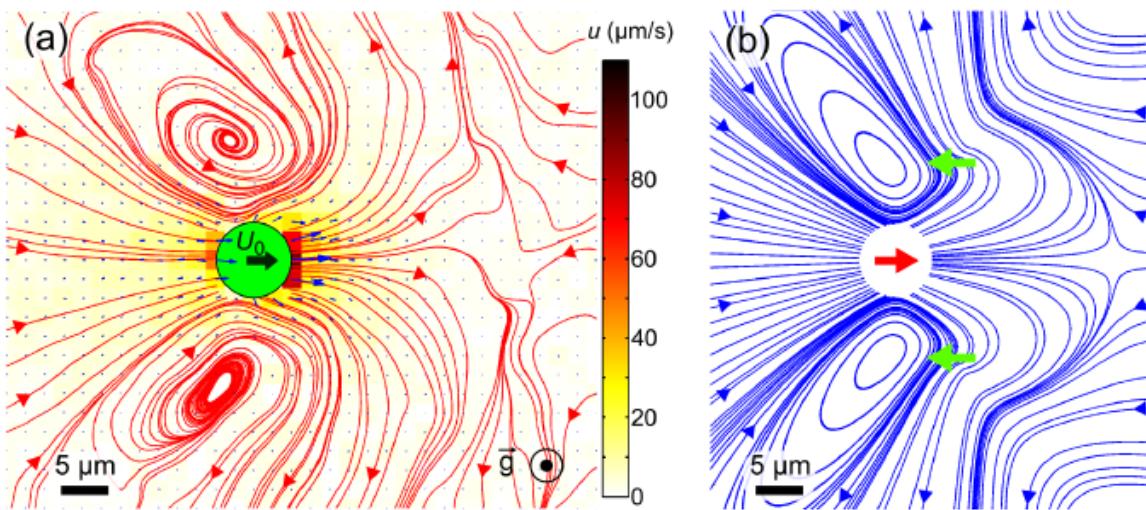
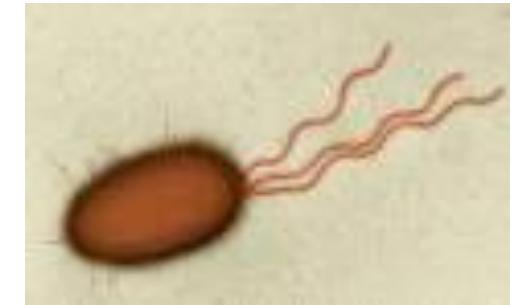
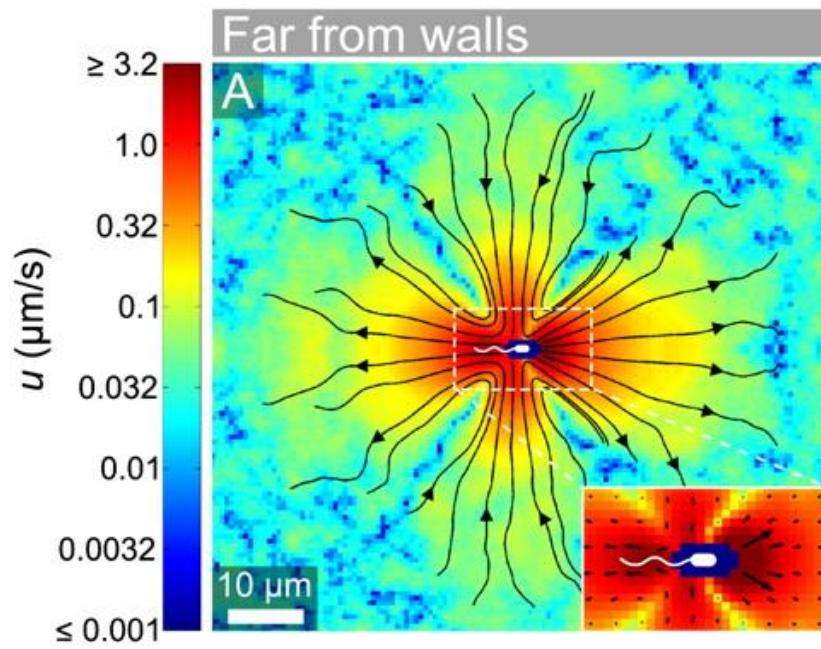


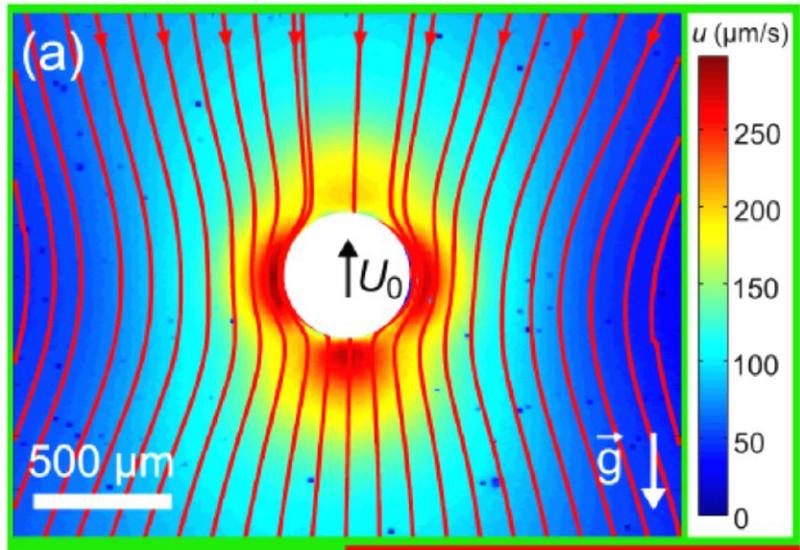
puller (contractile)



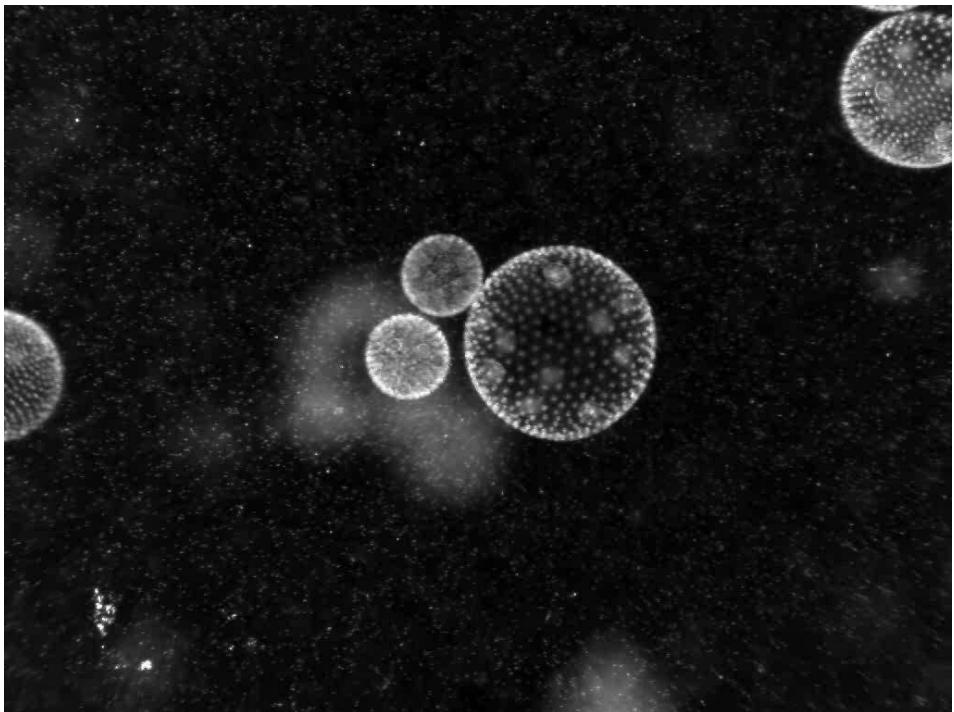
pusher (extensile)

$$v_r = \frac{f}{4\pi\mu} \cdot \frac{L}{r^2} \cdot (3\cos^2\theta - 1)$$

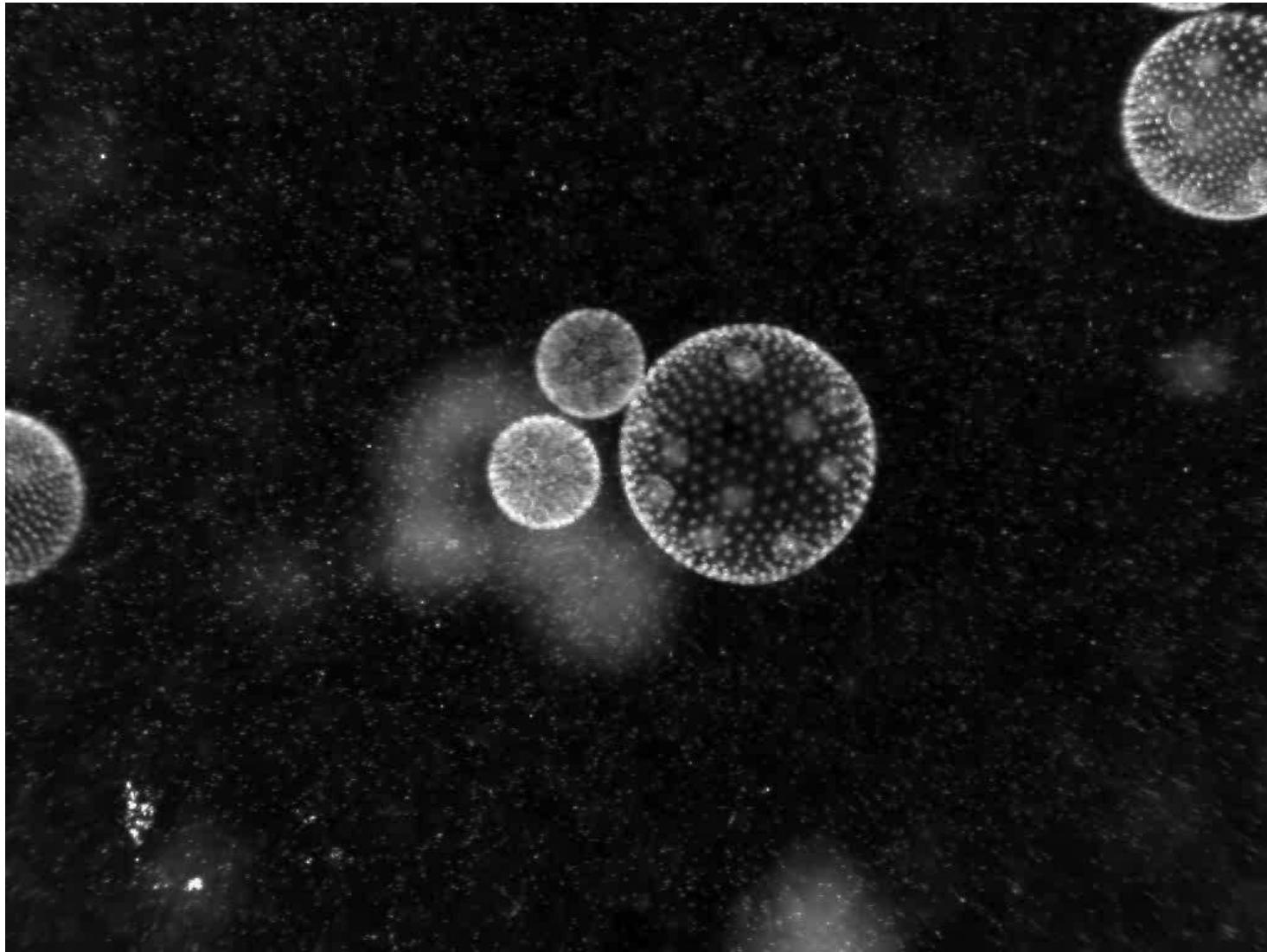




Volvox



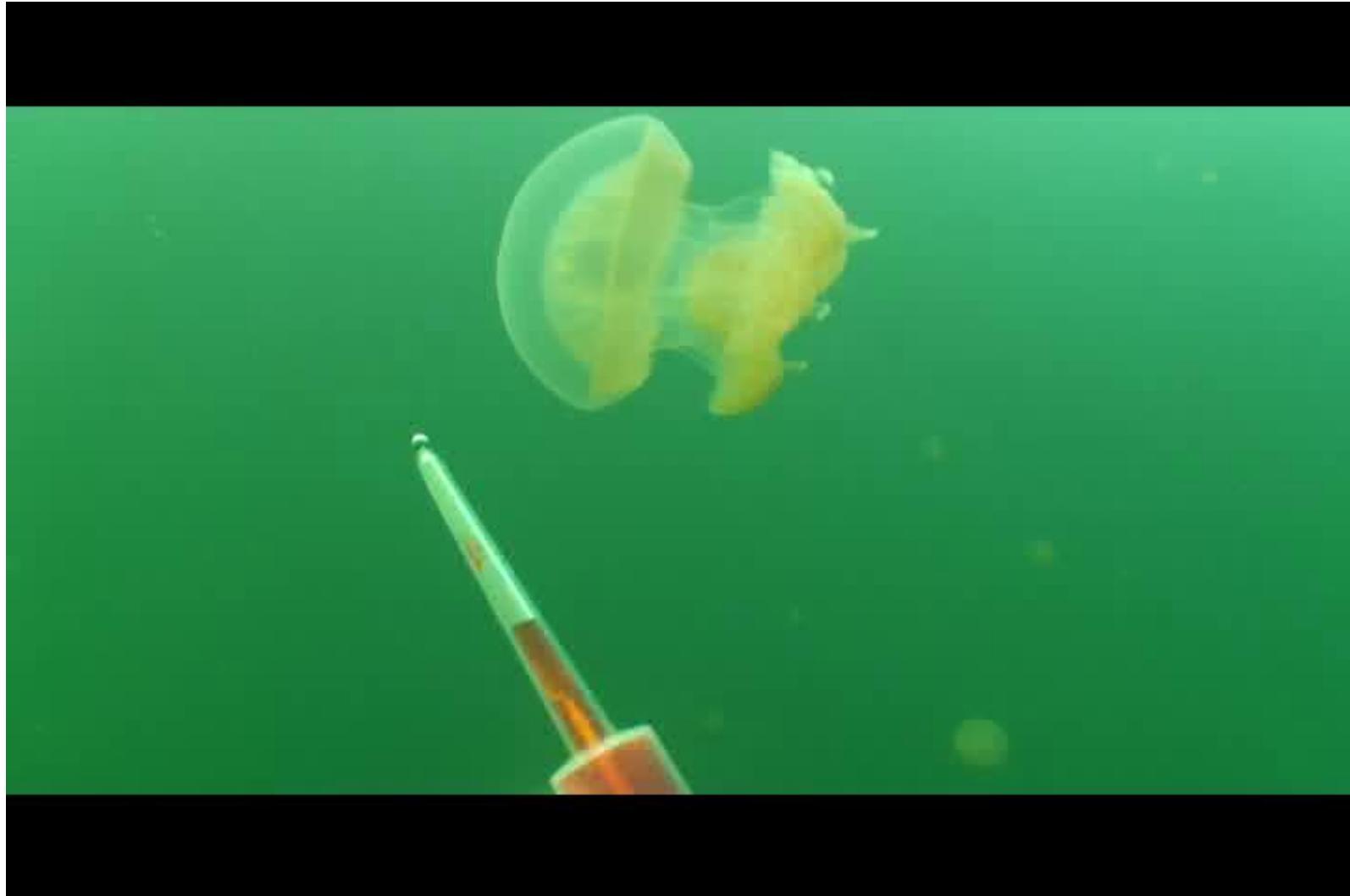
Dresher et al, PRL 105 (2010)
PNAS 108 (2011)

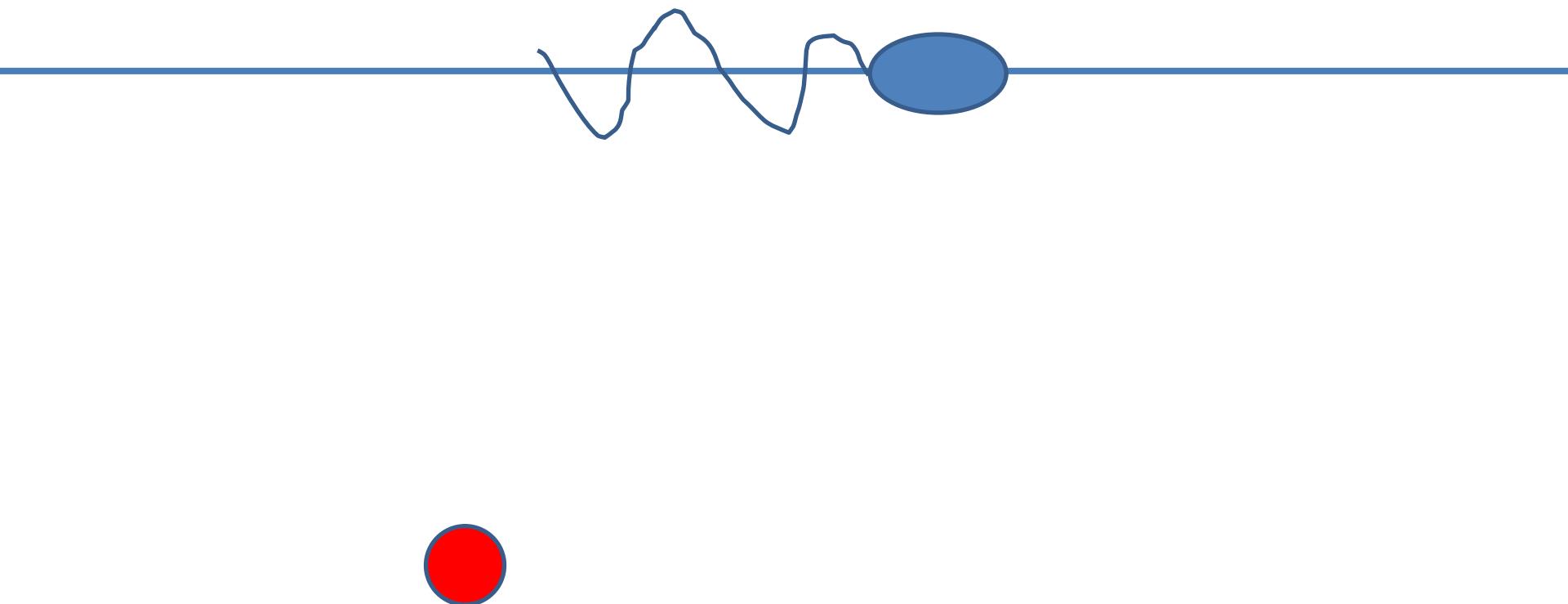


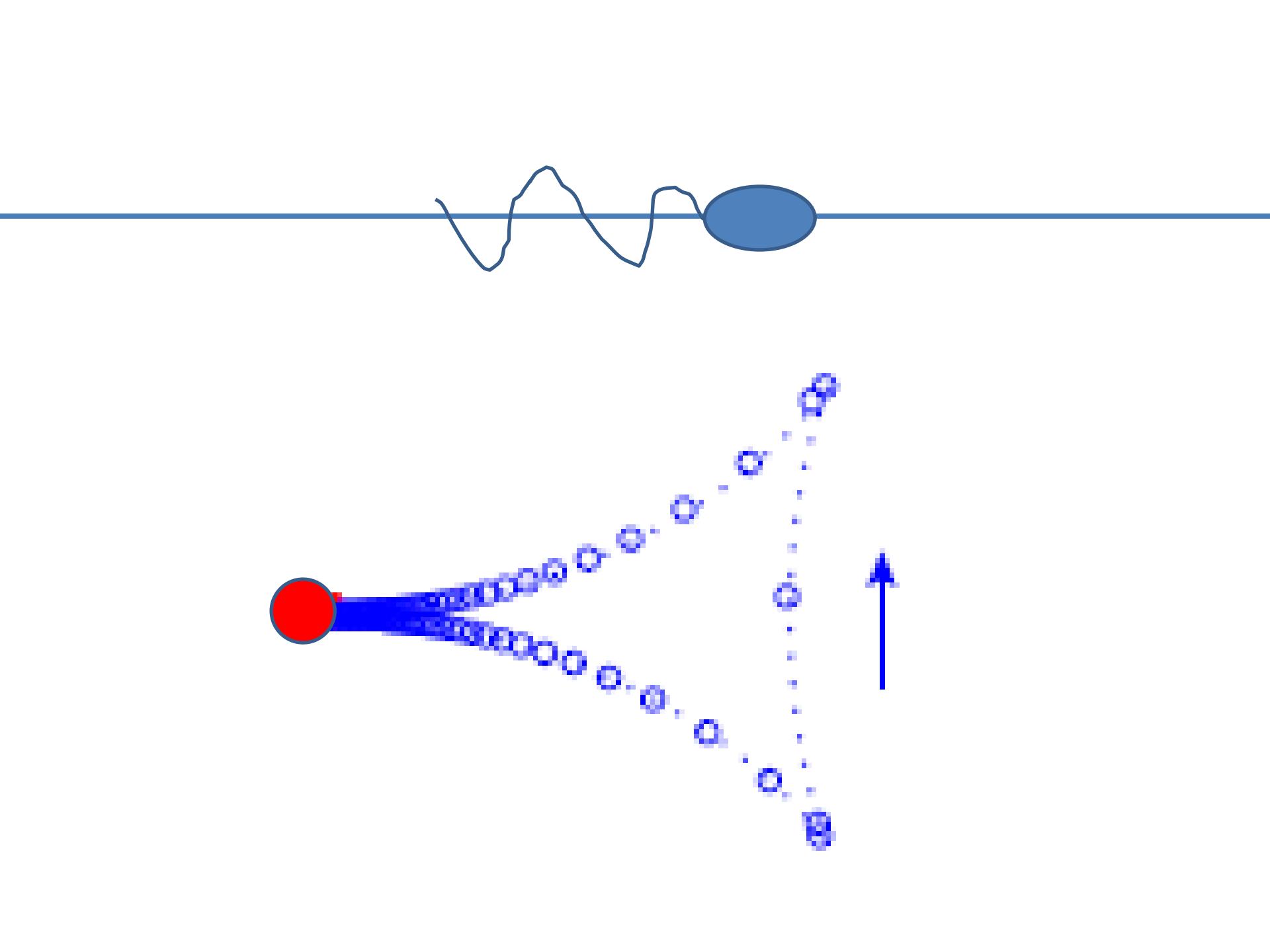
Volvox

Goldstein group, Cambridge

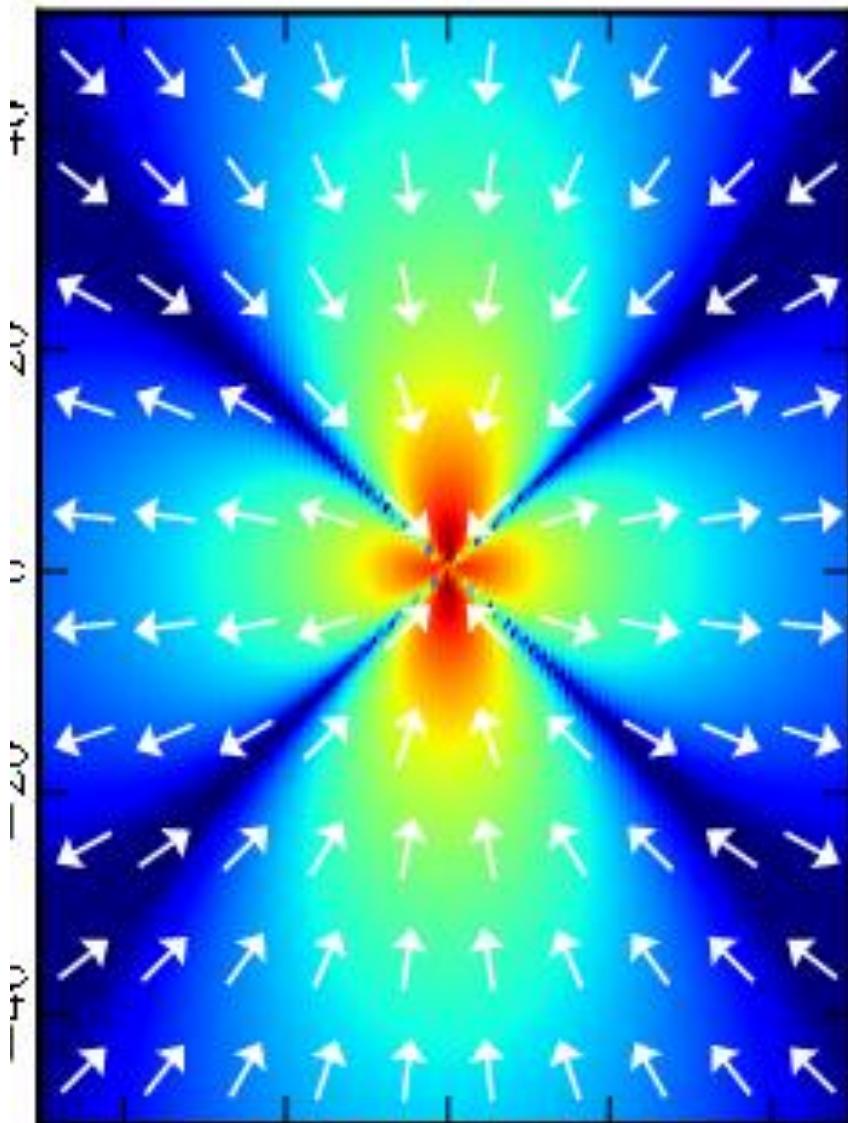
Do small swimmers mix the ocean? K. Katija, J.O. Dabiri, G. Subramanian,
A.M. Leshansky, L.M. Pismen, A.W. Visser





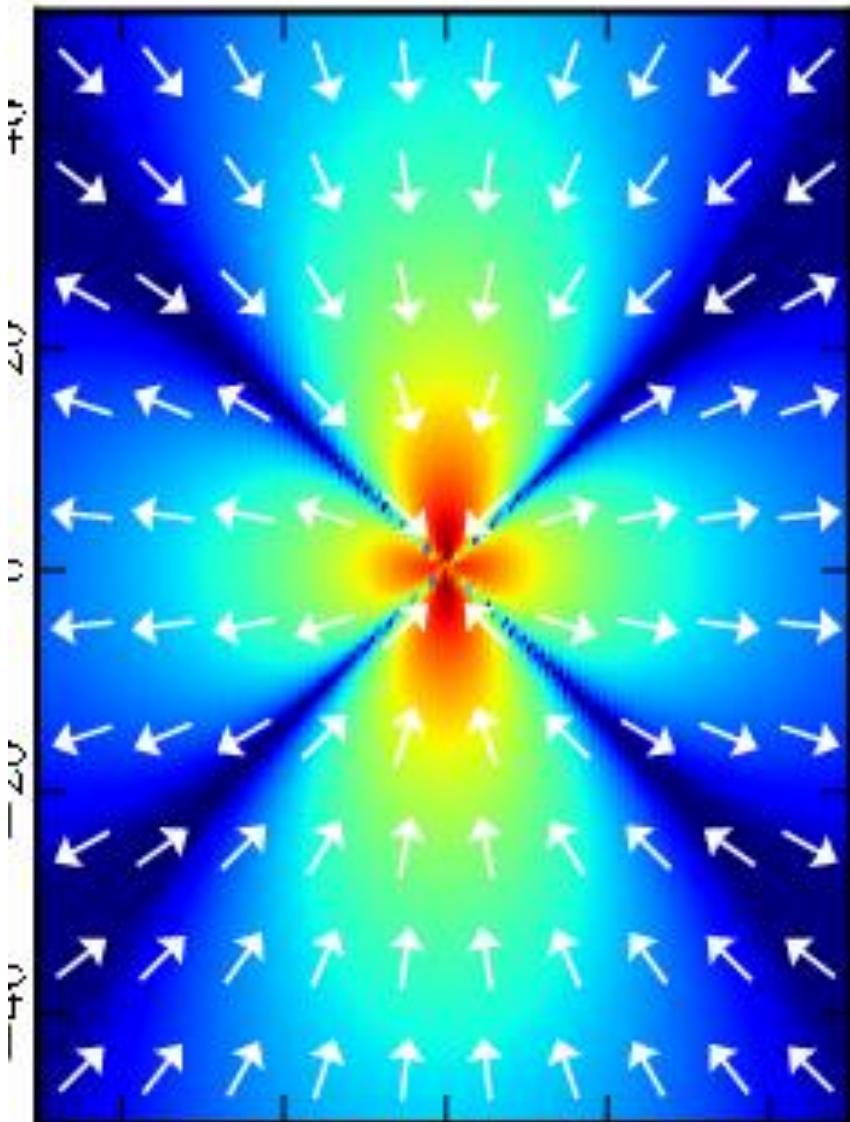


Multipole flow fields

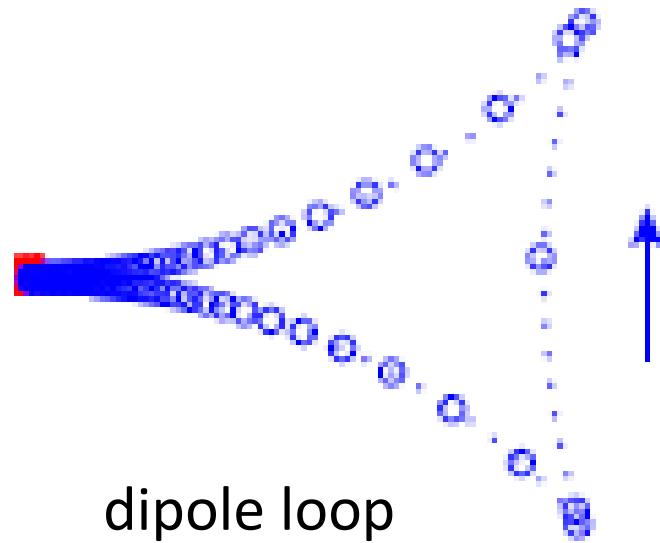


Dipole flow field

Multipole flow fields

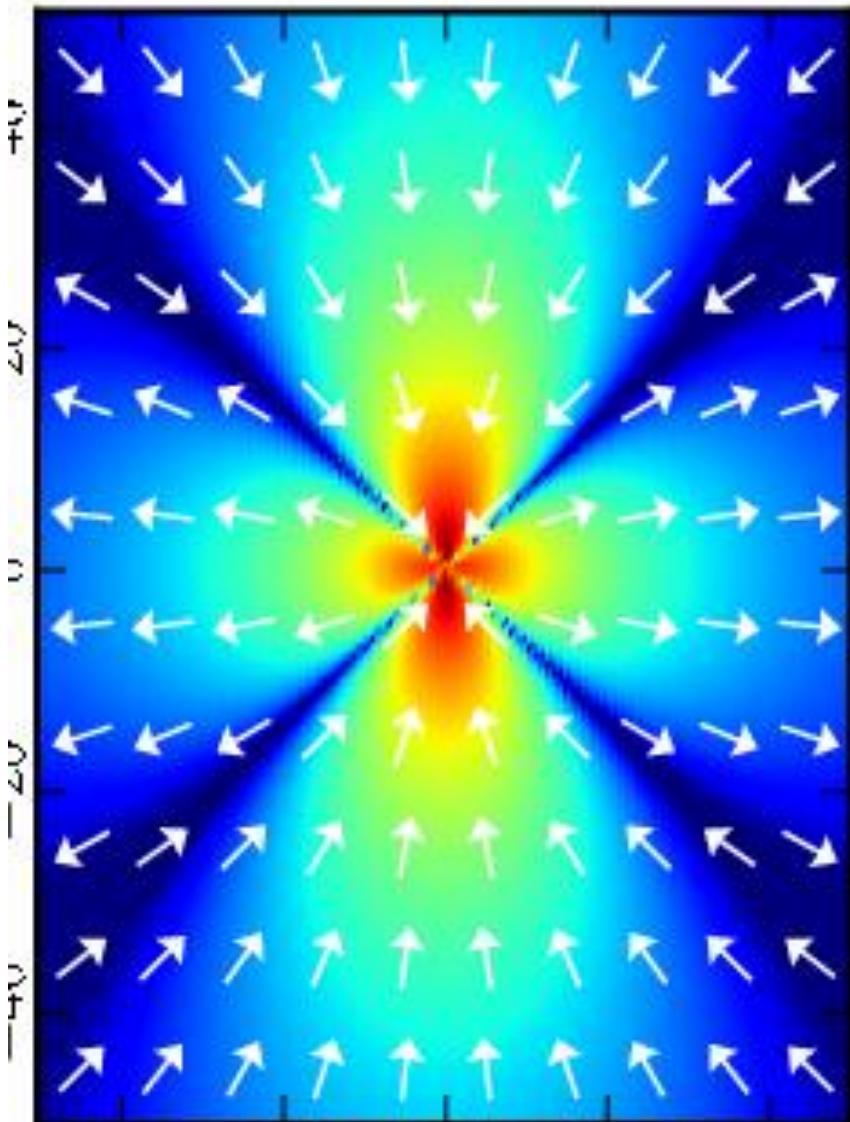


Dipole flow field

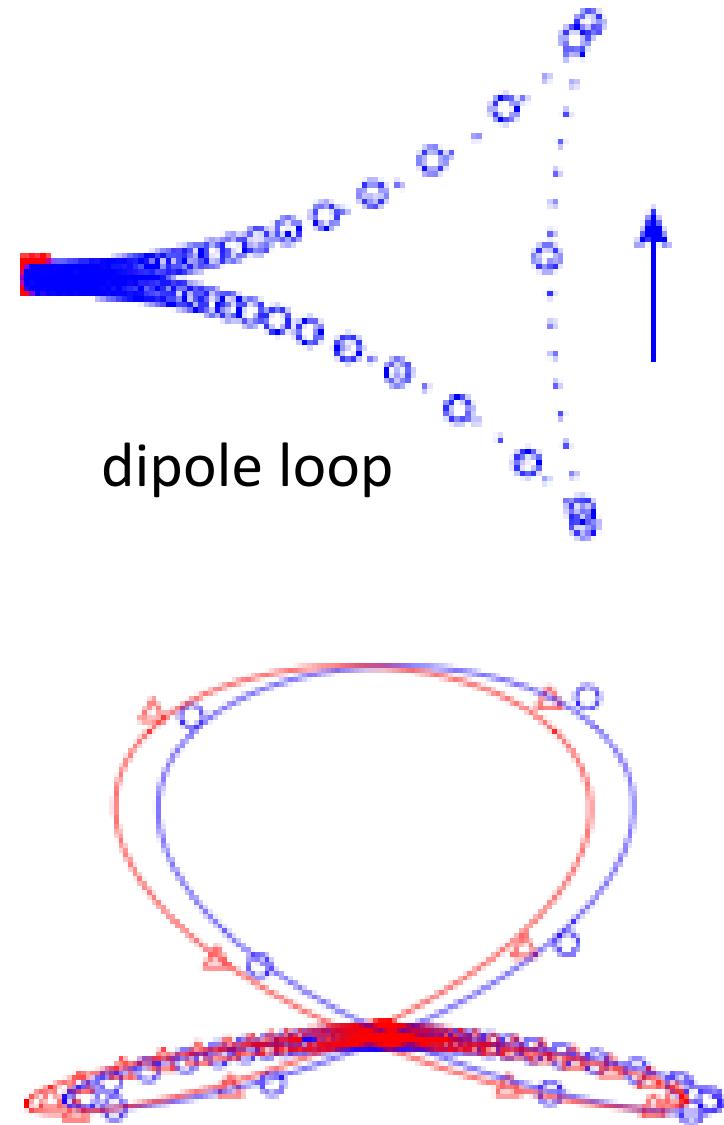


dipole loop

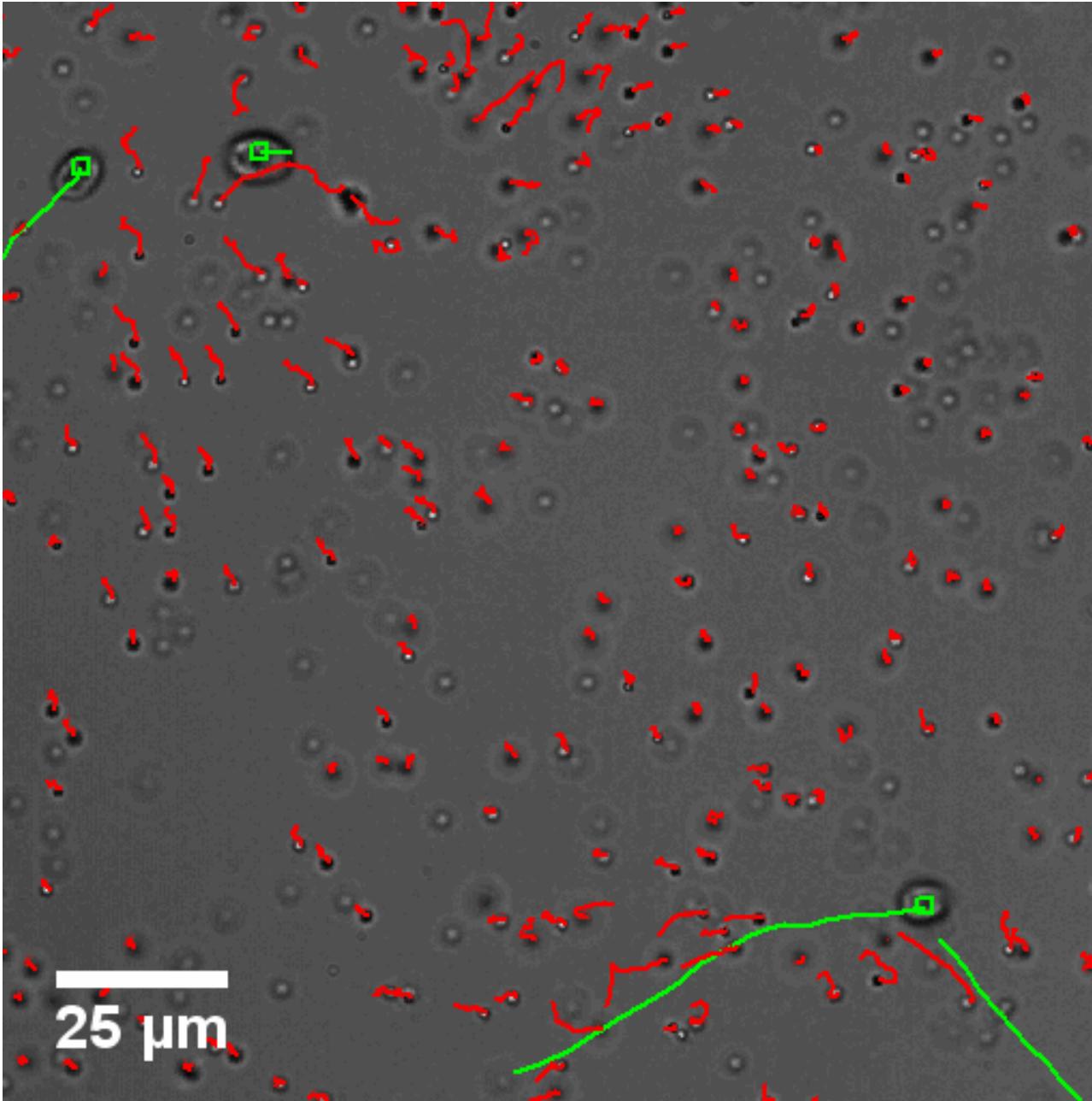
Multipole flow fields



Dipole flow field

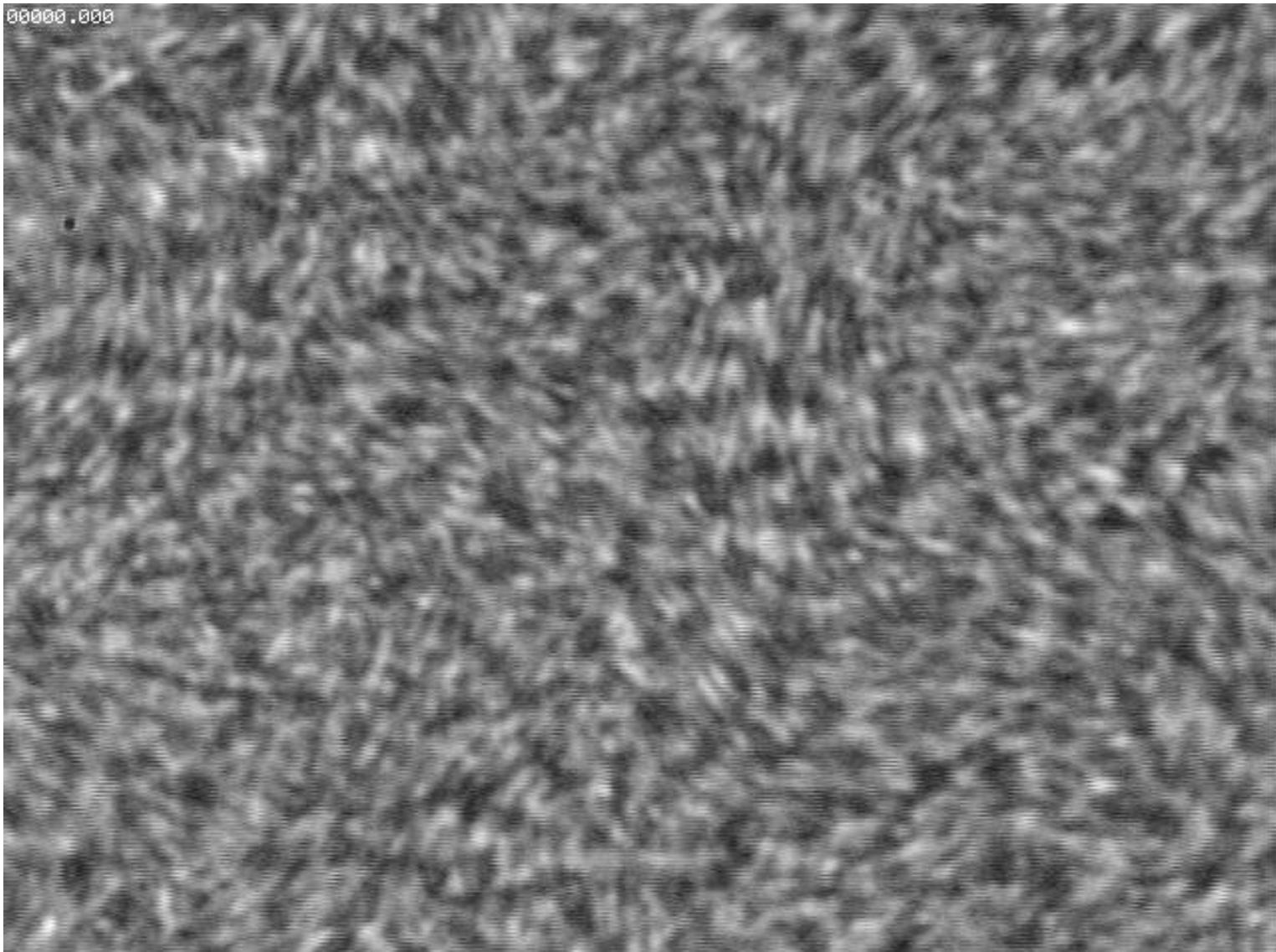


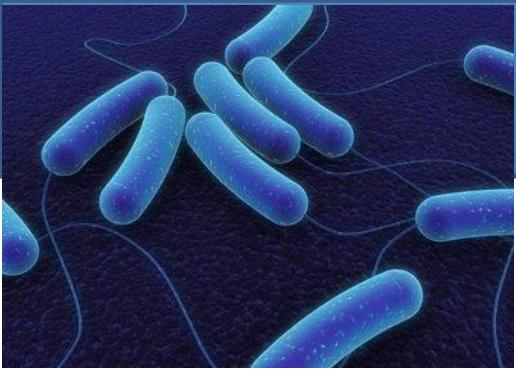
quadrupole loop



Guasto
website

Bacteria



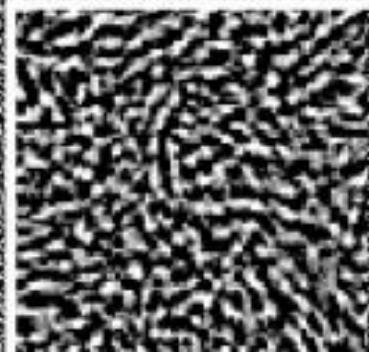


Bacteria

vorticity

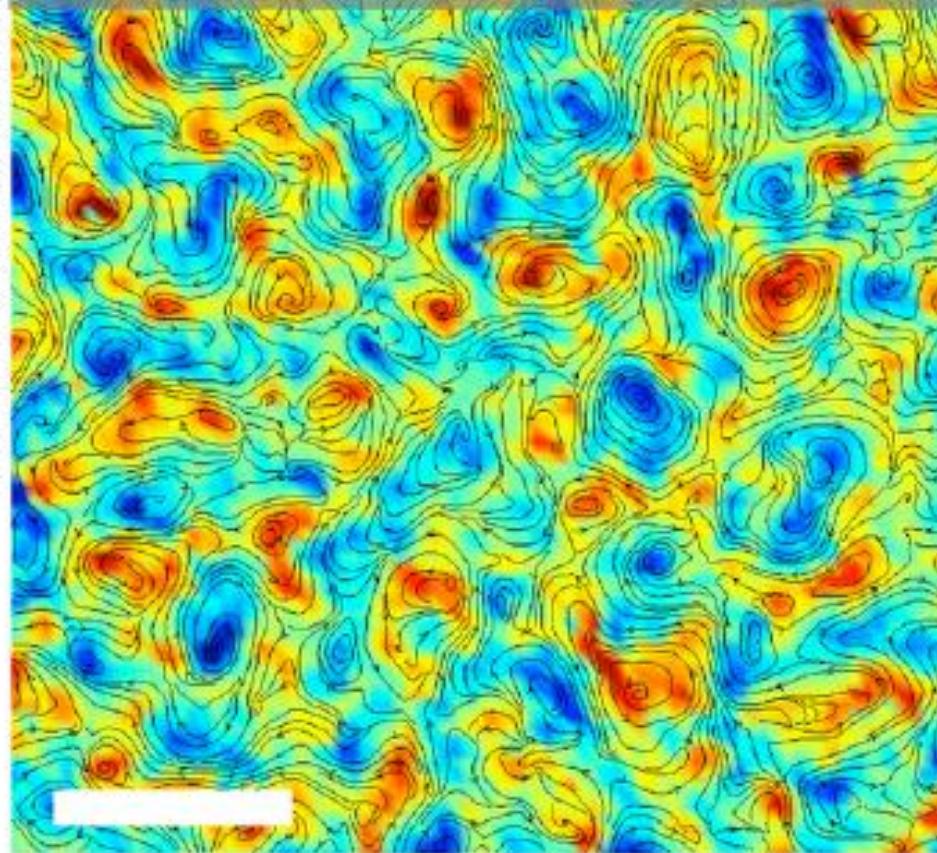
A

B. subtilis (quasi 2D)

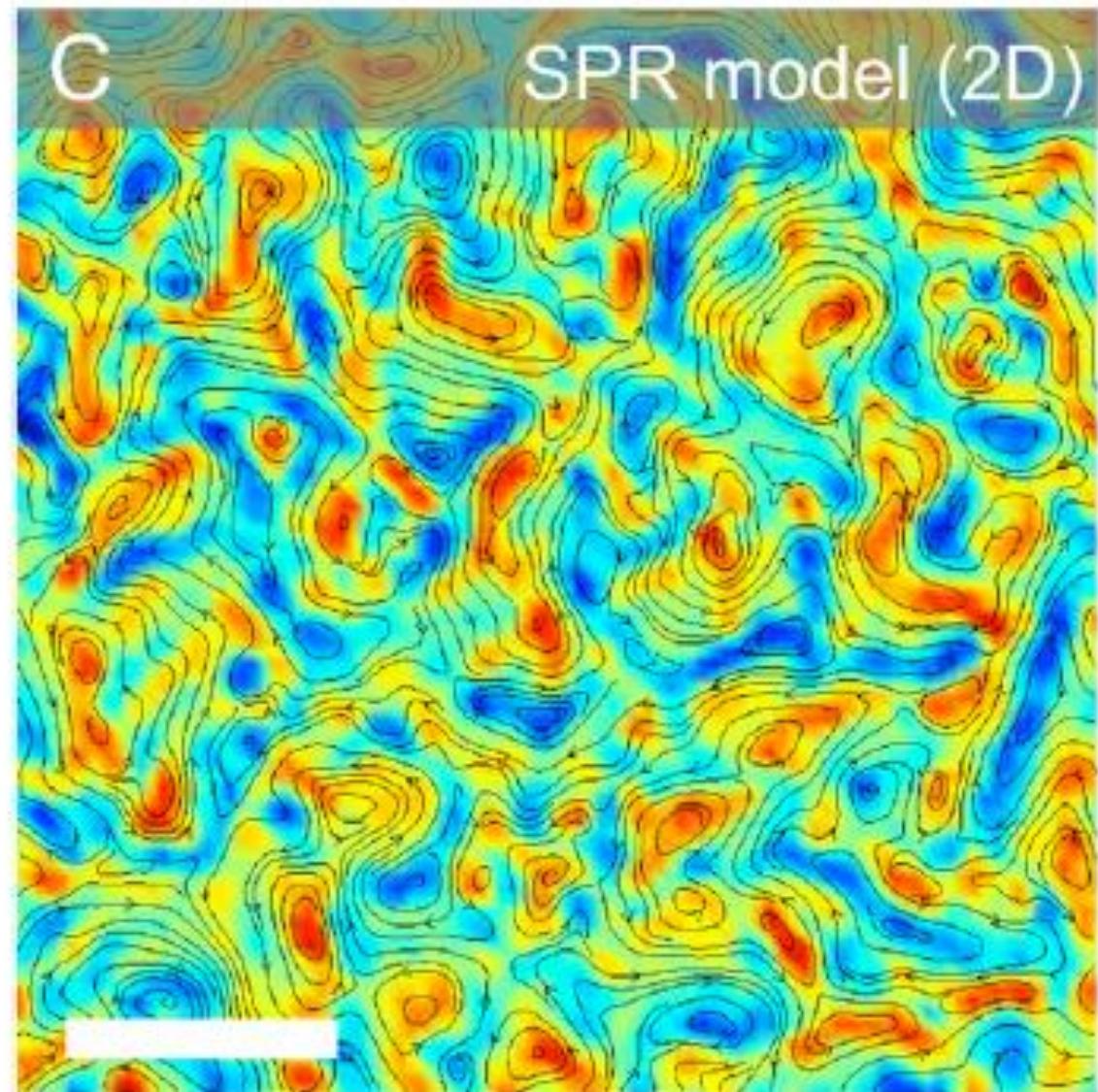


B

B. subtilis (quasi 2D)

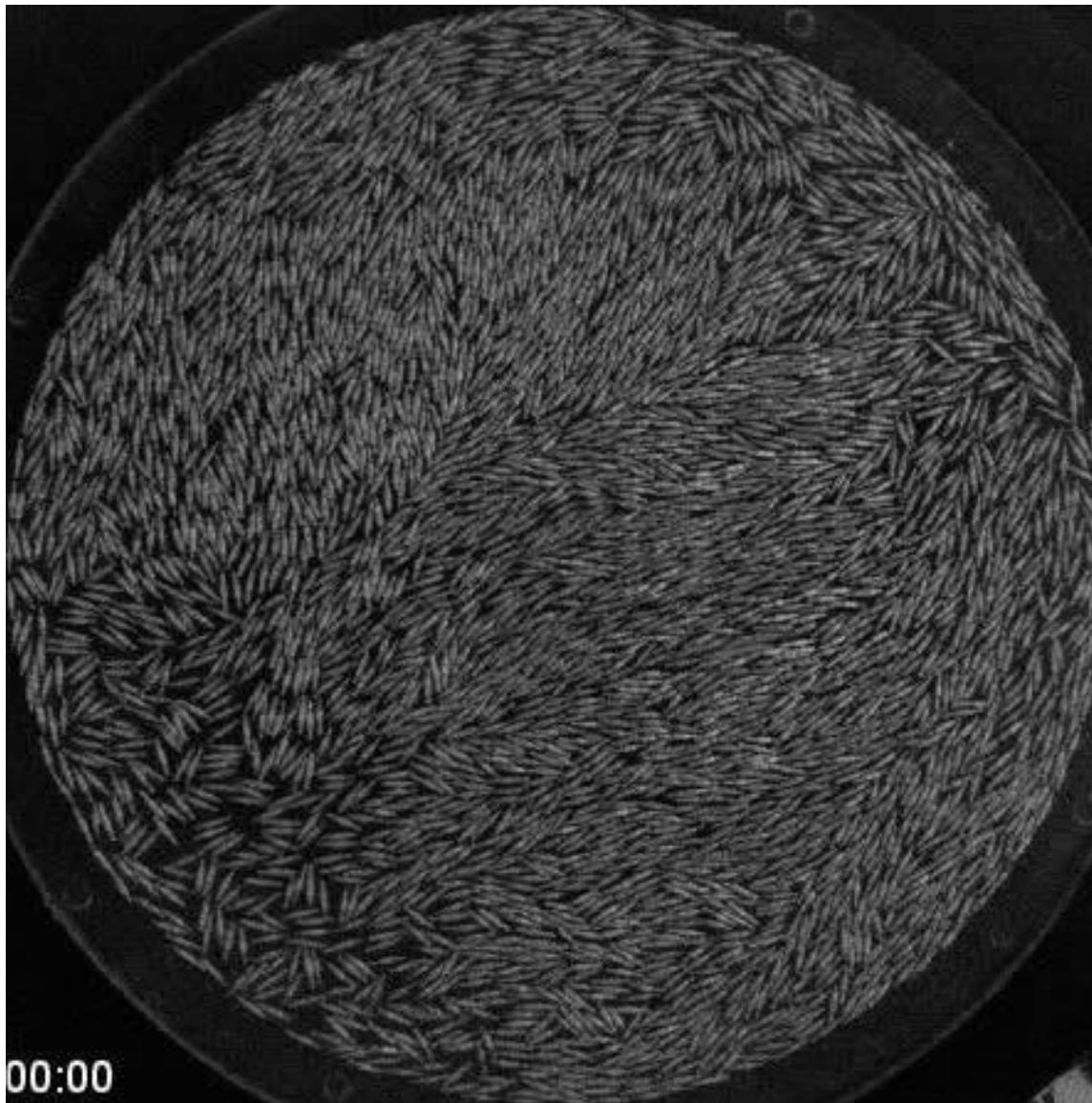


Discrete simulations

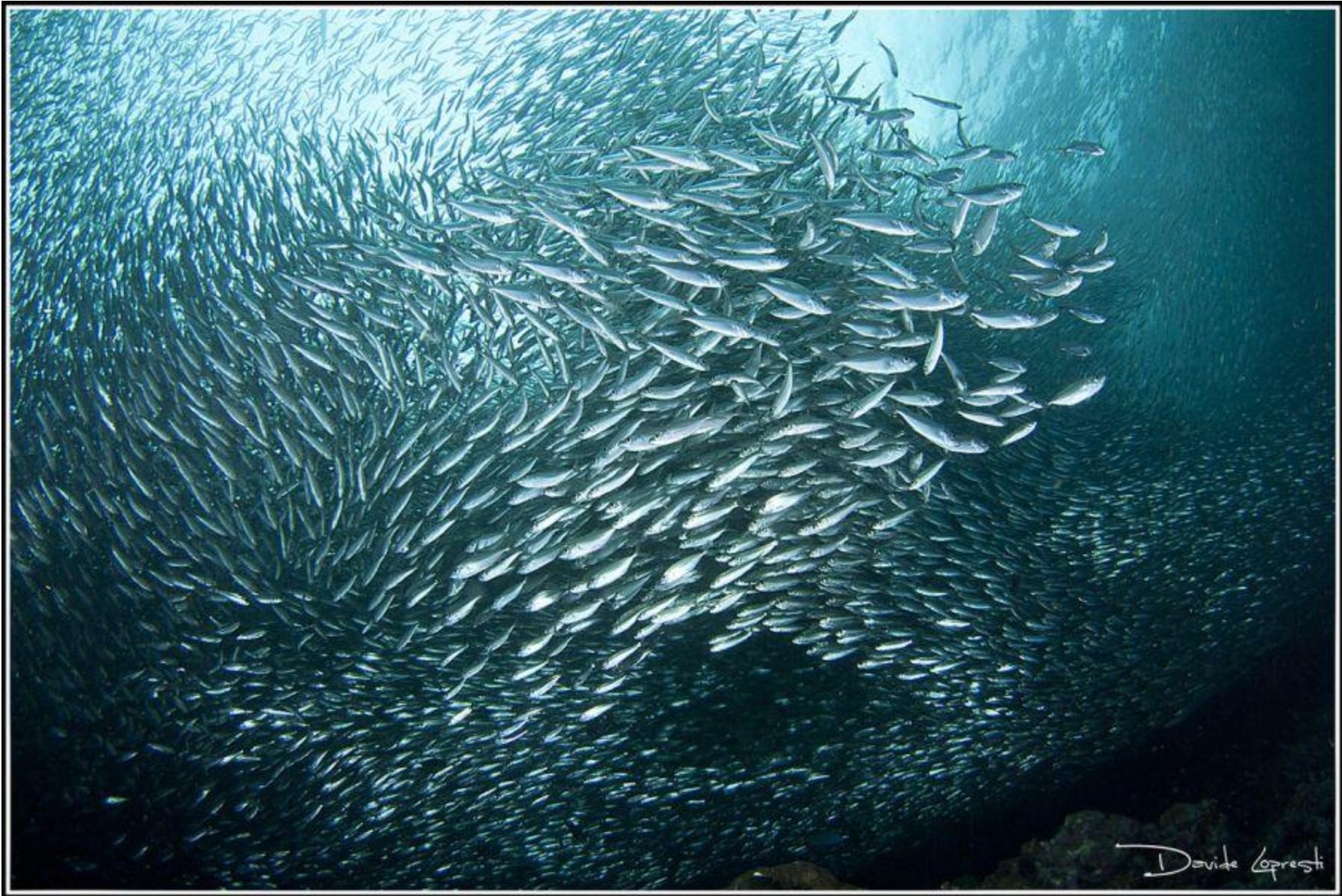


Wensink, Dunkel, Heidenreich,
Dresher, Goldstein, Lowen,
Yeomans, PNAS 2012

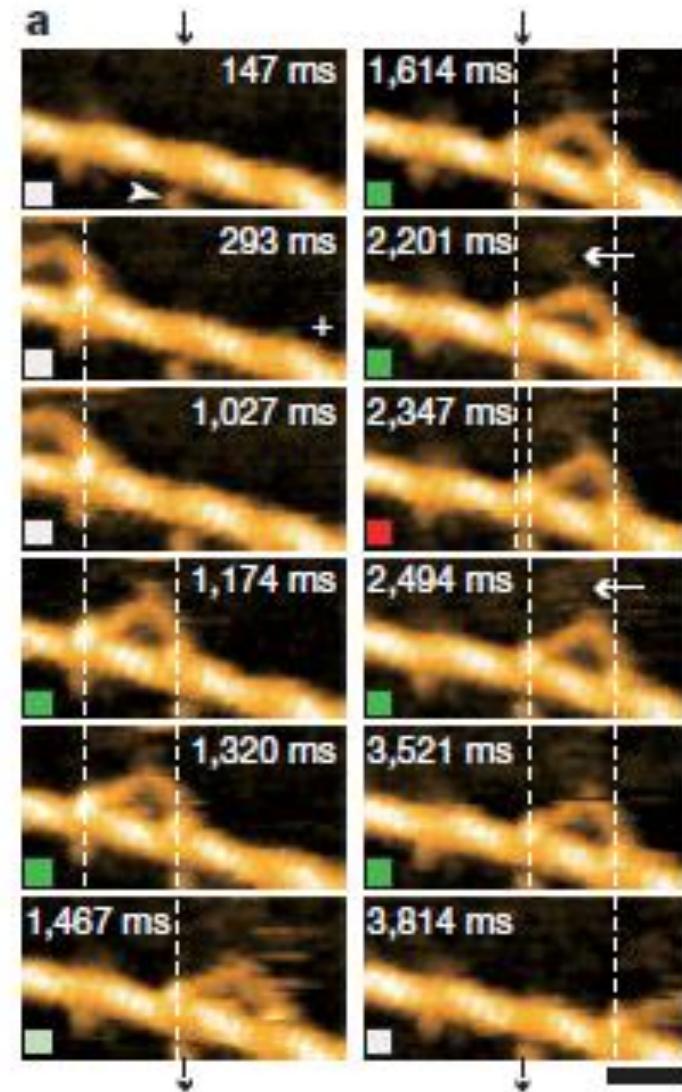
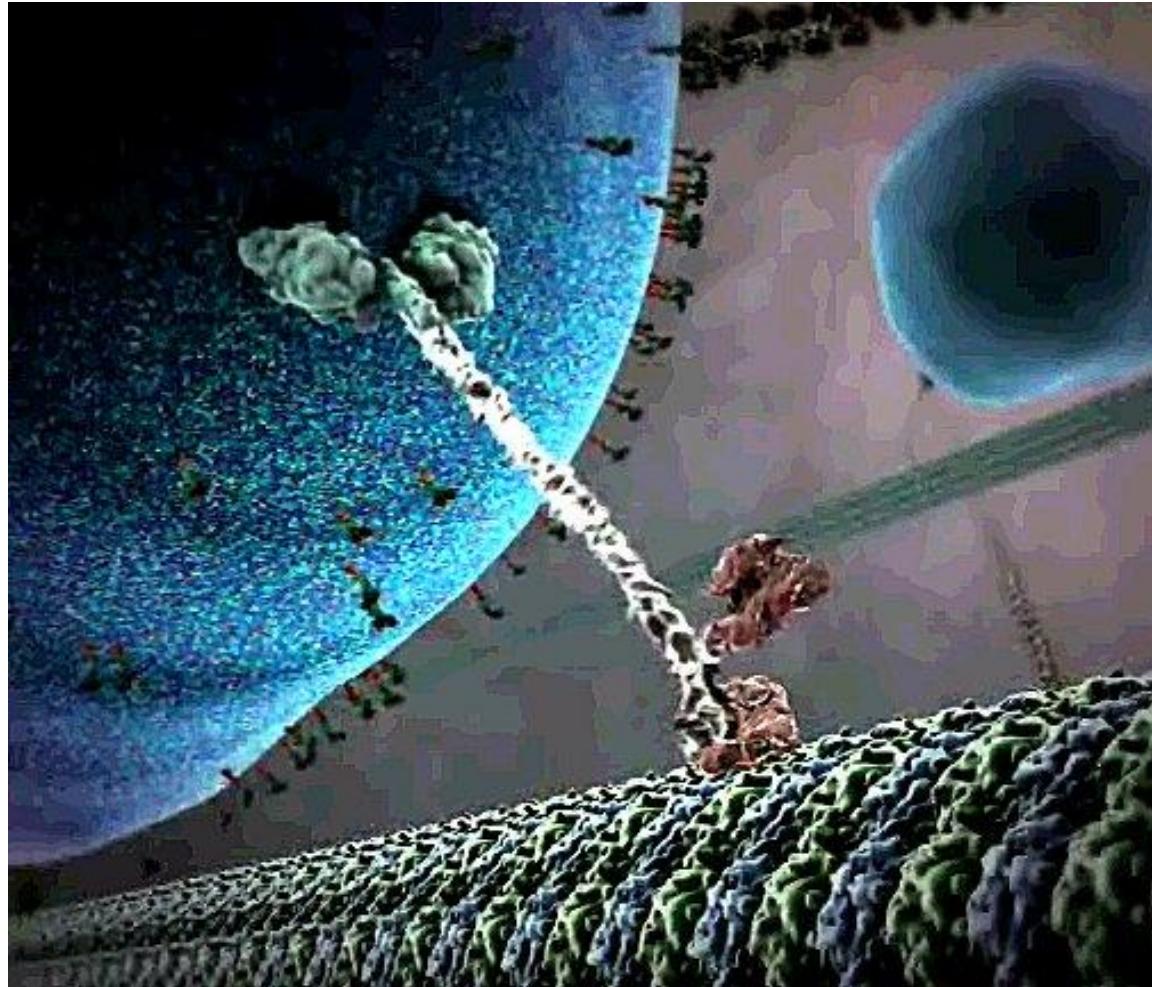
Driven grains



Fish?

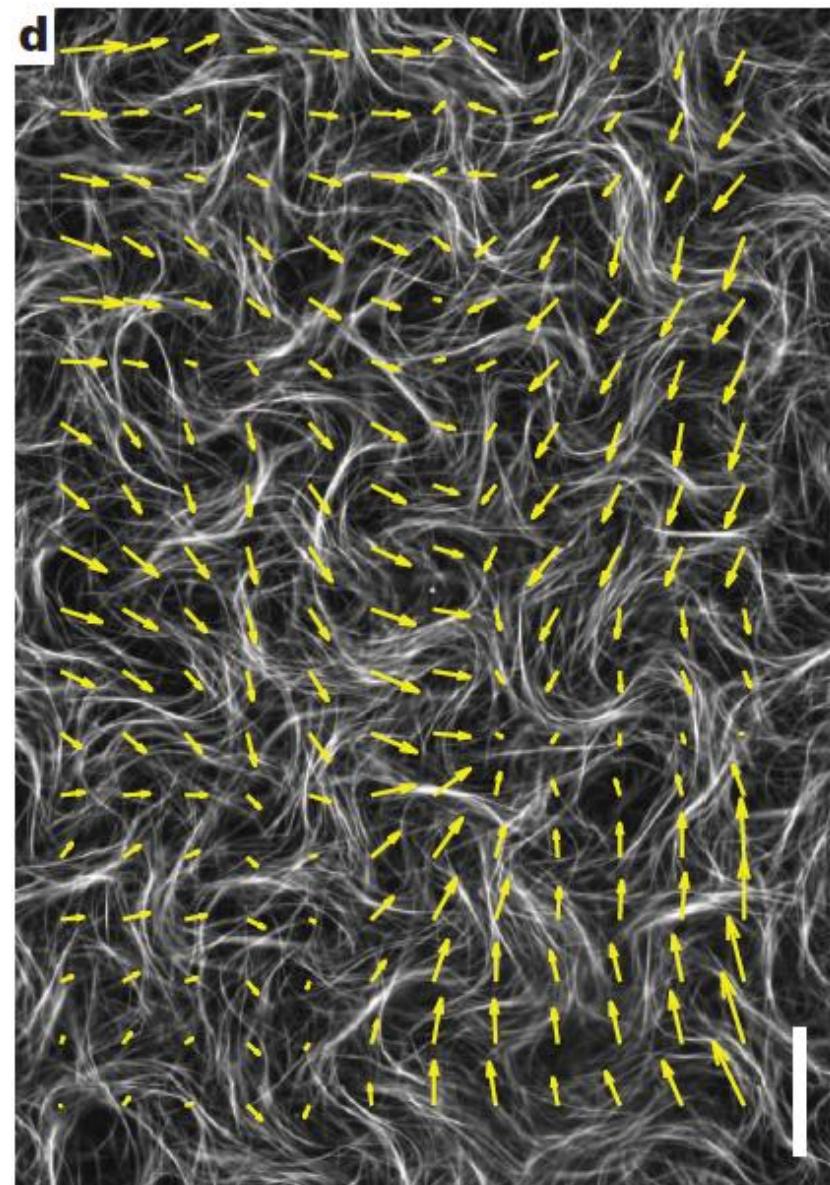
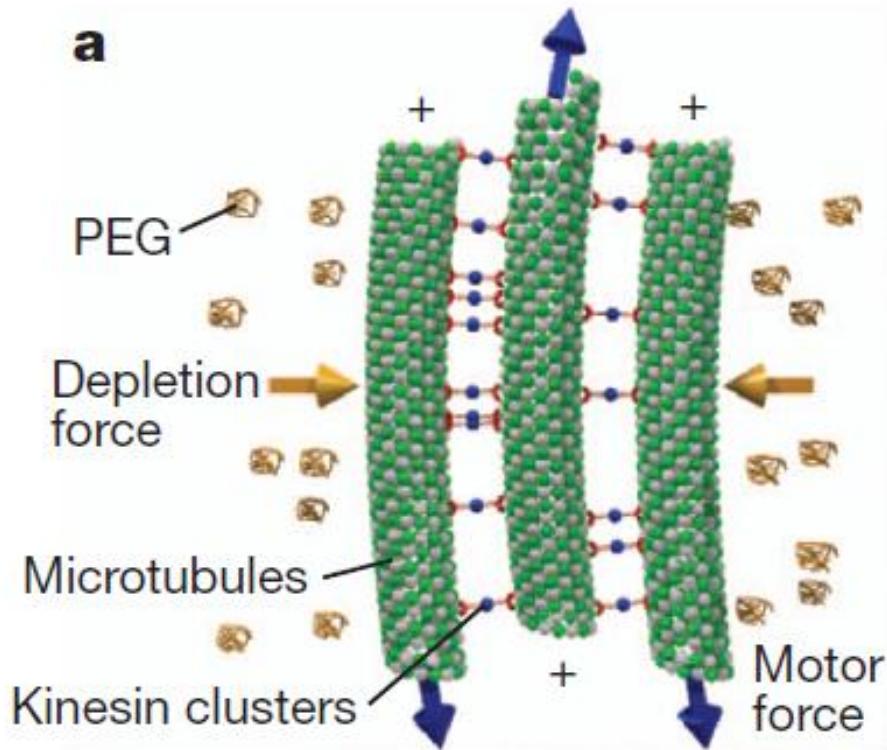


Molecular motors



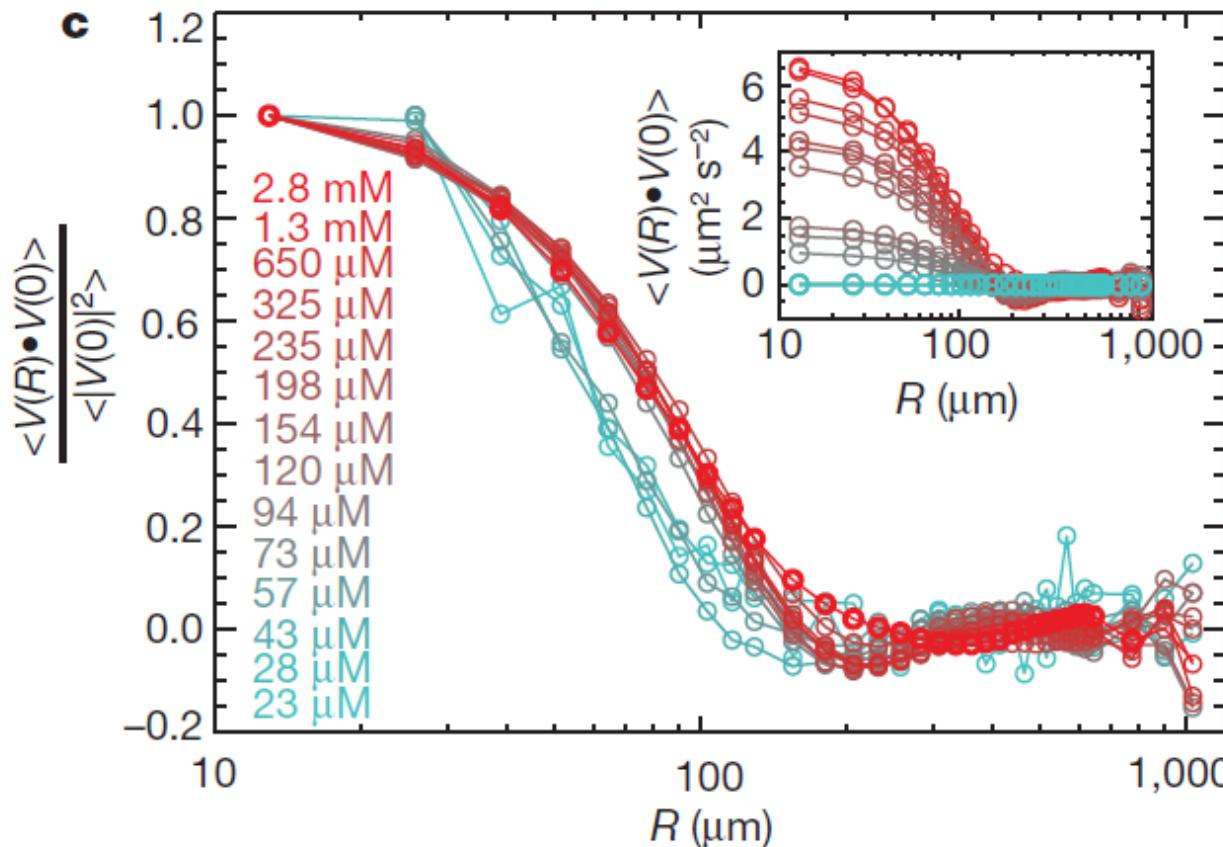
Inner life of a cell You tube

Molecular motors



Sanchez, Chen, DeCamp, Heymann, Dogic,
Nature 2012

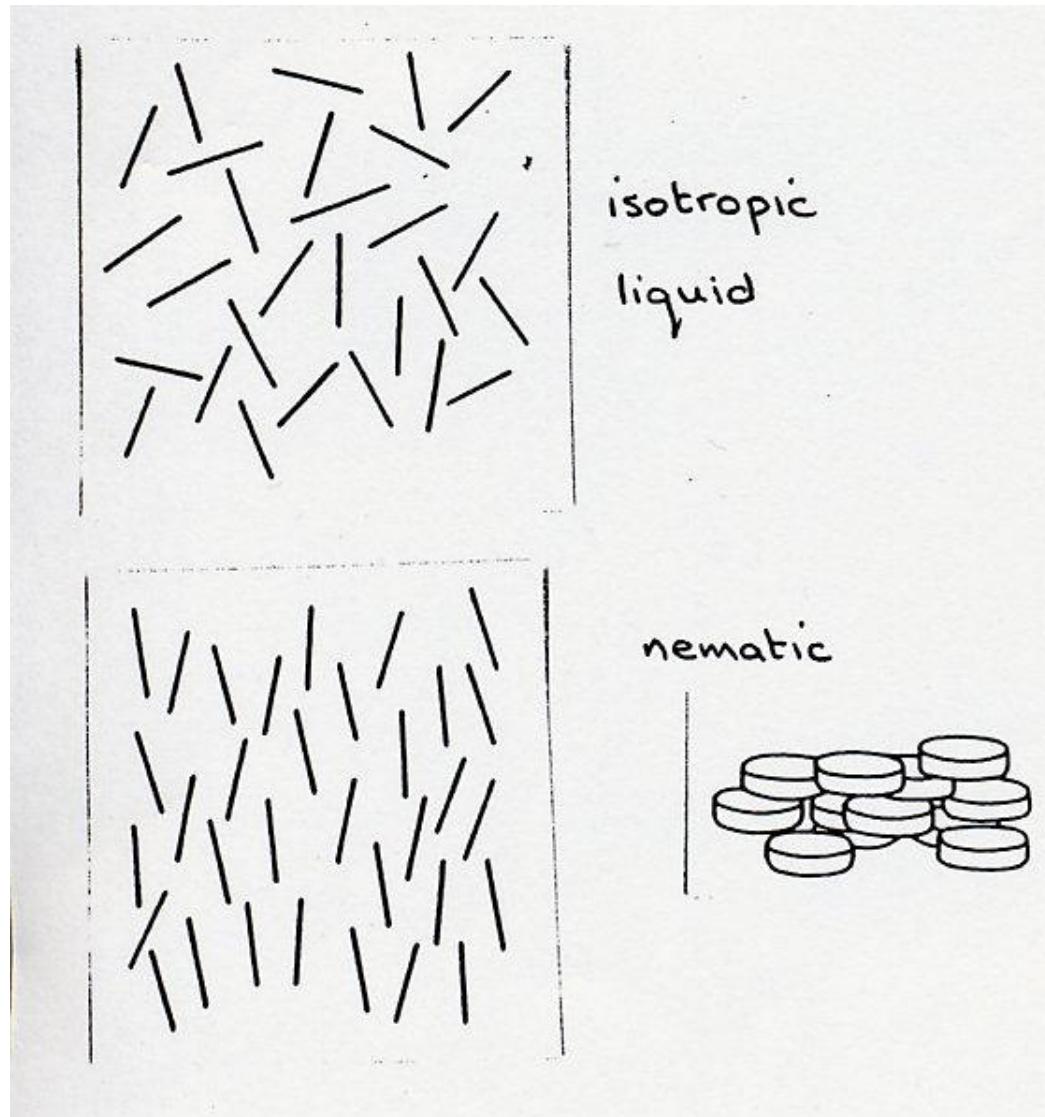
Molecular motors



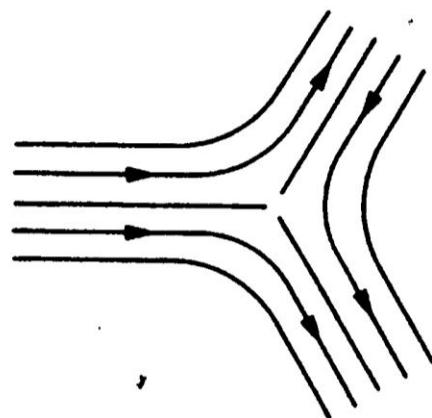
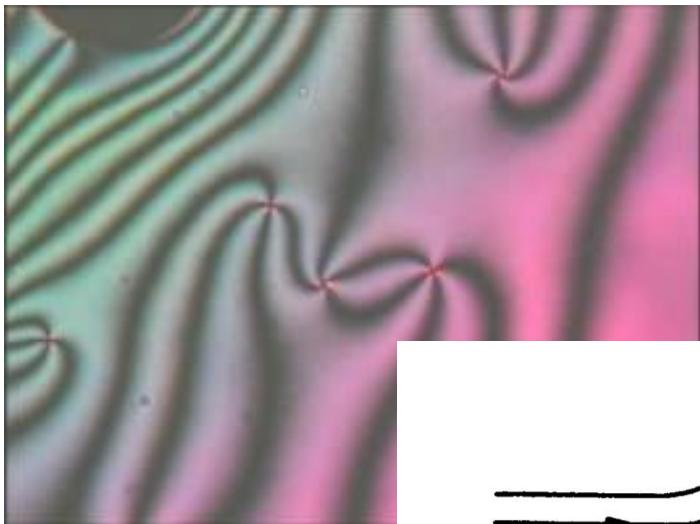
Velocity increases with activity

Length scale controlling decay of $\langle vv \rangle$ independent of activity

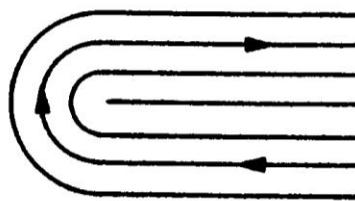
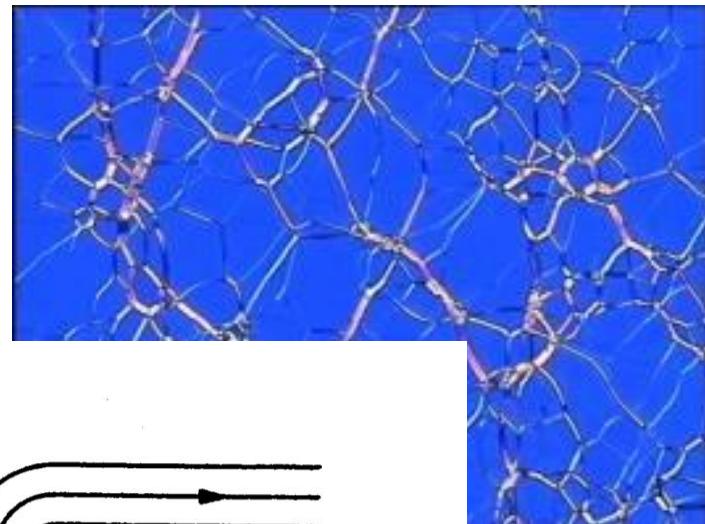
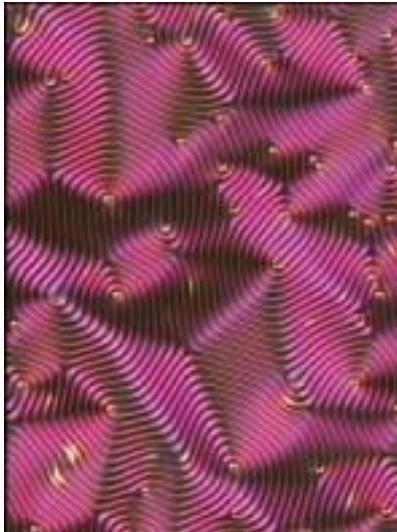
Liquid crystals



Topological defects



$$m = -\frac{1}{2}$$



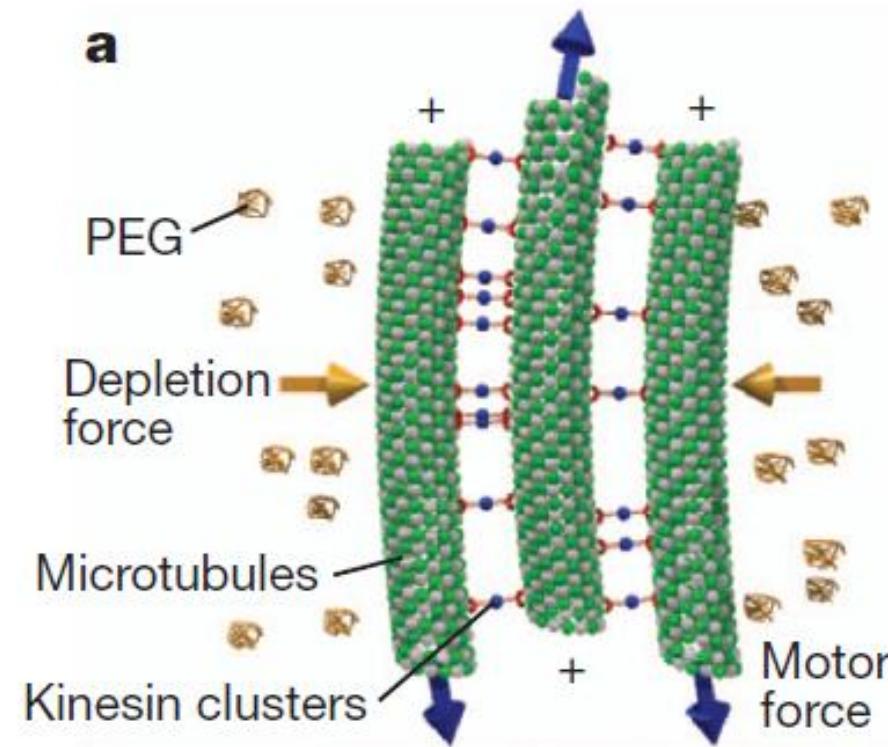
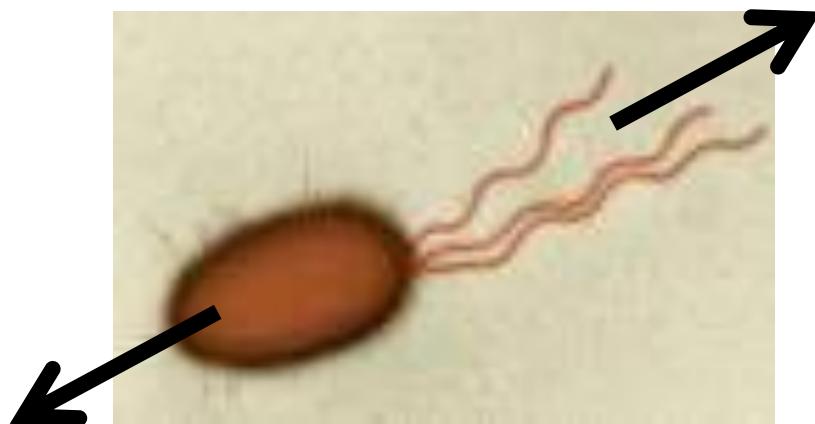
$$m = +\frac{1}{2}$$



Continuum equations of active nematics

Liquid crystal equations of motion +
additional term in the stress tensor

Consequence of a dipolar source term



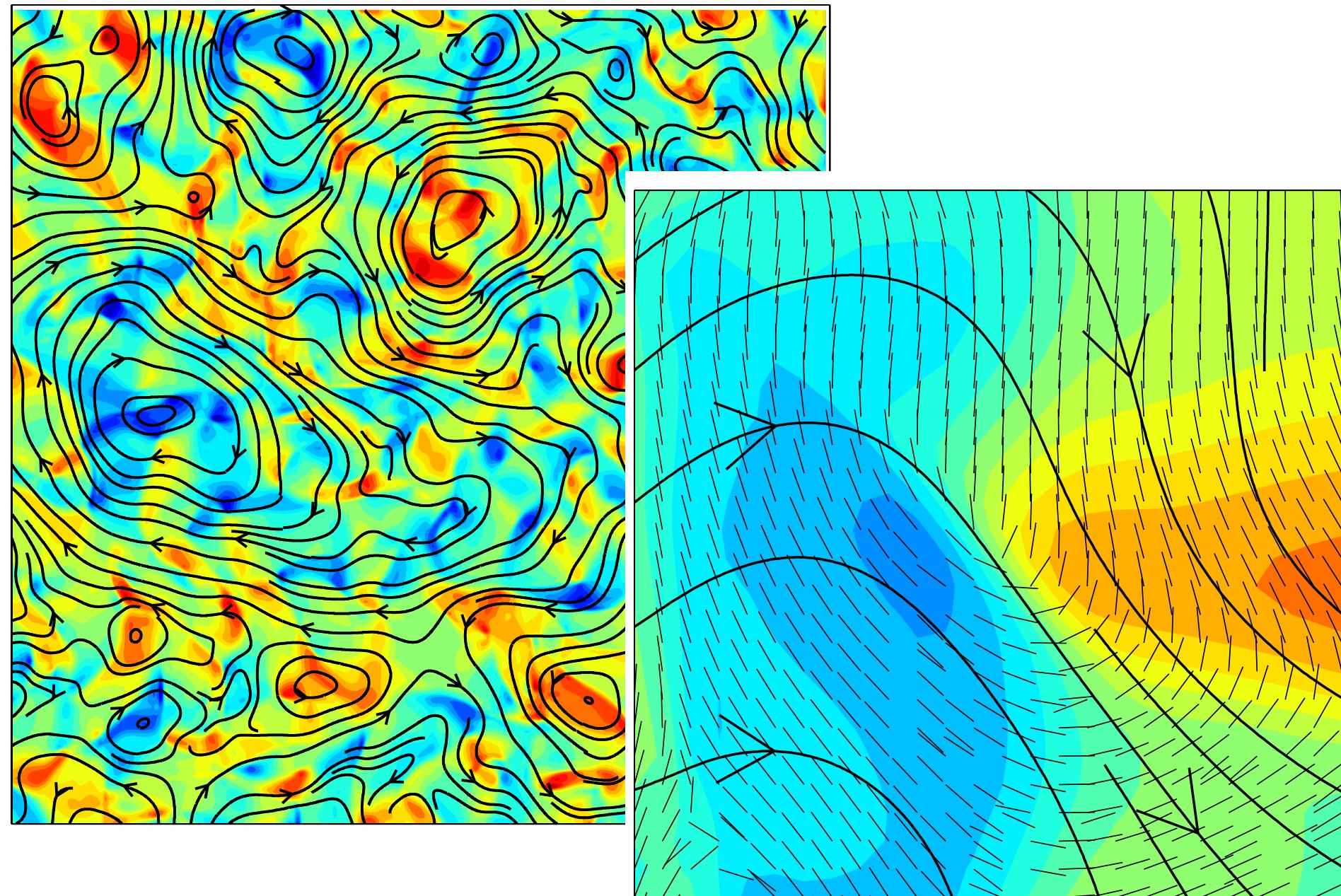
Continuum equations of active nematics

Liquid crystal equations of motion +
additional term in the stress tensor

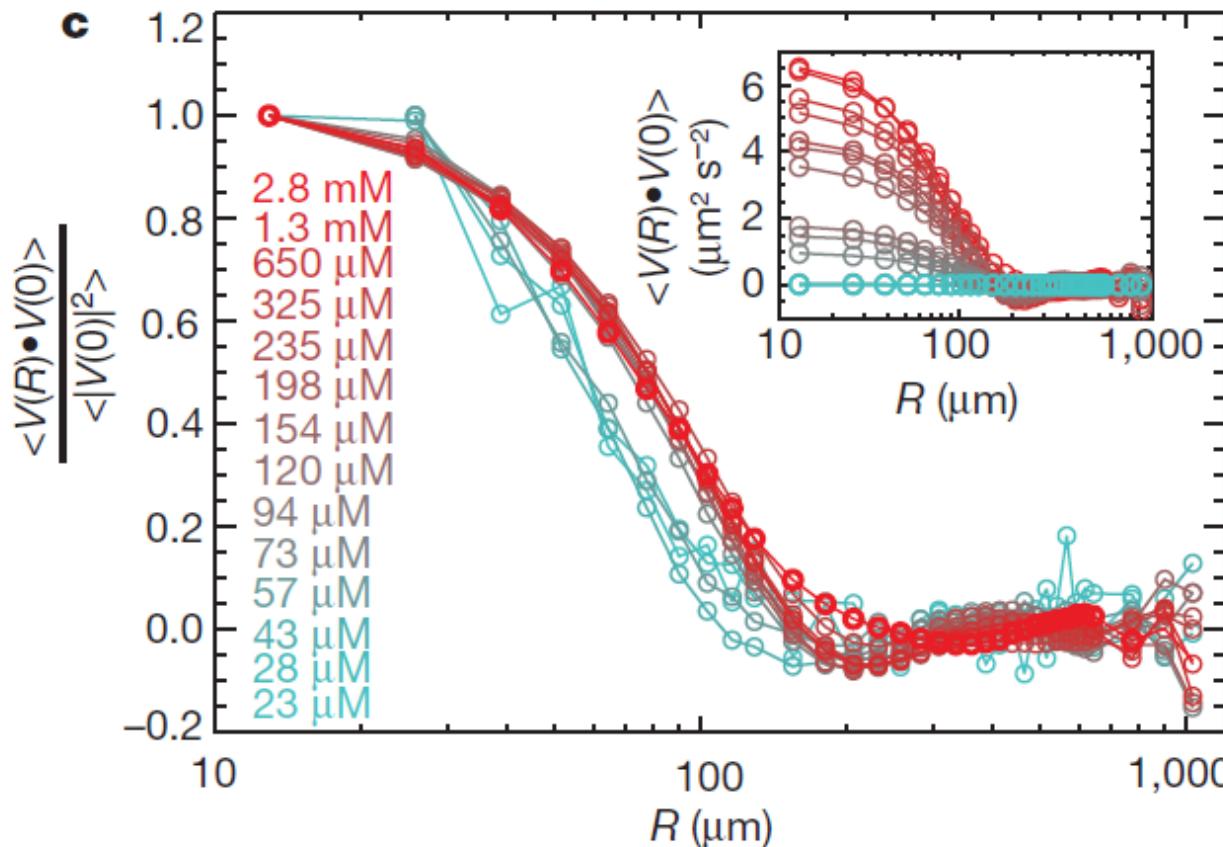
Gradients in the order parameter field induce a flow

Nematic state is unstable

Active turbulence in extensile suspensions



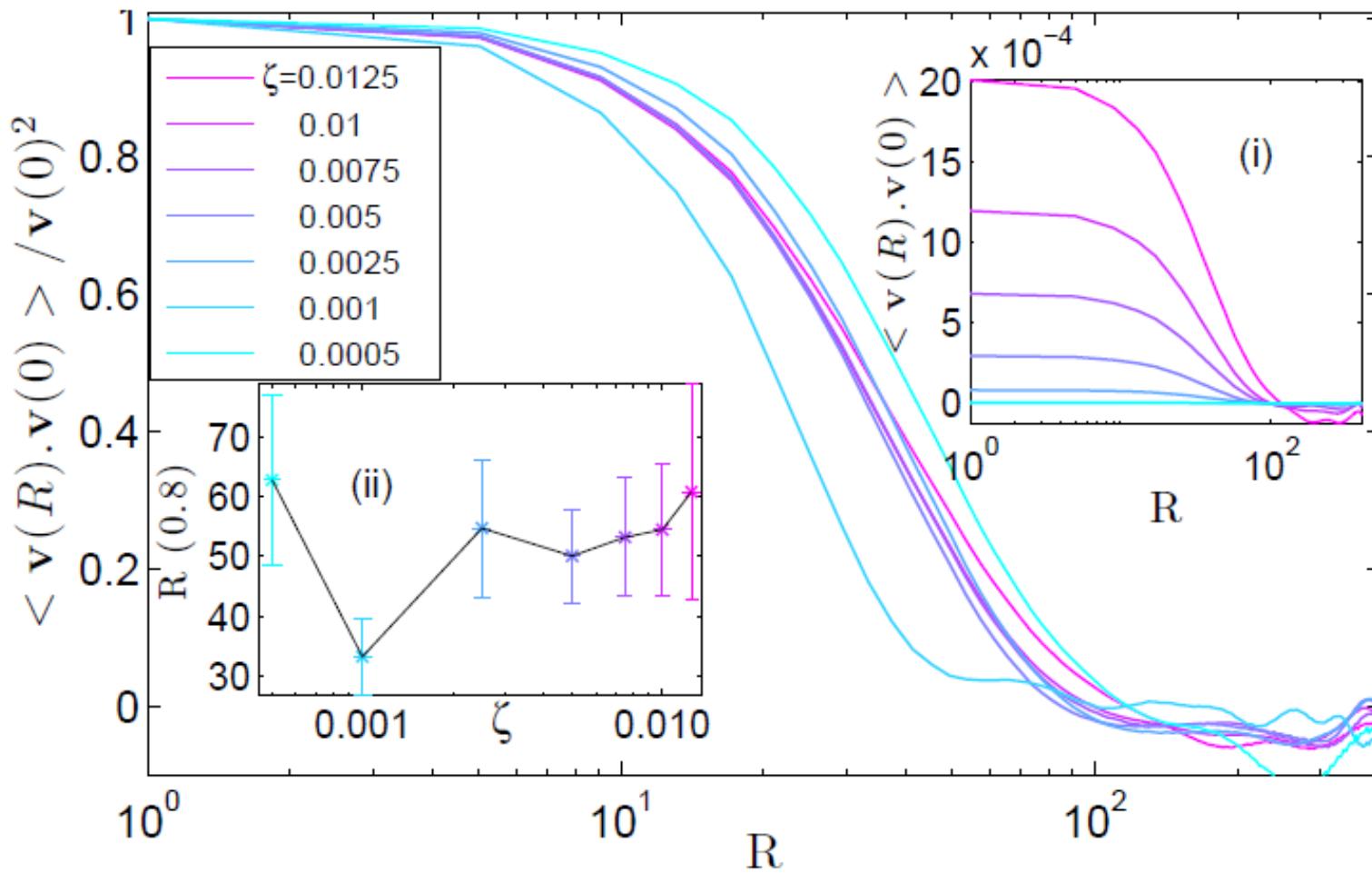
Molecular motors



Velocity increases with activity

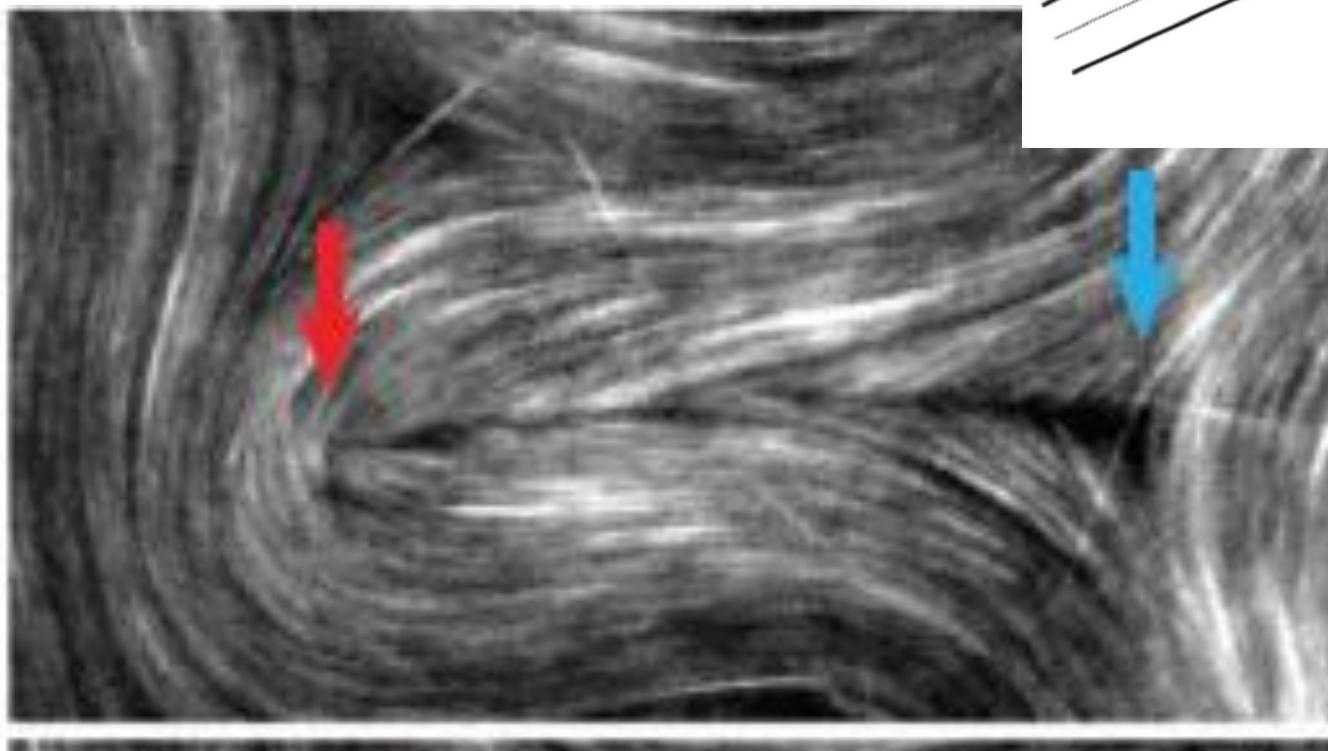
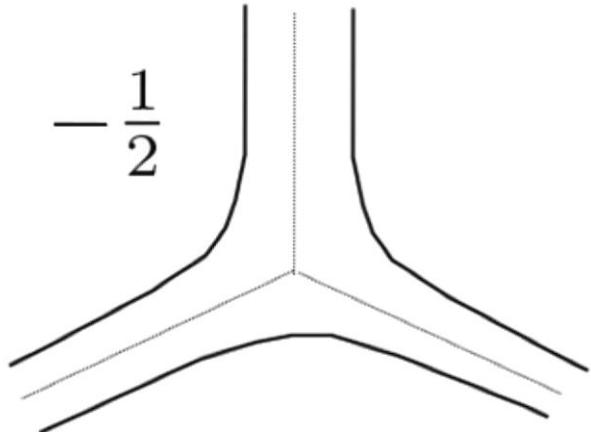
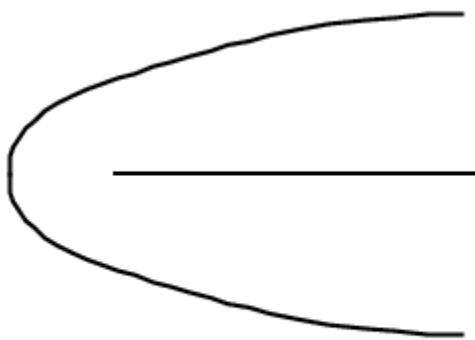
Length scale controlling decay of $\langle vv \rangle$ independent of activity

$\langle vv \rangle$: simulations



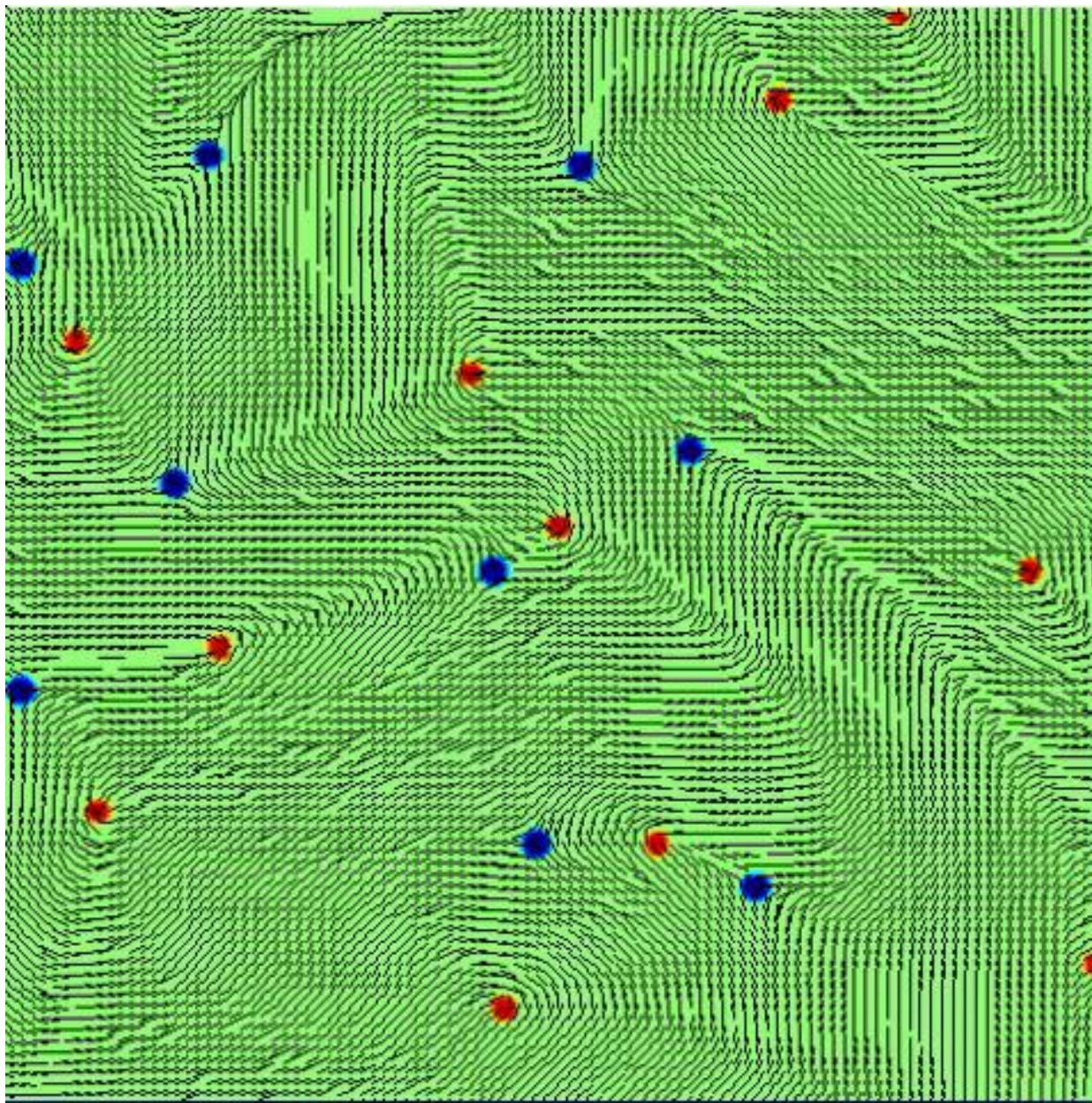
Topological defects in active systems

$\frac{1}{2}$



microtubule bundles driven by
molecular motors

L. Giomi, M.J. Bowick, Ma Xu, M.C. Marchetti, PRL 110, 228101
Sanchez, Chen, DeCamp, Heymann, Dogic, Nature 2012



Defect dynamics: steady state

$$\alpha \frac{\zeta}{K} = \beta \frac{\sigma \zeta \ell Q n^2}{\mu}$$

ℓ : independent of activity

Active nematics

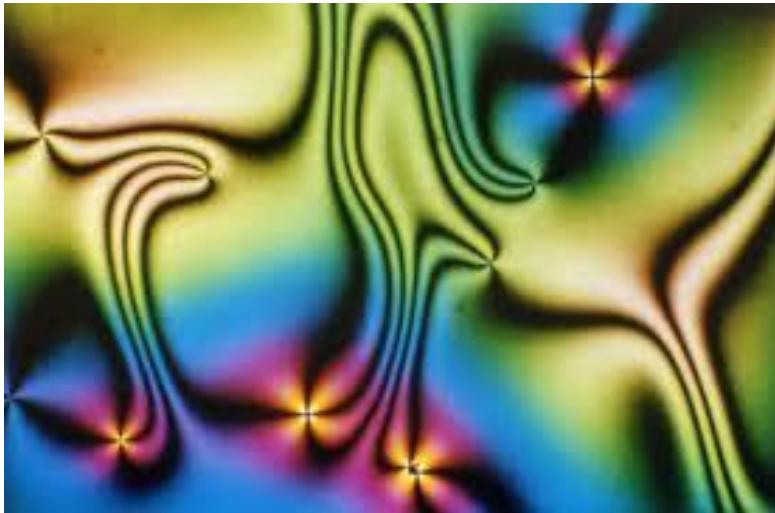
Experimental and simulation evidence that defects control active turbulence

Predicting the rate of defect formation?

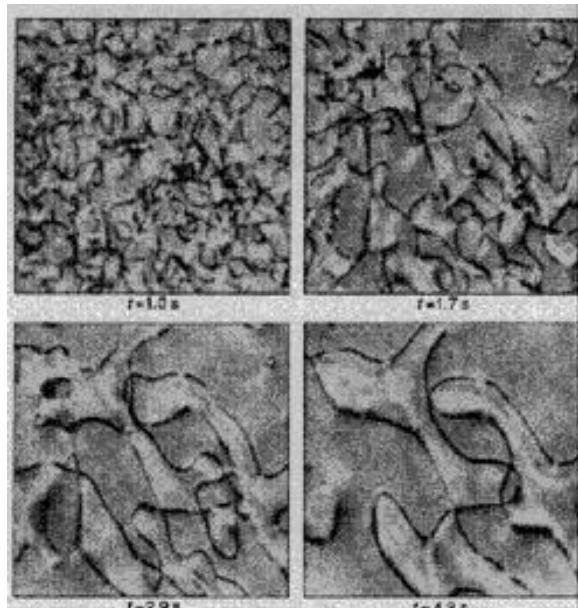
Predicting the cross section for annihilation?

Varying concentration?

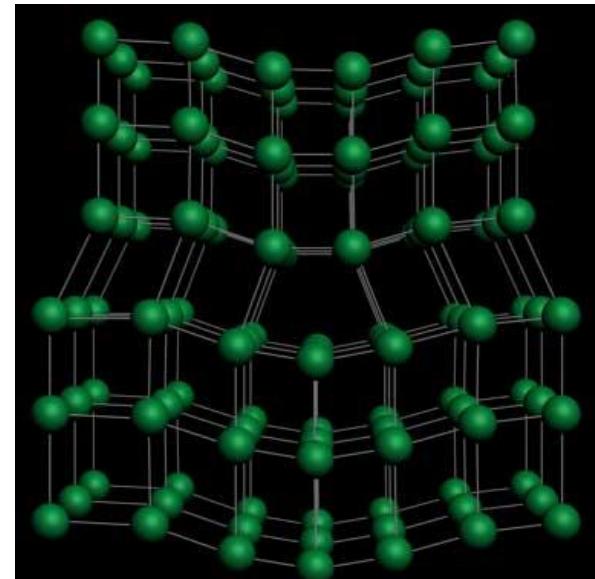
How generic is this picture?



liquid crystals



cosmic strings in the early universe



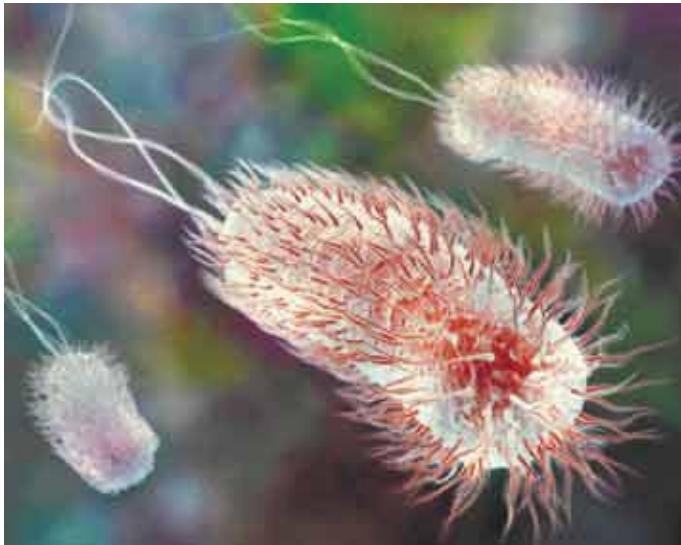
crystal dislocations

magnetic monopoles in spin ice

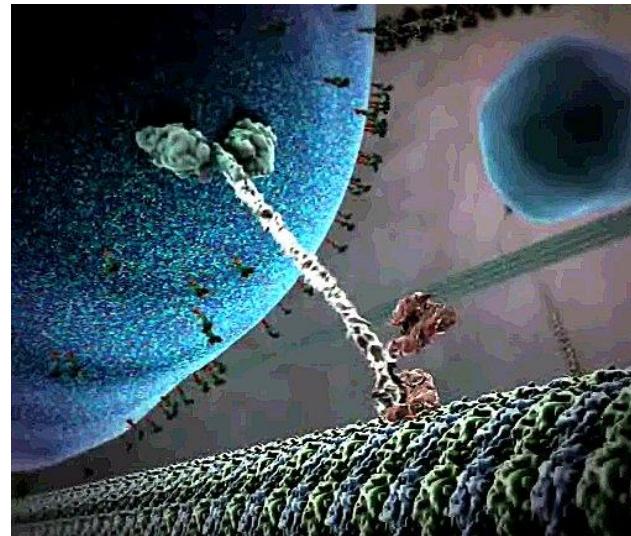
topological insulators

quantum vortex in a superfluid

Active matter



bacteria, self-propelled colloids



molecular motors, cells

active systems operate out of
thermodynamic equilibrium



birds, fish



Dmitri (Mitya) Pushkin
University of Oxford



Sumesh Thampi
University of Oxford



Henry Shum
University of Pittsburgh

Jorn Dunkel
MIT

Ramin Golestanian
University of Oxford

Pushkin, Shum, Yeomans, J. Fluid Mechanics **726** (2013) 5
Pushkin, Yeomans, arXiv:1307.6025
Thampi, Golestanian, Yeomans Phys. Rev. Lett. Sept 13

Funding: ERC Advanced Grant