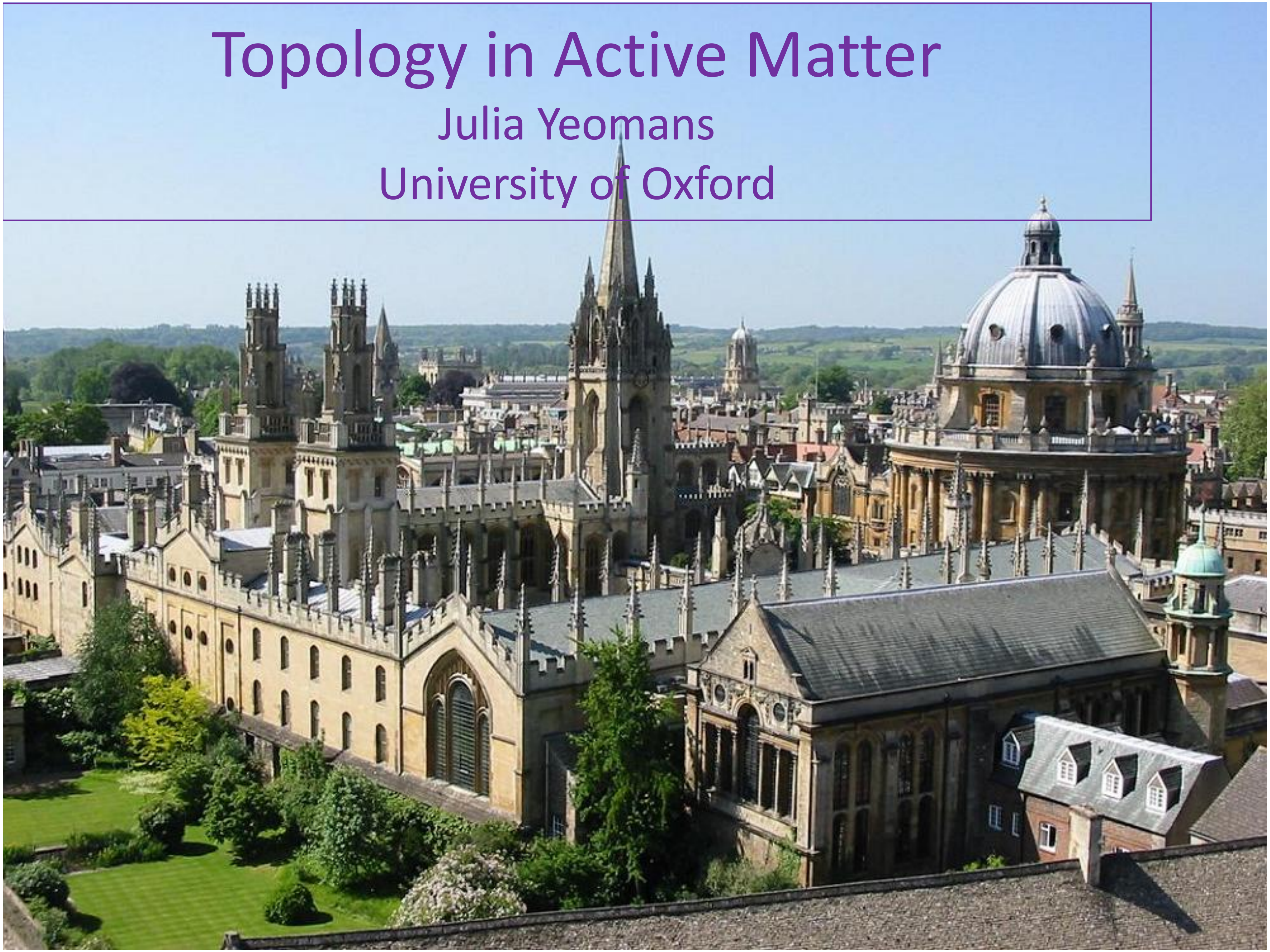
Topology in Active Matter

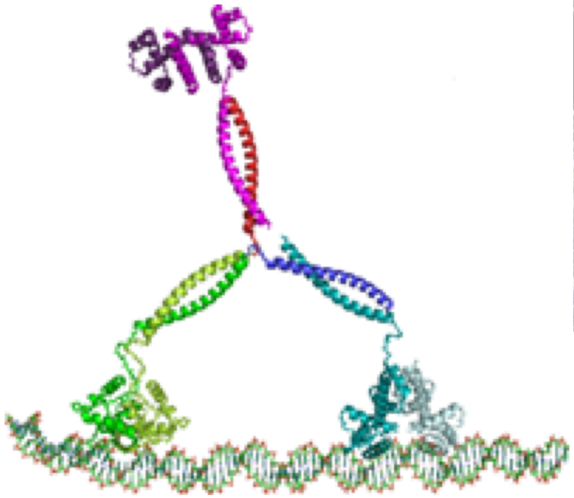
Julia Yeomans
University of Oxford

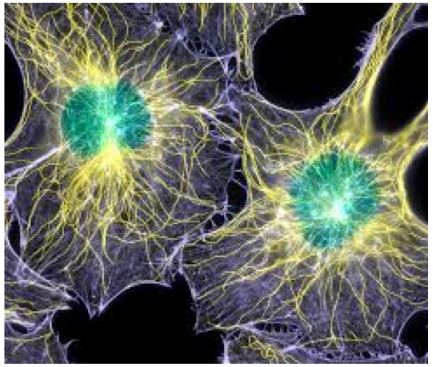


1. What is active matter and why is it interesting?
2. Background 1: nematic liquid crystals
3. Background 2: low Reynolds number hydrodynamics
4. Active nematics and active turbulence
5. Self-propelled topological defects
6. Confining active turbulence
7. Bacteria: the hare and the tortoise
8. Eukaryotic cells as an active system

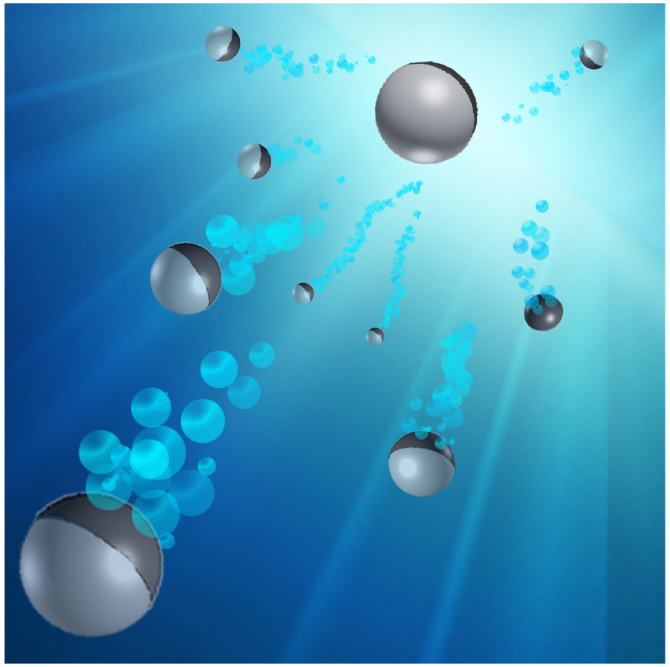
Active matter: takes energy from its surroundings on a single particle level and uses it to do work.

molecular motors



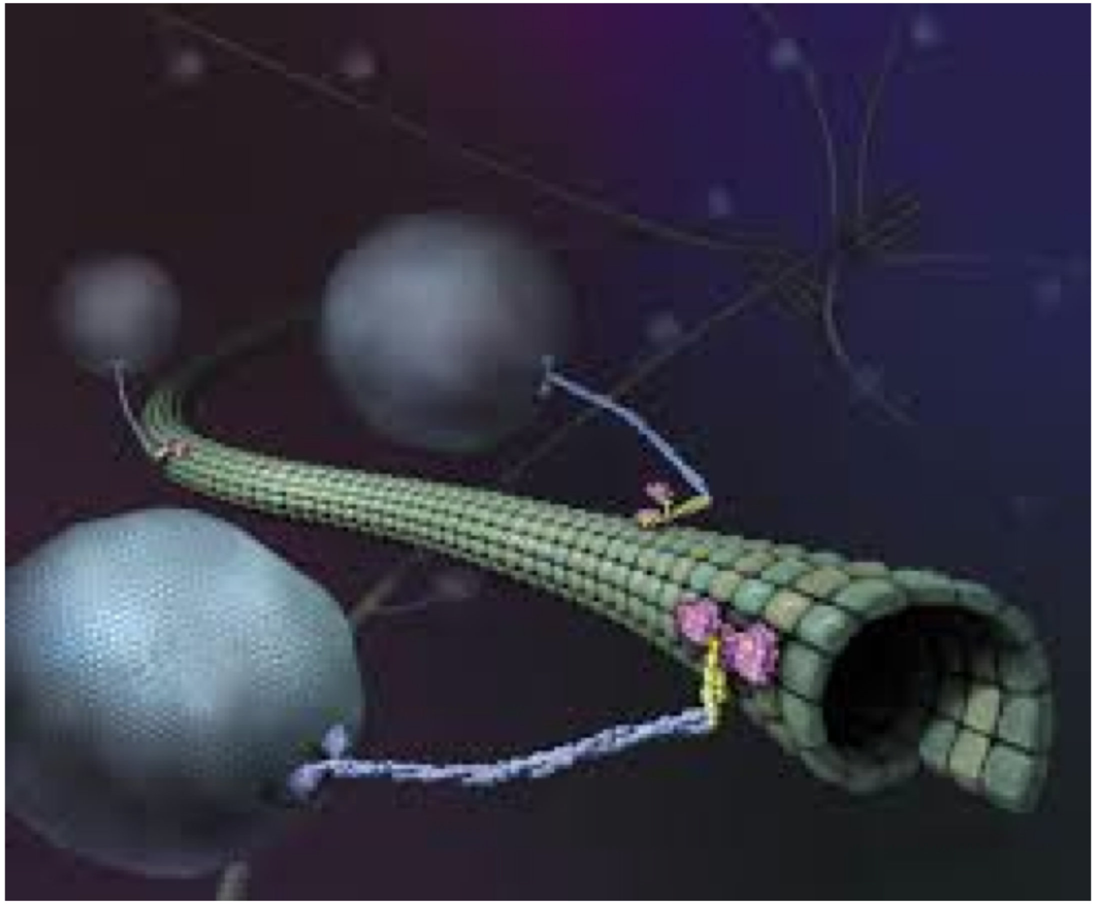


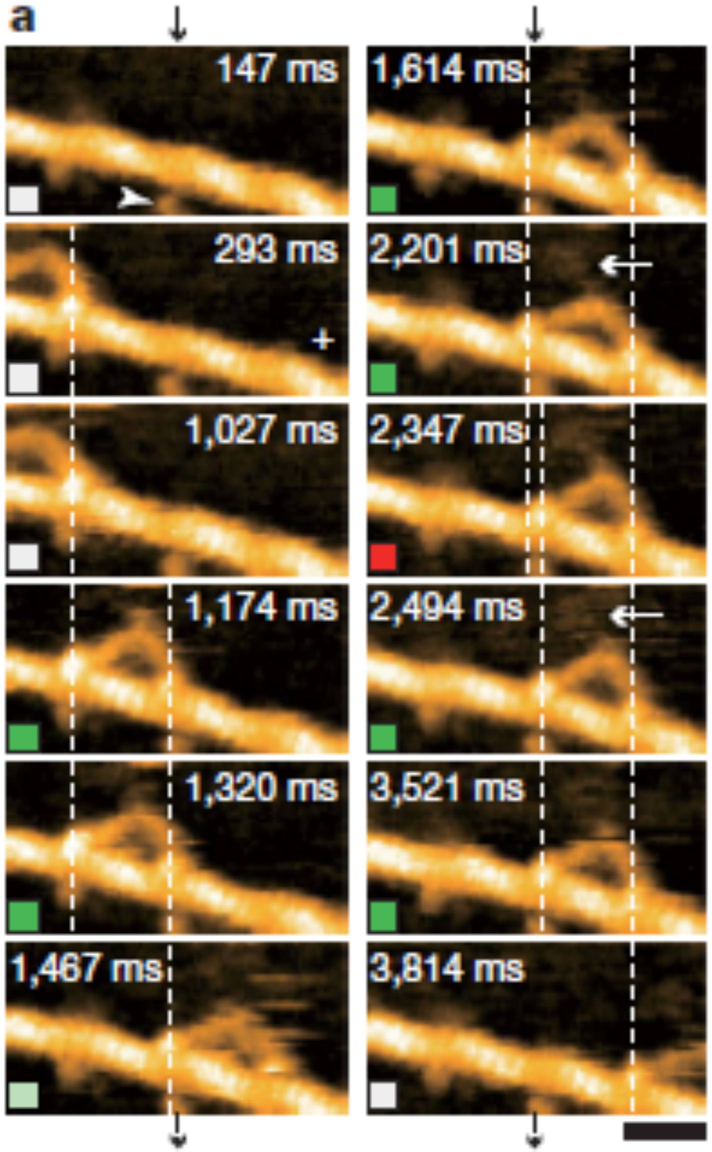
cells

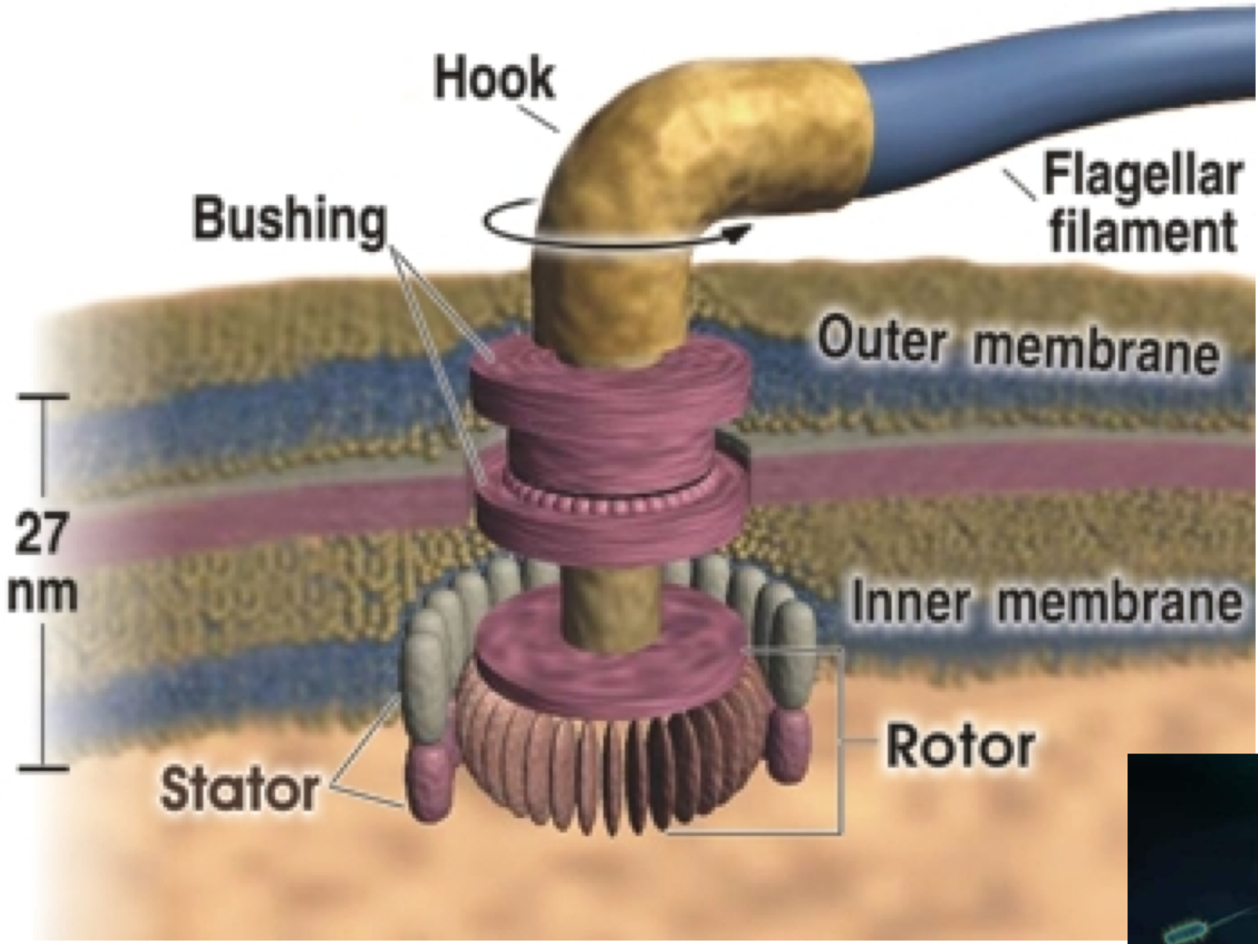


active colloids

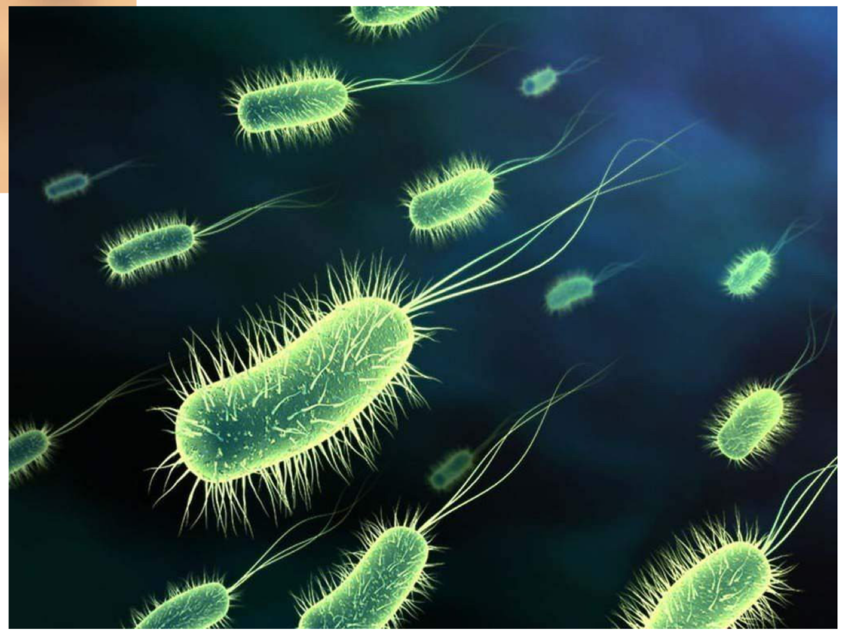
microswimmers



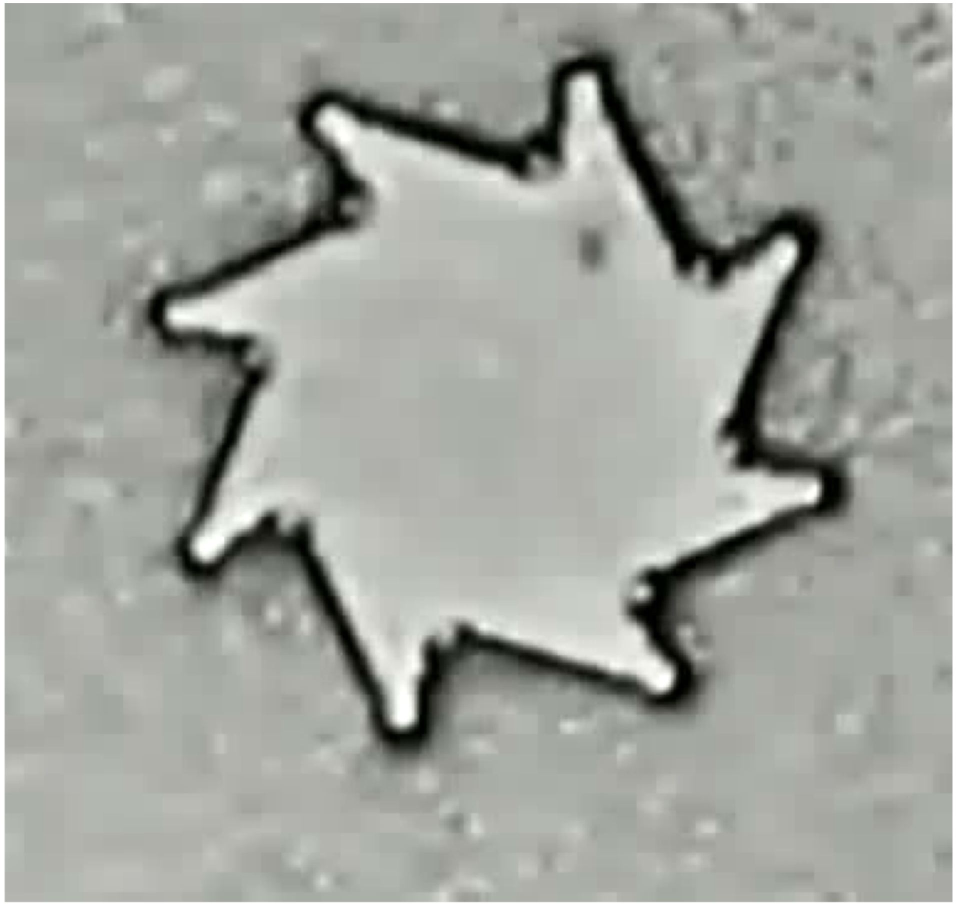

a
147 ms
293 ms
+
1,027 ms
1,174 ms
1,320 ms
1,467 ms
1,614 ms
2,201 ms
2,347 ms
2,494 ms
3,521 ms
3,814 ms



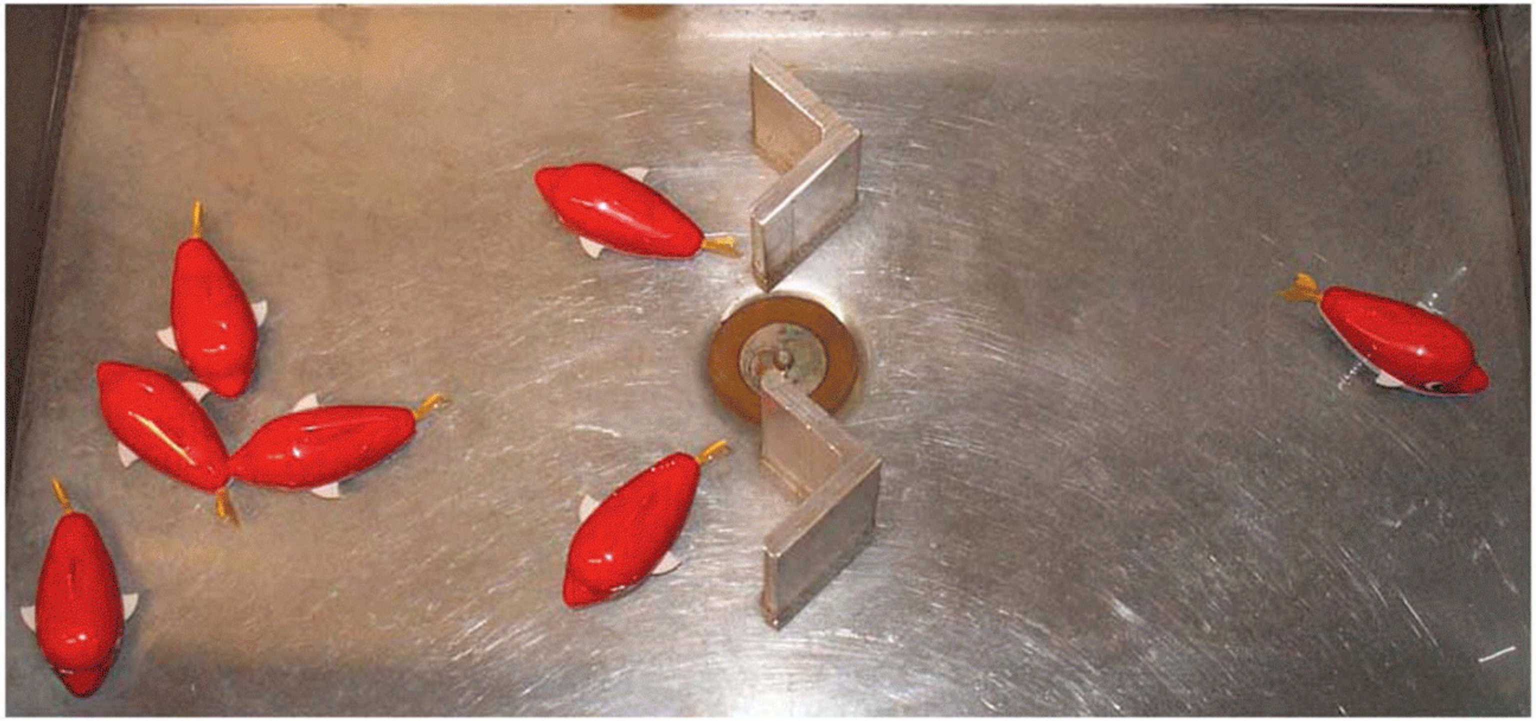
Bacterial flagellar motor

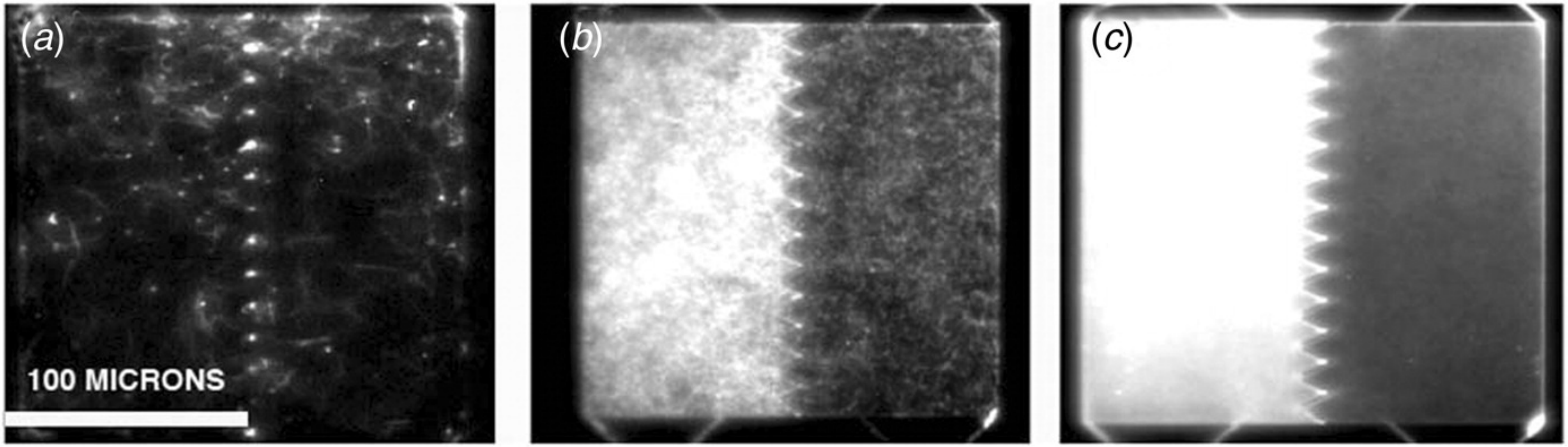


Active propulsion:



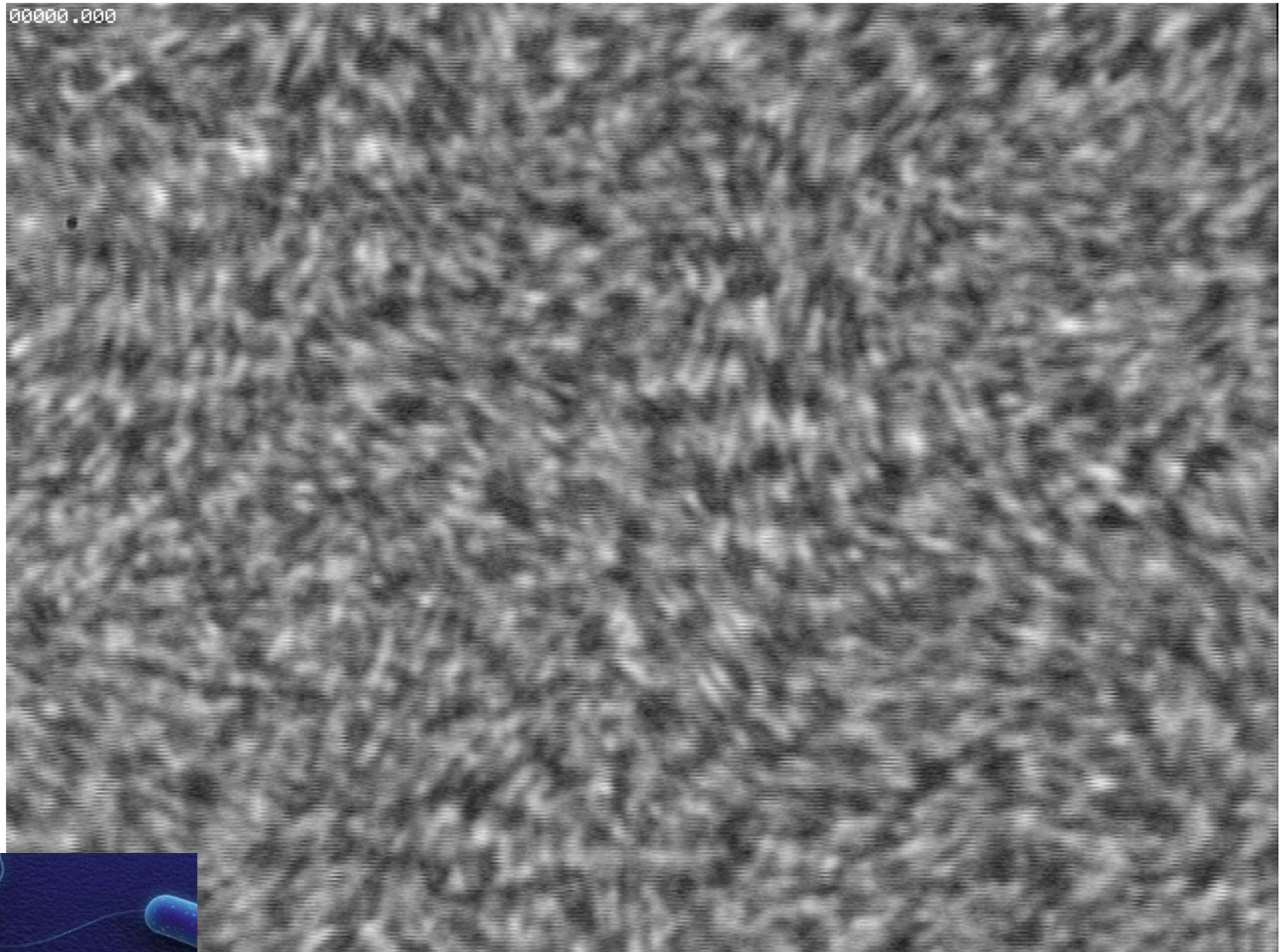
Di Leonardo, Sokolov,





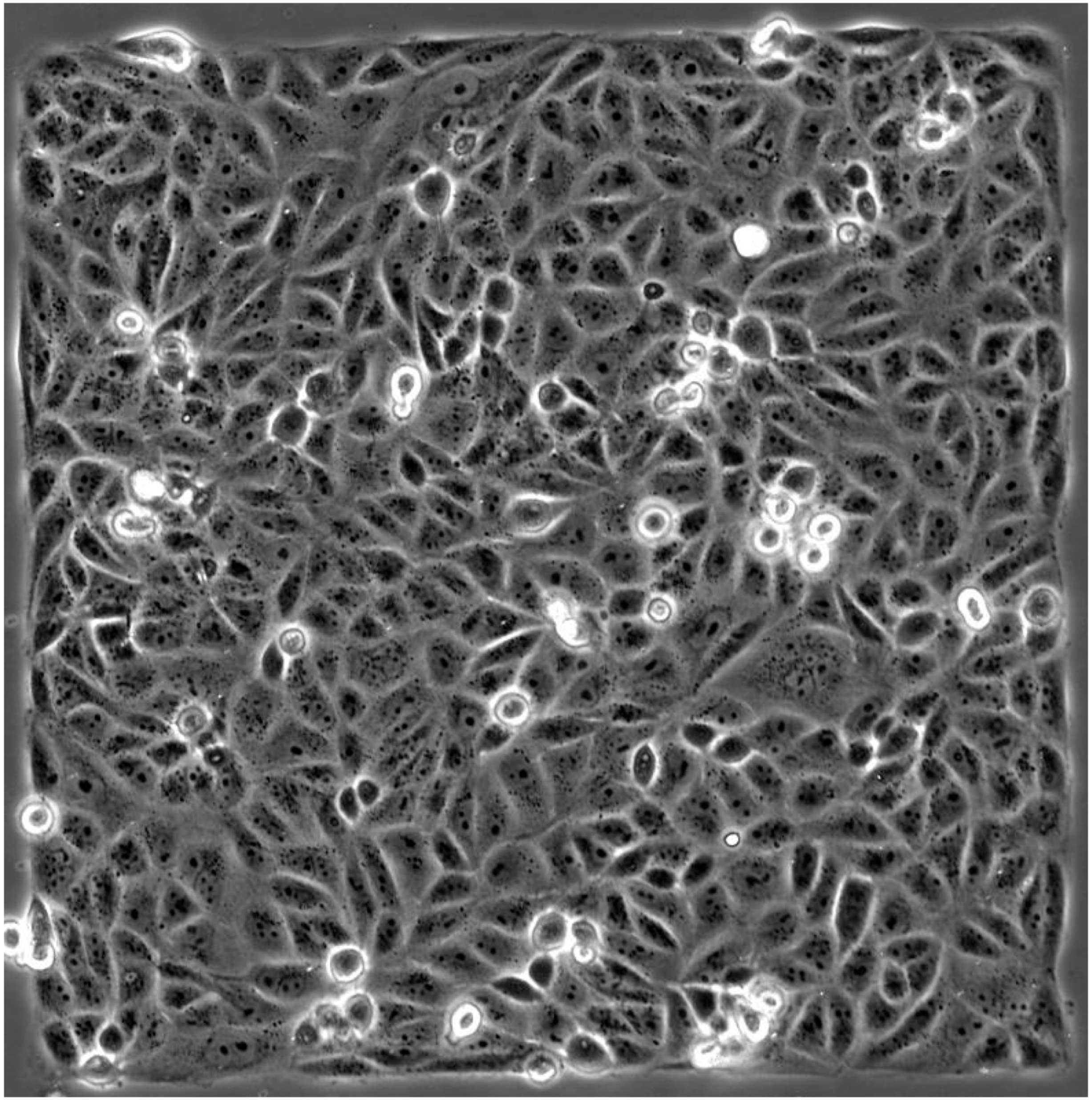
Galajda et al, J Modern Optics 2011

Active turbulence: bacteria



Dense suspension of microswimmers

Active turbulence: eukaryotic cells



Why study active matter:

1. to understand biological systems: biomechanics and self-assembly

2. To create new types of micro-engines

3. As examples of non-equilibrium statistical physics

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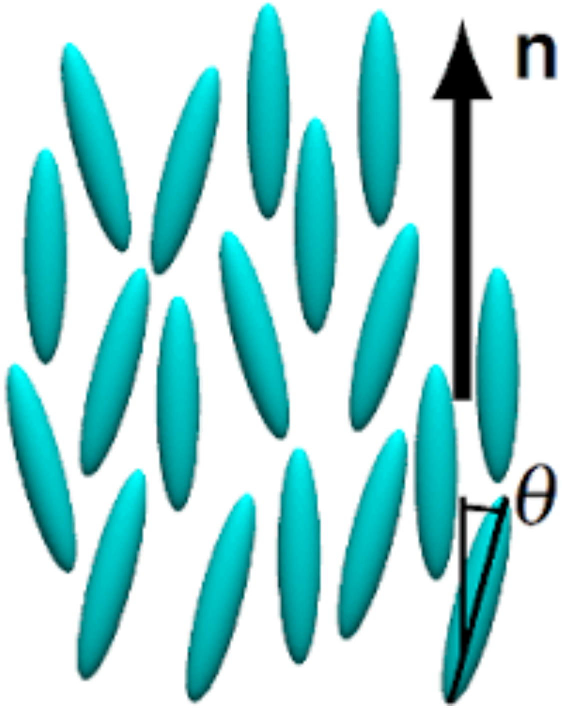
nematic symmetry

nematic symmetry

nematic phase



$$Q_{ij} = \langle n_i n_j - \frac{\delta_{ij}}{3} \rangle$$

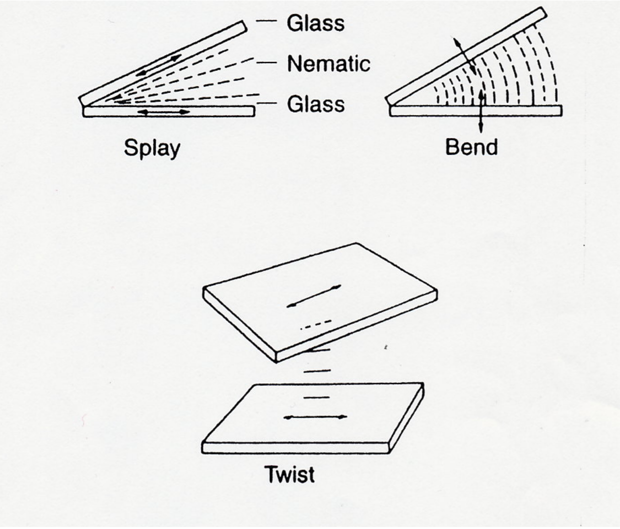
Tensor order parameter, Q

$$Q_{ij} = \langle n_i n_j - \frac{\delta_{ij}}{3} \rangle$$

Landau-de Gennes free energy

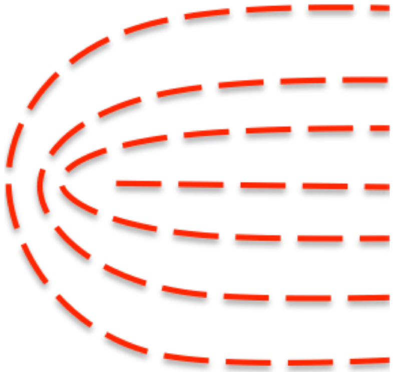
:

$$\mathcal{F} = \frac{K}{2}(\partial_k Q_{ij})^2 + \frac{A}{2} Q_{ij} Q_{ji} + \frac{B}{3} Q_{ij} Q_{jk} Q_{ki} + \frac{C}{4}(Q_{ij} Q_{ji})^2$$

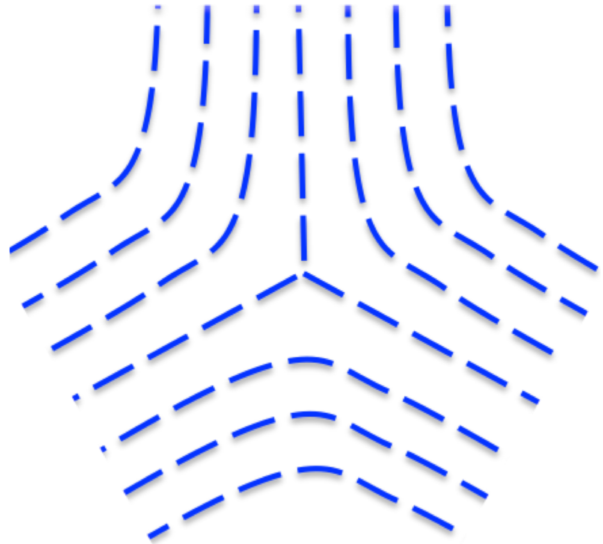


An ‘elastic liquid’

Topological defects in nematic liquid crystals



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



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

topological charge

$$\boxed{m = \frac{1}{2\pi}\int_{dS} d\theta}$$

Continuum equations of liquid crystal hydrodynamics

$$\boxed{(\partial_t + u_k \partial_k) Q_{ij} - S_{ij} = \Gamma H_{ij}}$$

Continuum equations of liquid crystal hydrodynamics

$$\boxed{(\partial_t + u_k \partial_k) Q_{ij} - S_{ij} = \Gamma H_{ij}}$$

$$S_{ij} = (\lambda E_{ik} + \Omega_{ik})(Q_{kj} + \delta_{kj}/3) +$$
$$(Q_{ik} + \delta_{ik}/3)(\lambda E_{kj} - \Omega_{kj}) - 2\lambda (Q_{ij} + \delta_{ij}/3)(Q_{kl} \partial_k u_l)$$

$$E_{ij} = (\partial_i u_j + \partial_j u_i)/2$$

$$\Omega_{ij} = (\partial_j u_i - \partial_i u_j)/2$$

Continuum equations of liquid crystal hydrodynamics

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$$E_{ij} = (\partial_i u_j + \partial_j u_i)/2$$

$$\Omega_{ij} = (\partial_j u_i - \partial_i u_j)/2$$

$$H_{ij} = -\delta \mathcal{F} / \delta Q_{ij} + (\delta_{ij}/3) \mathrm{Tr}(\delta \mathcal{F} / \delta Q_{kl})$$

$$\mathcal{F} = K(\partial_k Q_{ij})^2/2 + A Q_{ij} Q_{ji}/2 + B Q_{ij} Q_{jk} Q_{ki}/3 + C (Q_{ij} Q_{ji})^2/4$$

Continuum equations of liquid crystal hydrodynamics

$$\boxed{\rho(\partial_t + u_k \partial_k) u_i = \partial_j \Pi_{ij}}$$

Continuum equations of liquid crystal hydrodynamics

$$\boxed{\rho(\partial_t + u_k \partial_k) u_i = \partial_j \Pi_{ij}}$$

$$\Pi_{ij}^{viscous} = 2\mu E_{ij}$$

Continuum equations of liquid crystal hydrodynamics

$$\boxed{\rho(\partial_t + u_k\partial_k)u_i = \partial_j \Pi_{ij}}$$

$$\Pi_{ij}^{viscous} = 2\mu E_{ij}$$

$$\begin{aligned}\Pi_{ij}^{passive} = & -P\delta_{ij} + 2\lambda(Q_{ij} + \delta_{ij}/3)(Q_{kl}H_{lk}) - \lambda H_{ik}(Q_{kj} + \delta_{kj}/3) \\ & -\lambda(Q_{ik} + \delta_{ik}/3)H_{kj} - \partial_i Q_{kl}\frac{\delta\mathcal{F}}{\delta\partial_j Q_{lk}} + Q_{ik}H_{kj} - H_{ik}Q_{kj}\end{aligned}$$

Tumbling parameter

Continuum equations of liquid crystal hydrodynamics

$$\boxed{(\partial_t + u_k \partial_k) Q_{ij} - S_{ij} = \Gamma H_{ij}}$$

couples nematic order and shear flows

relaxation to minimum of Landau-de Gennes free energy

$$\boxed{\rho(\partial_t + u_k \partial_k) u_i = \partial_j \Pi_{ij}}$$

viscous + passive

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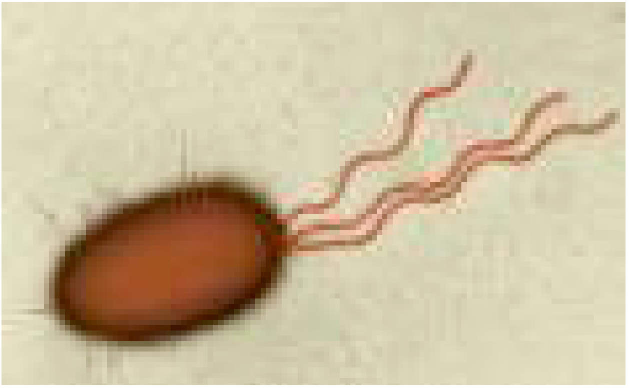
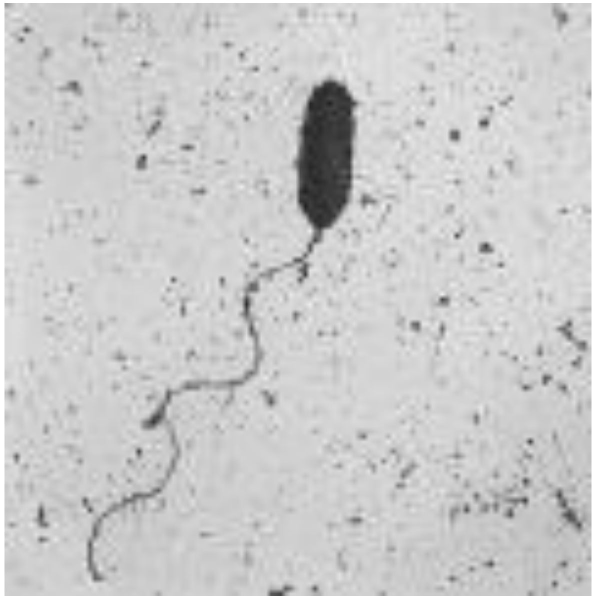
Stokes equations

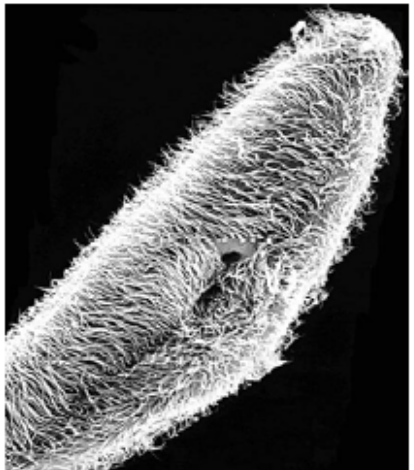
$$\nabla p = \mu \nabla^2 \mathbf{v} + \mathbf{f} \qquad \nabla \cdot \mathbf{v} = 0$$

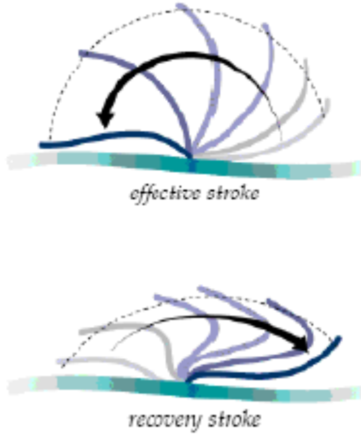
Purcell's Scallop Theorem

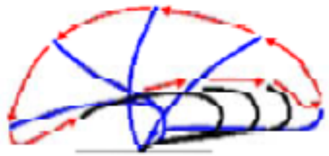
A swimmer strokes must be non-invariant under time reversal



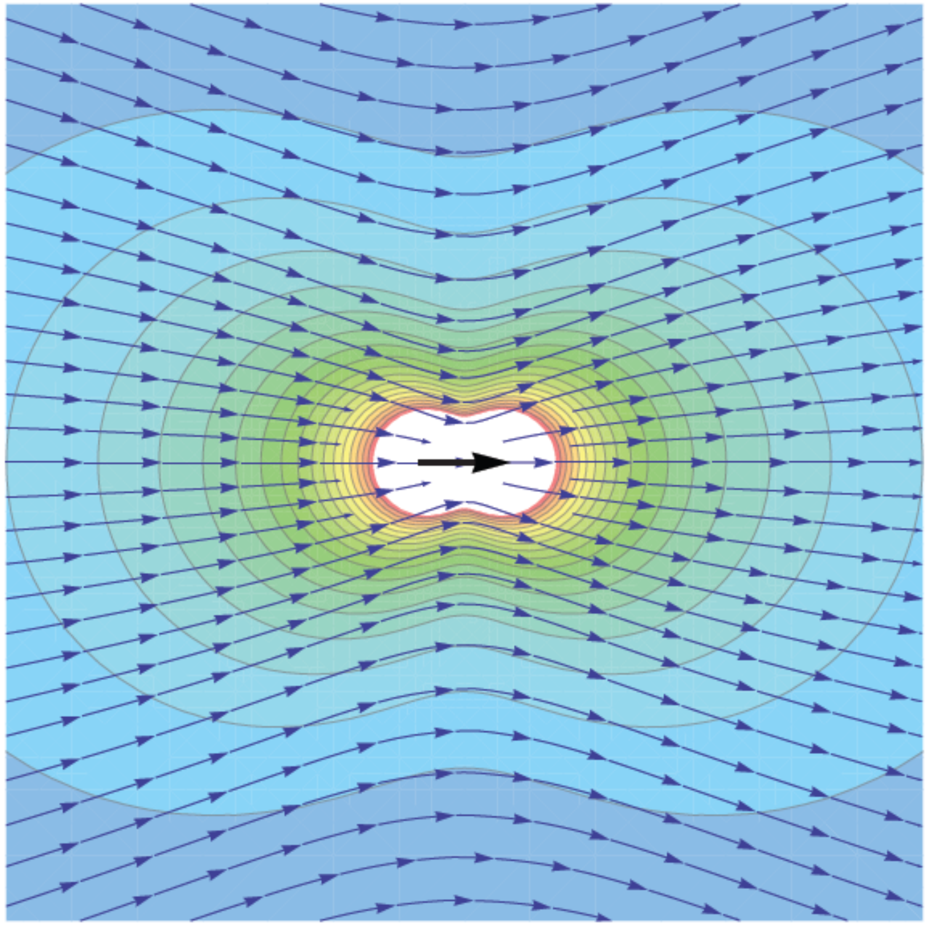






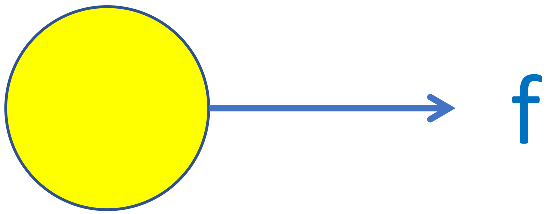


Green function of the Stokes equation (Stokeslet)



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

$$v_i(\mathbf{r}) = \frac{f_j}{8\pi\mu} \left(\frac{\delta_{ij}}{r} + \frac{r_i r_j}{r^3} \right) \equiv G_{ij}(\mathbf{r}) f_j$$

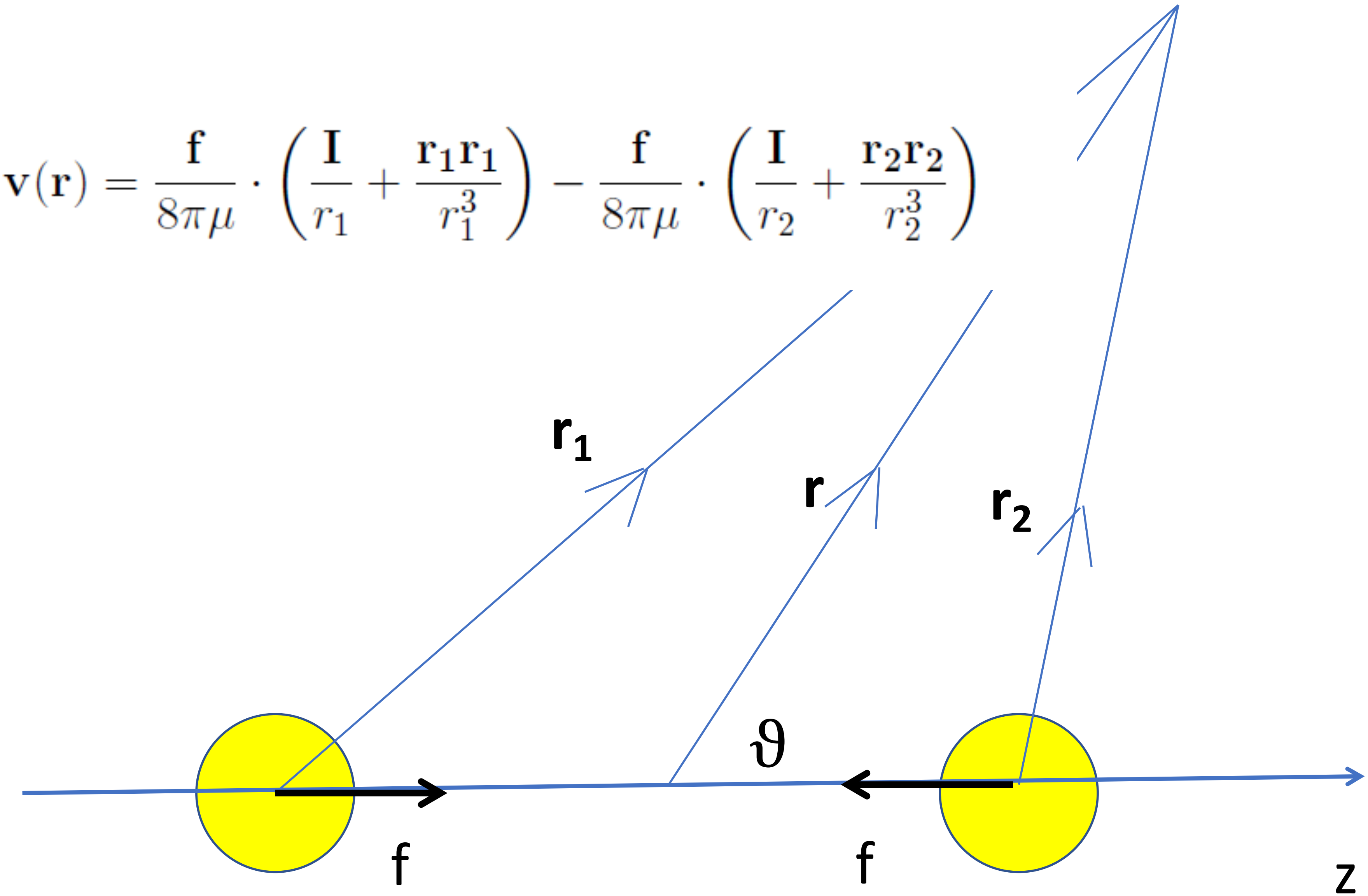


Far flow field of a swimmer

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

Dipolar far flow field

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

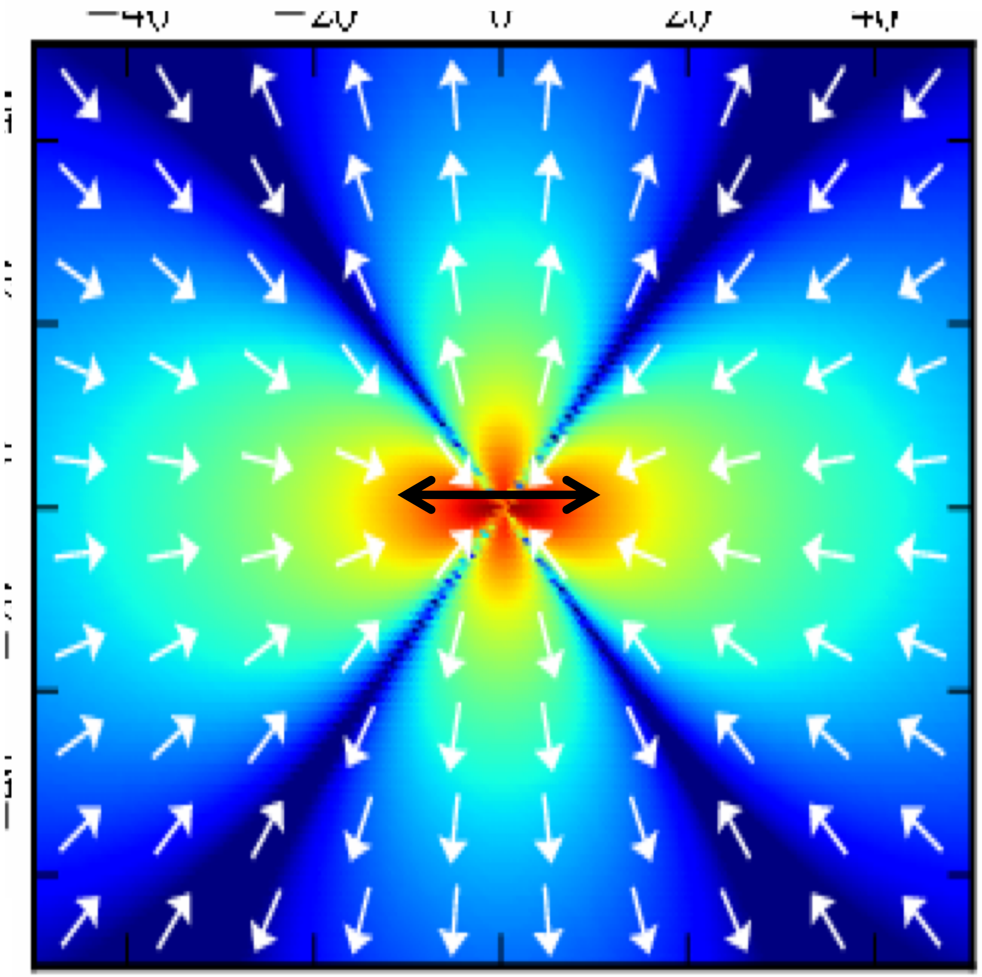


Far flow field of a swimmer

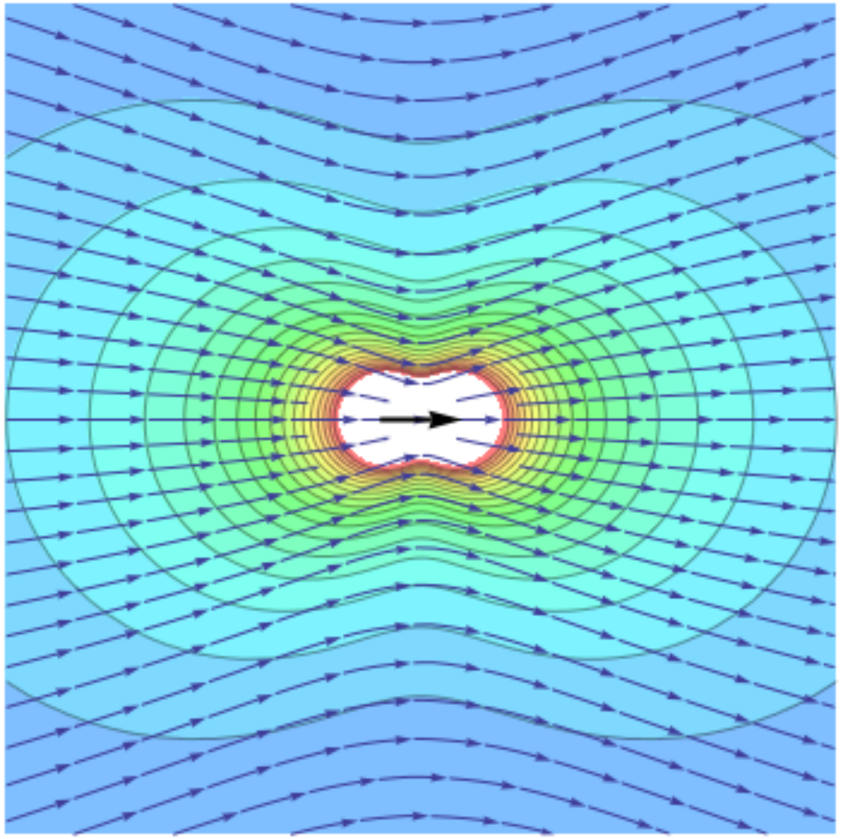
Swimmers have dipolar far flow fields because they have no net force acting on them

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

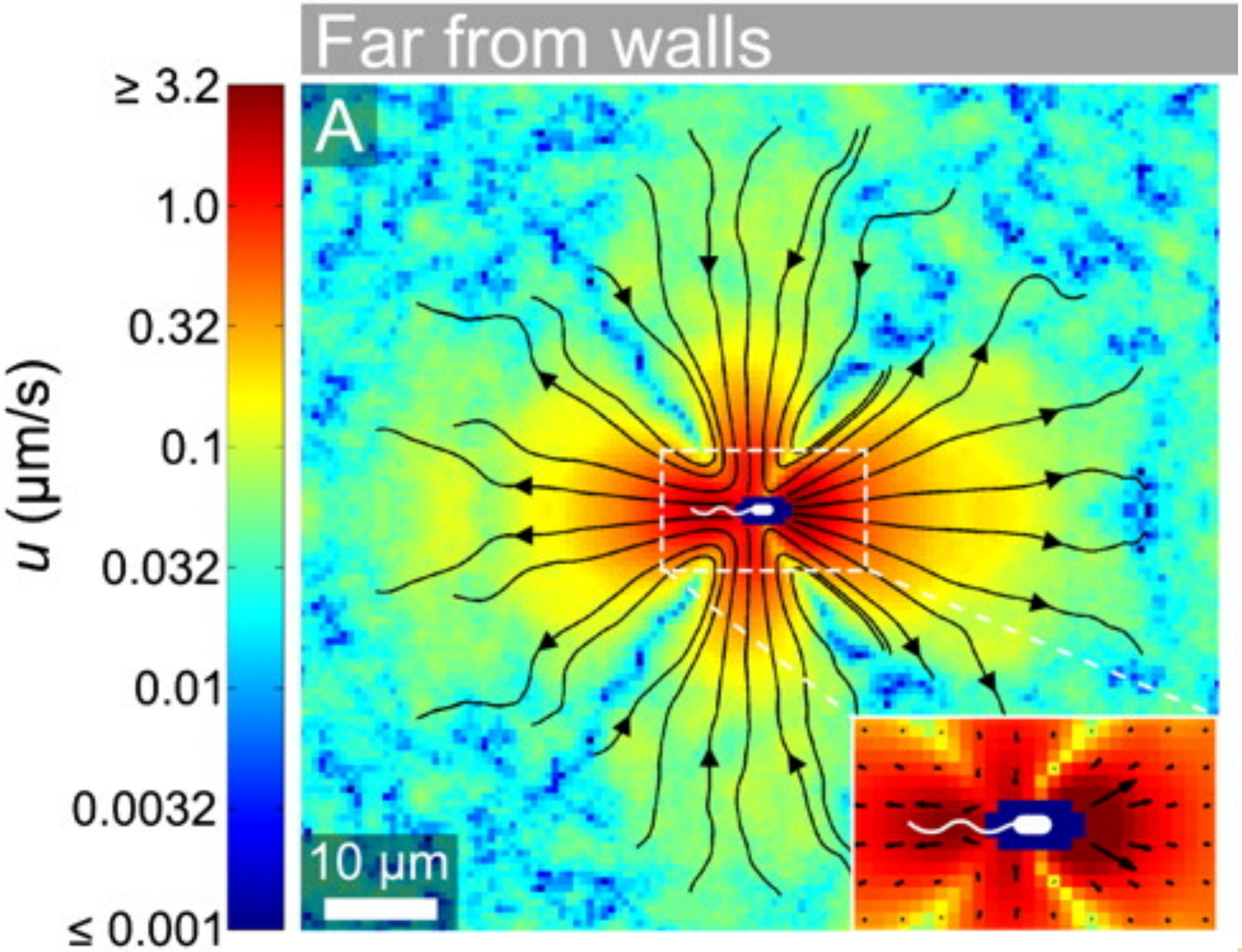
Swimmer and colloidal flow fields



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

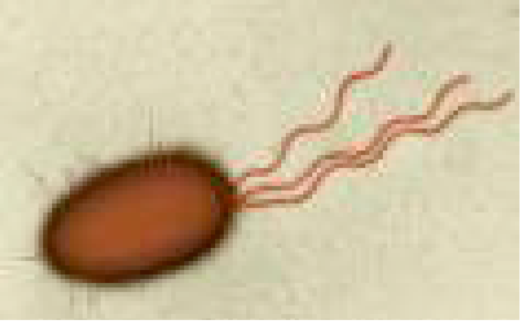


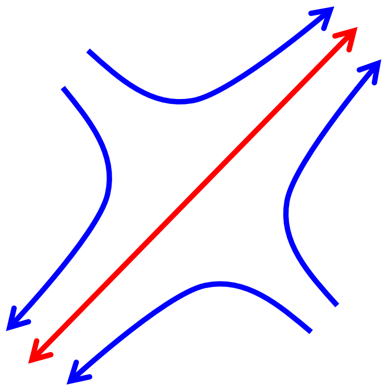
$$v \sim \frac{1}{r}$$

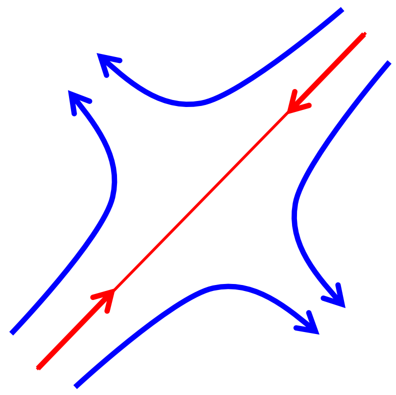


Goldstein group, Cambridge

E-coli





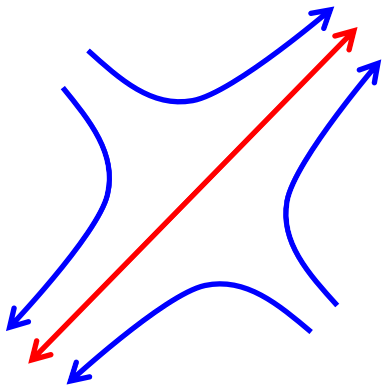


Extensile
Pusher

$\zeta > 0$

Contractile
Puller

$\zeta < 0$



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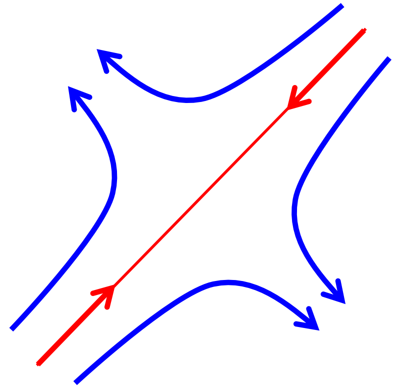


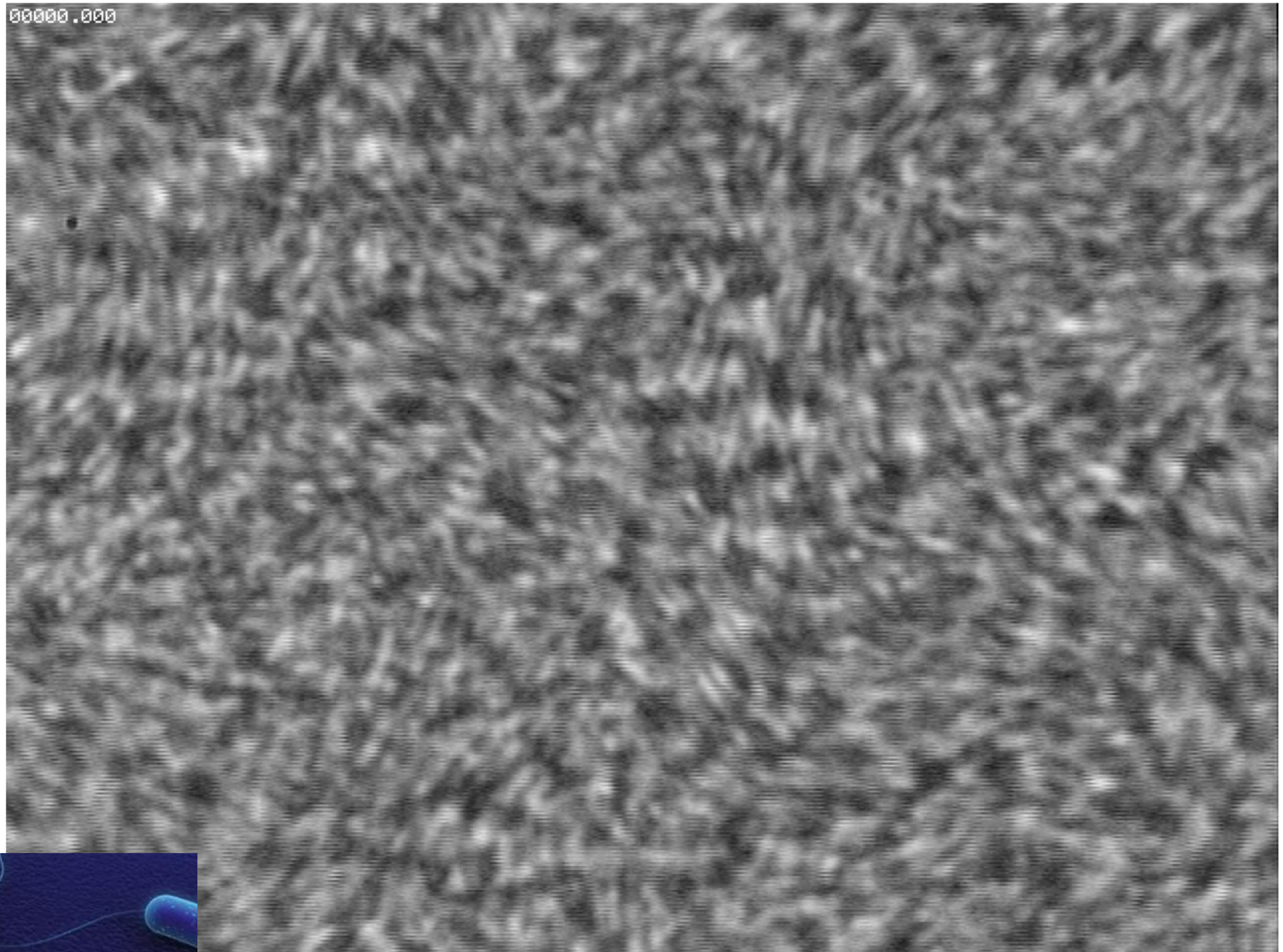
Contractile

Puller

$\zeta < 0$

Flow field has nematic symmetry

Active turbulence: bacteria



Dense suspension of microswimmers

Continuum equations of liquid crystal hydrodynamics

$$\boxed{(\partial_t + u_k \partial_k) Q_{ij} - S_{ij} = \Gamma H_{ij}}$$

couples nematic order and shear flows

relaxation to minimum of Landau-de Gennes free energy

$$\boxed{\rho(\partial_t + u_k \partial_k) u_i = \partial_j \Pi_{ij}}$$

viscous + passive

Continuum equations of active liquid crystal hydrodynamics

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viscous + passive + active stress

$$\boxed{\Pi_{ij}^{active} = -\zeta Q_{ij}}$$

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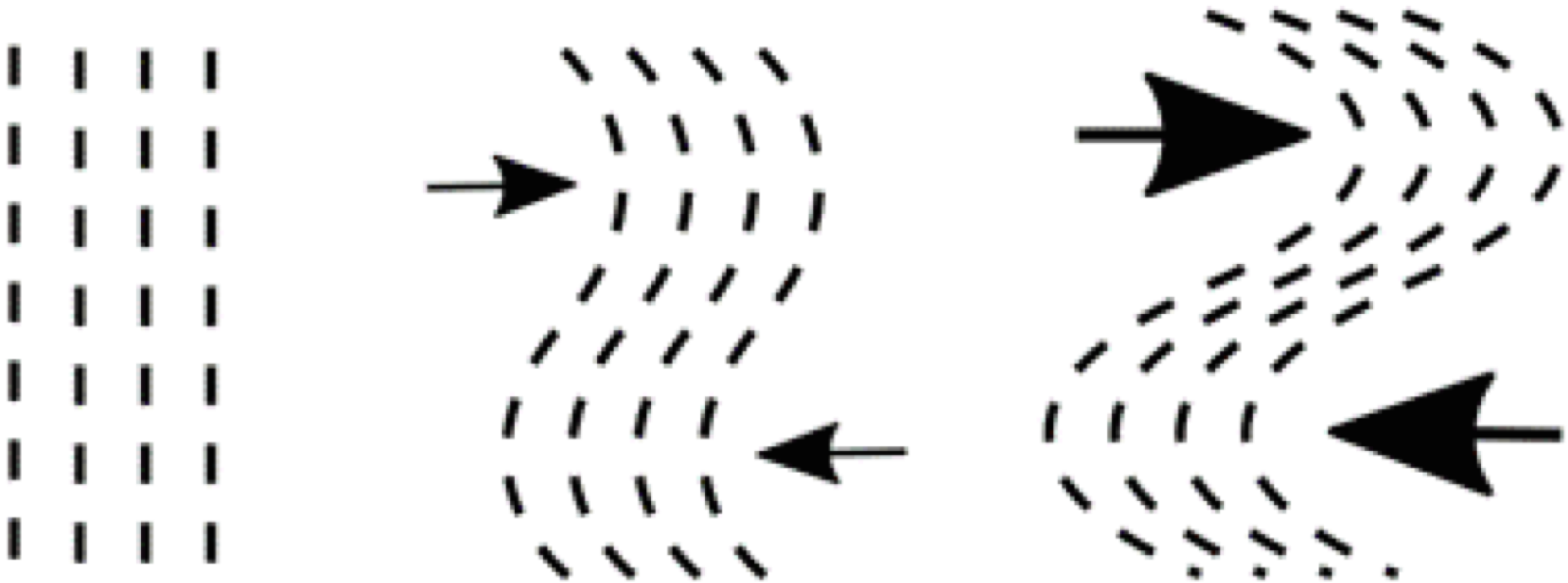
Active stress => active turbulence

Active contribution to the stress $$-\zeta \mathbf{Q}$$

Gradients in the magnitude or direction of the order parameter induce flow.

Hatwalne, Ramaswamy,
Rao, Simha, PRL 2004

nematic ordering is unstable to bend instabilities



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Linear stability analysis =>
nematic state is unstable to vortical flows

Hatwalne, Ramaswamy, Rao, Simha, PRL 2004

Active stress => active turbulence

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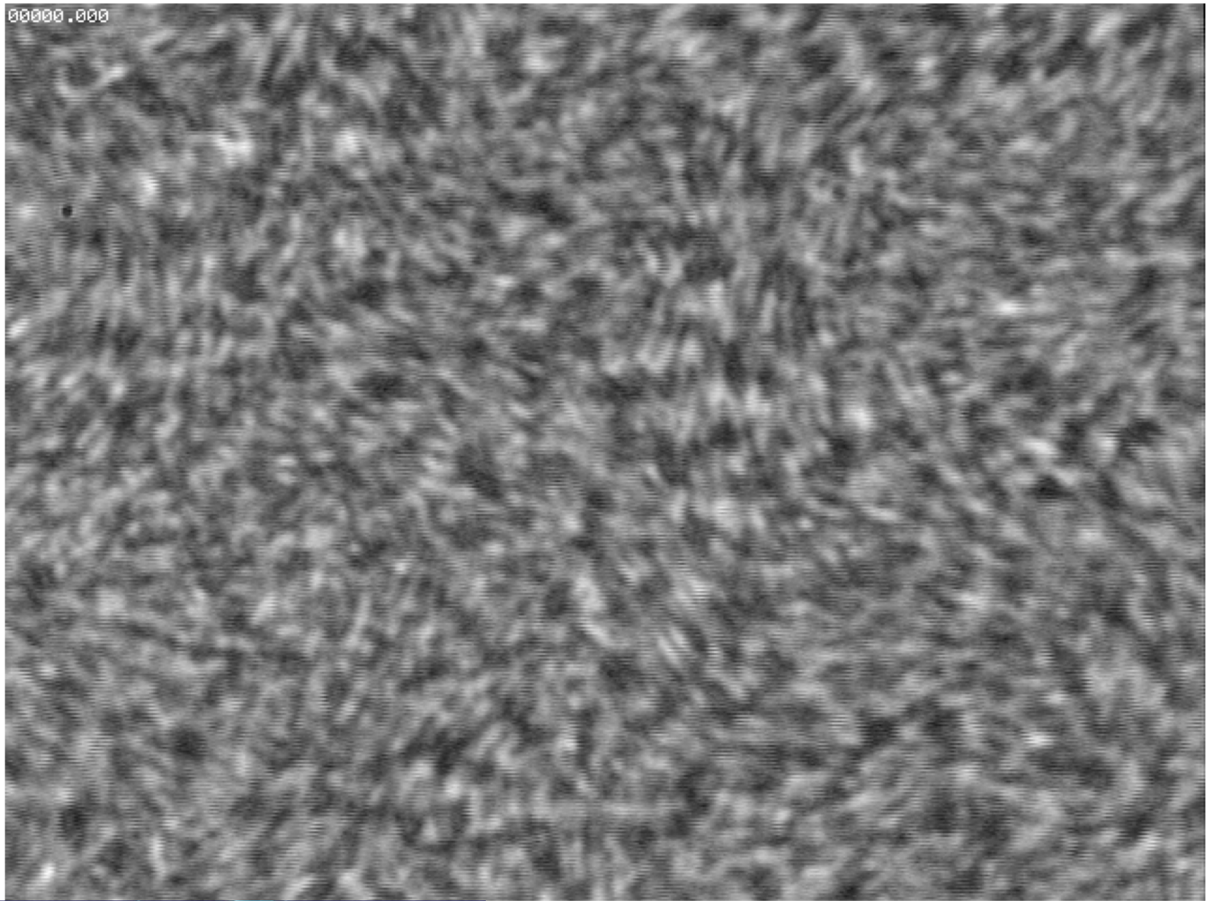
What happens instead is active turbulence

Hatwalne, Ramaswamy,
Rao, Simha, PRL 2004

Active turbulence



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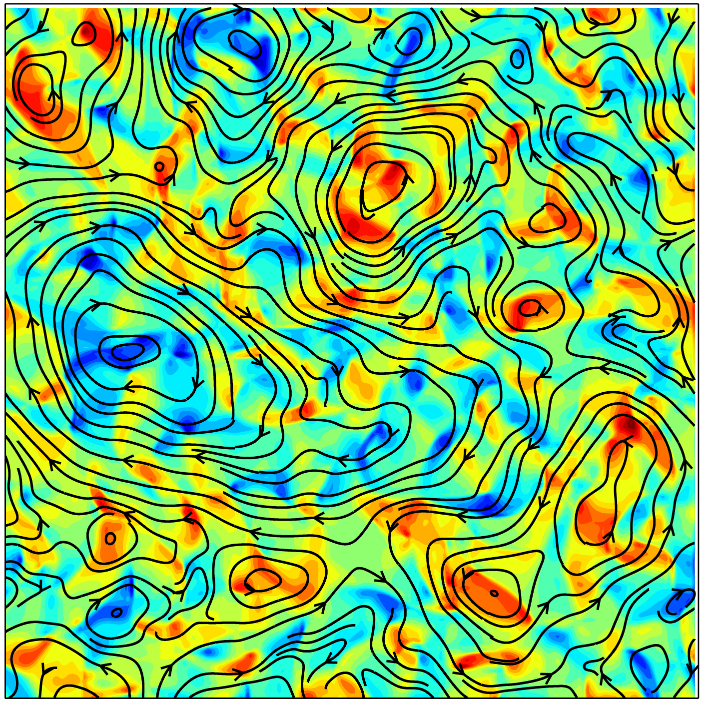
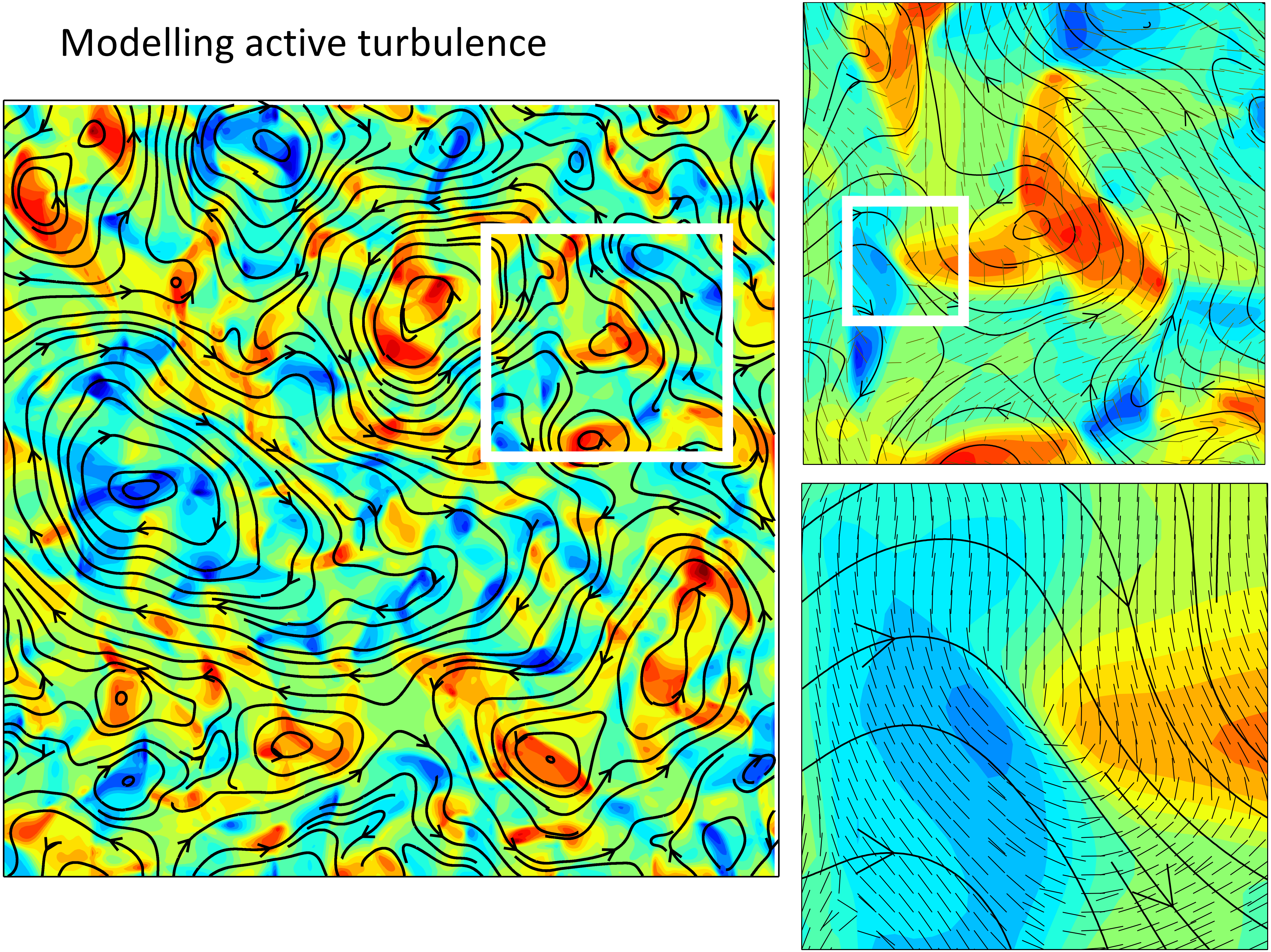
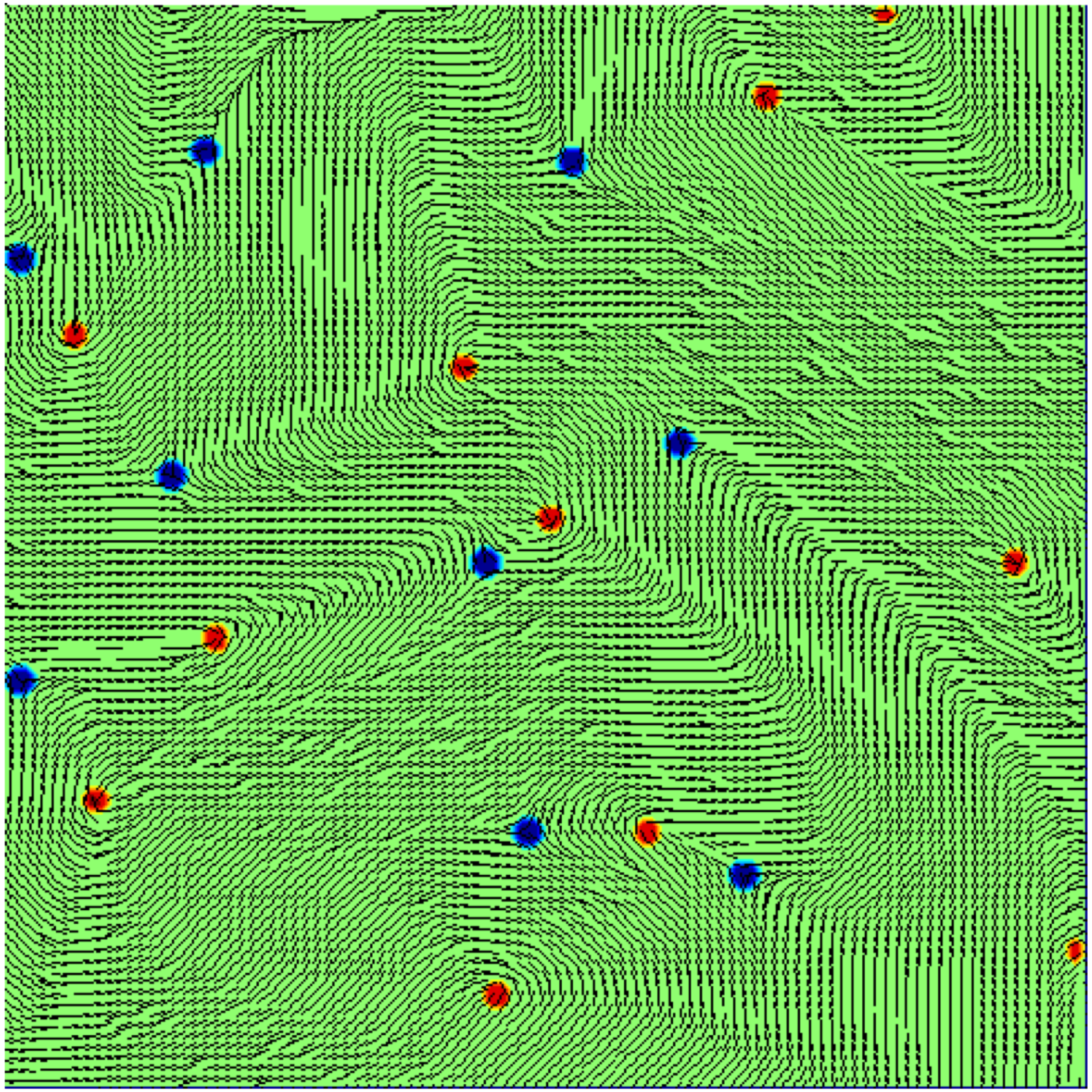


Vorticity field

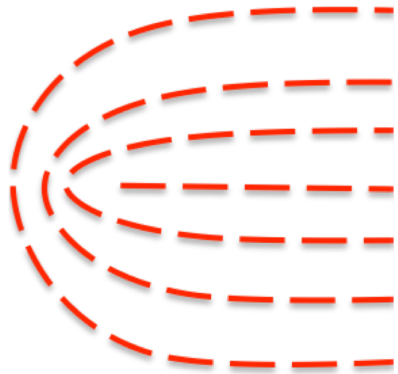
Modelling active turbulence



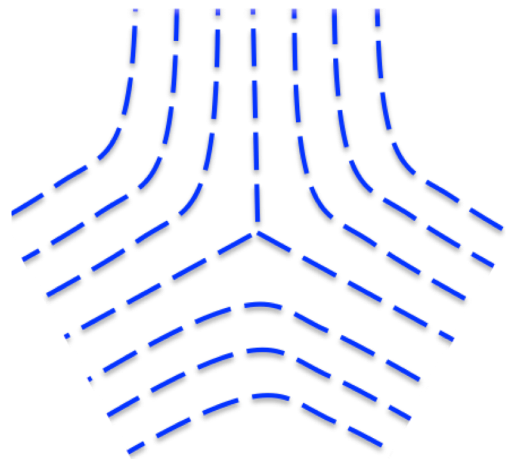
Active turbulence: topological defects are created and destroyed



Topological defects are self motile



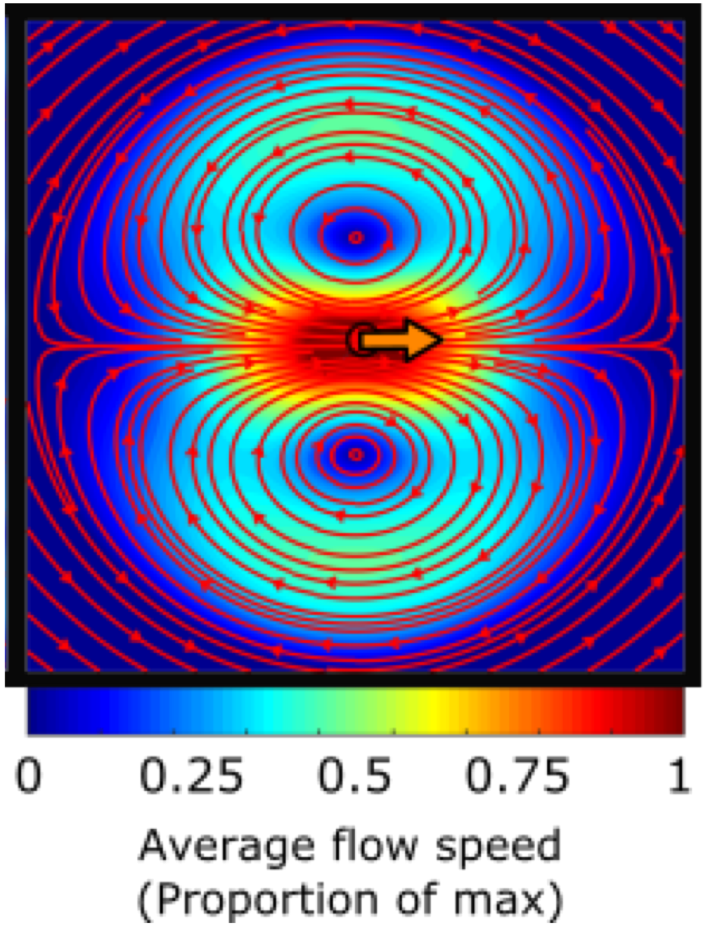
$$m = +\frac{1}{2}$$



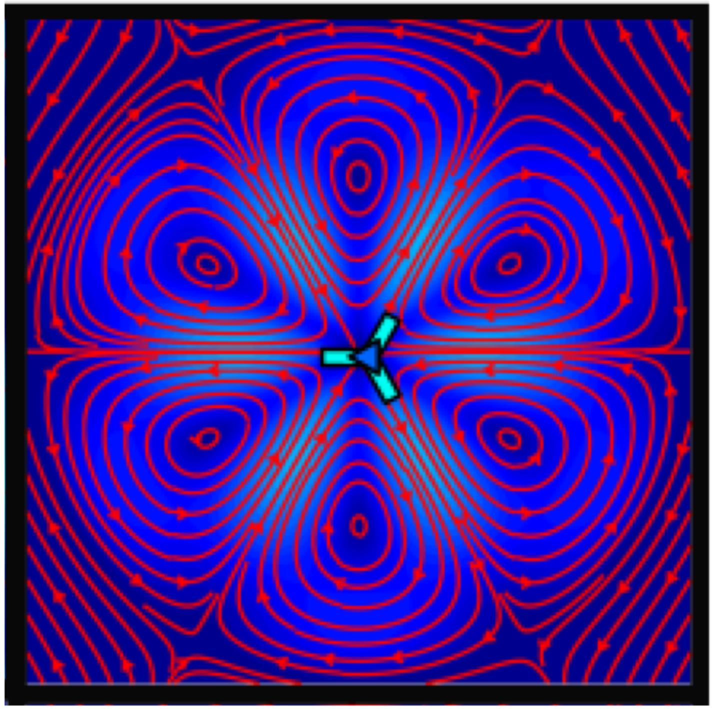
$$m = -\frac{1}{2}$$

Flow fields around defects

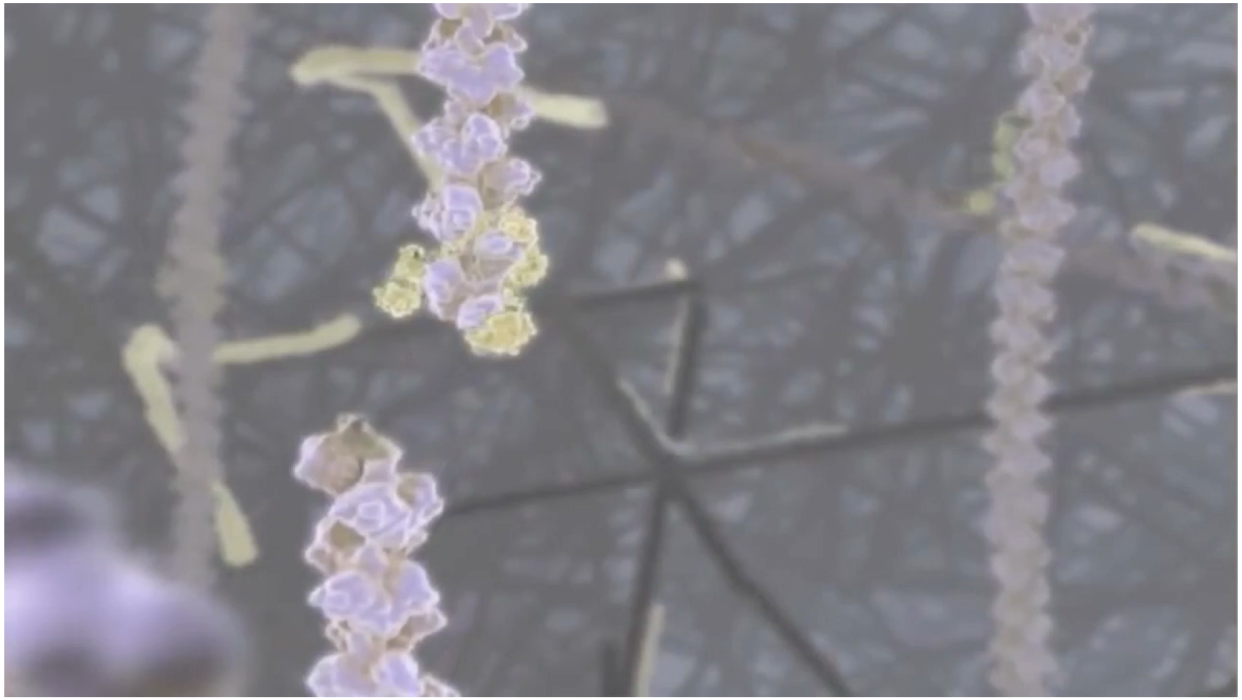
$$m = +\frac{1}{2}$$

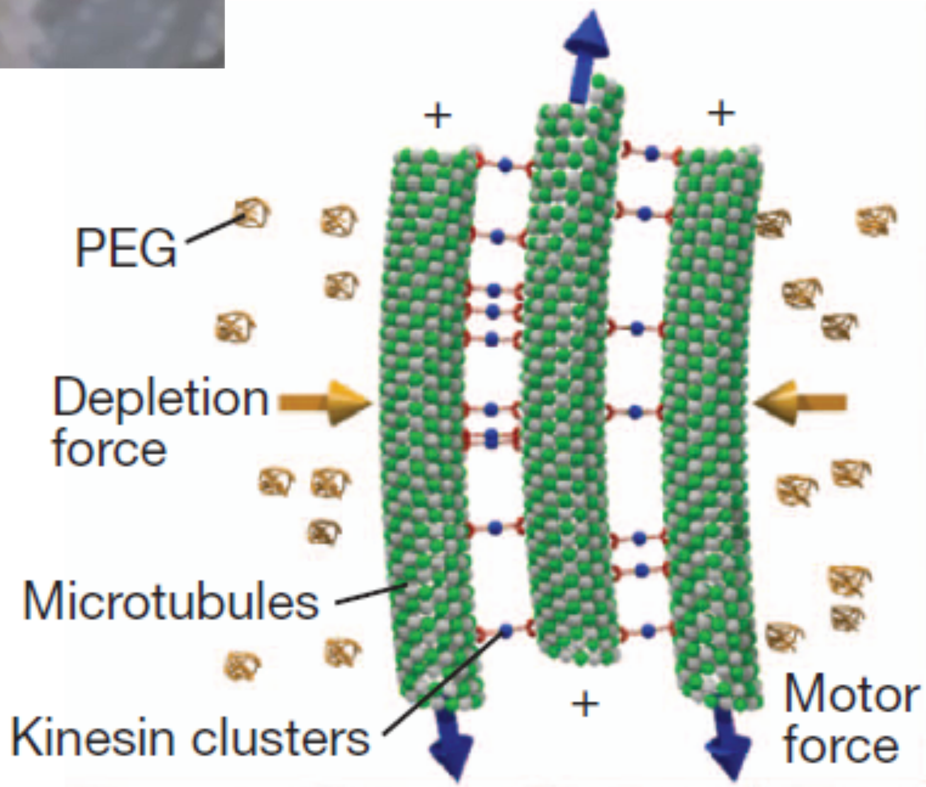


$$m = -\frac{1}{2}$$

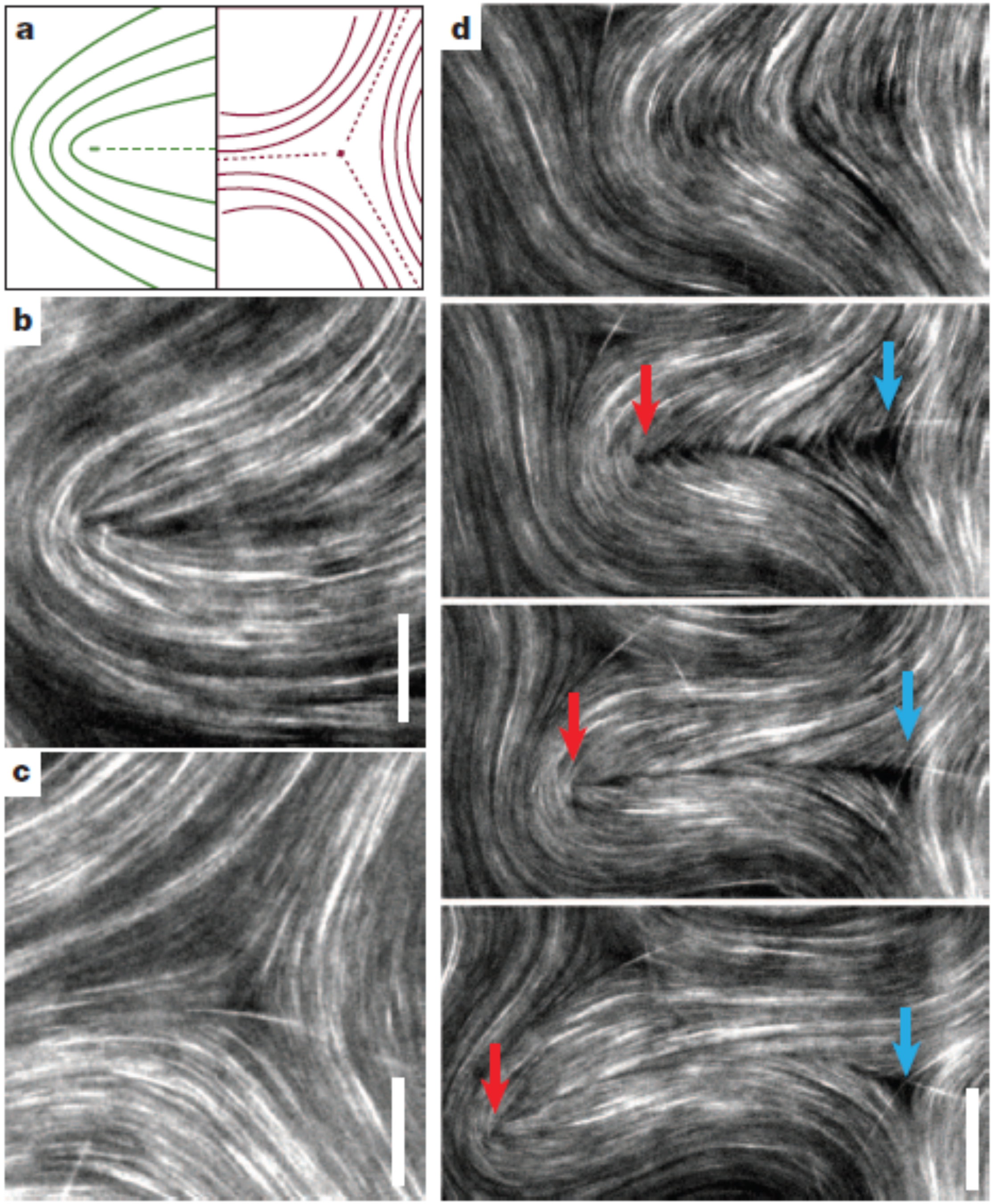


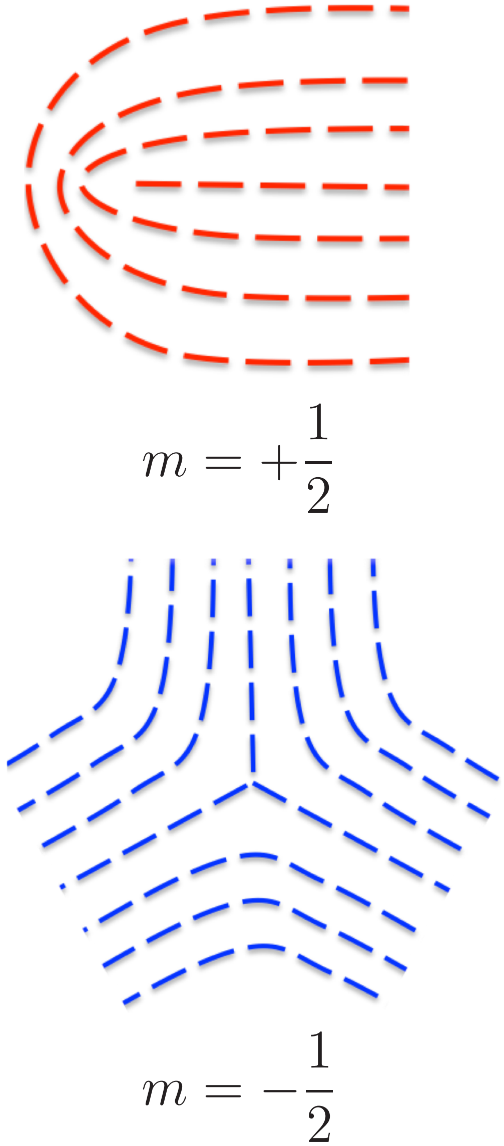
L. Giomi





+
+
PEG
Depletion
force
Microtubules
Kinesin clusters
+
Motor
force





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

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Amin Doostmohammadi
Tyler Shendruk
Kristian Thyssen
Sumesh Thampi
Santhan Chandragiri
Jerome Hardouin
Rian Hughes

Justine Laurent
Jordi Ignes-Mullol
Teresa Lopex-Leon
Francesc Sagues

Why study confined active systems?

To control active turbulence

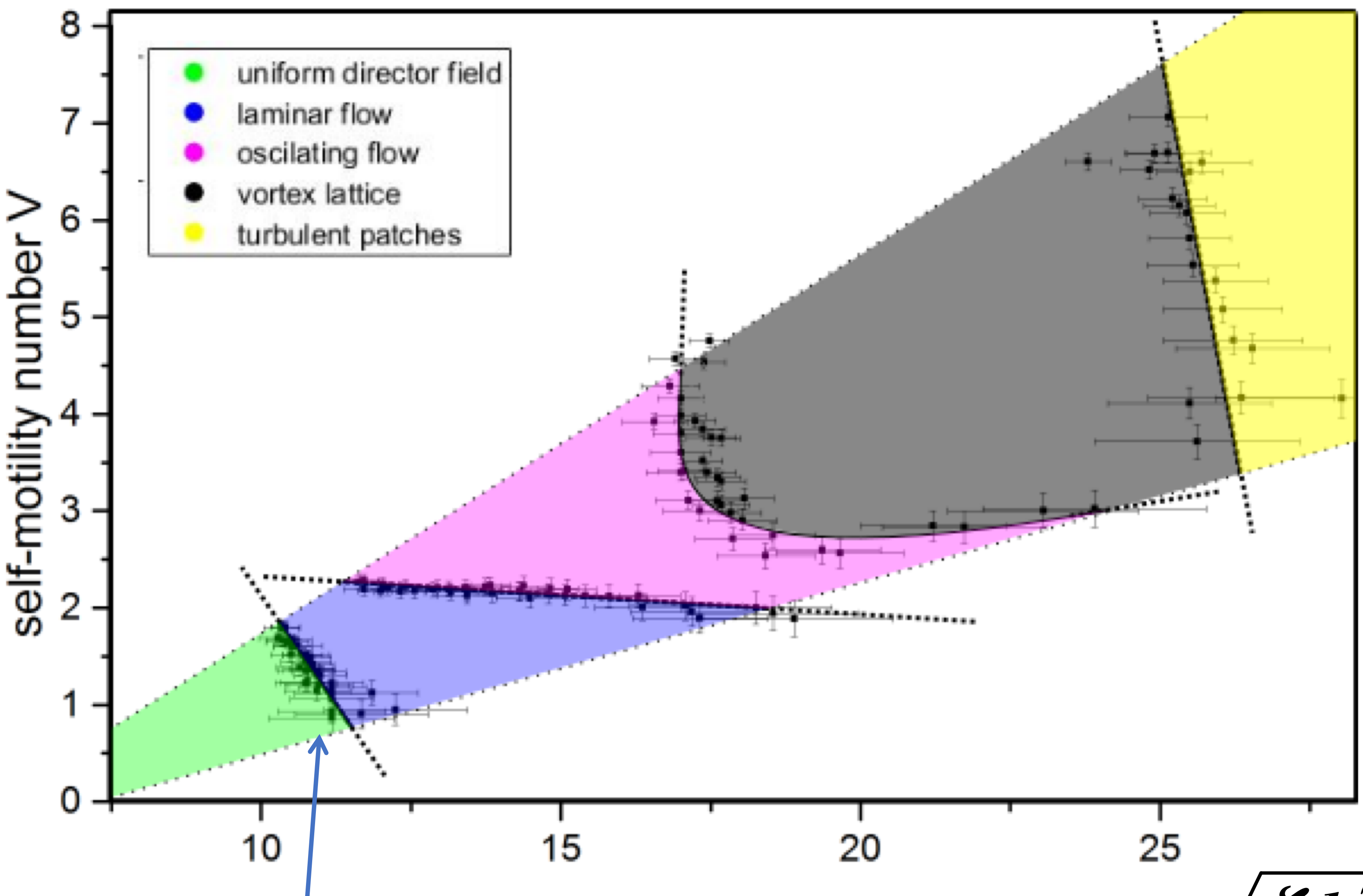
Many active systems are finite in extent – tissues,
organoids, tumours

The physics:

Two competing length scales

Motile topological defects

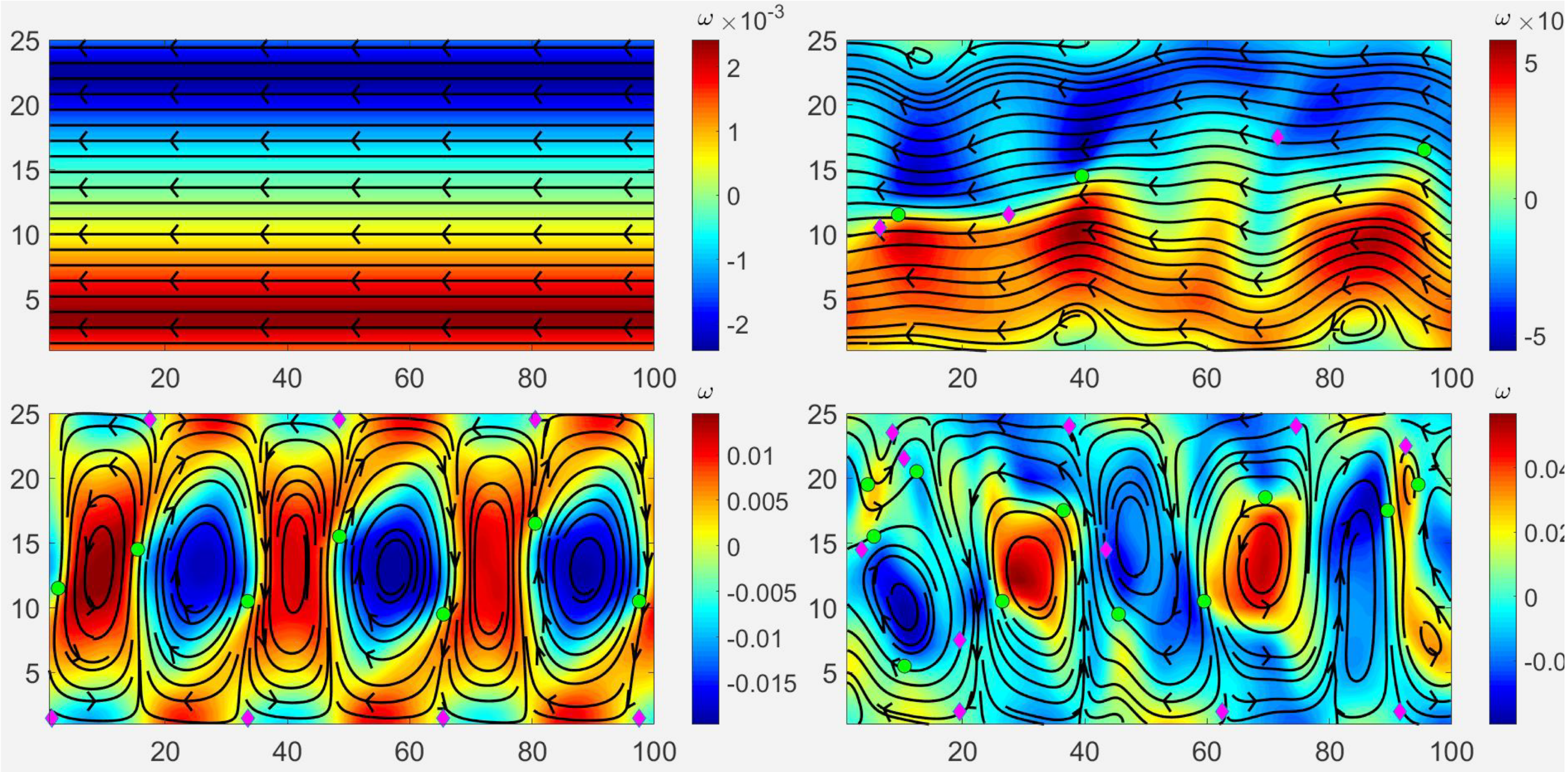
States of an Active Nematic in a Channel



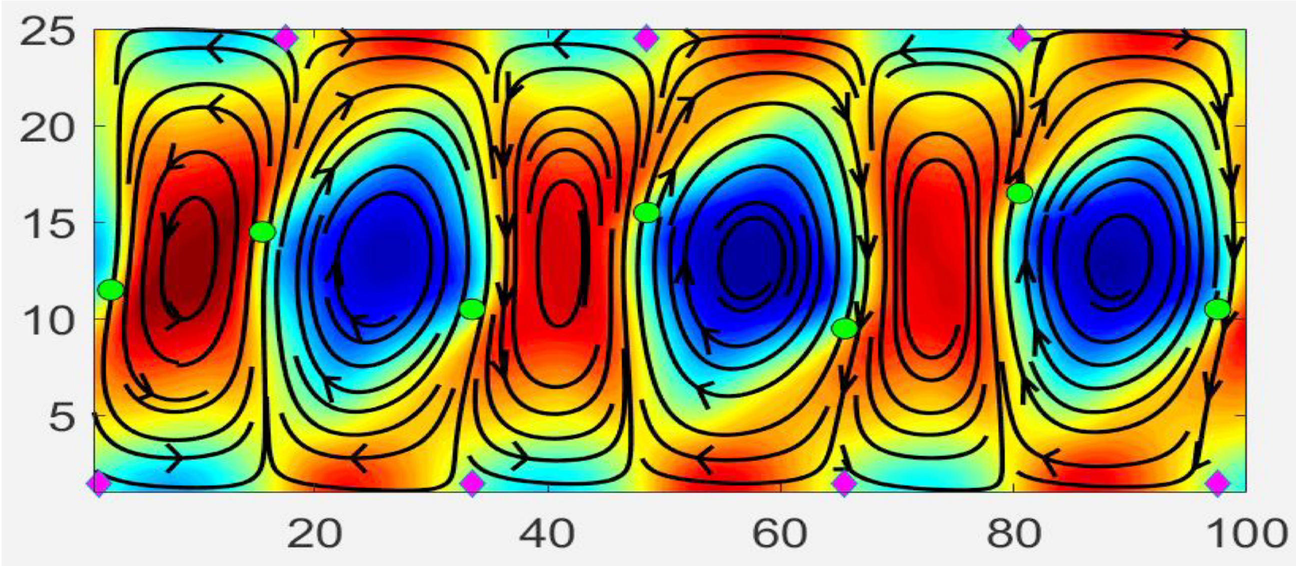
$= \sqrt{\zeta h^2 / K}$

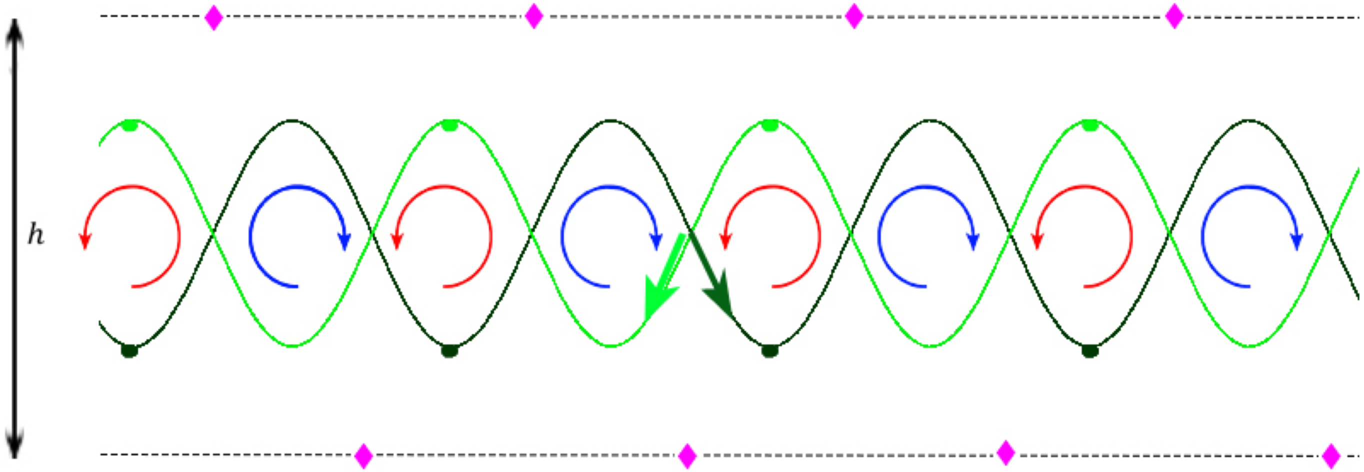
Voituriez et al
EPL (2005)

States of an Active Nematic in a Channel

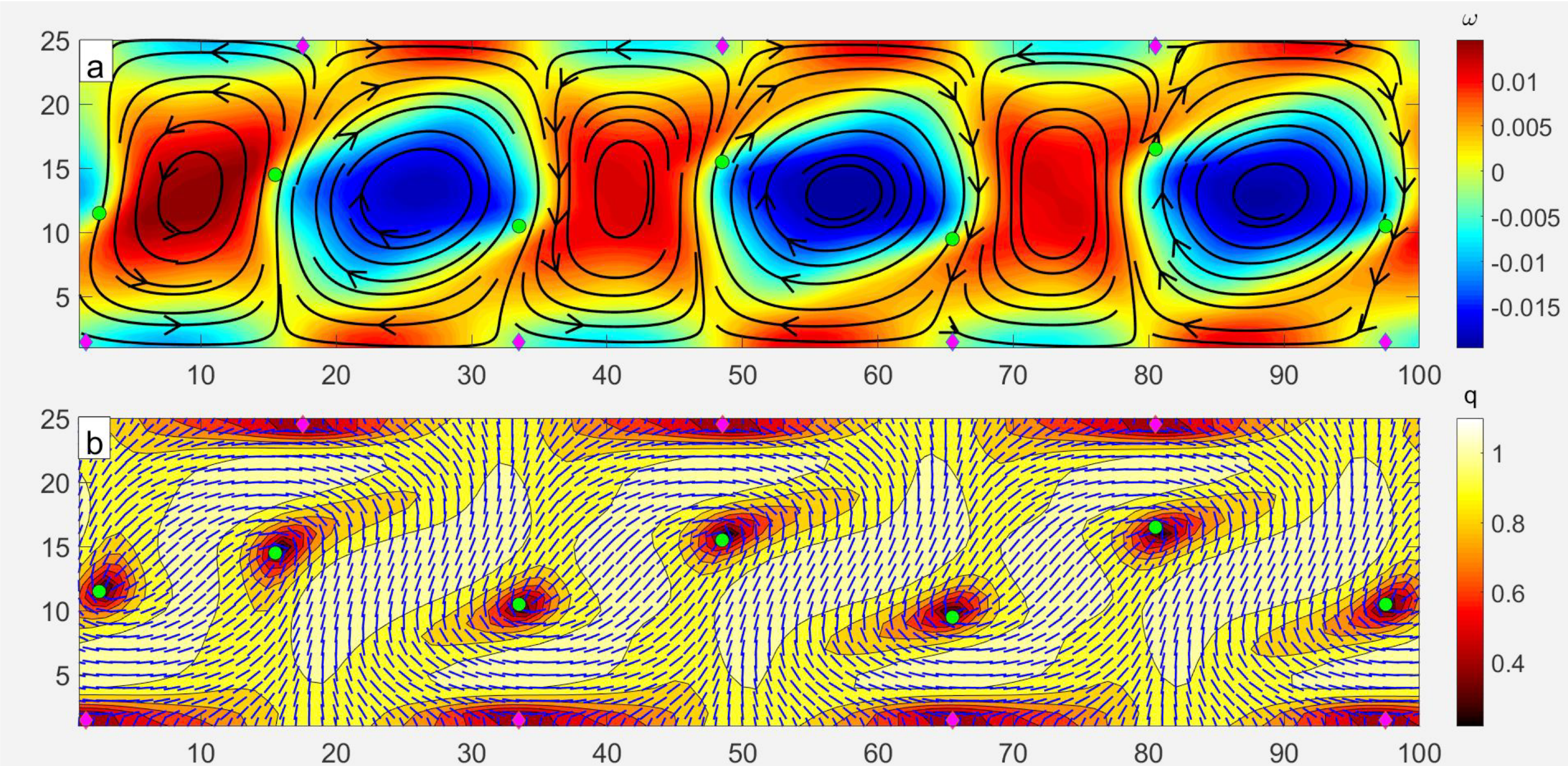


Ceilidh Dance

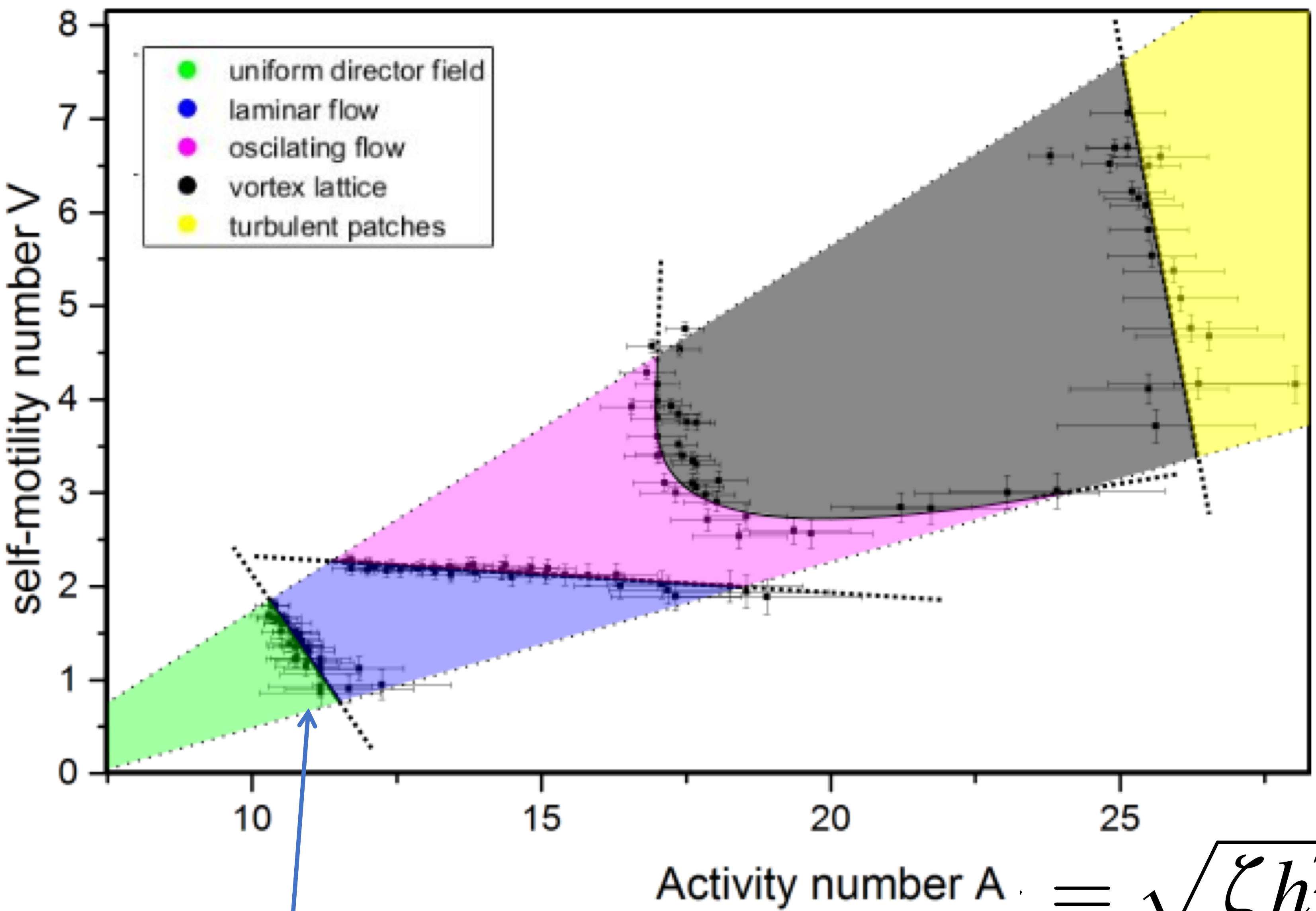




Vortex lattice and active topological microfluidics



States of an Active Nematic in a Channel



$= \sqrt{\zeta h^2 / K}$

Voituriez et al
EPL (2005)

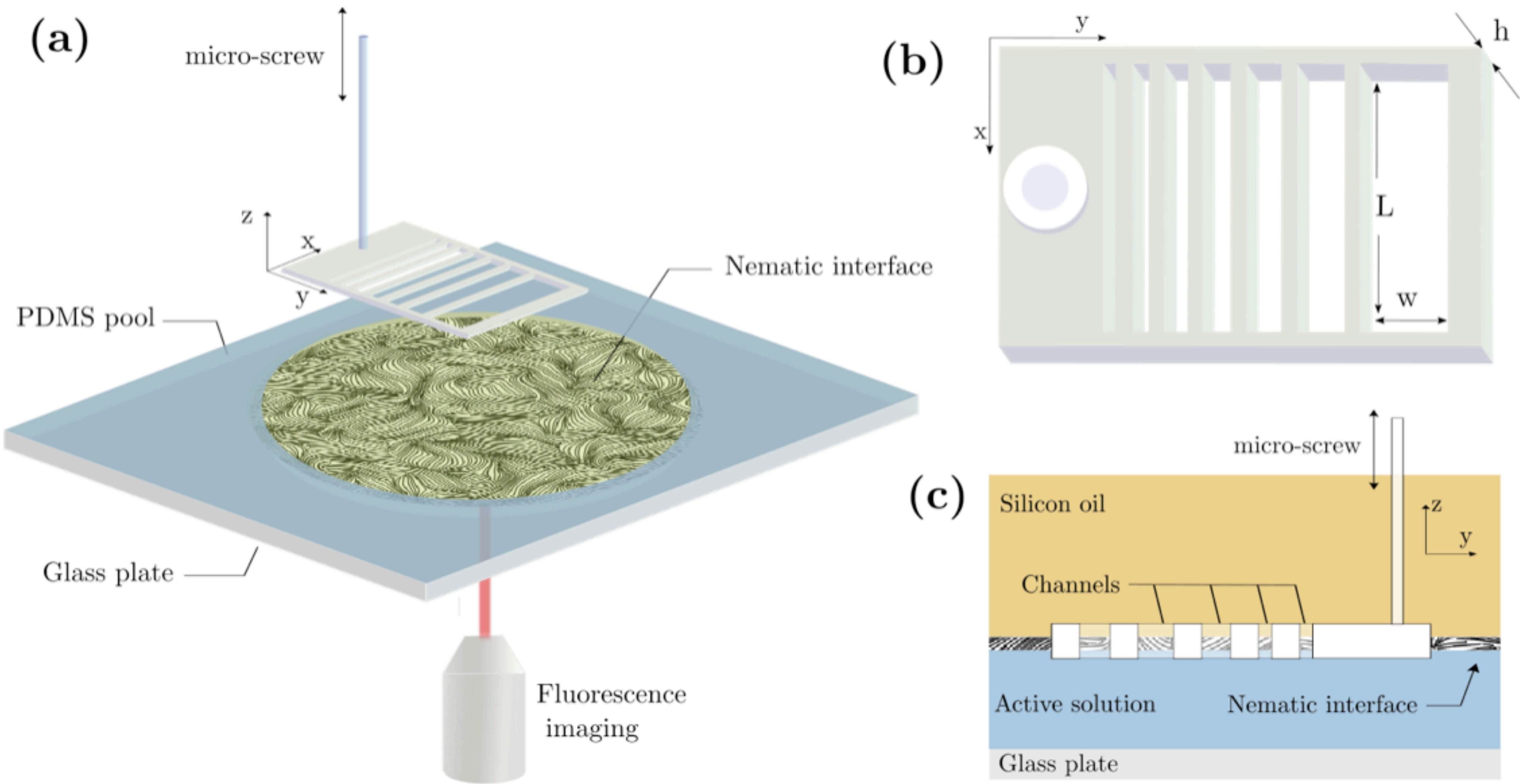
No flow => laminar flow => the Ceilidh dance => active turbulence

Increasing activity =>

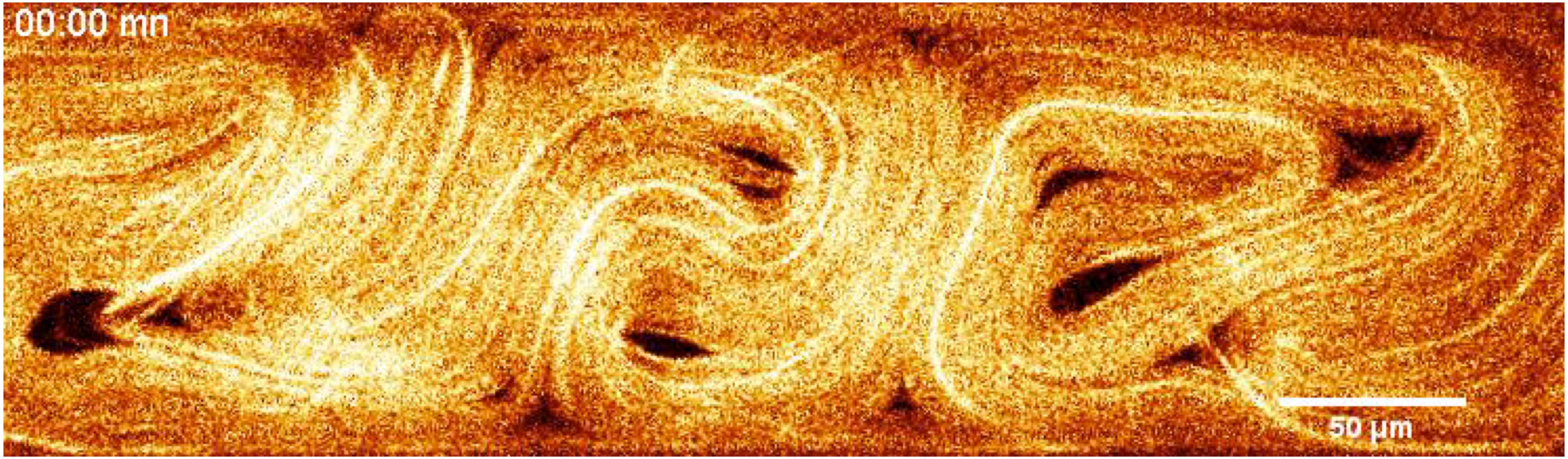
<= Increasing confinement

Microtubules and kinesin motors in channels

Widths 30 – 400 microns



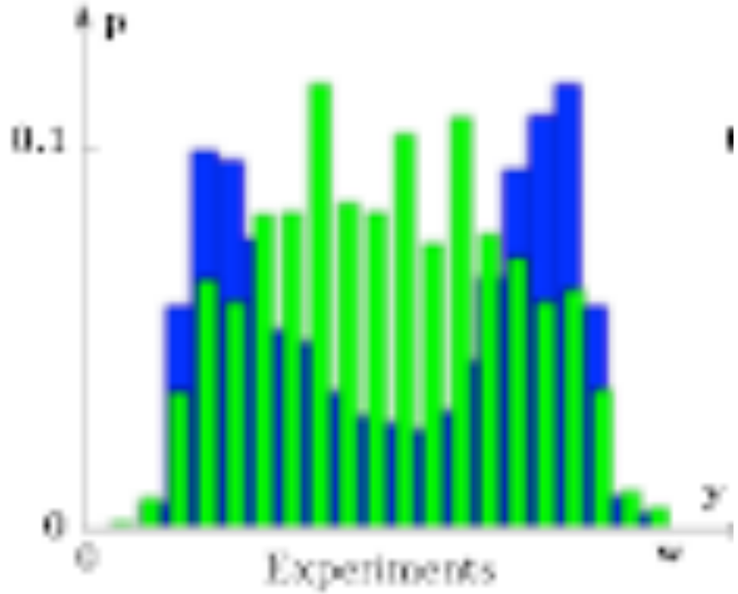
The dancing state in confined microtubule – kinesin mixtures

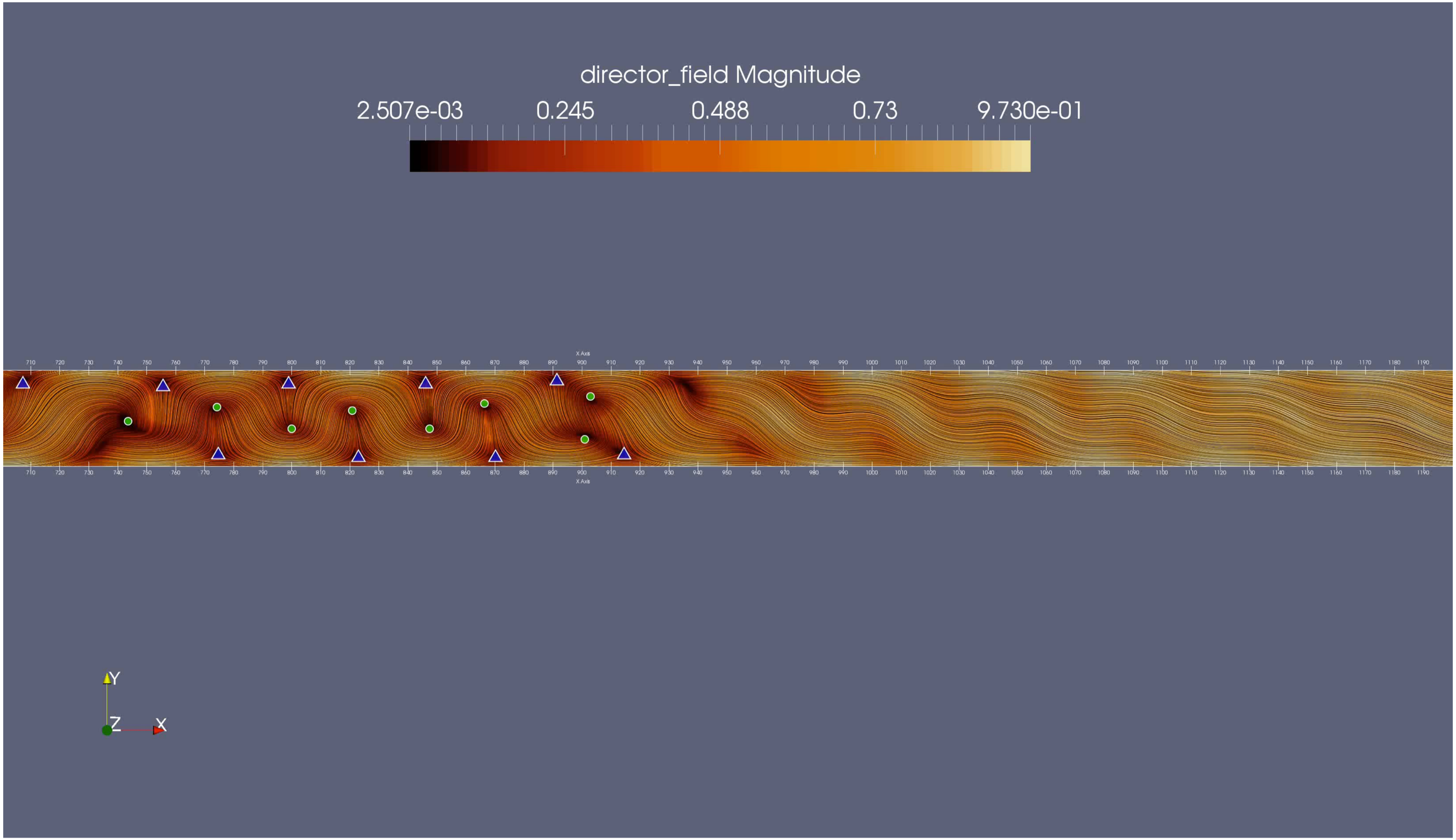


Distribution of defects across
 the channel:

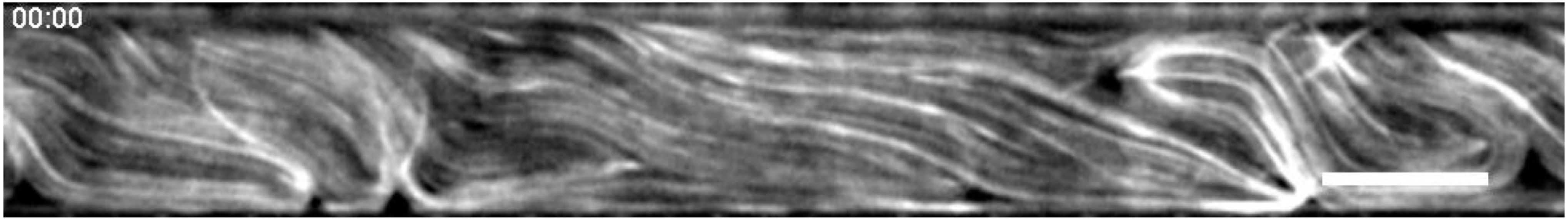
Blue -1/2

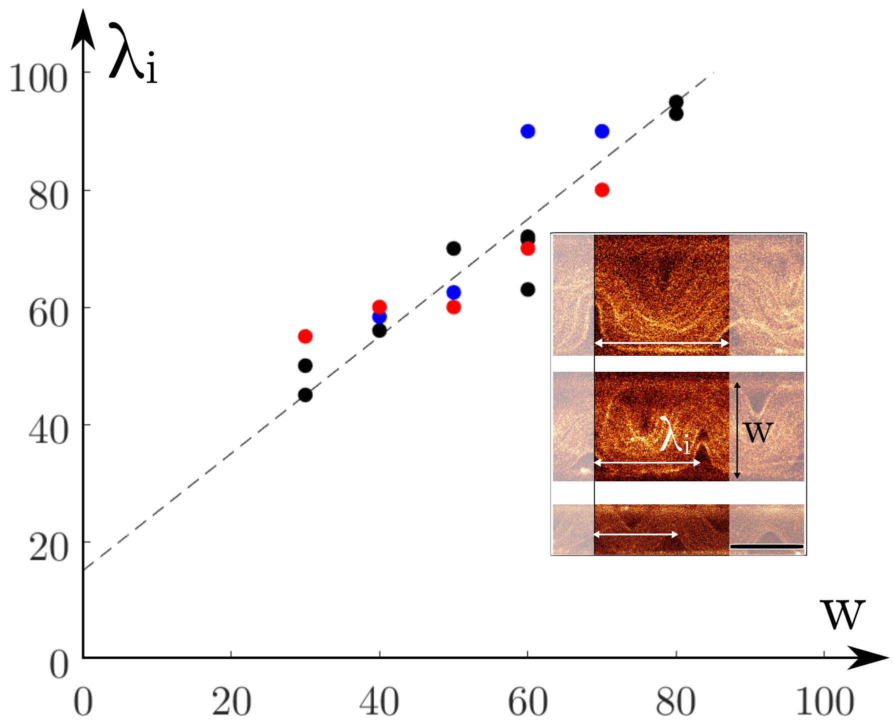
Green +1/2




director_field Magnitude
2.507e-03
0.245
0.488
0.73
9.730e-01
X Axis
Y
Z
X

Shear + periodic bursts of defects

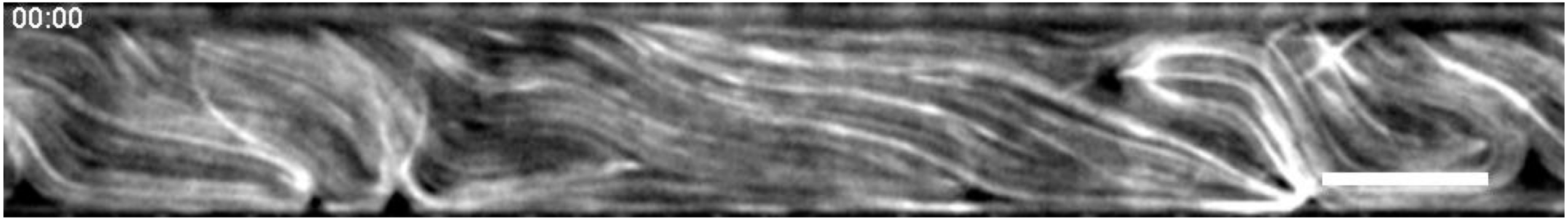


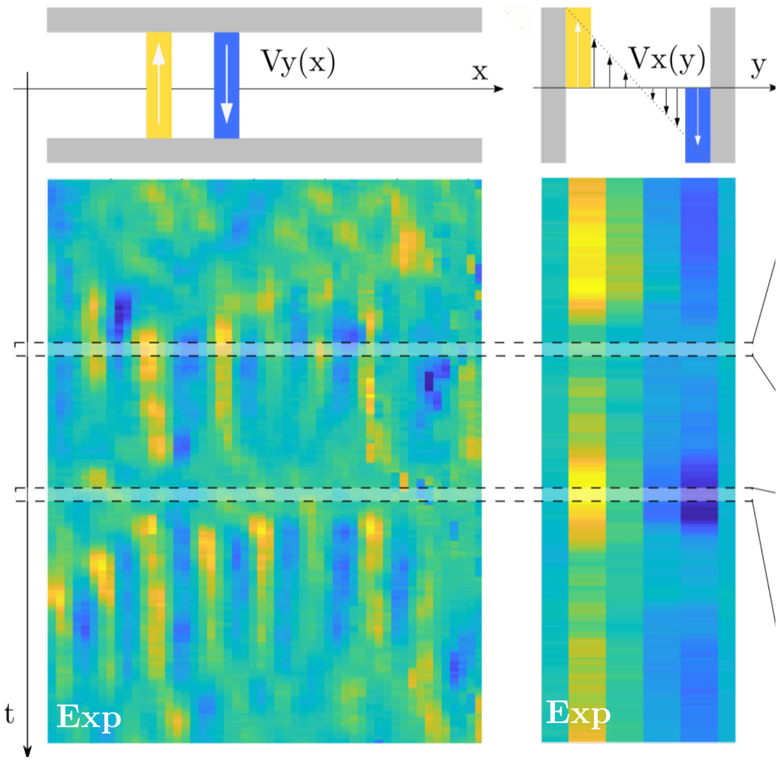


Distance between defects is set by the channel width

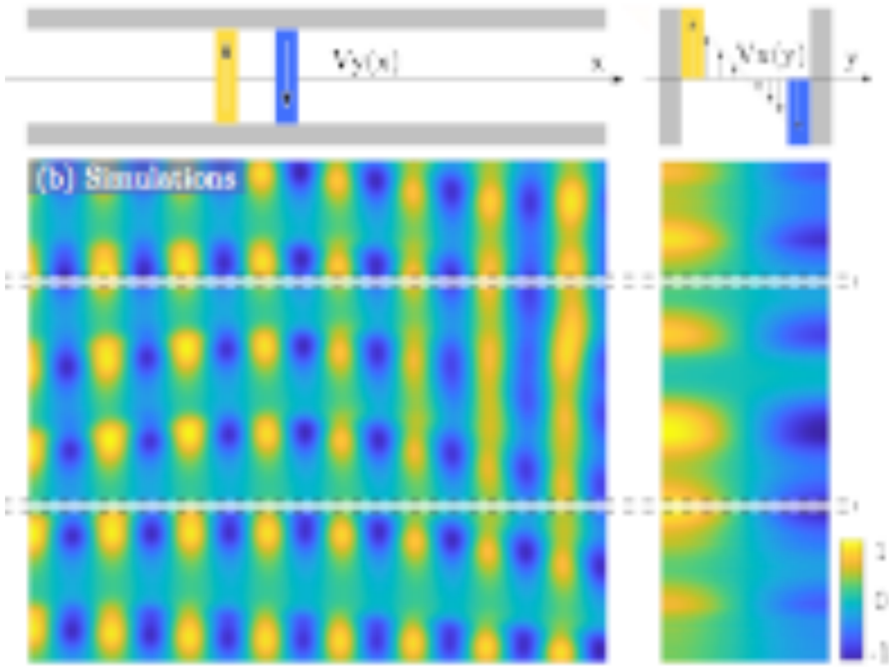
Shear + bursts of defects

Defect bursts are periodic



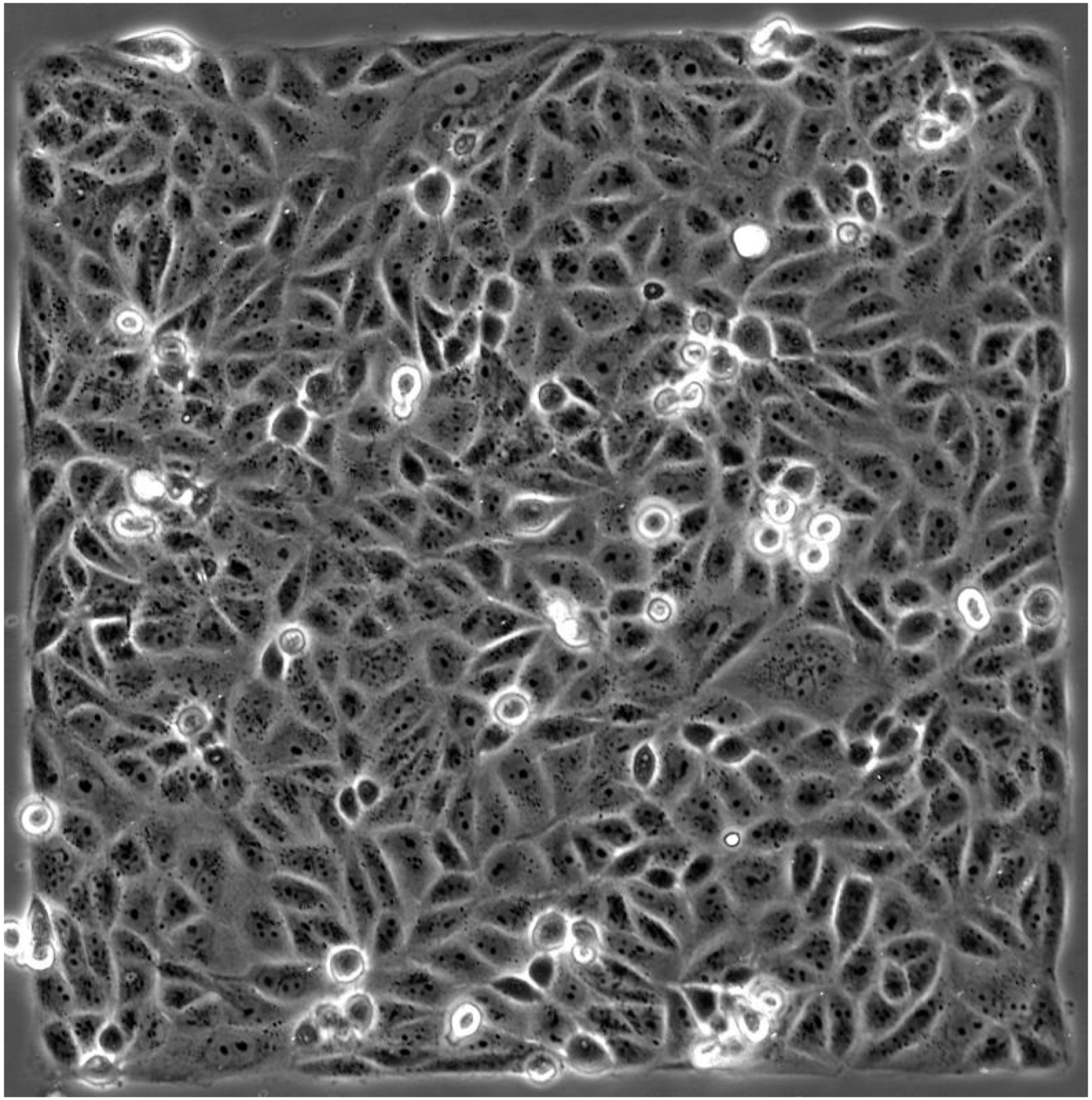


time



1. What is active matter and why is it interesting?
2. Background 1: nematic liquid crystals
3. Background 2: low Reynolds number hydrodynamics
4. Active nematics and active turbulence
5. Self-propelled topological defects
6. Confining active turbulence
7. Bacteria: the hare and the tortoise
8. Eukaryotic cells as an active system

Active turbulence: eukaryotic cells



Thank You

Amin Doostmohammadi

Guanming Zhang

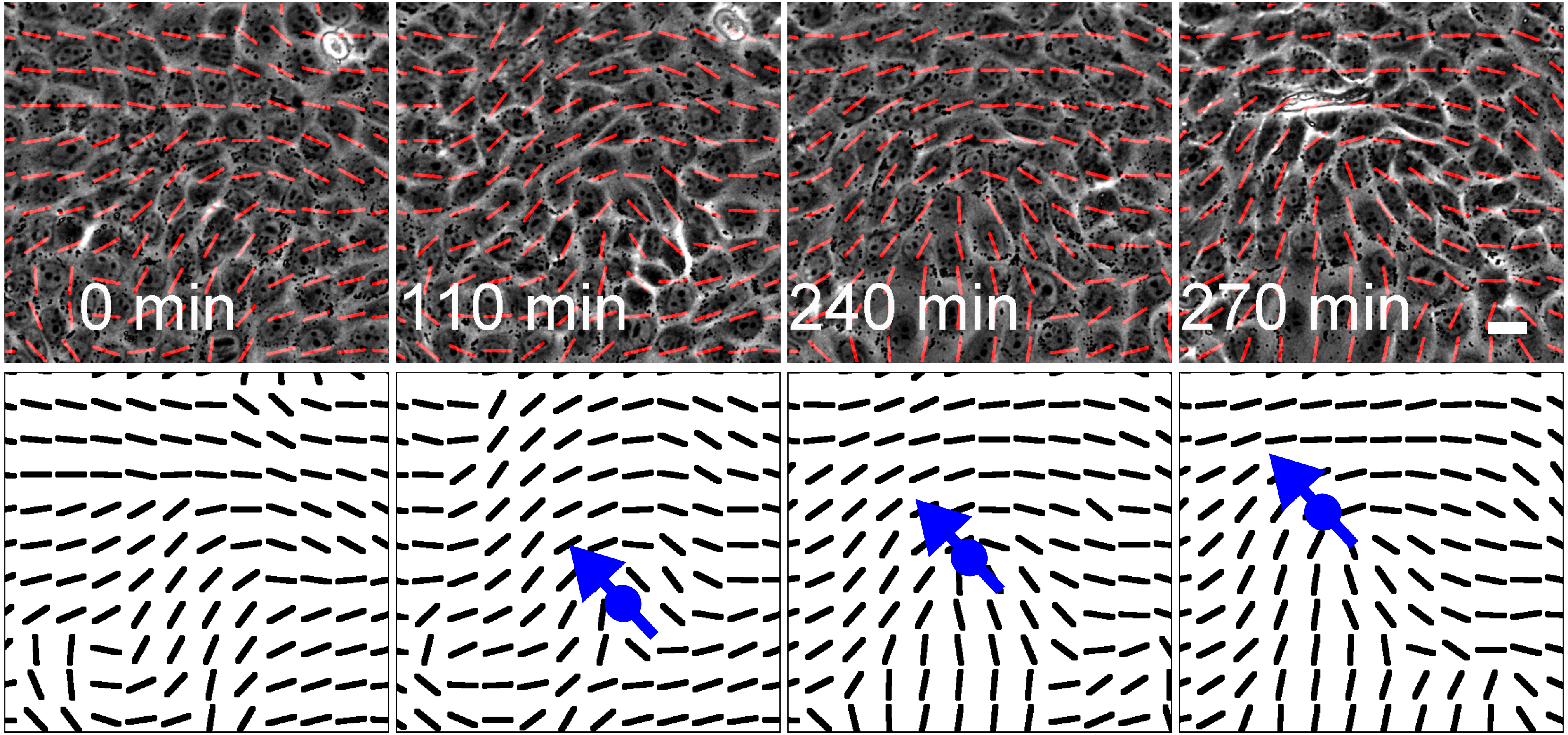
Romain Mueller

Benoit Laboux

Thuan Beng Saw

Saw et al Nature, 2017
Mueller et al Physical Review Letters 2019

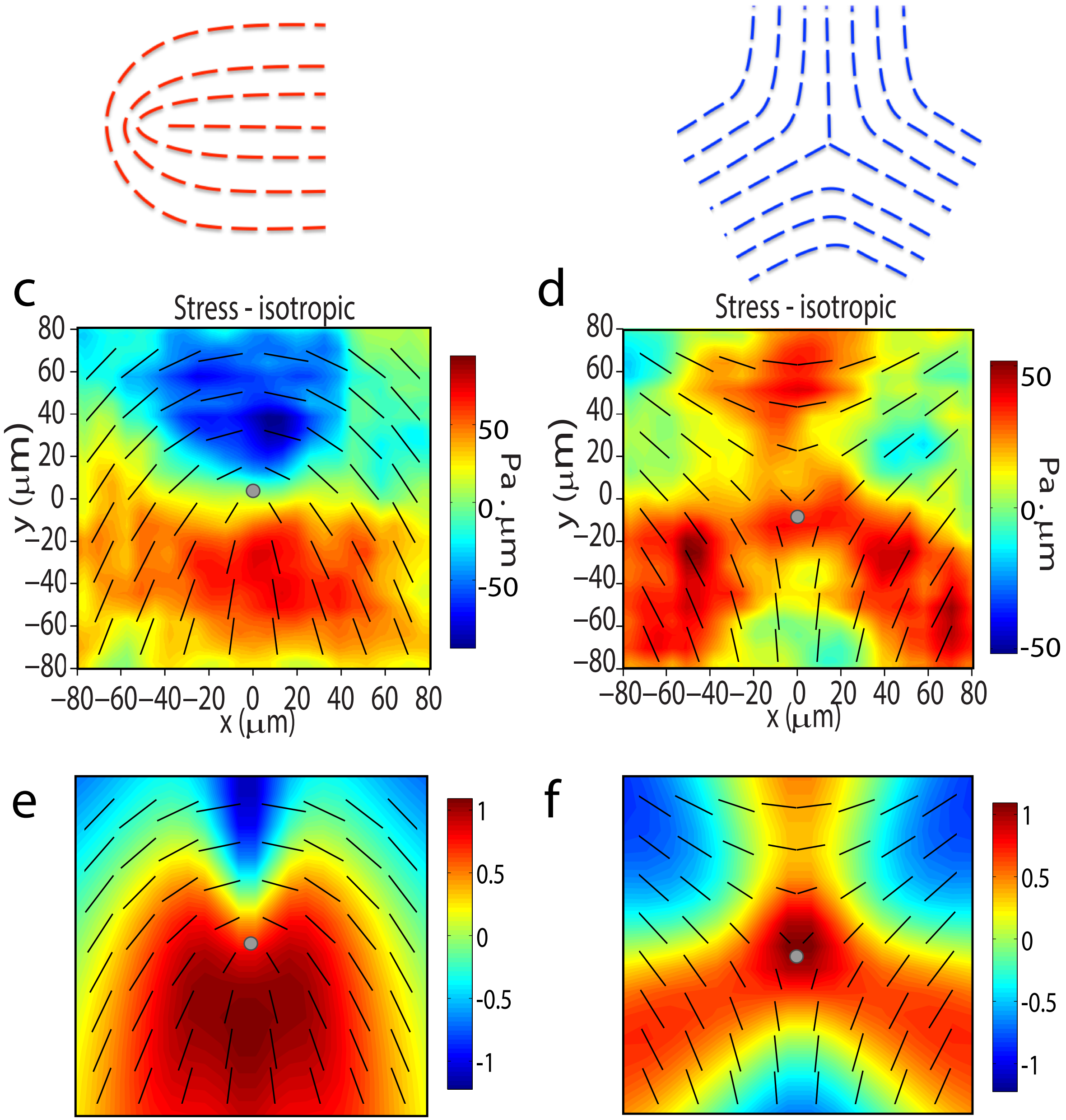
Topological defects in cell layers



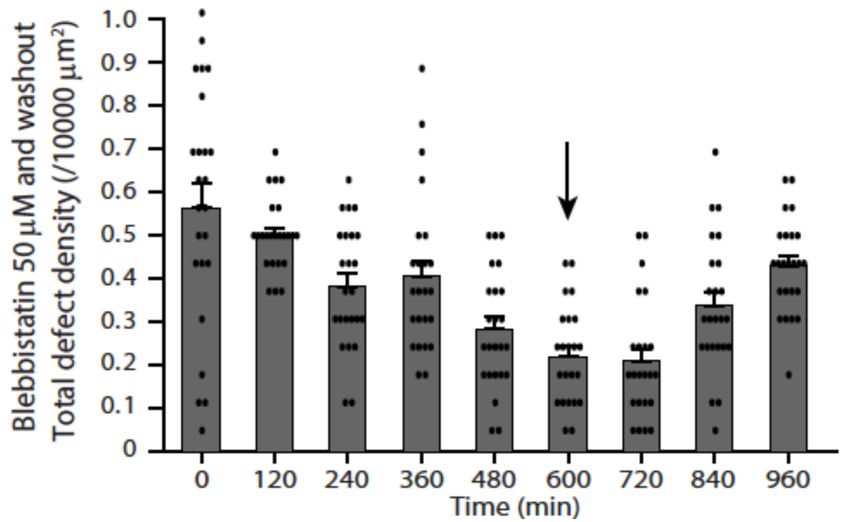
Isotropic stress around a topological defect

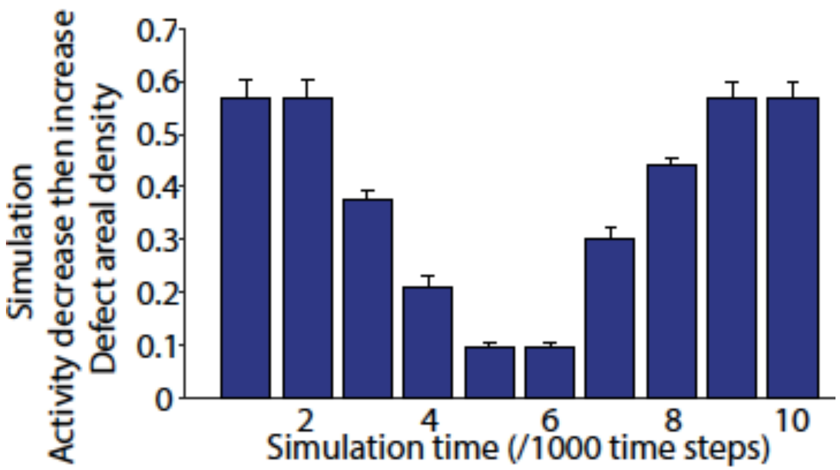
experiment

simulations



‘Turning off’ motility

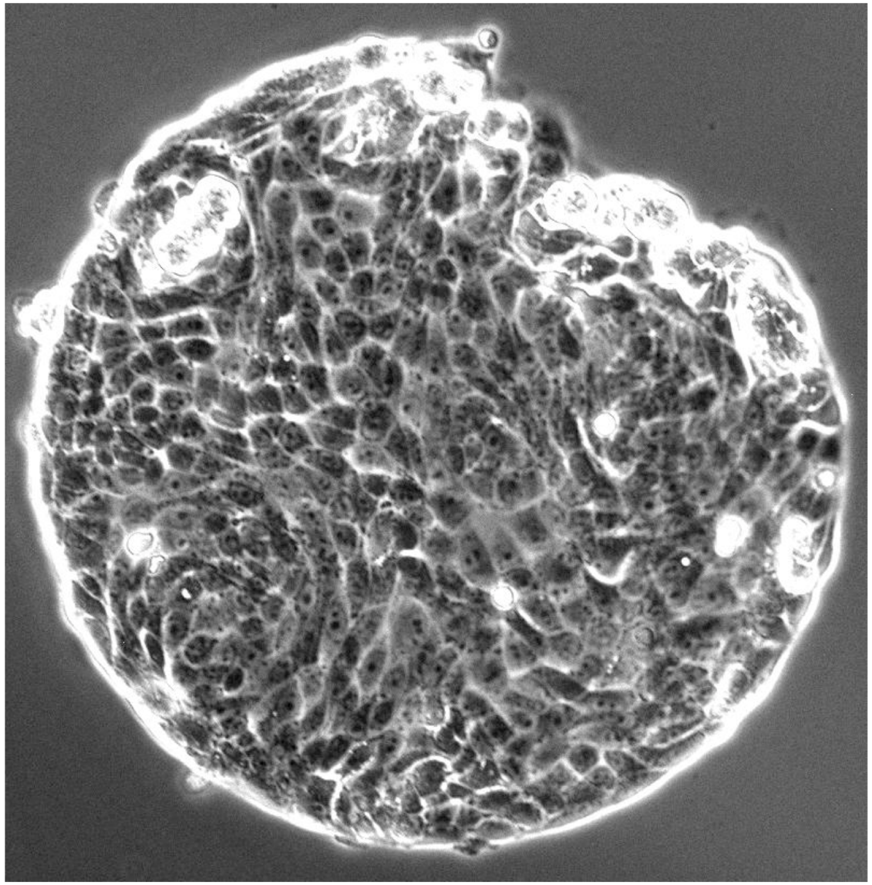




Topological defects in epithelia govern the extrusion of dead cells

T. Beng Saw, A. Doostmohammadi et al, Nature 544 212 (2017)

Topology in biology?



Positions of apoptosis correlated with +1/2 topological defects

High stress drives YAP from nucleus to cytoplasm which is a signal for cell death

Cell dies and is ejected from the monolayer

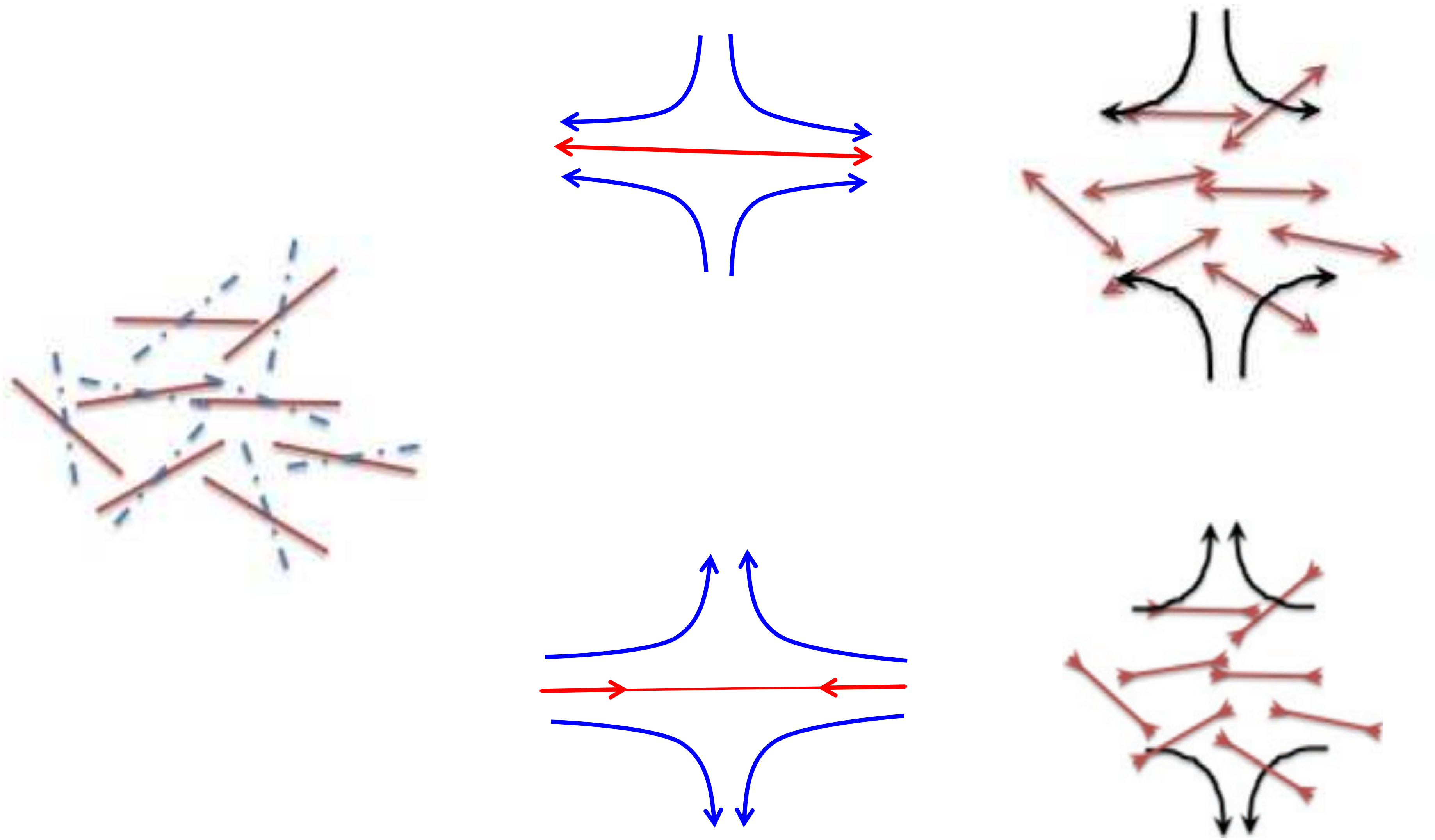
Questions

Why do isotropic cells give nematic defects?

Why are the defects extensile?

Can we model cell mechanics as an active system?

Extensile forces enhance nematic fluctuations



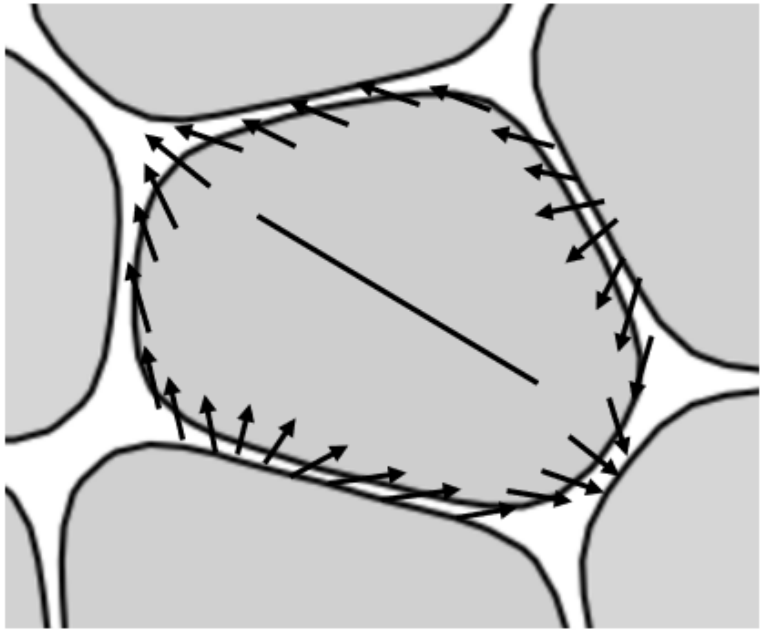
Active dipolar force

active dipolar stress for cell i:

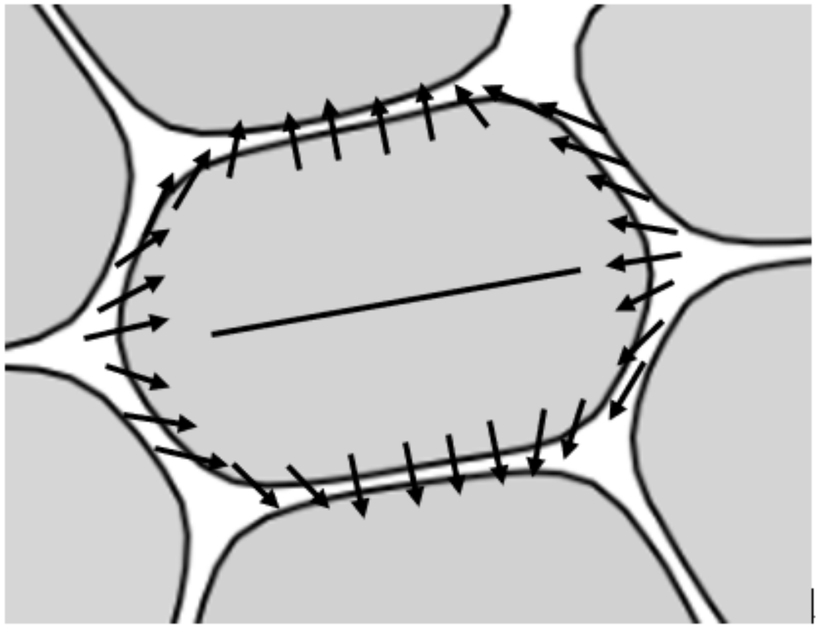
$$\sigma_{Q,i} = -\zeta \varphi_i(\mathbf{x}) \mathcal{Q}_i$$

active dipolar force density:

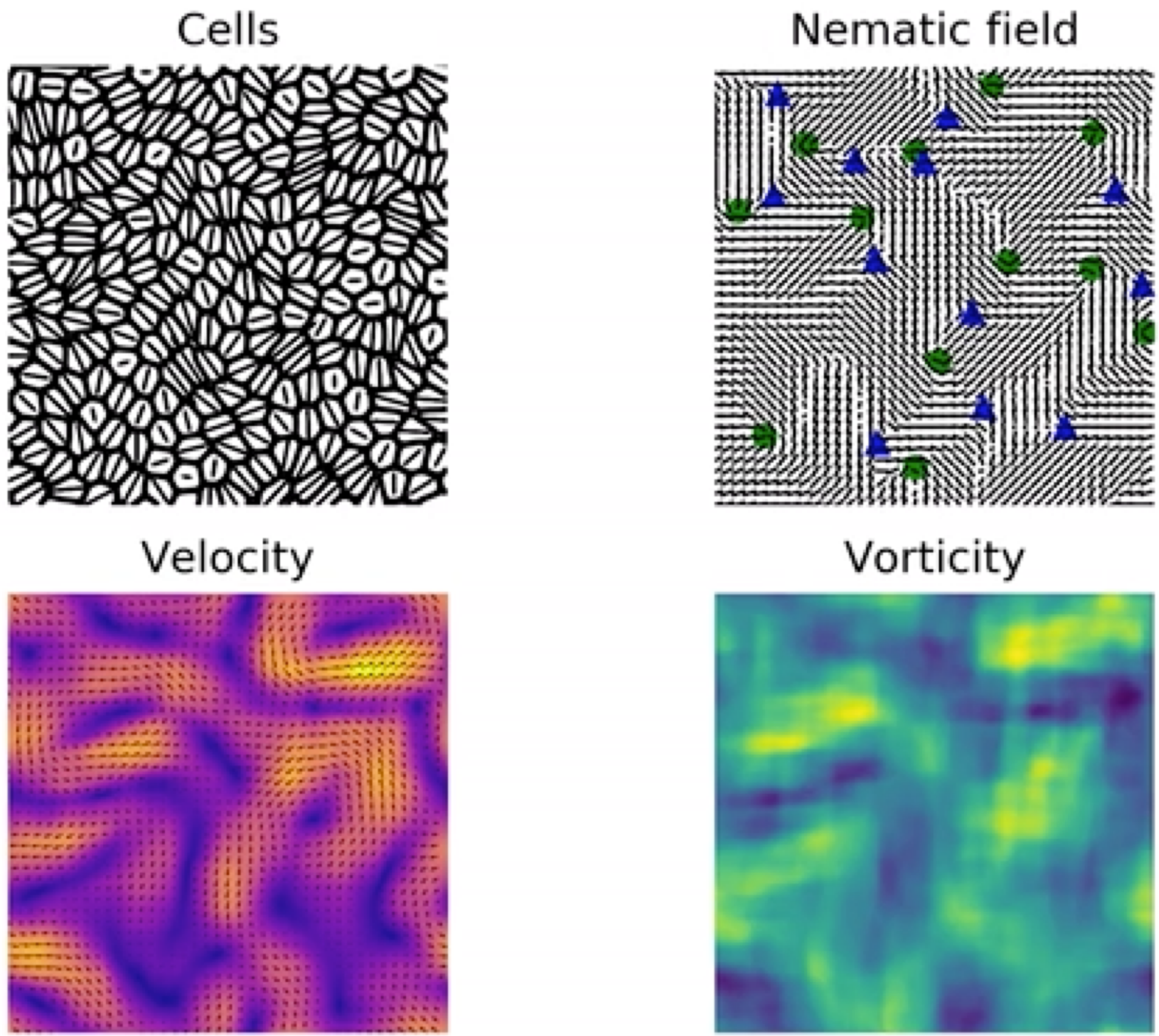
$$\mathbf{f}_i^{\text{dipolar}} = \nabla \cdot \sigma_{Q_i} = -\zeta \mathcal{Q}_i \cdot \nabla \varphi_i$$



(a) extensile

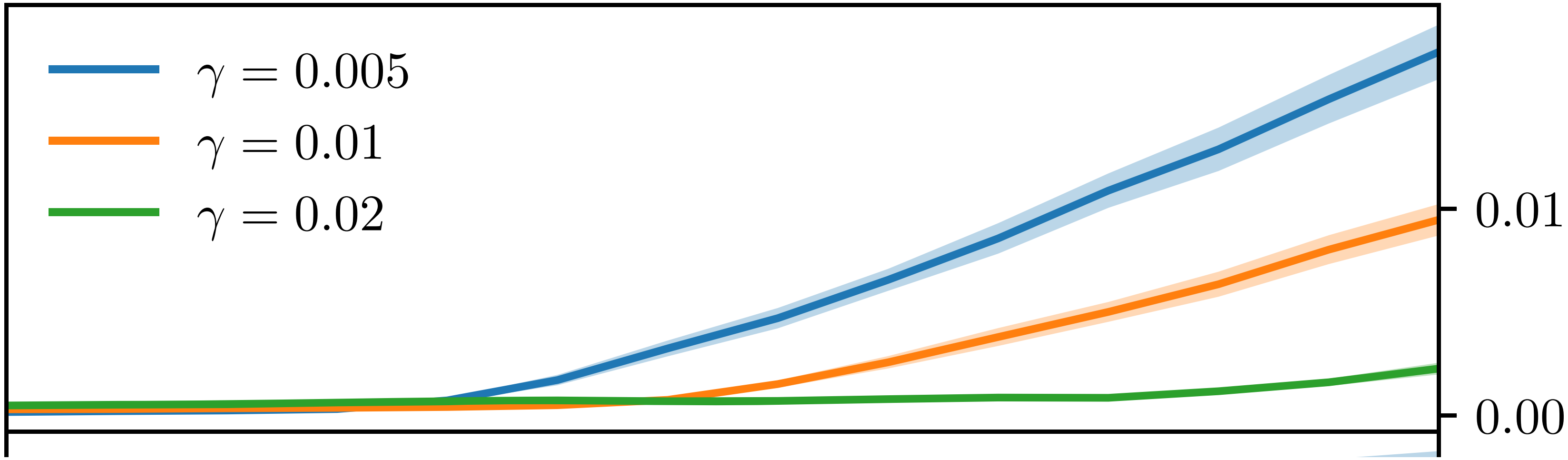


(b) contractile


Cells
Nematic field
Velocity
Vorticity

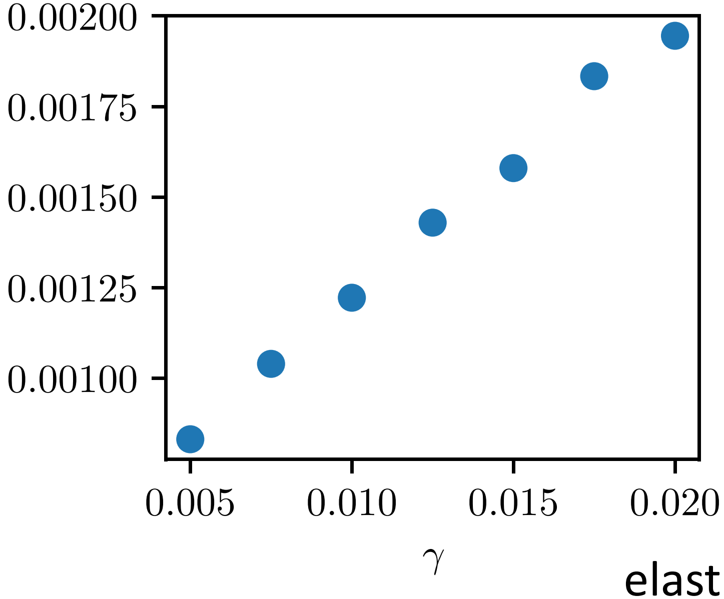
Onset of active turbulence

r m s
velocity



extensile activity

threshold for active
turbulence



elasticity

Questions and some answers

Why do isotropic cells give nematic defects

Bootstrap effect of extensile forces

Why are the defects extensile?

Due to interactions between cells

Why don't we see walls?

Hydrodynamic instability weak

Can we model cell mechanics as an active system?

??

Polarisation dynamics

Cf vertex models

Confinement, cell division ….