Discussion session: Bacterial "Sheets"

Jörn Dunkel

dunkel@mit.edu

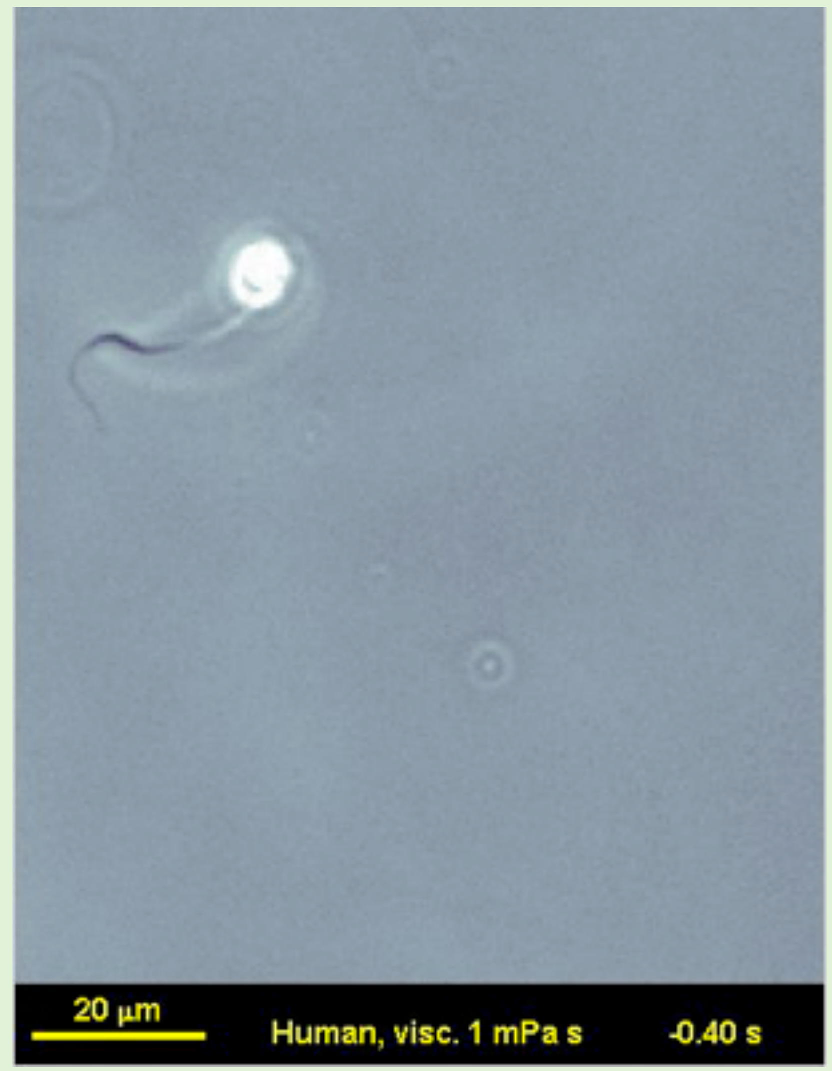
- effects of spatial dimensionality on individual microbial swimming (2D vs. 3D)
- intrinsic vortex scale selection in bacterial suspensions
- confinement & collective dynamics of quasi-2D suspensions (edge currents, magnetic order, quasi-“superfluidity”, etc.)
- defect dynamics and long-range order in 2D planar/curved active nematics

Model organisms

Chlamydomonas alga

Drescher et al (2010) PRL
Guasto et al (2010) PRL

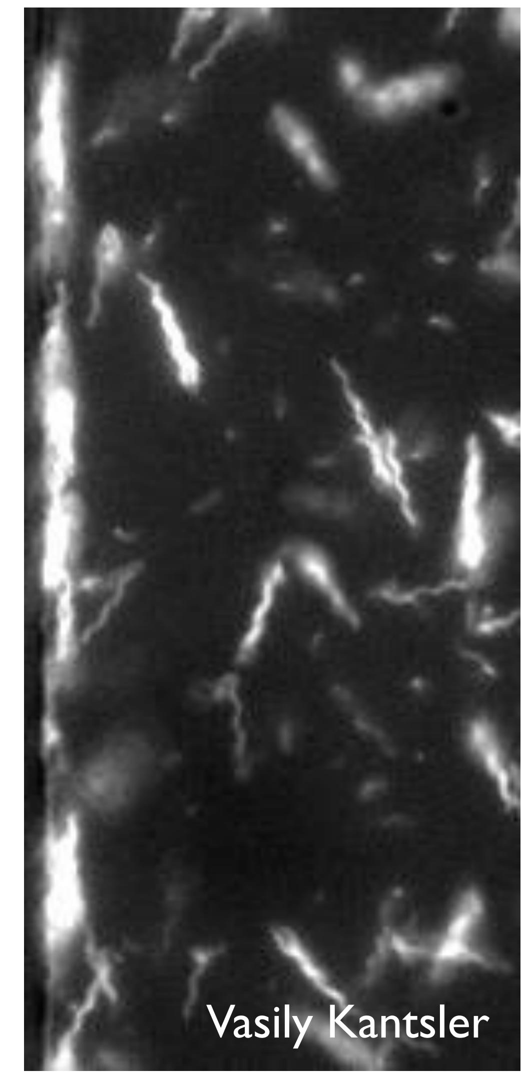
Human sperm cell



Kantsler et al (2014) eLife
Friedrich et al (2010) JEB

Eukaryotes

Bacteria

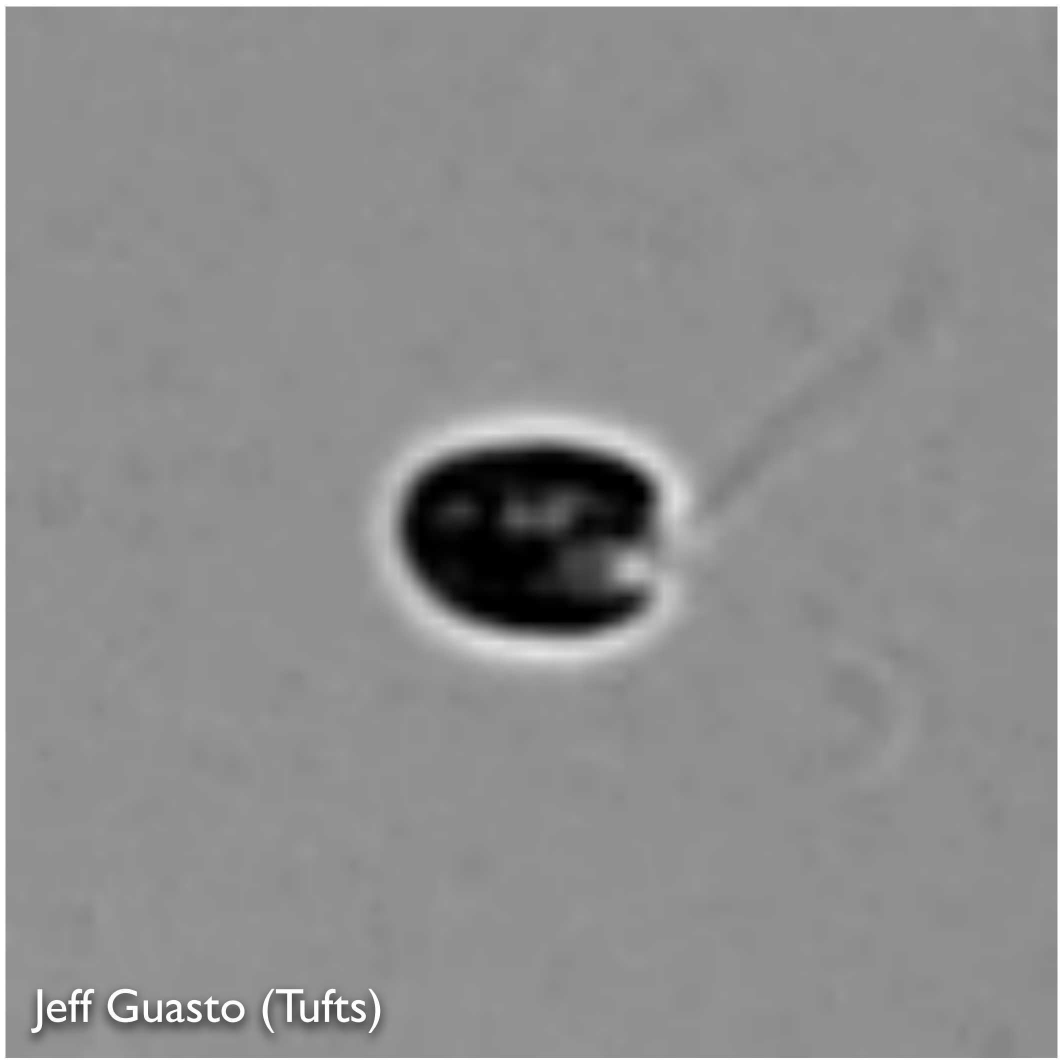


Drescher et al (2011) PNAS

Prokaryote

Swimming strategies

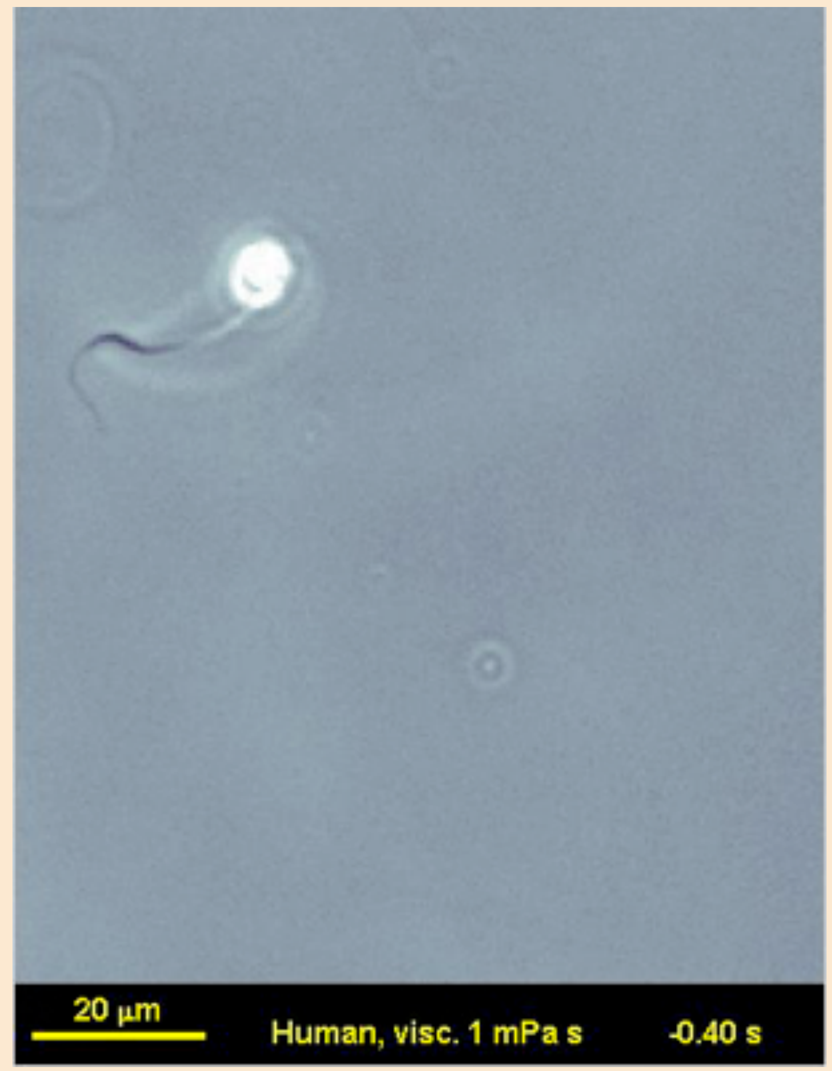
Chlamydomonas alga



Drescher et al (2010) PRL
Guasto et al (2010) PRL

Puller

Human sperm cell



Kantsler et al (2014) eLife
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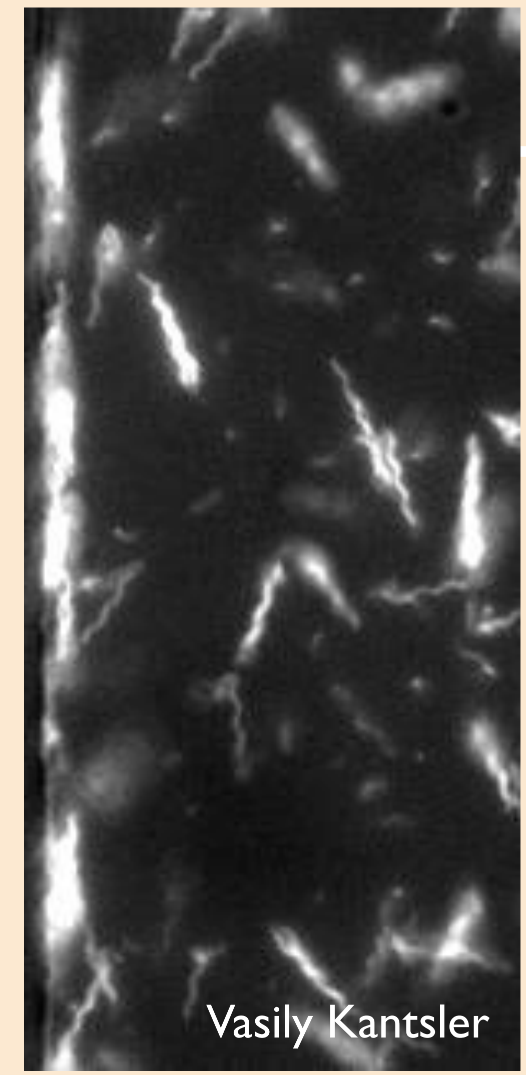
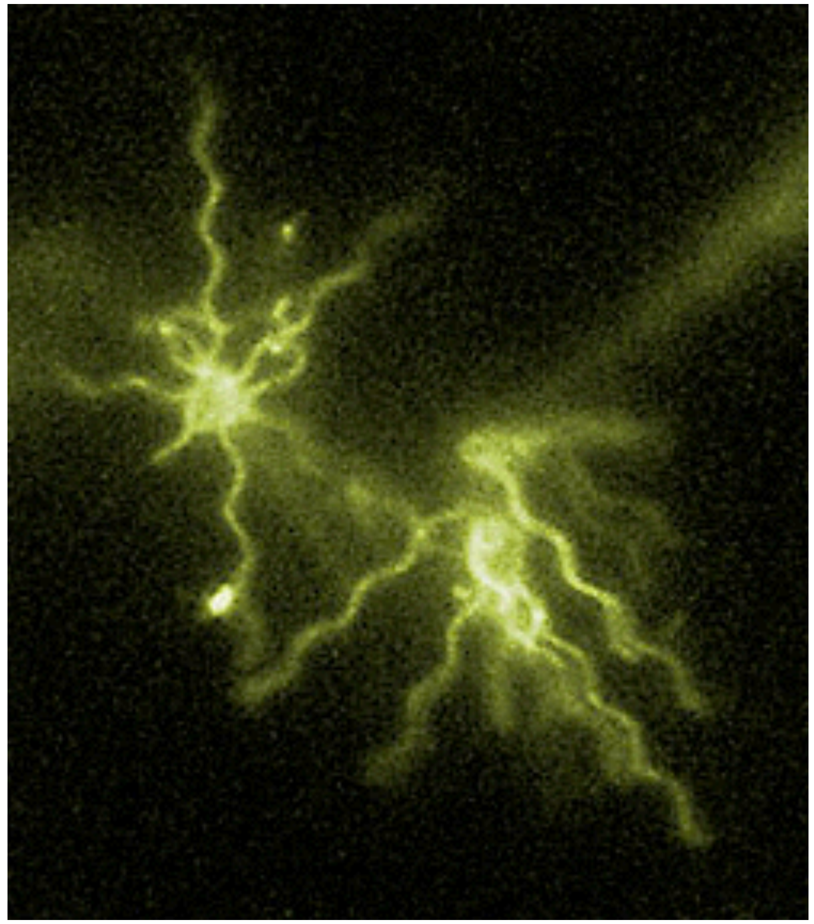
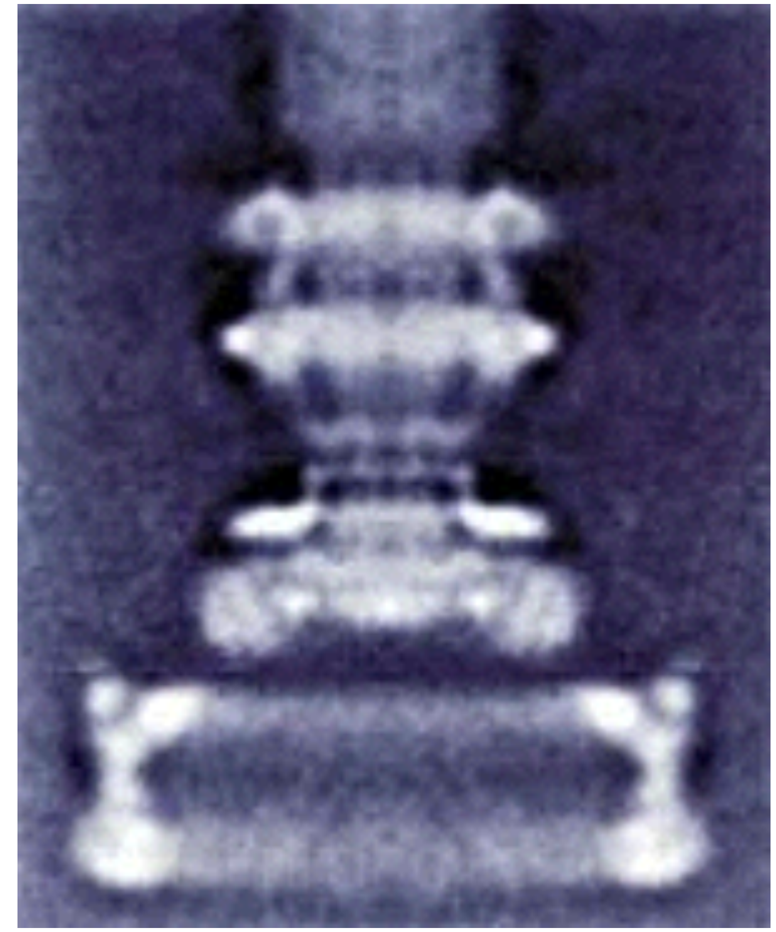
Bacteria



Drescher et al (2011) PNAS

Pusher





Berg (1999) Physics Today

Bacterial Hydrodynamics*

Eric Lauga†

Department of Applied Mathematics and Theoretical Physics, Centre for Mathematical Sciences, University of Cambridge, Wilberforce Road, Cambridge, CB3 0WA, United Kingdom

http://arxiv.org/pdf/1509.02184v1.pdf

Swimming at low Reynolds number

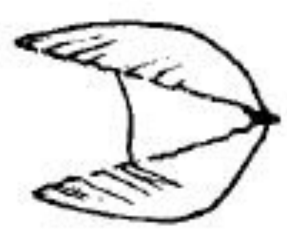
Navier - Stokes:

$$-\nabla p + \eta \nabla^2 \vec{v} = \cancel{\rho \frac{\partial \vec{v}}{\partial t}} + \cancel{\rho (\vec{v} \cdot \nabla) \vec{v}}$$

If $\mathcal{R} \sim UL\rho/\eta \ll 1$

Time doesn't matter. The pattern of motion is the same, whether slow or fast, whether forward or backward in time.

The Scallop Theorem



American Journal of Physics, Vol. 45, No. 1, January 1977

Geoffrey I Taylor

James Lighthill

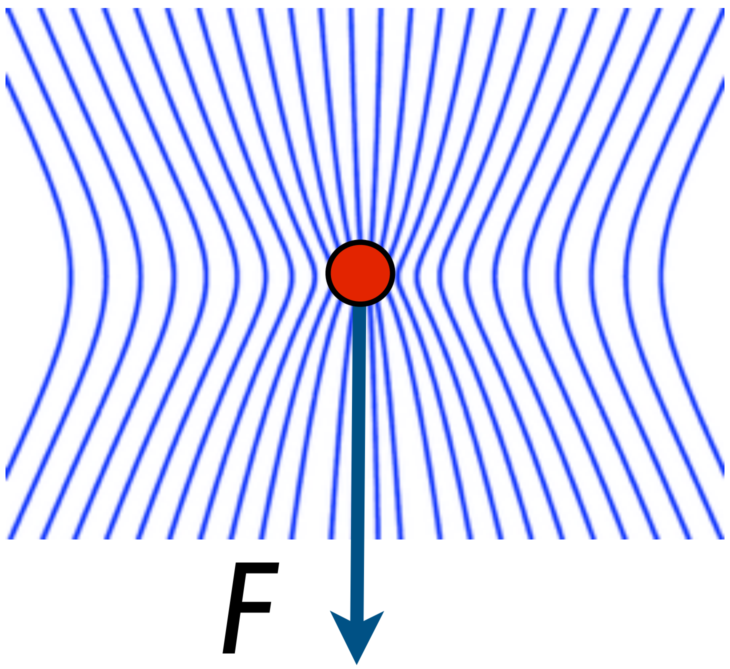
Edward Purcell

$$0 = \mu \nabla^2 \boldsymbol{u} - \nabla p + \boldsymbol{f},$$
$$0 = \nabla \cdot \boldsymbol{u}.$$

+ time-dependent BCs

Superposition of singularities

3D stokeslet



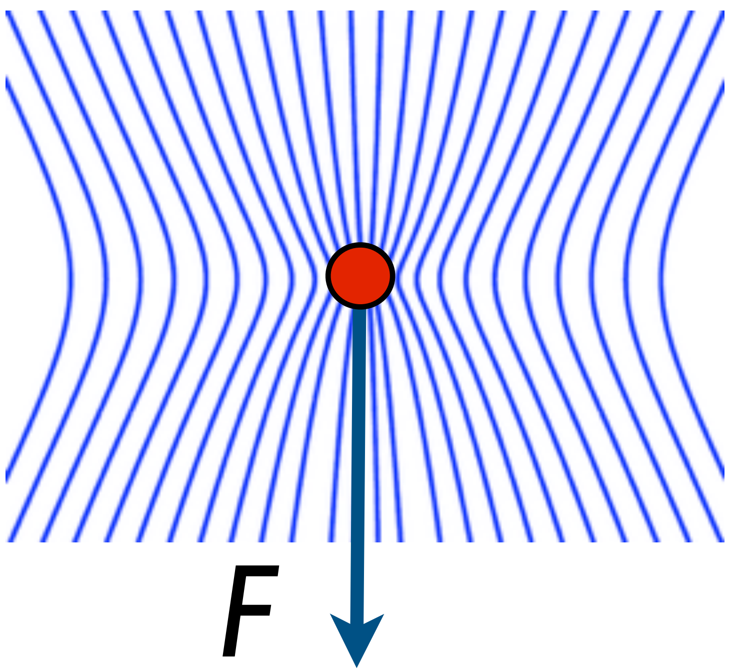
$$p(\boldsymbol{r}) = \frac{\hat{\boldsymbol{r}} \cdot \boldsymbol{F}}{4\pi r^2} + p_0$$

$$v_i(\boldsymbol{r}) = \frac{(8\pi\mu)^{-1}}{r}[\delta_{ij} + \hat{r}_i\hat{r}_j]F_j$$

flow ~ r^{-1}

Superposition of singularities

3D stokeslet



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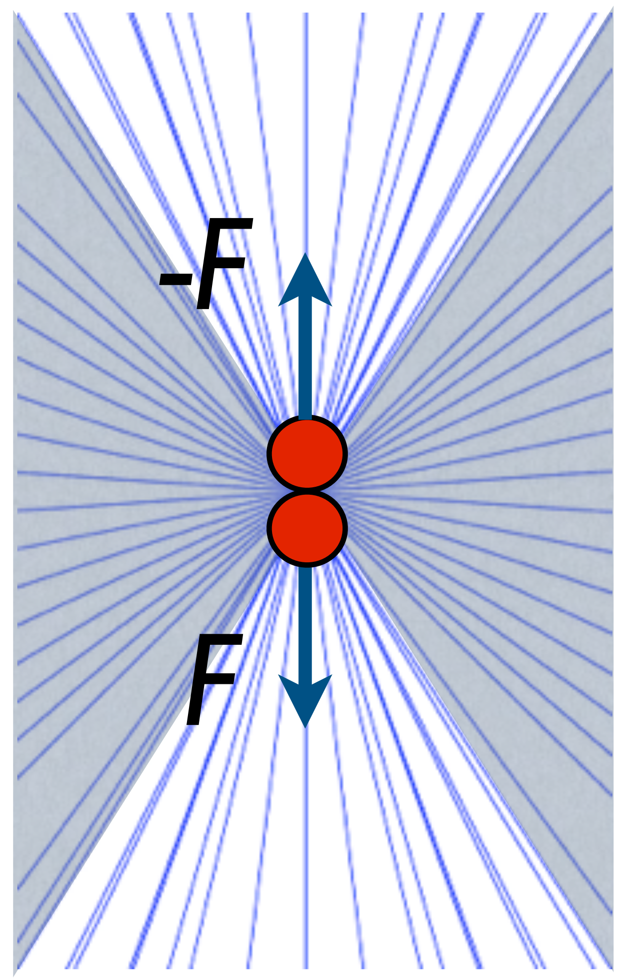
flow ~ r^{-1}

2 x stokeslet = symmetric dipole

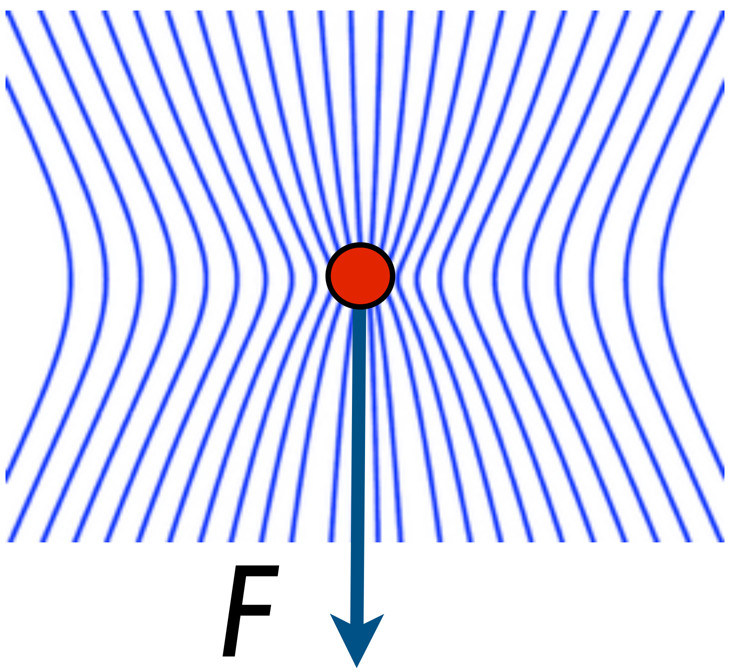


r^{-2}

'pusher' dipole

Superposition of singularities

stokeslet



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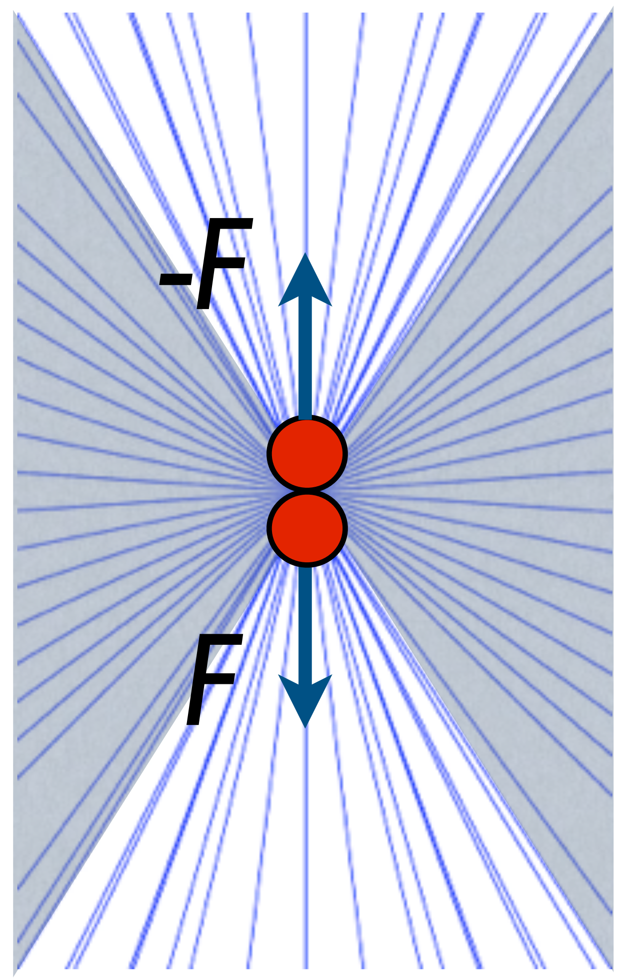

r^{-2}

'pusher' dipole

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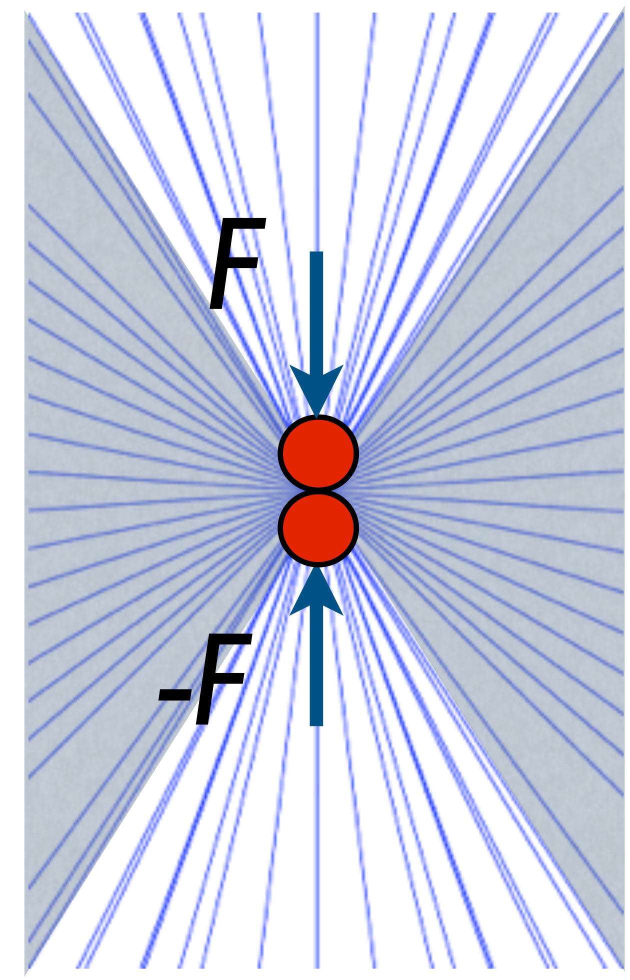
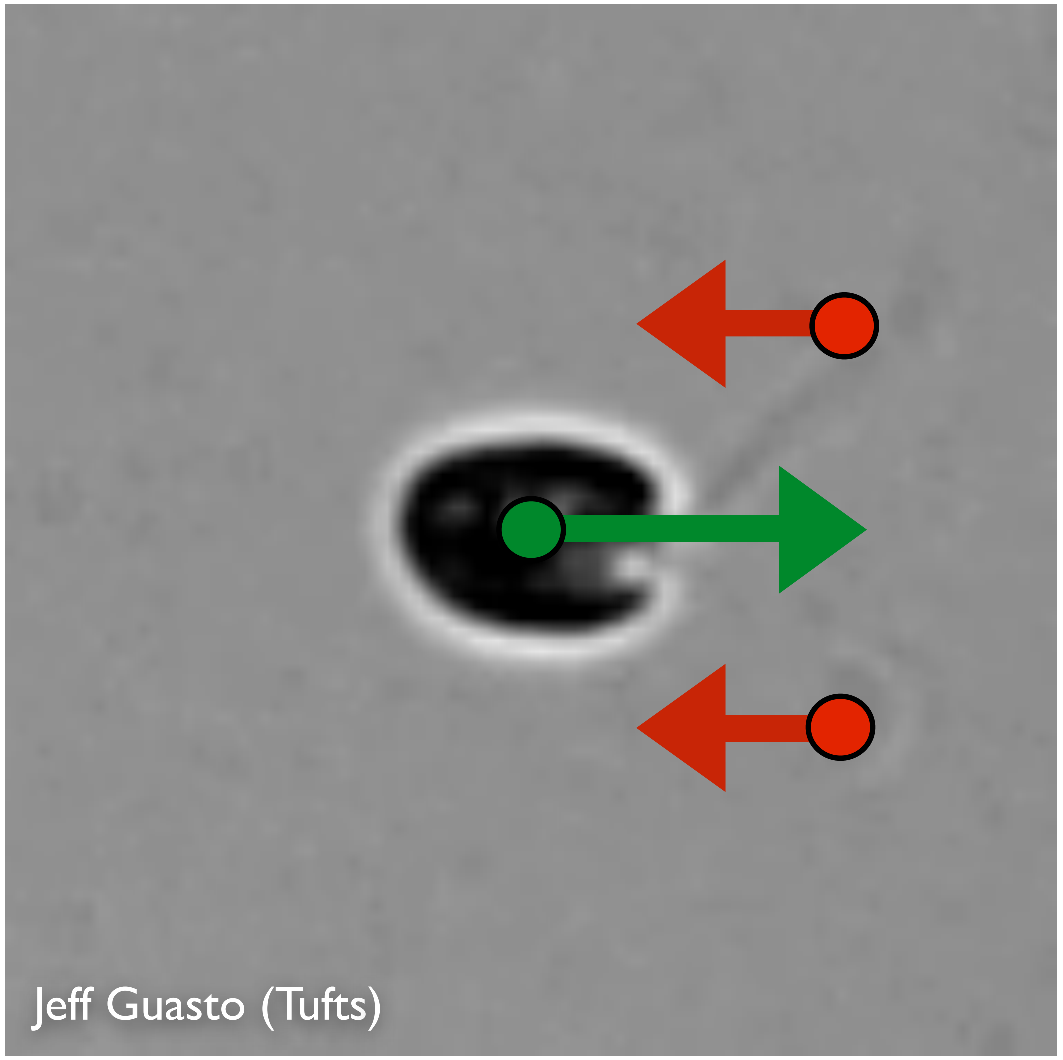


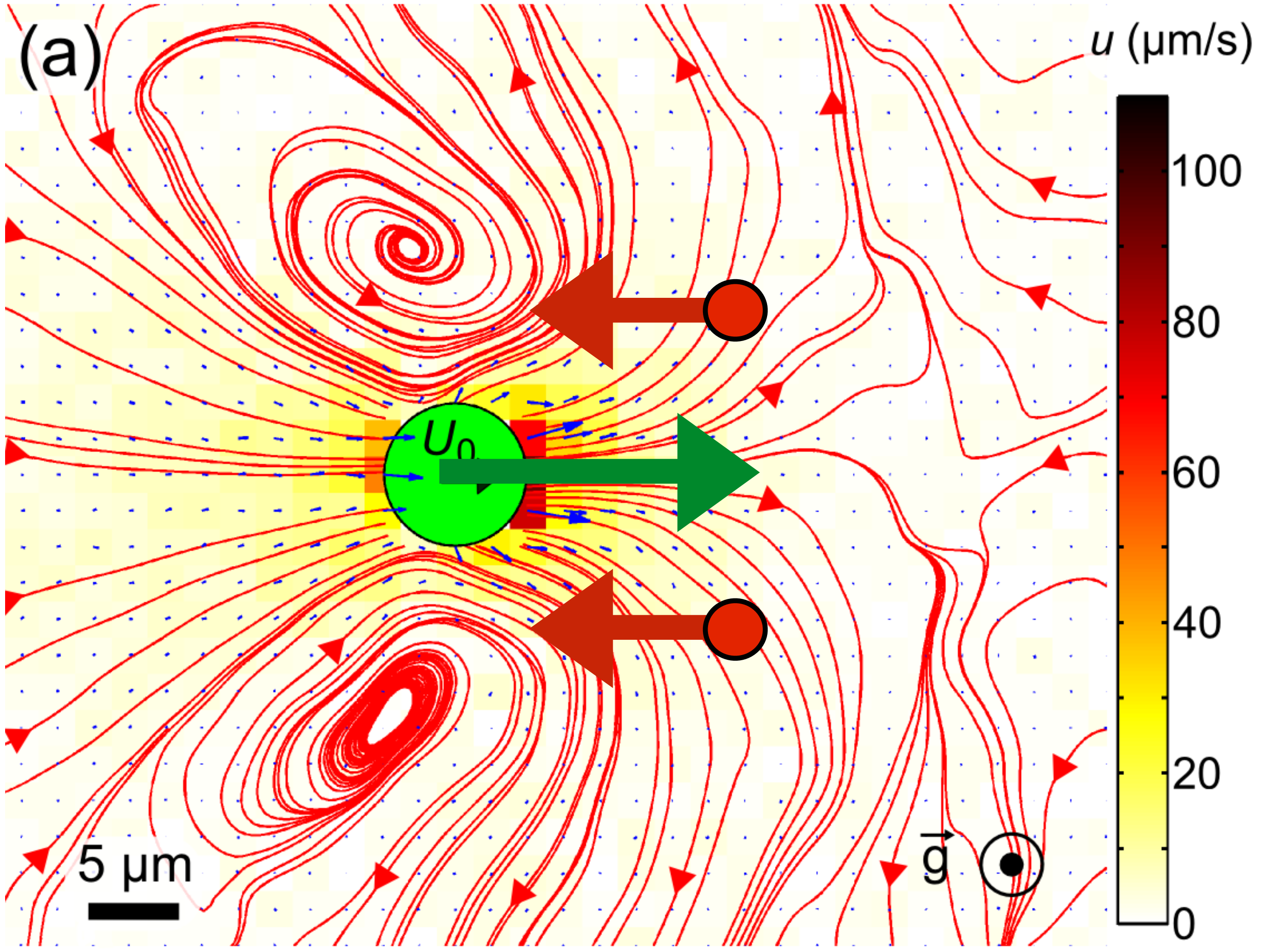
r^{-2}

'puller' dipole

Algal flow field: not a dipole

Chlamydomonas alga



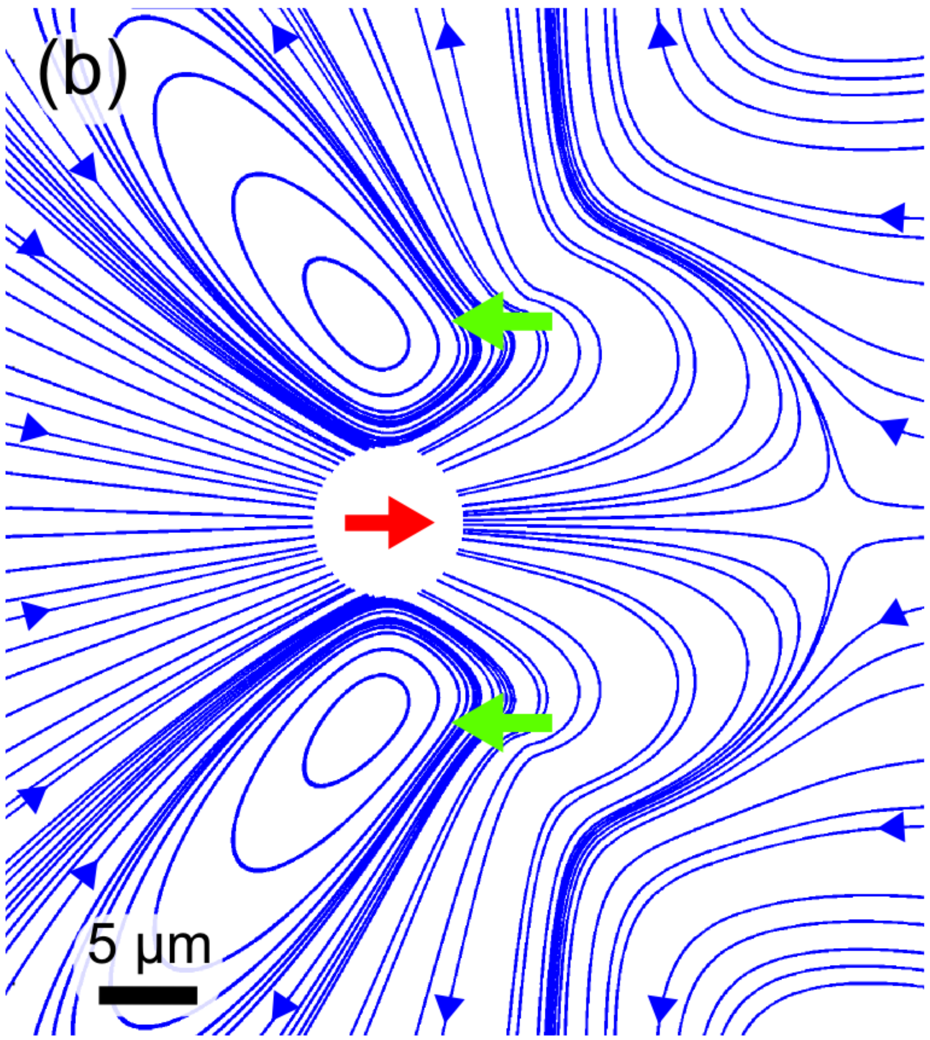


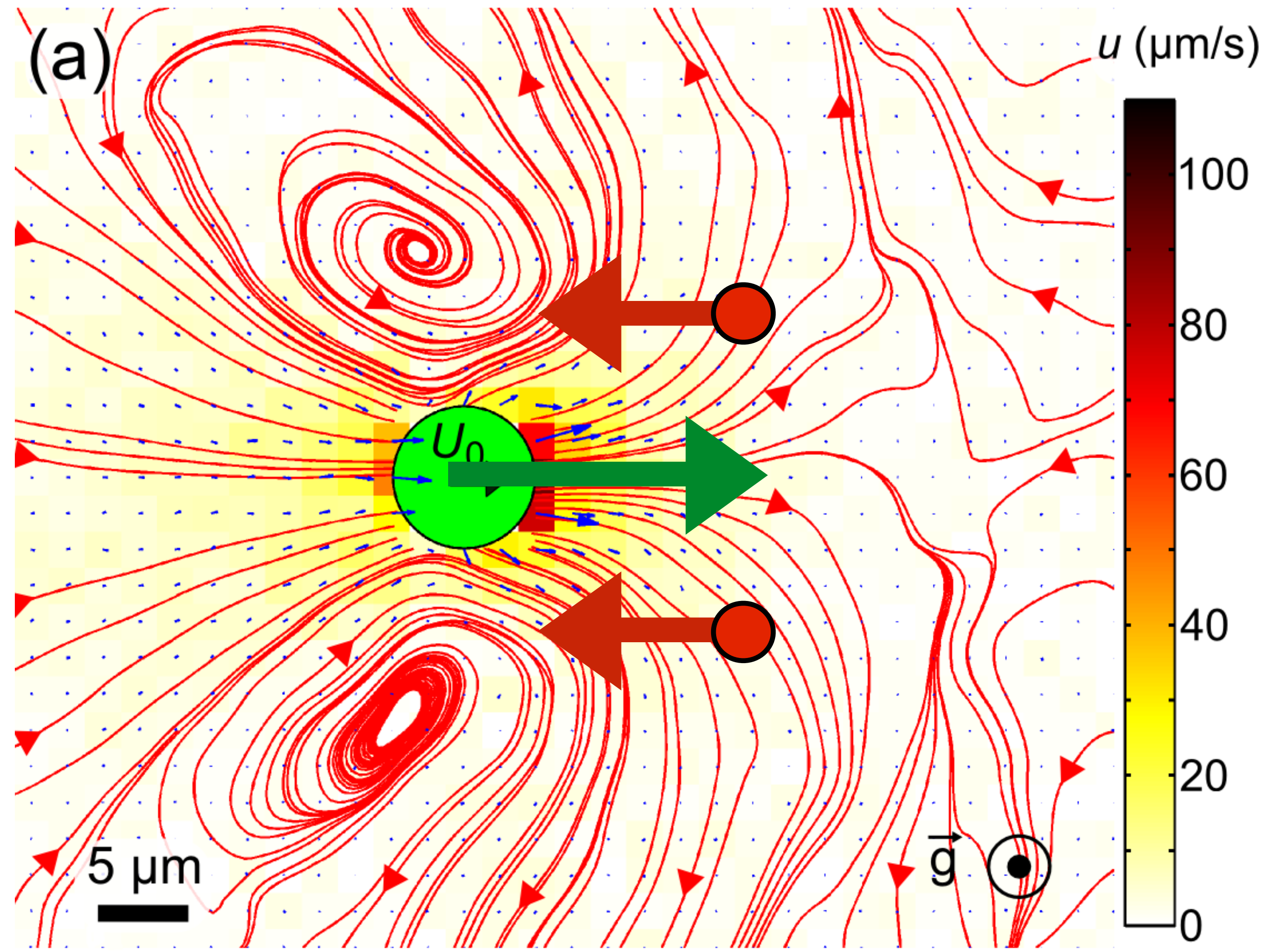
Drescher et al (2010) PRL
Guasto et al (2010) PRL

size: 20 μm
speed: 100 μm/s
beat frequency: 30 Hz

Algal flow field: not a dipole

Chlamydomonas alga





Drescher et al (2010) PRL
Guasto et al (2010) PRL

size: 20 μm
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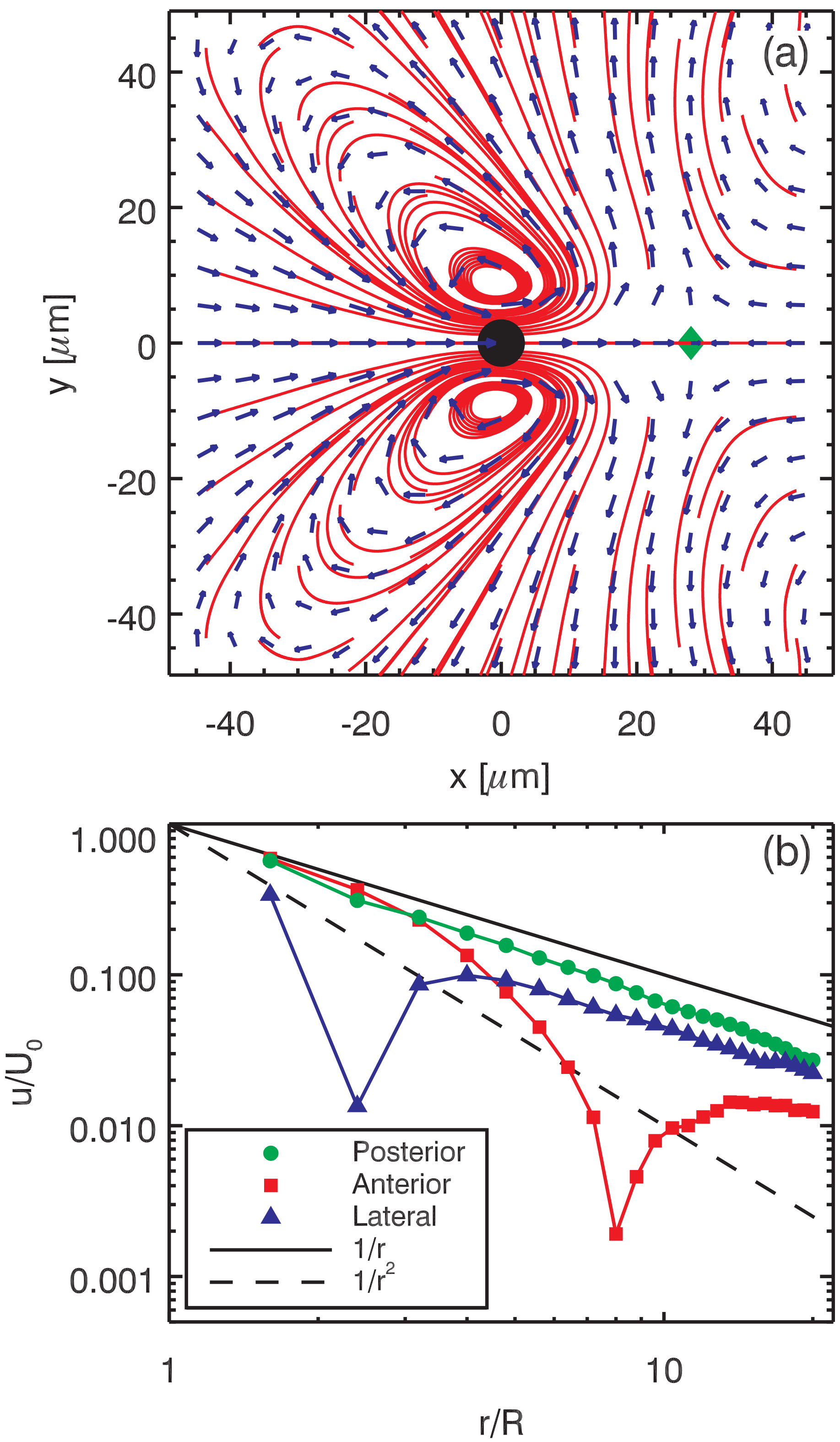
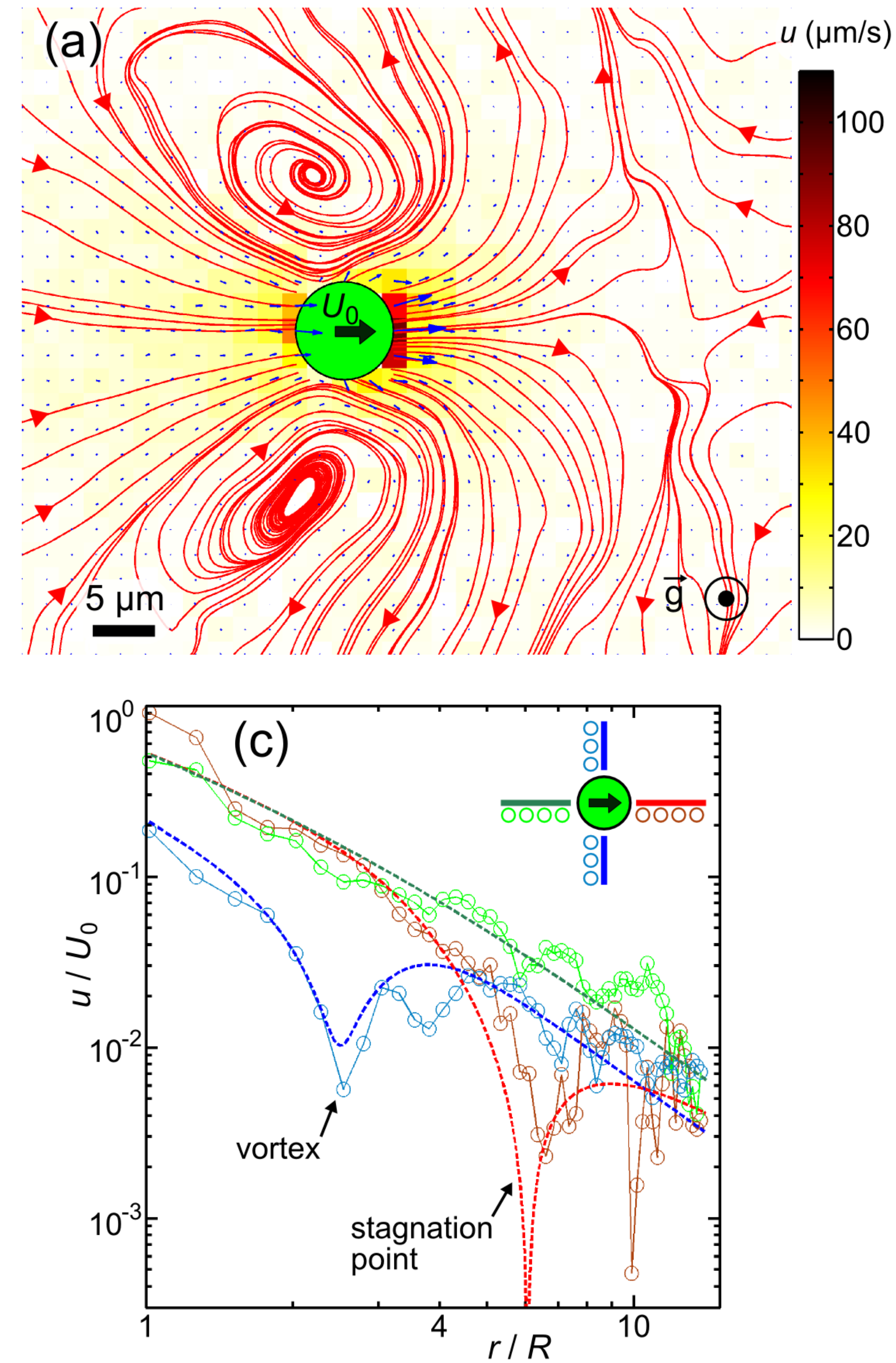
beat frequency: 30 Hz

2D *vs.* 3D

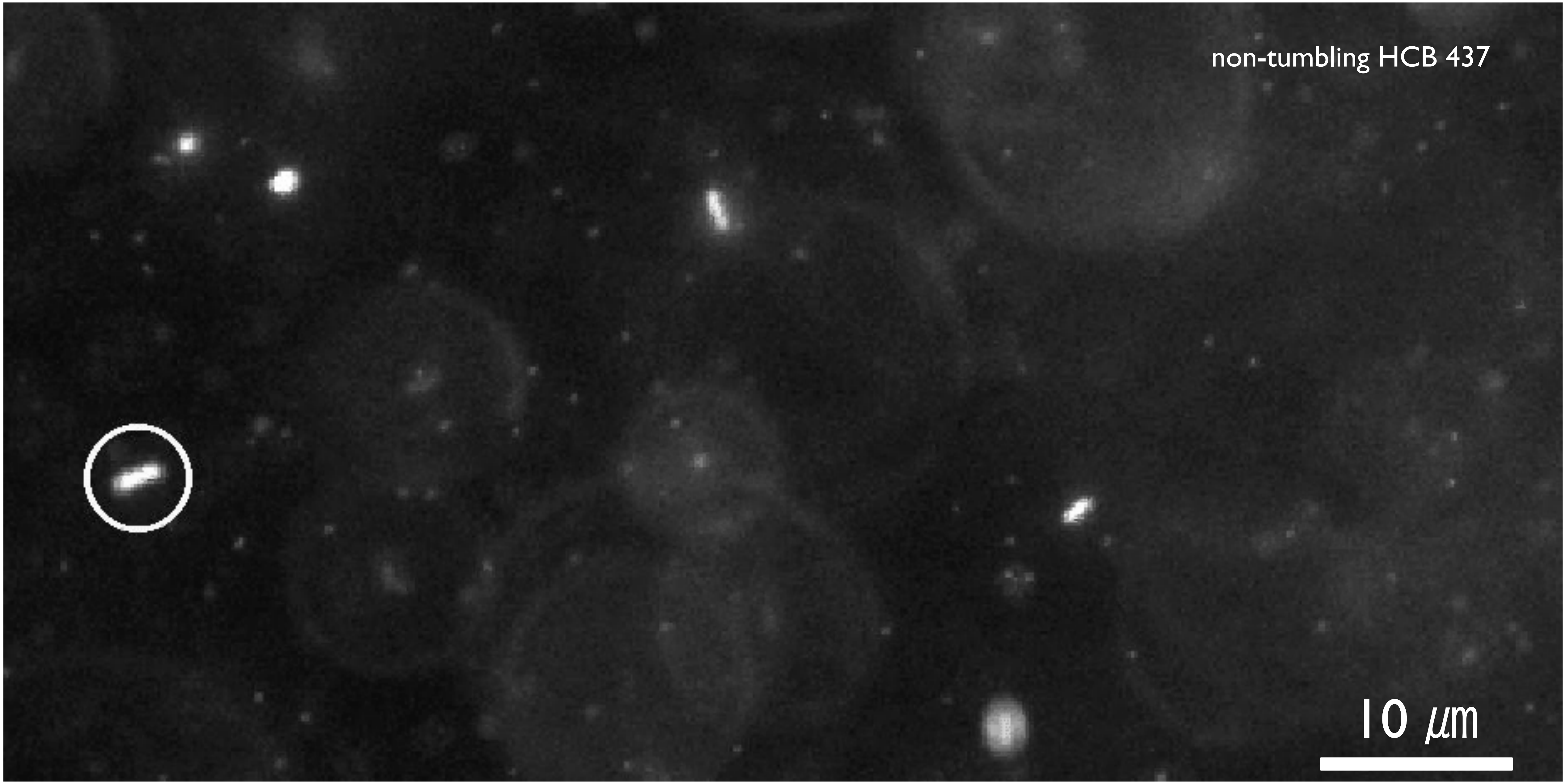


Guasto et al (2010) PRL



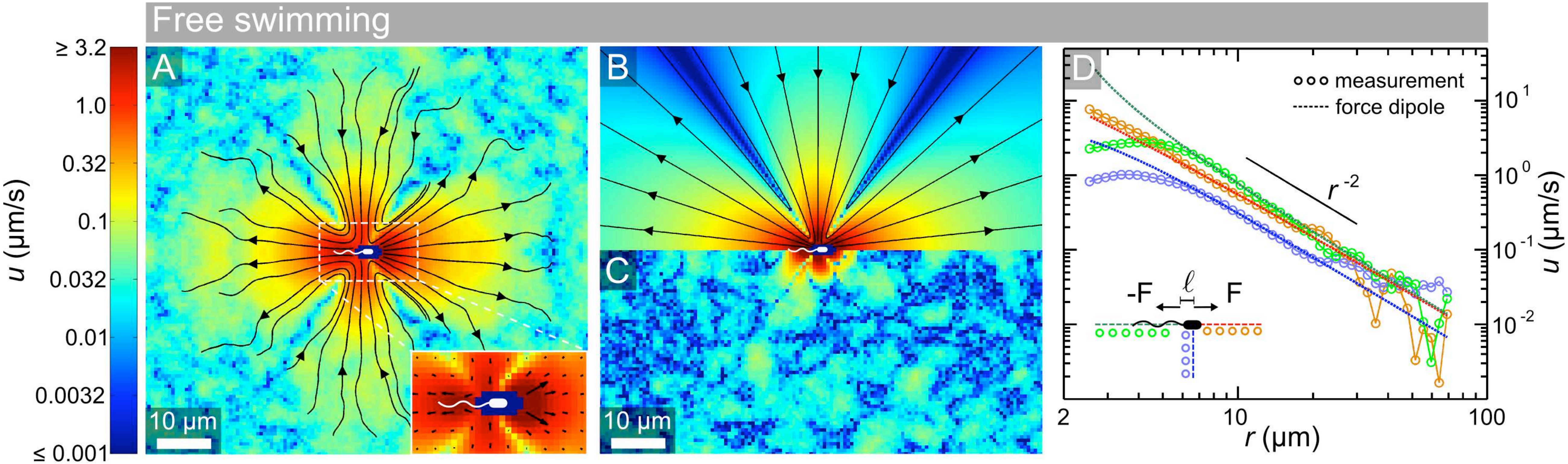
Drescher et al (2010) PRL

E. coli (non-tumbling)



Drescher et al (2011) PNAS

E.coli (non-tumbling HCB 437)



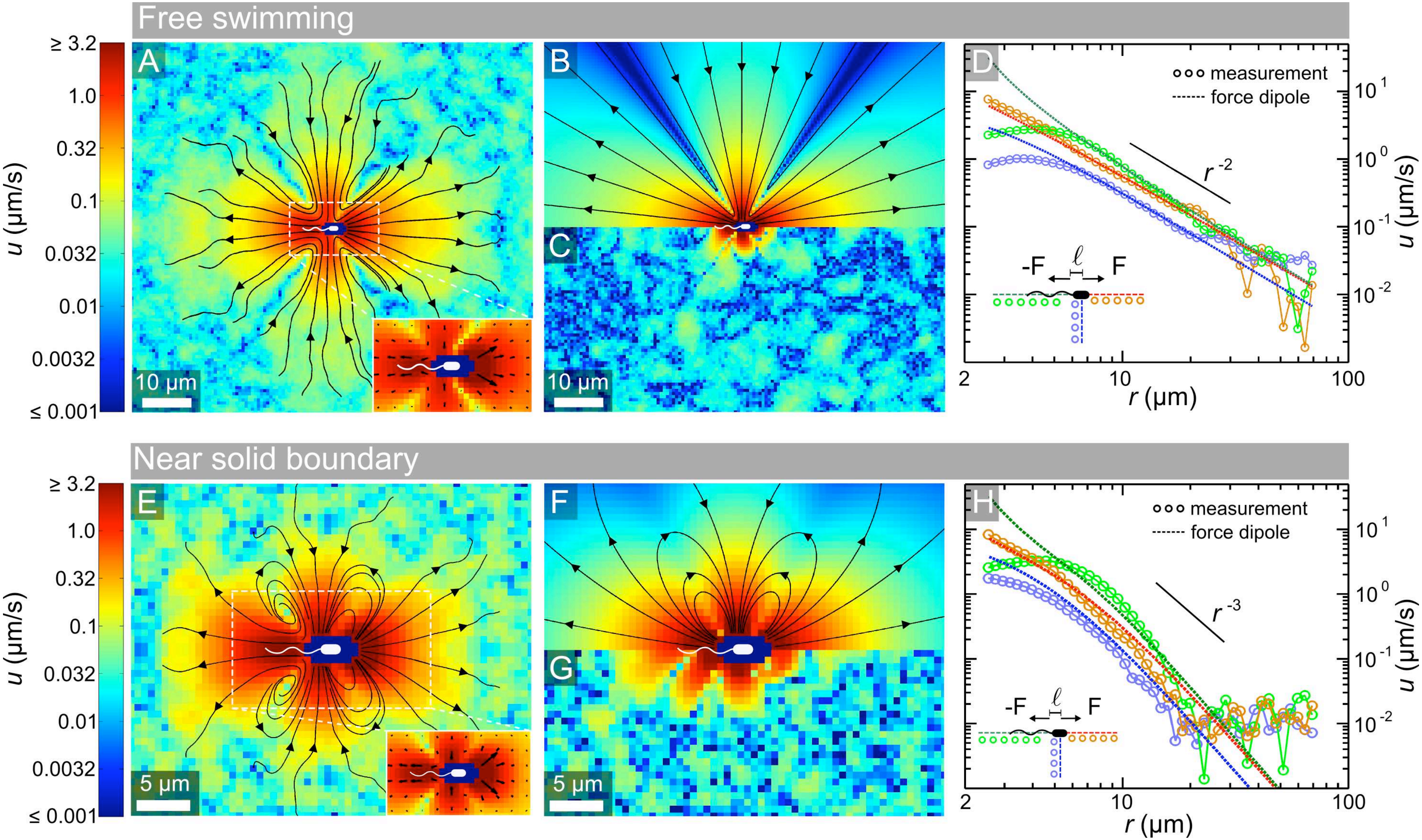
$$\boldsymbol{u}(\boldsymbol{r}) = \frac{A}{|\boldsymbol{r}|^2}\left[3(\hat{\boldsymbol{r}}.\hat{\boldsymbol{d}})^2 - 1\right]\hat{\boldsymbol{r}}, \quad A = \frac{\ell F}{8\pi\eta}, \quad \hat{\boldsymbol{r}} = \frac{\boldsymbol{r}}{|\boldsymbol{r}|}$$

$$V_0 = 22 \pm 5 \ \mu\text{m/s}$$
$$\ell = 1.9 \ \mu\text{m}$$
$$F = 0.42 \ \text{pN}$$

'pusher' dipole

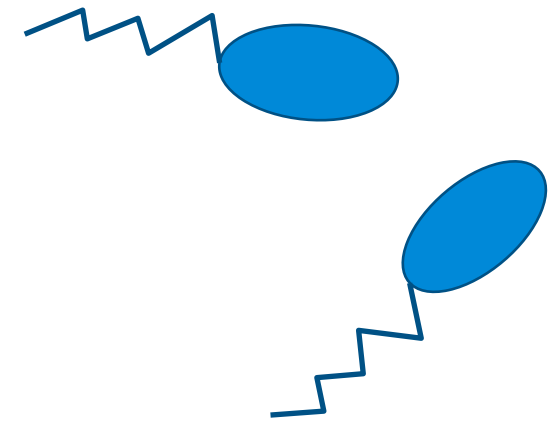
Drescher et al (2011) PNAS

E.coli (non-tumbling HCB 437)



Drescher et al (2011) PNAS

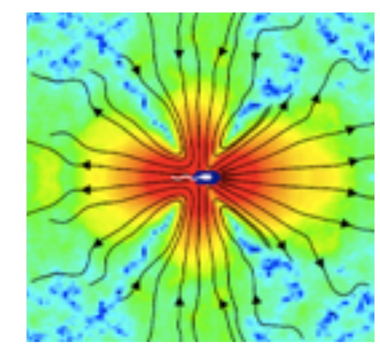
Hydrodynamic scattering



dipole flow $\boldsymbol{v} \sim \dfrac{A}{r^2}$

vorticity $\omega = \nabla \times \boldsymbol{v} \sim \dfrac{A}{r^3}$

encounter time $\tau \sim \ell / V$



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

rotational diffusion $\langle |\Delta\phi|^2 \rangle \sim D_r\tau$ $D_r = 0.057\ \mathrm{rad}^2/\mathrm{s}$

balance

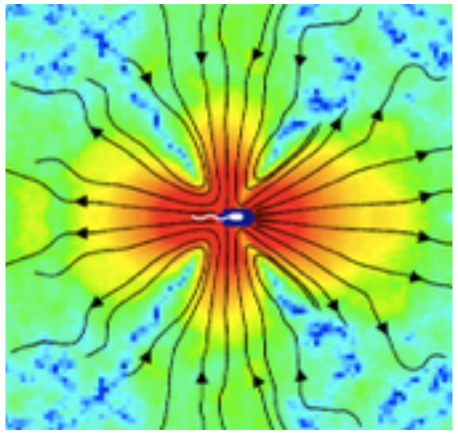
$$\boxed{r_H \sim \left(\frac{A^2\tau}{D_r}\right)^{1/6}}$$

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

Drescher et al (2011) PNAS

Implications for collective swimming

✓ hydrodynamic advection $\boldsymbol{v} \sim \frac{A}{r^2}$



✓ steric alignment

- hydrodynamic alignment less important $\omega = \nabla \times \boldsymbol{v} \sim \frac{A}{r^3}$

✓ intrinsic rotational noise
much larger than thermal noise $D_r = 0.057 \text{ rad}^2/\text{s}$

Drescher et al (2011) PNAS

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VOLUME 93, NUMBER 9 PHYSICAL REVIEW LETTERS week ending 27 AUGUST 2004

Self-Concentration and Large-Scale Coherence in Bacterial Dynamics

Christopher Dombrowski,[1] Luis Cisneros,[1] Sunita Chatkaew,[1] Raymond E. Goldstein,[1,2] and John O. Kessler[1]
[1]*Department of Physics, University of Arizona, Tucson, Arizona 85721, USA*
[2]*Program in Applied Mathematics, University of Arizona, Tucson, Arizona 85721, USA*
(Received 23 December 2003; published 24 August 2004)

B. subtilis

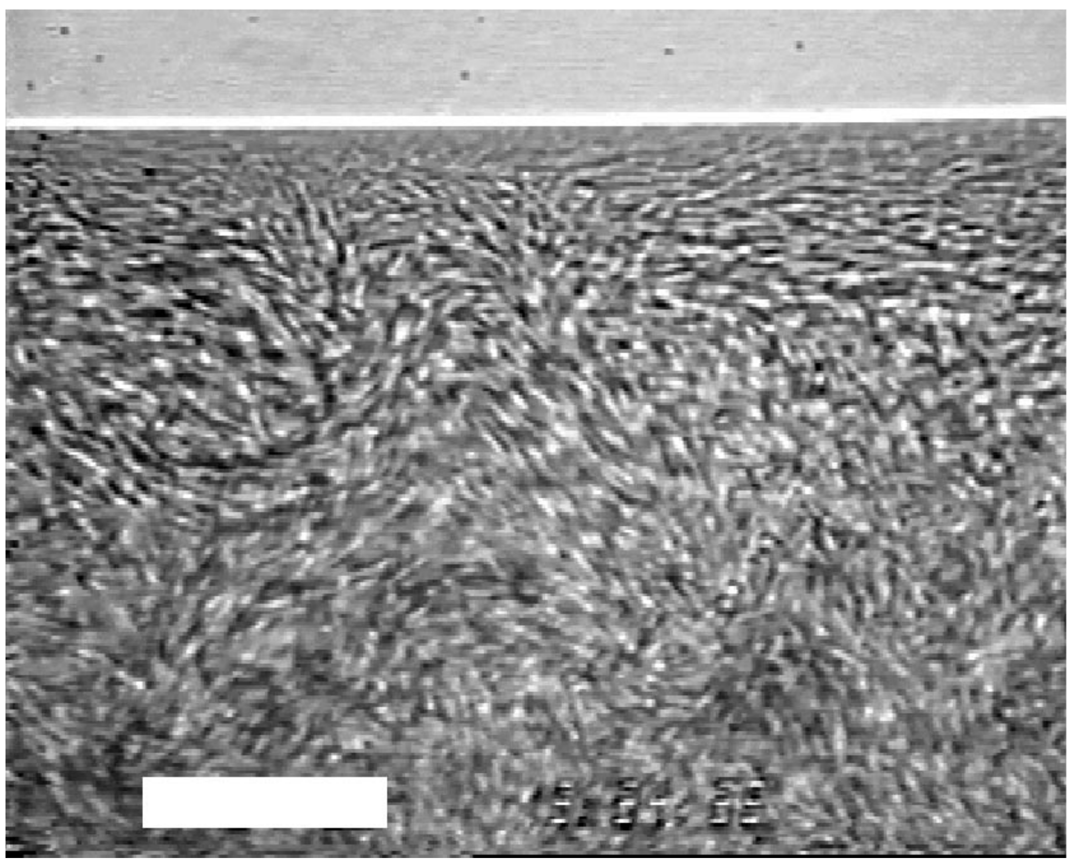
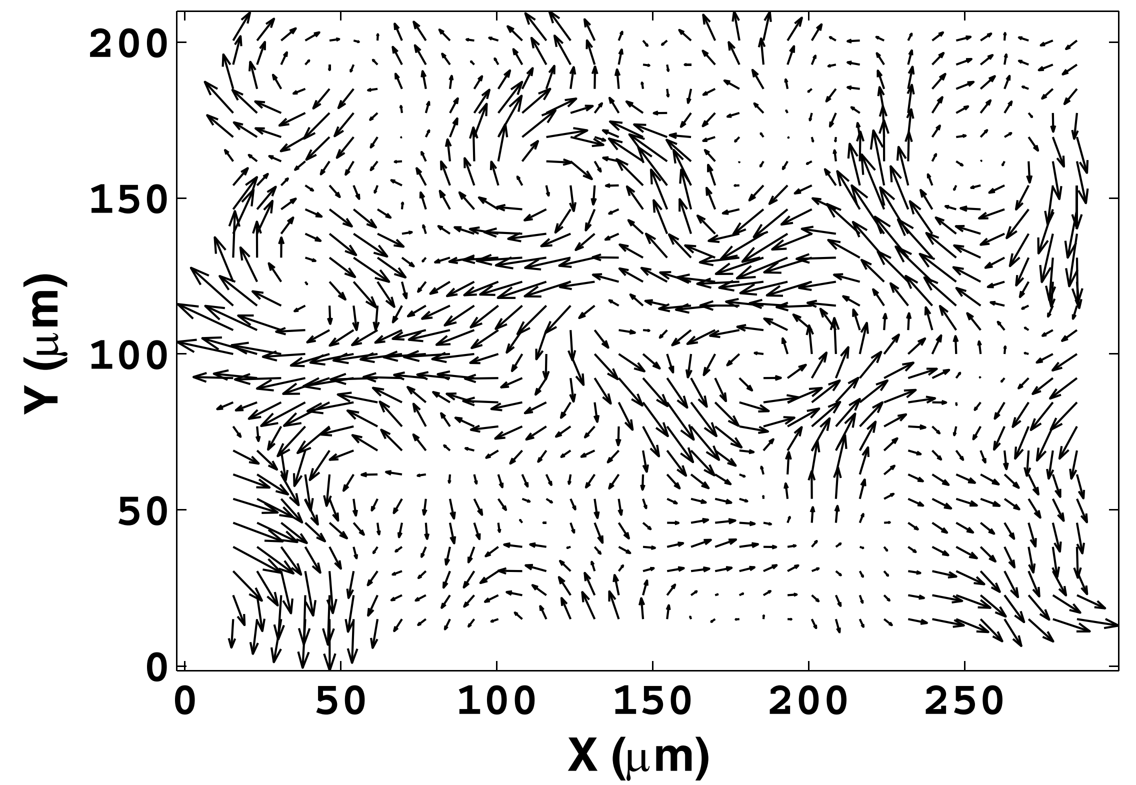
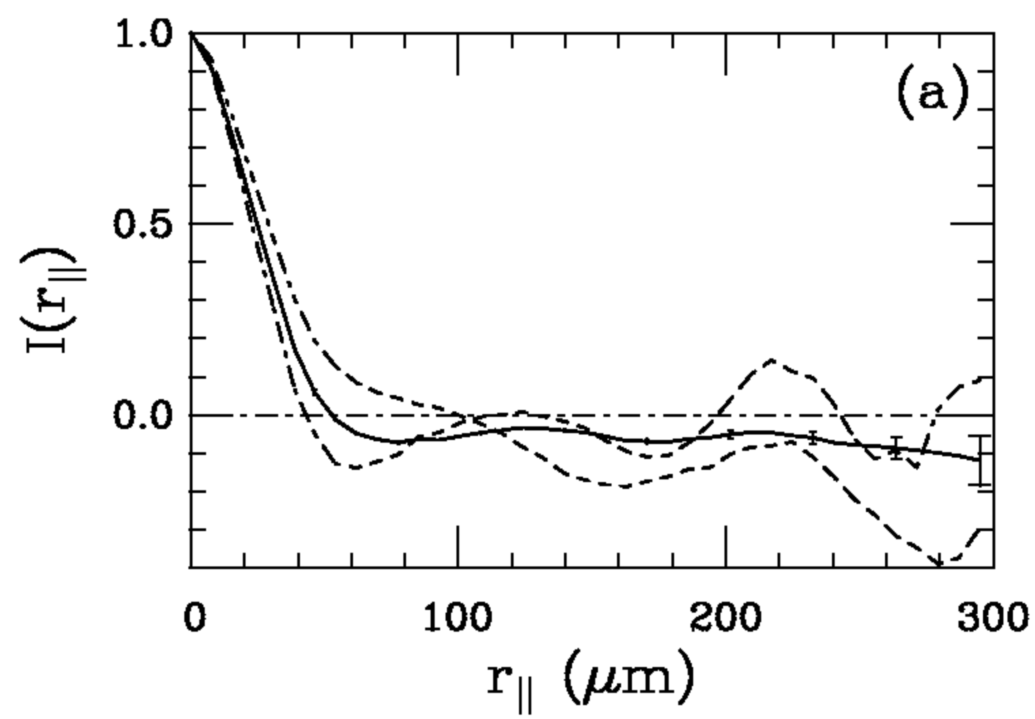
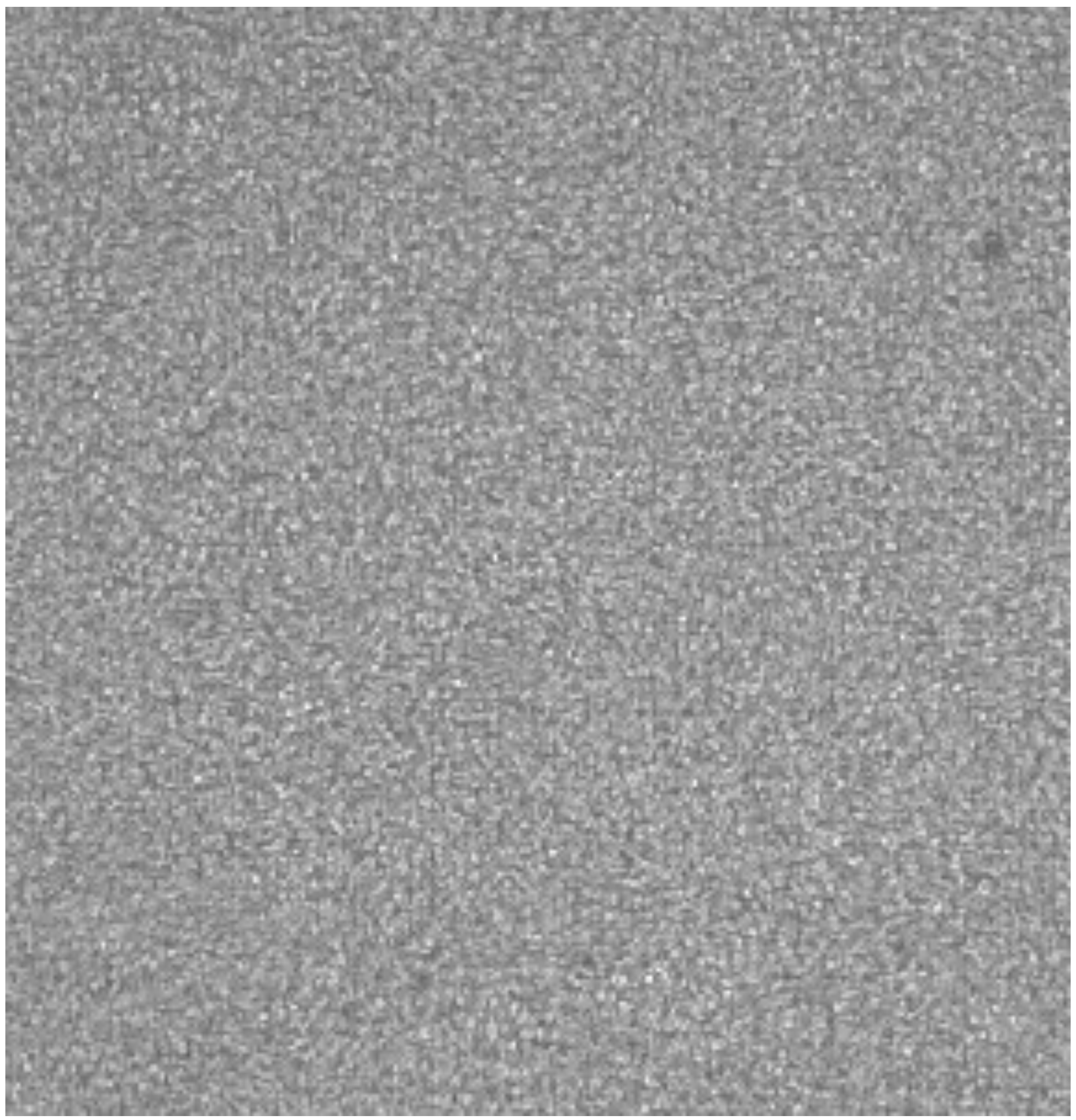
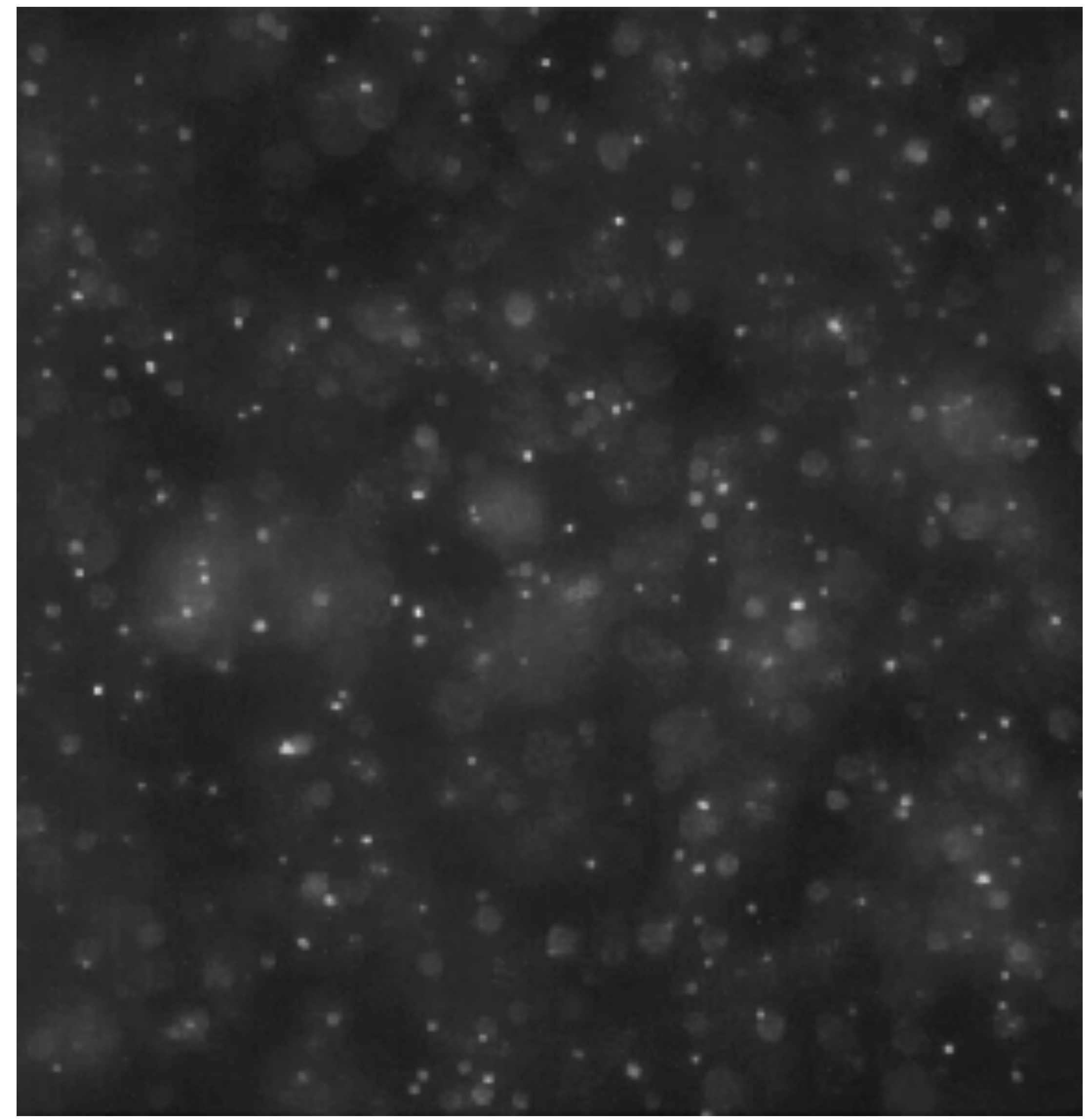


FIG. 3. Bacterial "turbulence" in a sessile drop, viewed from below through the bottom of a petri dish. Gravity is perpendicular to the plane of the picture, and the horizontal white line near the top is the air-water-plastic contact line. The central fuzziness is due to collective motion, not quite captured at the frame rate of 1/30 s. The scale bar is 35 μm.



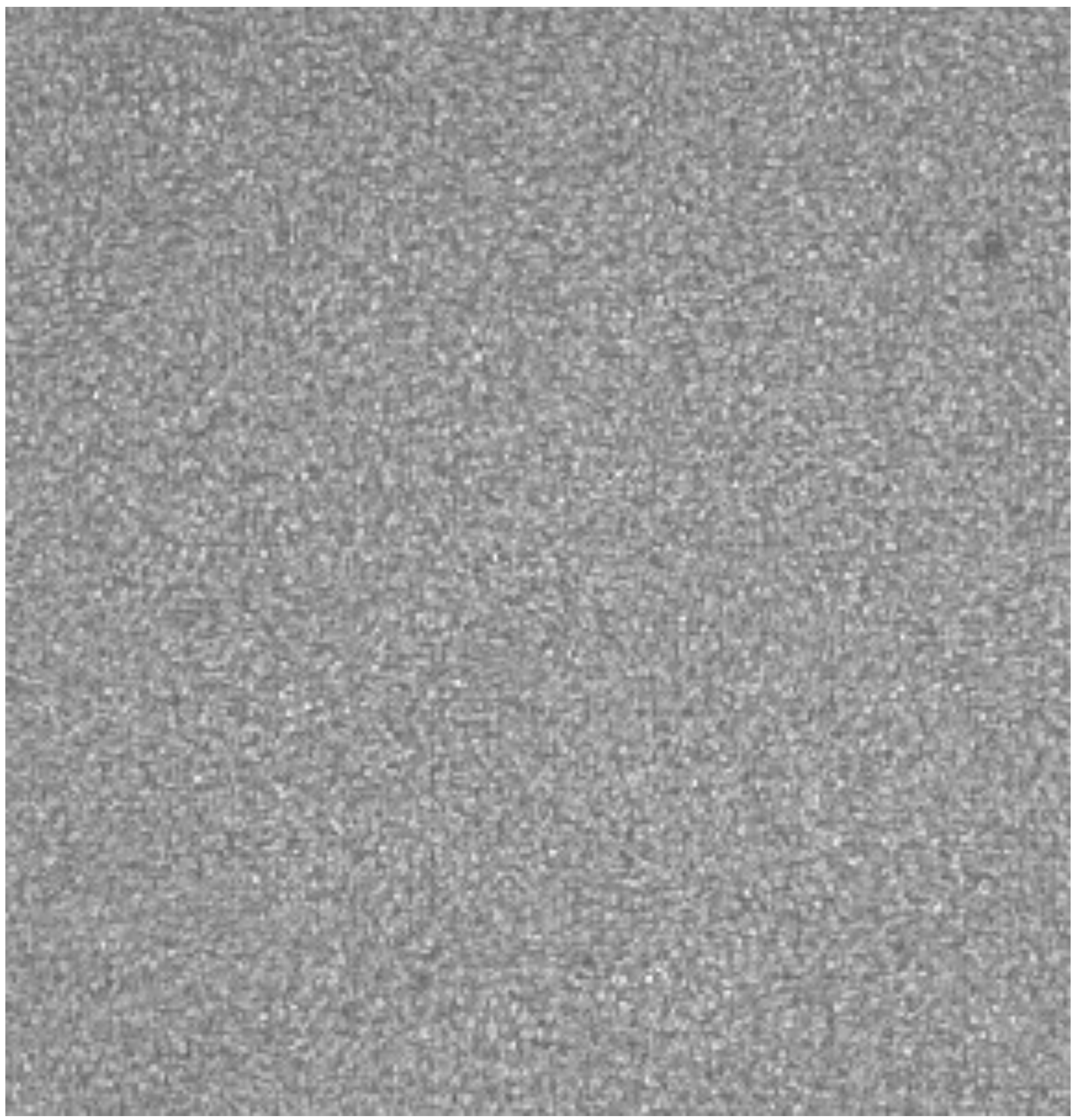


Bacterial 'turbulence'

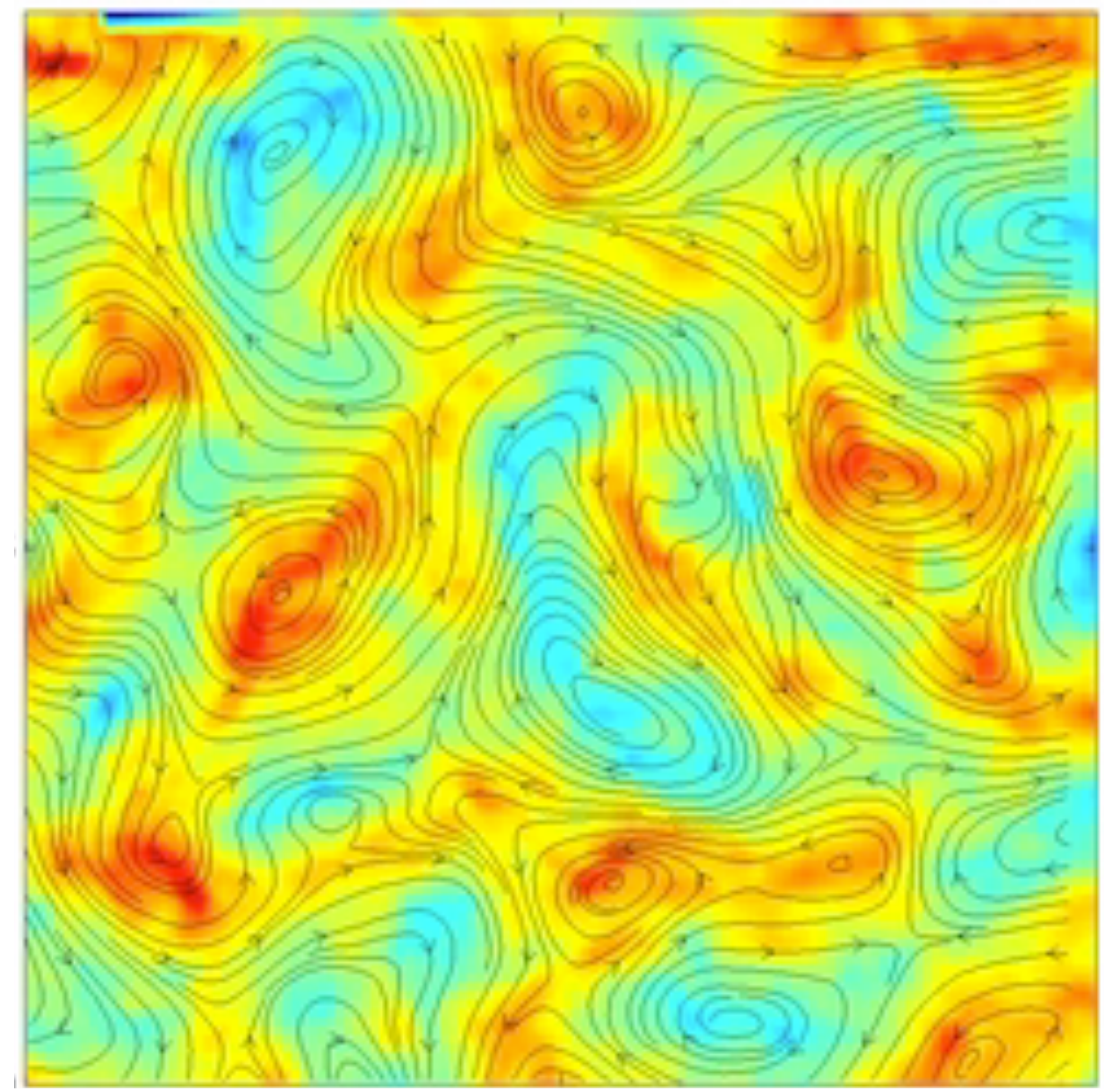
B. subtilis	tracers
	
bright field	fluorescence
Wensink et al PNAS 2012	Dunkel et al PRL 2013

Bacterial ‘turbulence’

B. subtilis



bright field

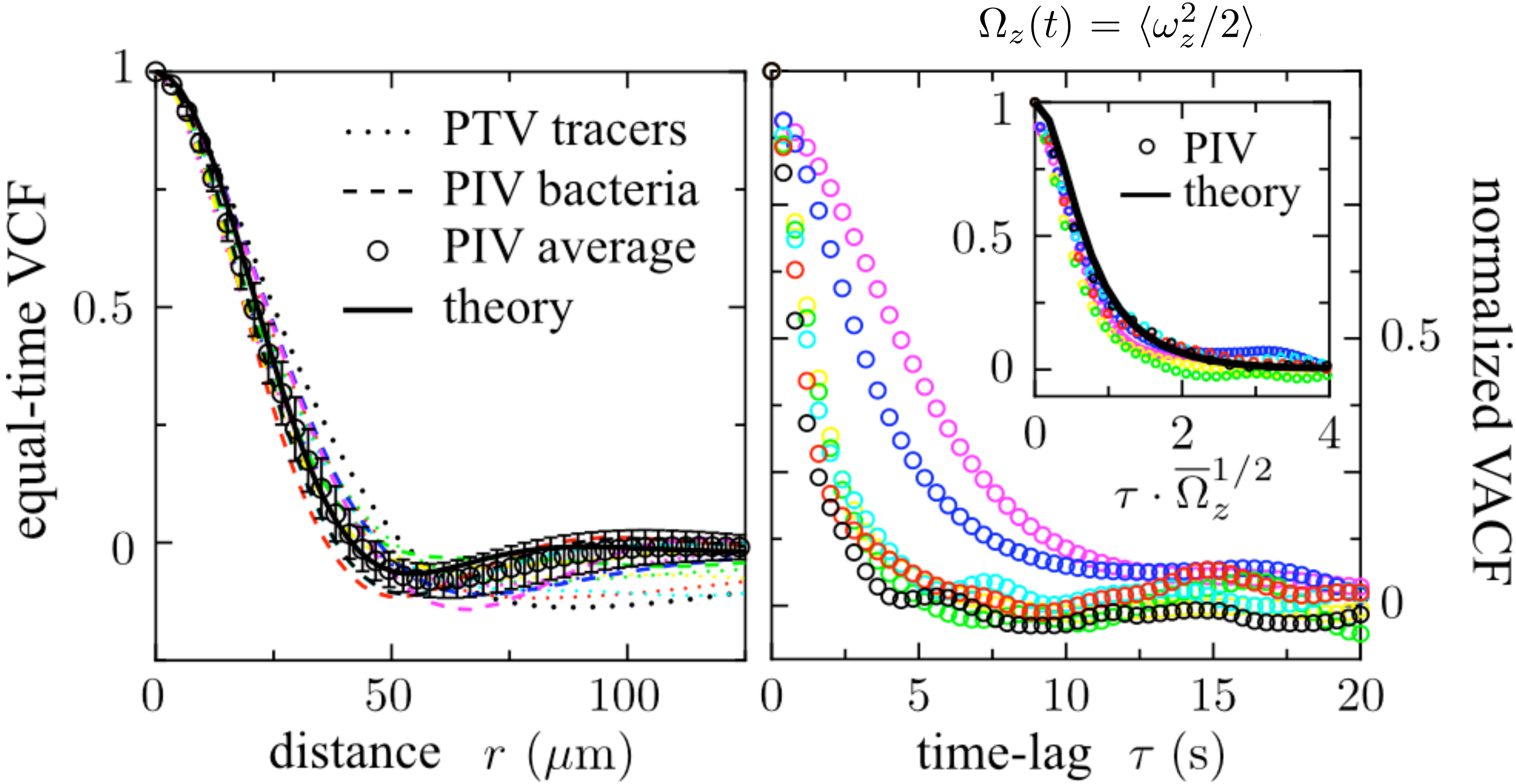


PIV

Wensink et al PNAS 2012
Dunkel et al (2013) PRL

see also:
Sokolov & Aronson (2012) PRL

Velocity correlations



Vortex diameter ~ 70 μm

Life time ~ seconds

Dunkel et al (2013) PRL

consistent with Sokolov & Aronson (2012) PRL

Minimal continuum theory for bacterial velocity field

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

nematic stresses

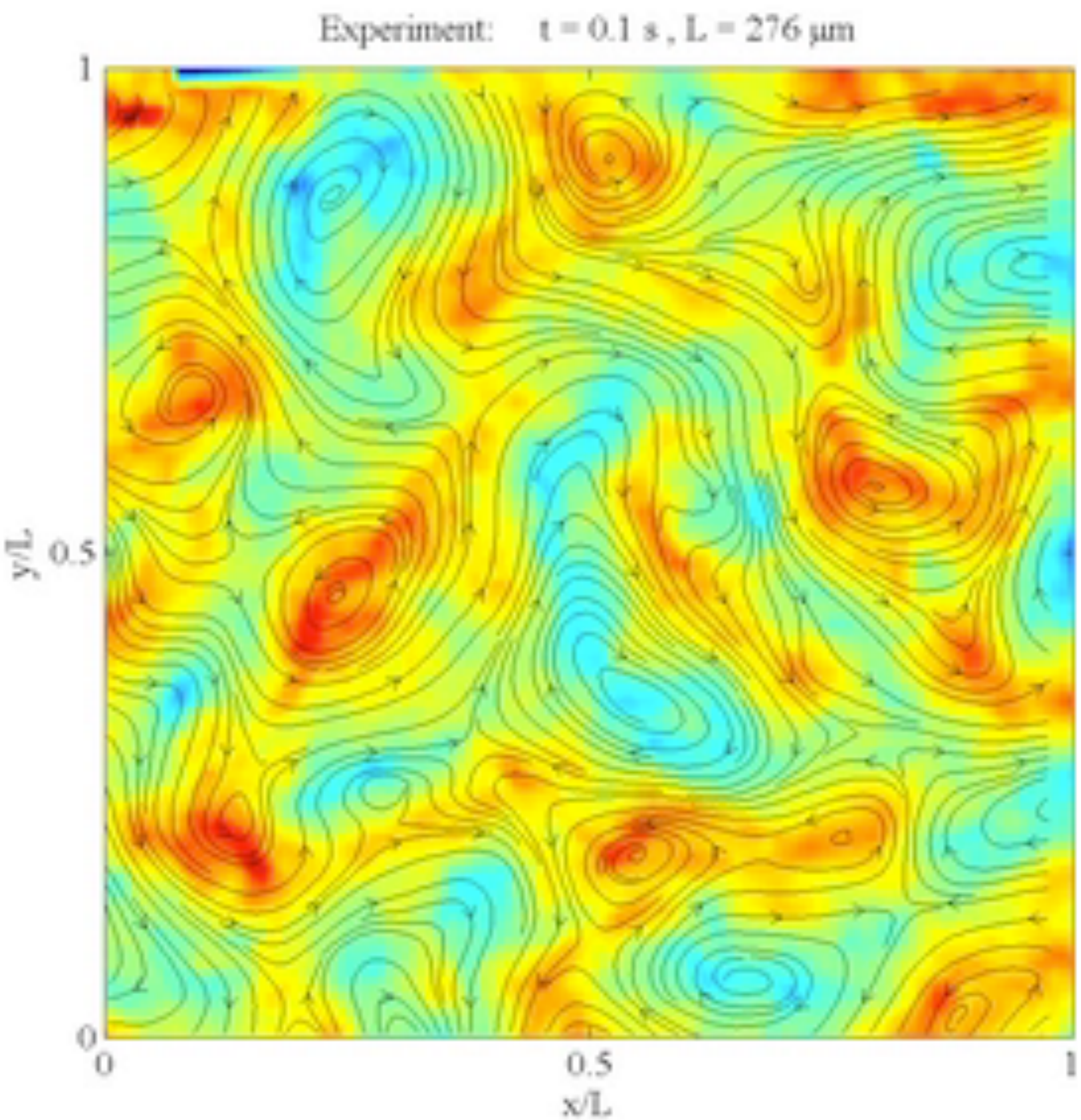
polar alignment

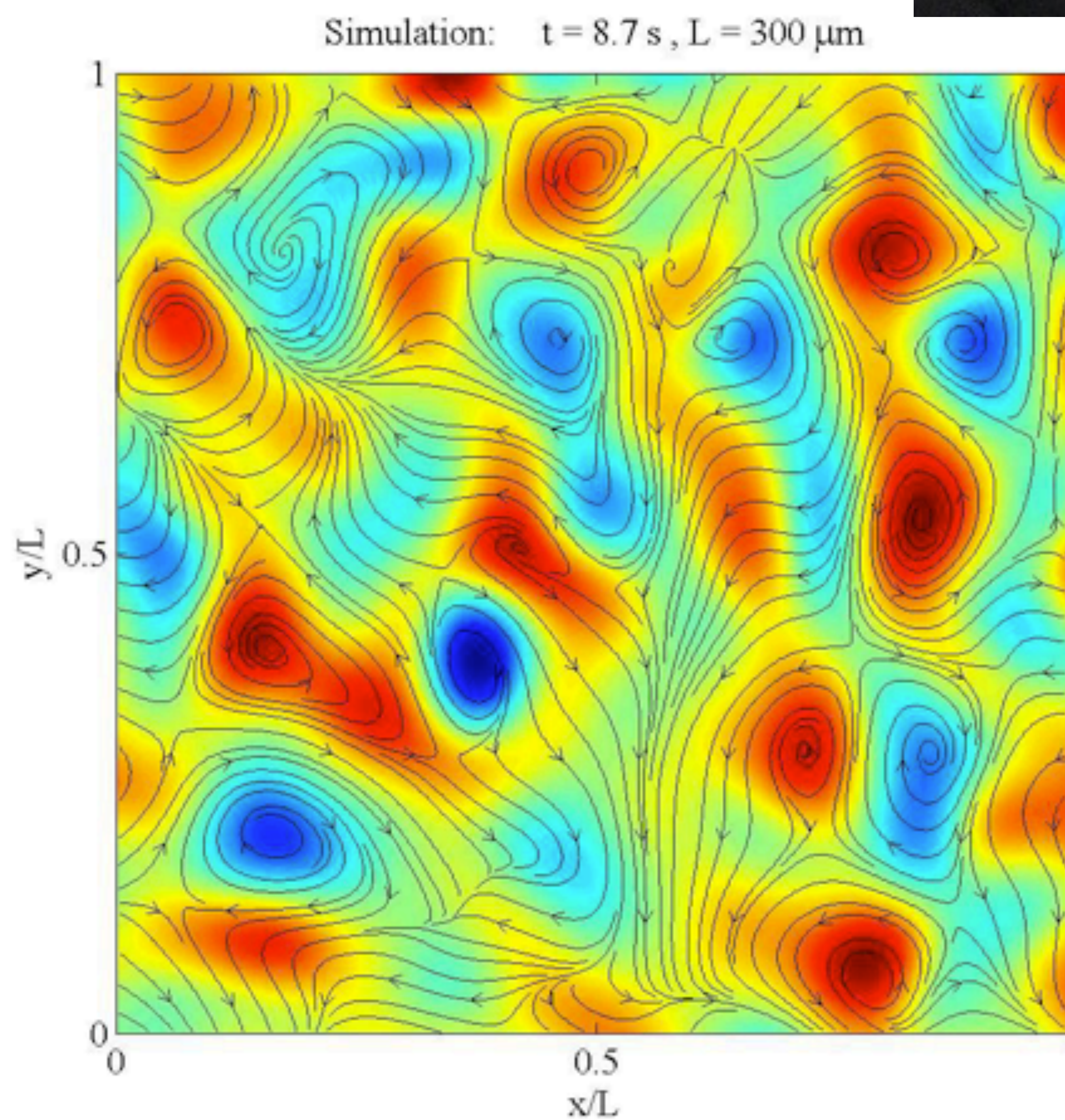
$$(\partial_t + \lambda_0 \boldsymbol{v} \cdot \nabla)\boldsymbol{v} = -\nabla(p + \lambda_1 \boldsymbol{v}^2) - (\beta \boldsymbol{v}^2 + \alpha)\boldsymbol{v} + \Gamma_0 \nabla^2 \boldsymbol{v} - \Gamma_2 (\nabla^2)^2 \boldsymbol{v}$$

vortices

Dunkel et al (2014) PRL
Wensink et al (2012) PNAS

experiment *vs.* theory



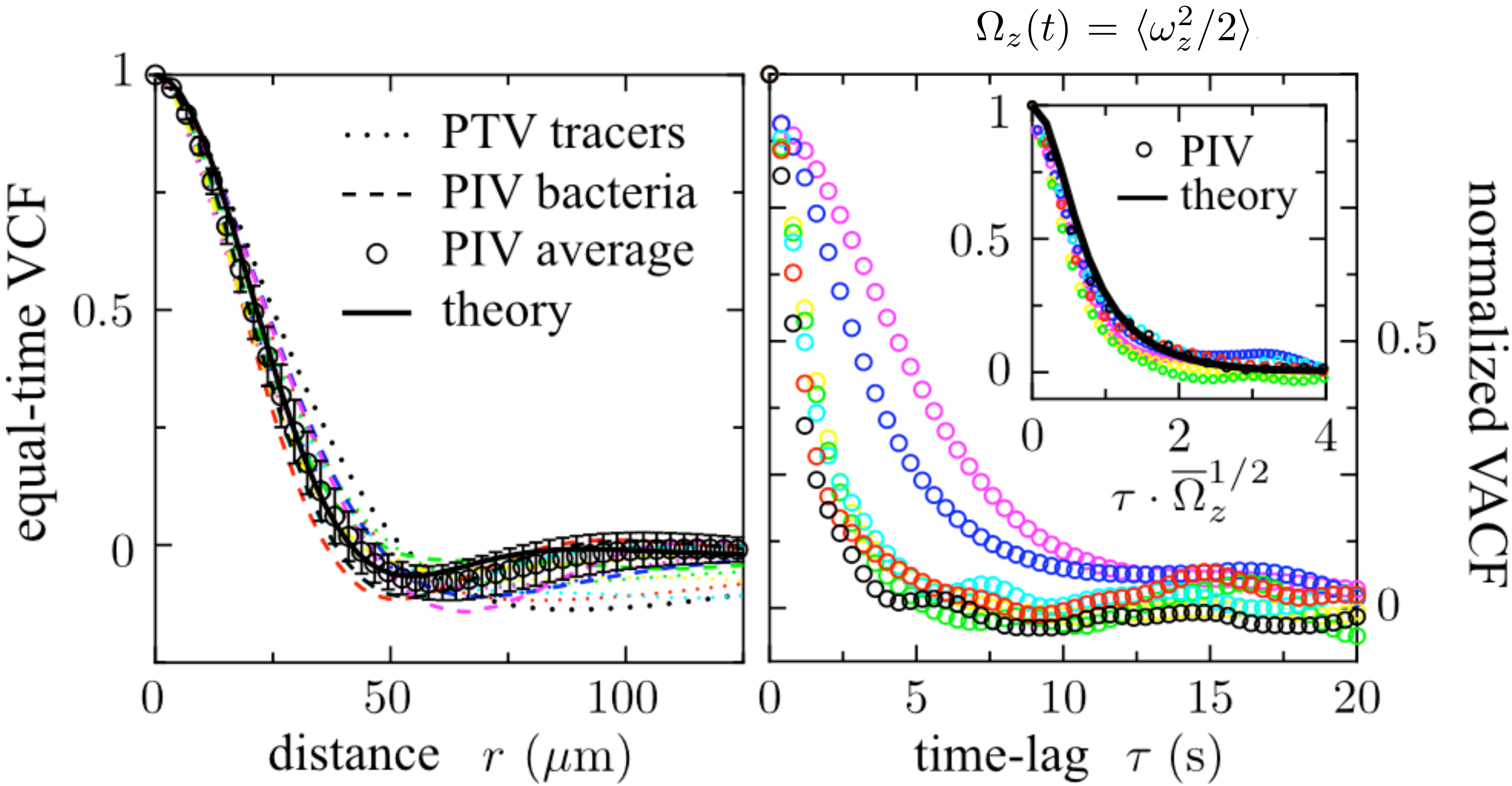


quasi-2D slice

2D slice
from 3D simulation

Dunkel, Heidenreich et al PRL 2013

Velocity correlations



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Dunkel et al (2013) PRL

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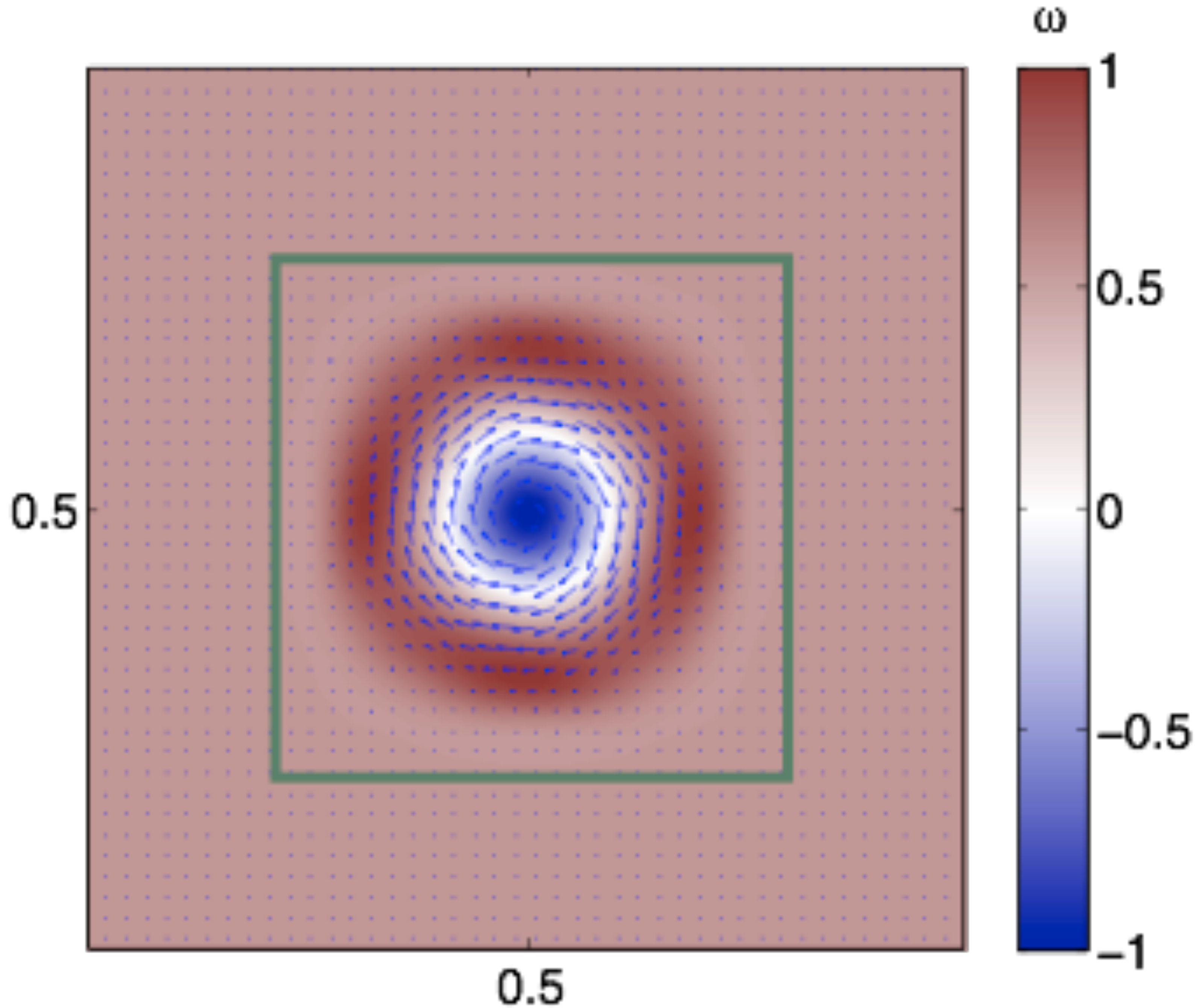
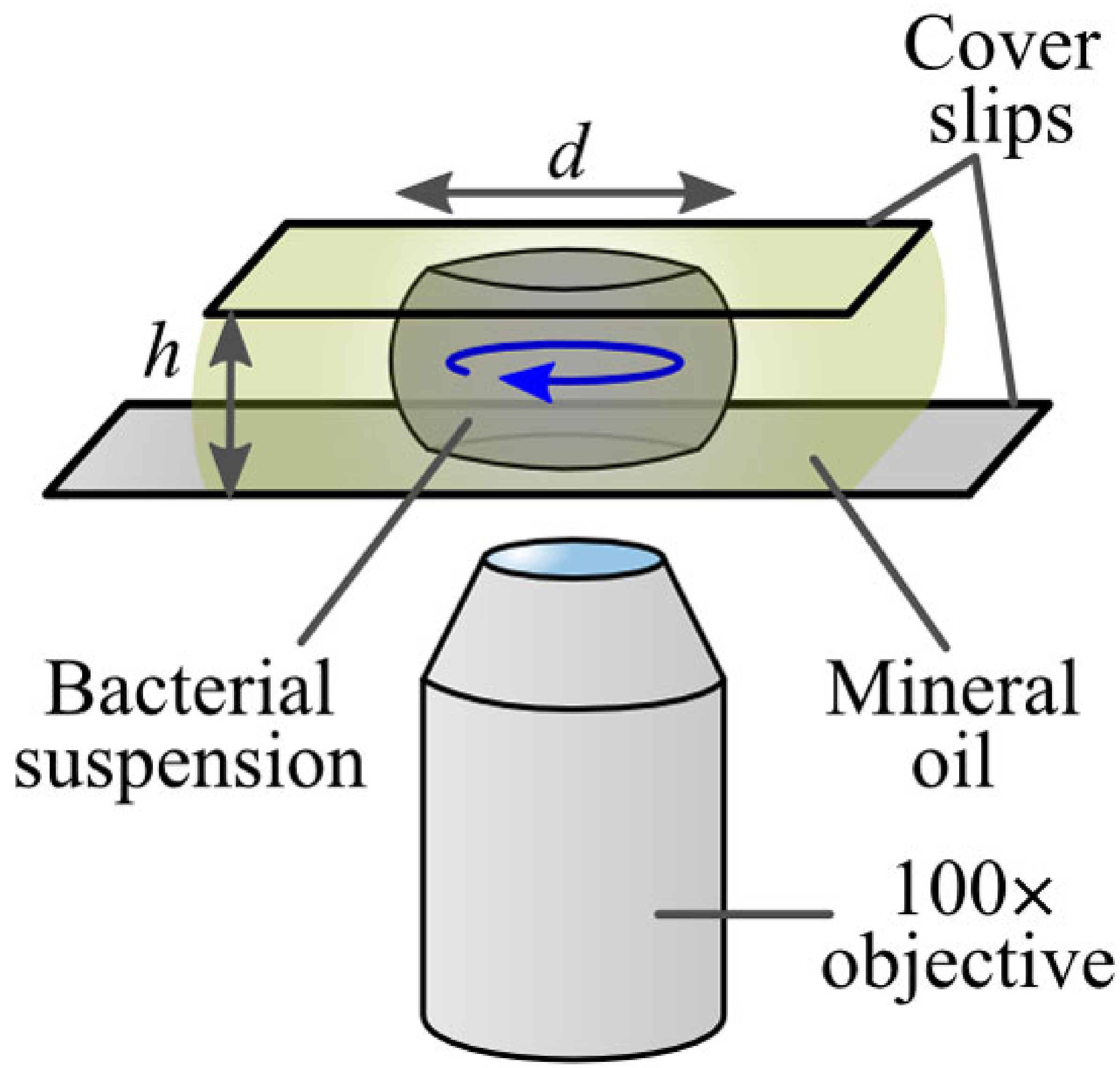
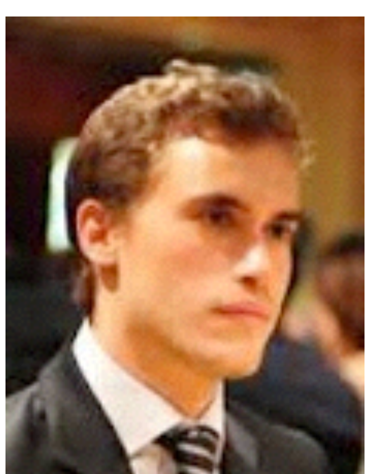
Vortex stabilization

'prediction' of many models



Can we stabilize vortices ?

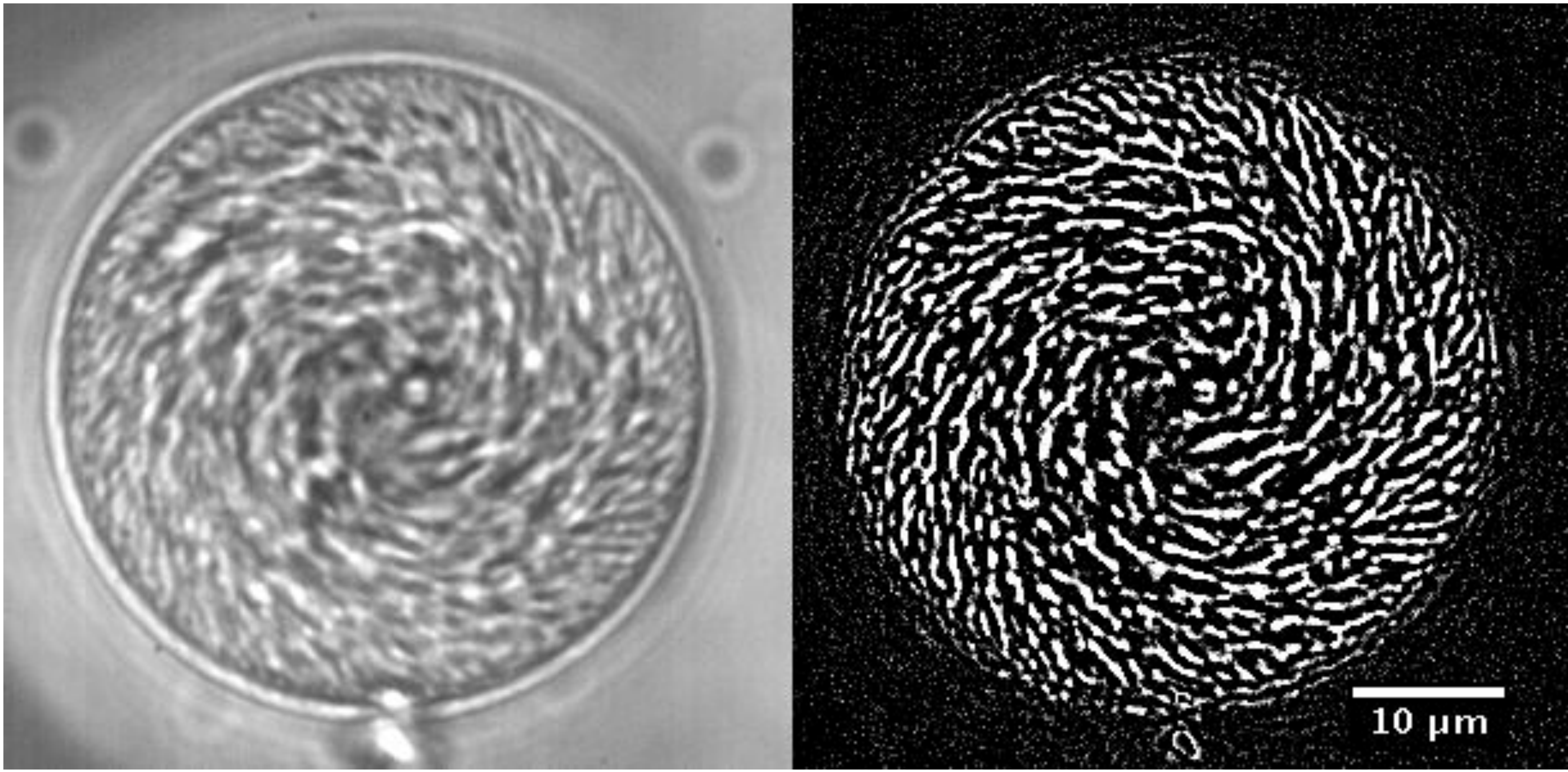




Wioland et al (2013) PRL

Stable bacterial spiral vortex

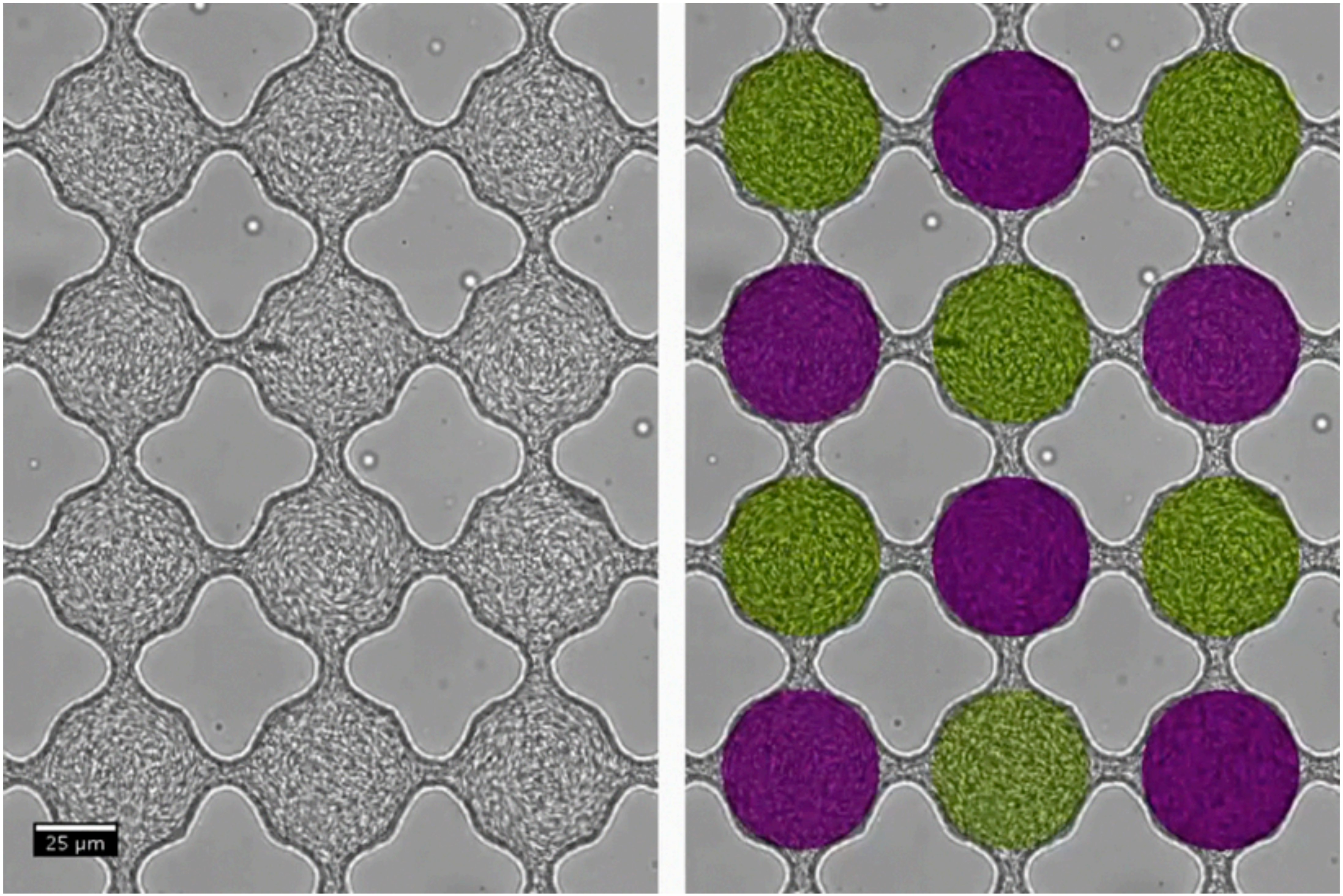
Vortex life time ~ minutes



Wioland et al (2013) PRL
Lushi et al (2014) PNAS

Edge currents !

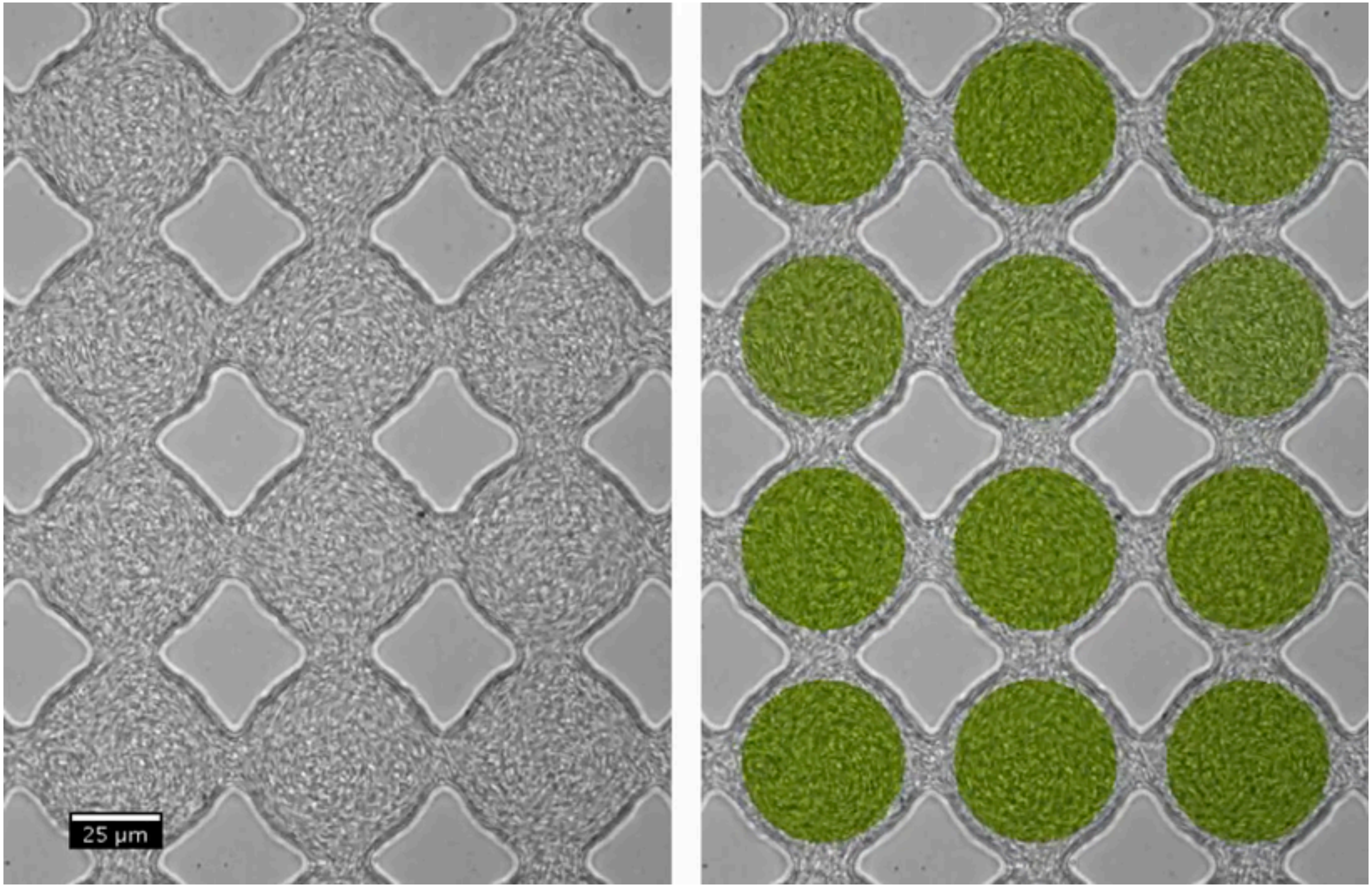
Anti-ferromagnetic order



Wioland et al (2016)
Nature Physics

… but only for weak coupling (small gaps)

Ferromagnetic order

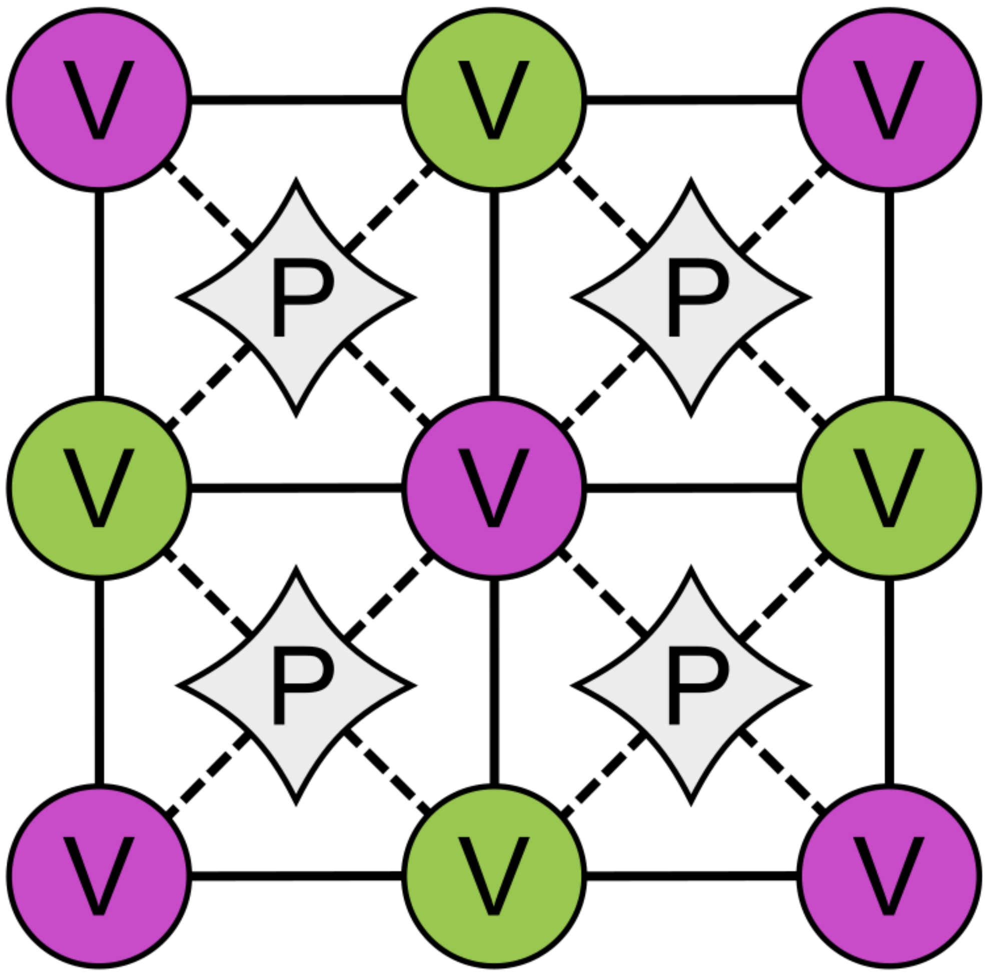


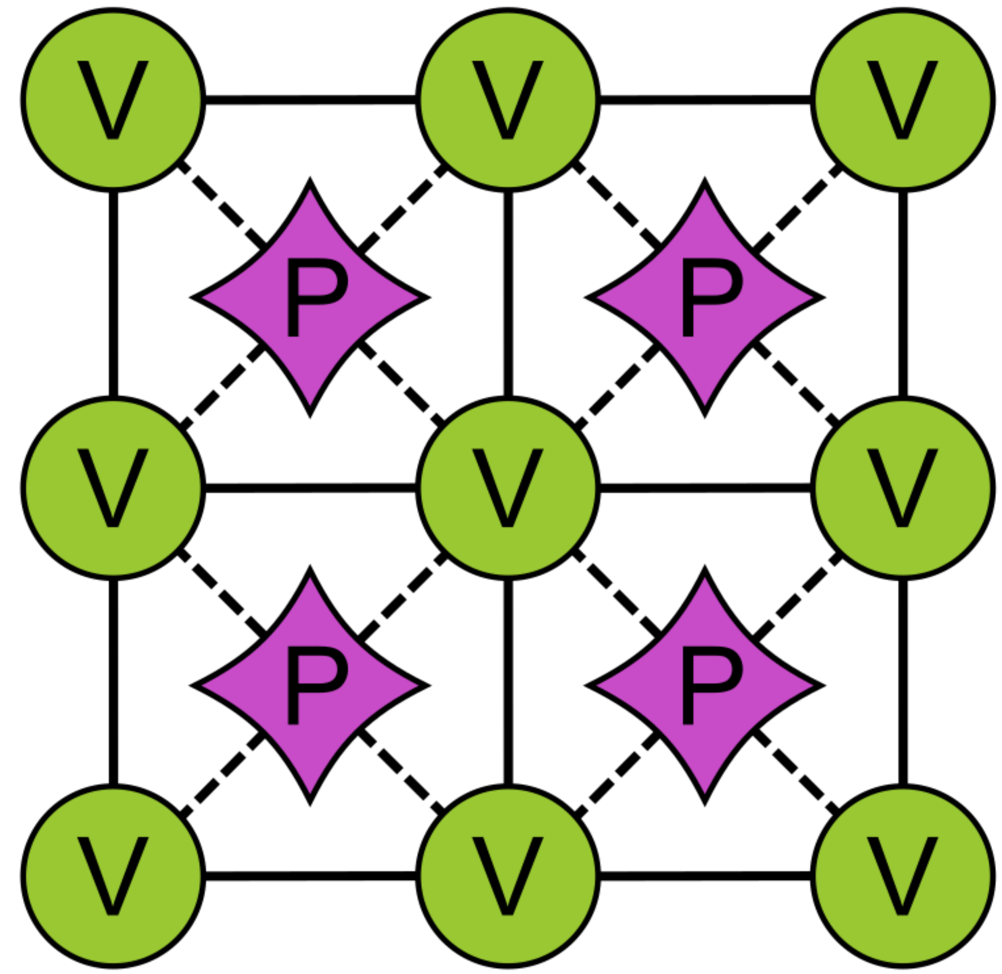
Wioland et al (2016)
Nature Physics

… driven by edge currents around pillars

Wioland et al (2016) Nat Phys

anti-ferro *vs.* ferro

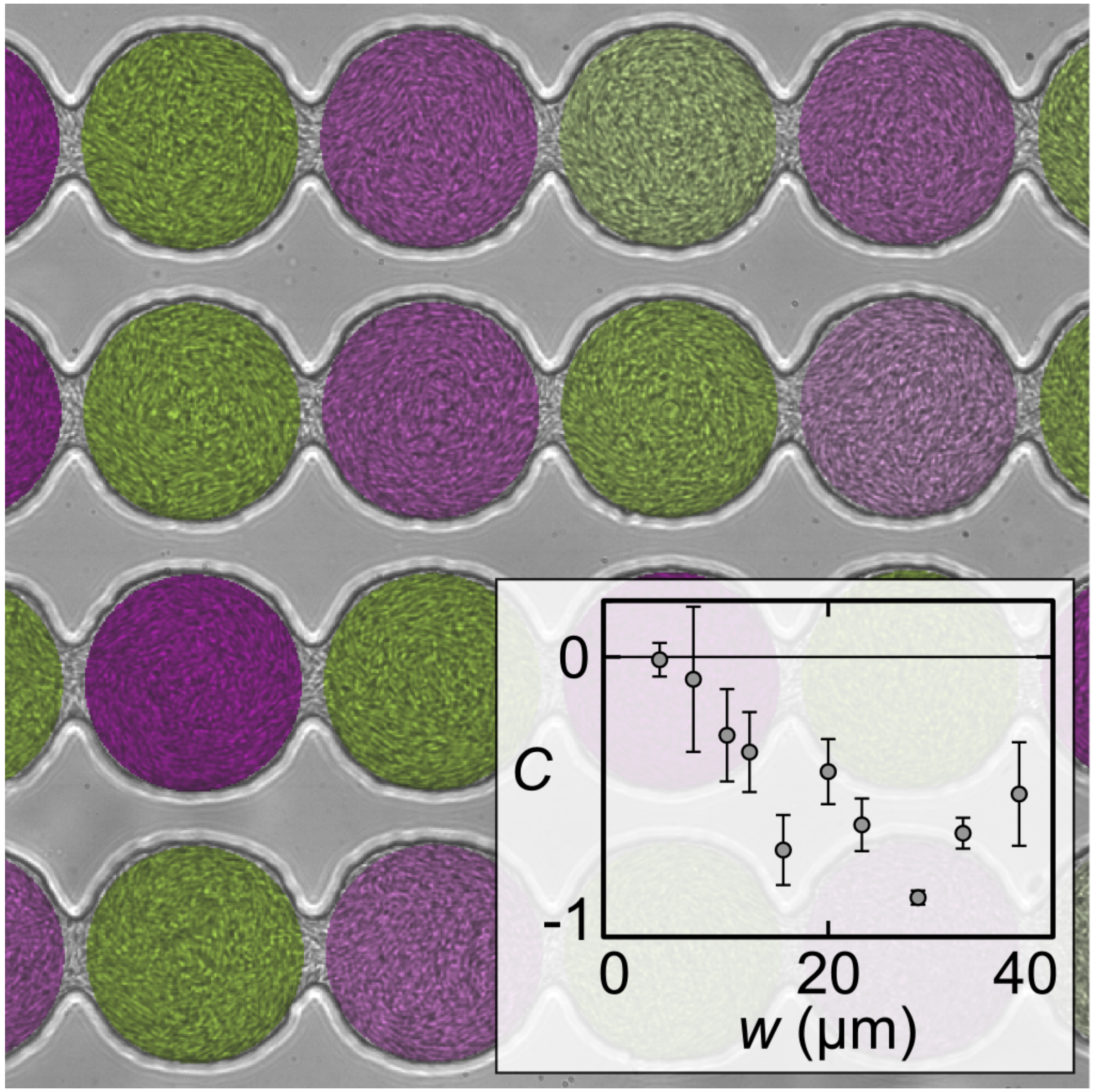


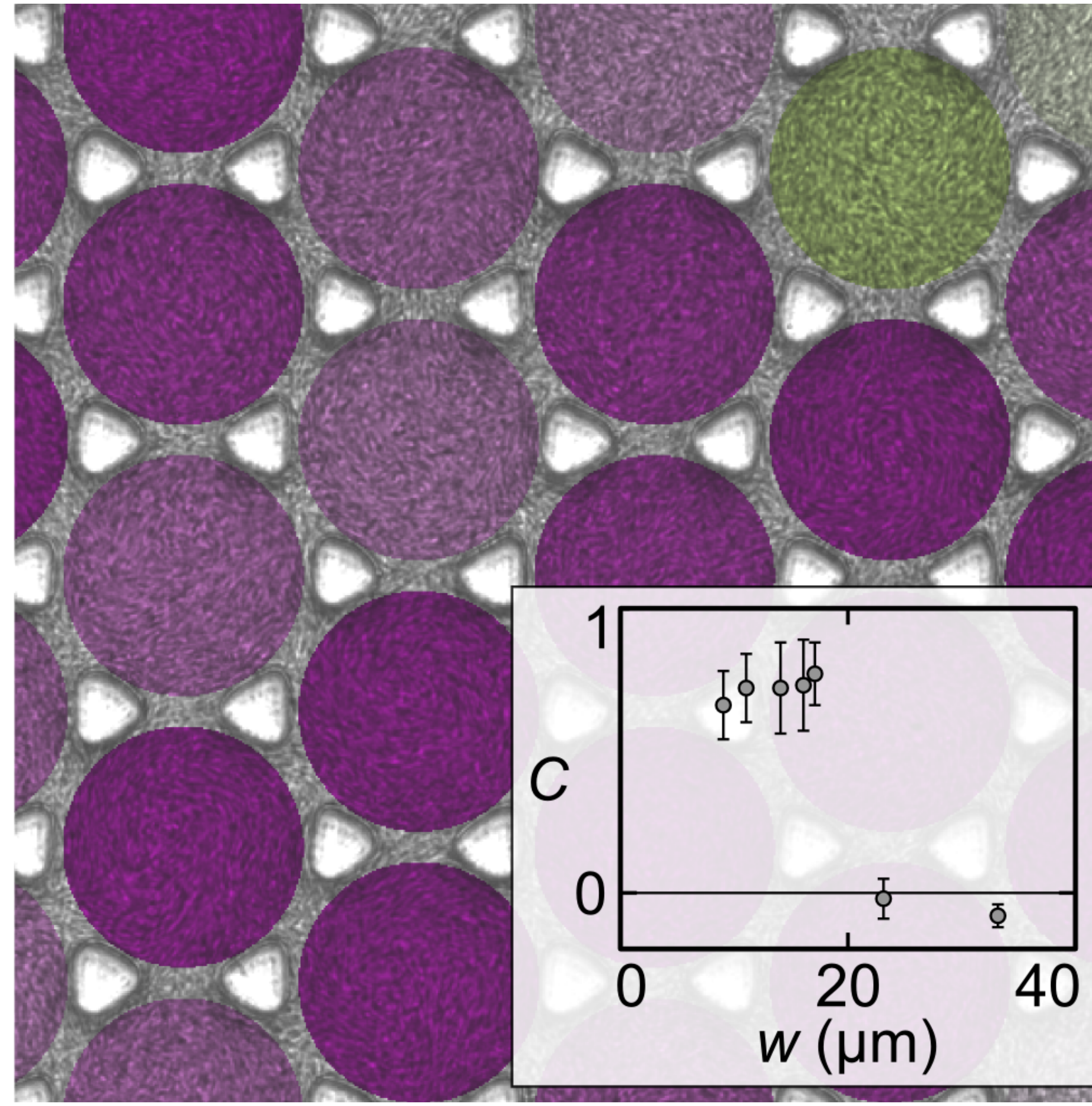


$$H(\mathbf{V},\mathbf{E}) = -J_v \sum_{V_i \sim V_j} V_i V_j - J_e \sum_{V_i \sim E_j} V_i E_j$$

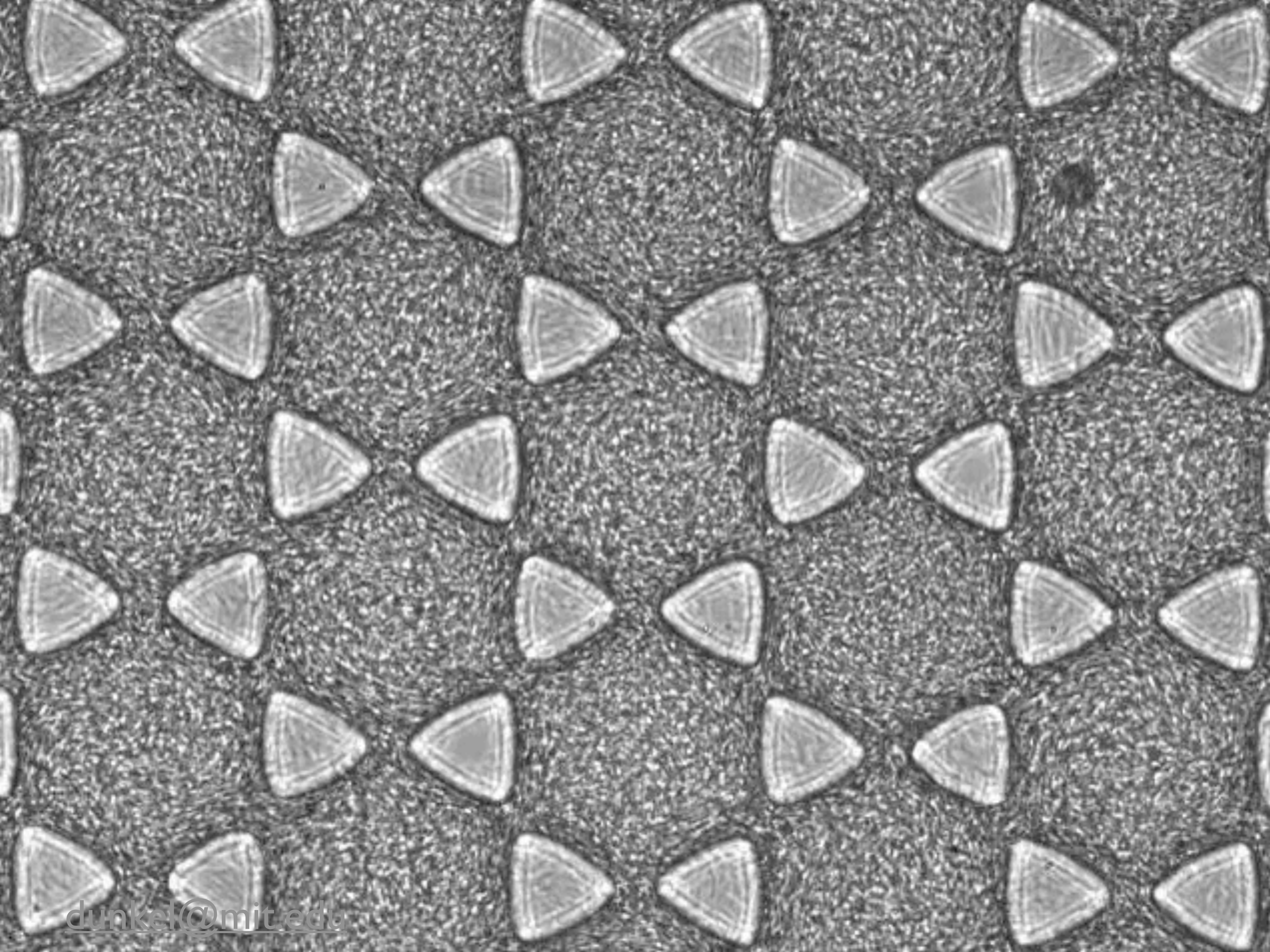
$$+ \sum_{V_i} \left(\tfrac{1}{2} a_v V_i^2 + \tfrac{1}{4} b_v V_i^4 \right) + \sum_{E_i} \tfrac{1}{2} a_p E_i^2$$

Geometry & frustration





$$C = \overline{\langle V_i V_j \rangle_{i \sim j}}$$


dunkel@mit.edu

Reduction of Viscosity in Suspension of Swimming Bacteria

Andrey Sokolov[1,2] and Igor S. Aranson[2]

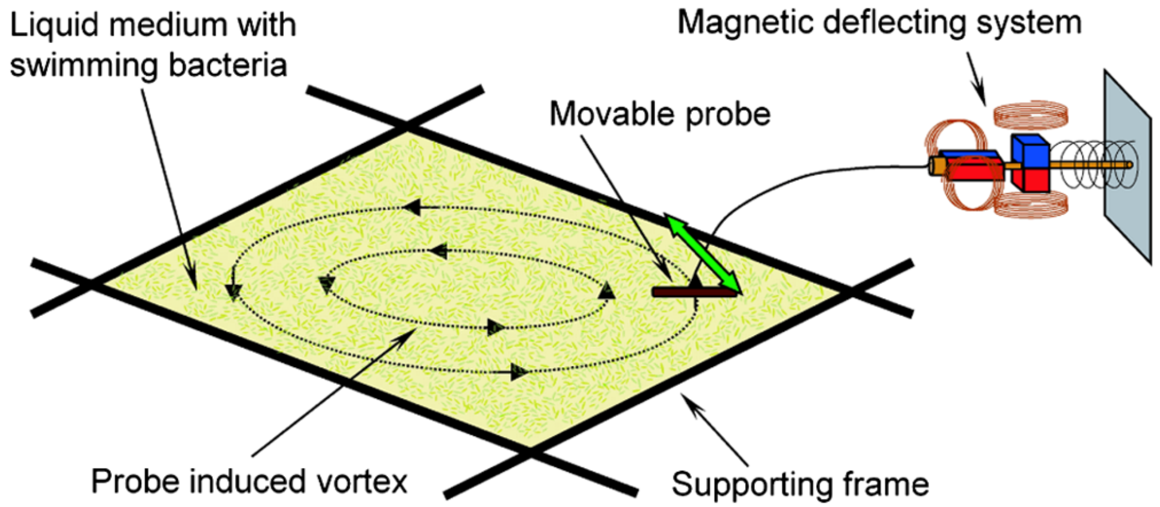


FIG. 1 (color online). Experimental setup 1: a thin liquid film with bacteria spans between four movable fibers. A micromanipulator with a magnetic deflecting system is used to initiate a large vortex through movement of the probe.

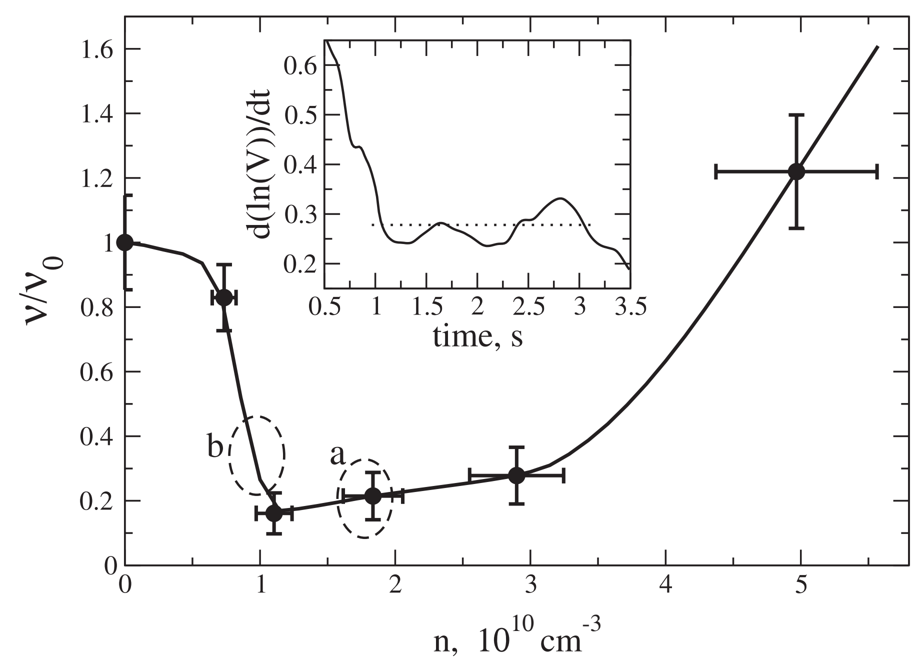


FIG. 3. Viscosity for 6 different concentrations of bacteria. ν_0 is the viscosity of the liquid without bacteria. Inset: instant viscosity vs time during decay of the vortex for density $n = 2.9 \times 10^{10}$. The dashed line is the average value of the viscosity during the slow phase of decay. See movies 1 and 2 in [19].

Non-Newtonian Viscosity of *Escherichia coli* Suspensions

Jérémie Gachelin, Gastón Miño, Hélène Berthet, Anke Lindner,* Annie Rousselet, and Éric Clément
PMMH-ESPCI, UMR 7636 CNRS-ESPCI-Universities Pierre et Marie Curie and Denis Diderot, 10 rue Vauquelin, 75005 Paris, France
(Received 5 October 2012; published 26 June 2013)

$$\eta_r = \frac{\eta_1}{\eta_0} = \frac{d_1}{d_0}. \quad (1)$$

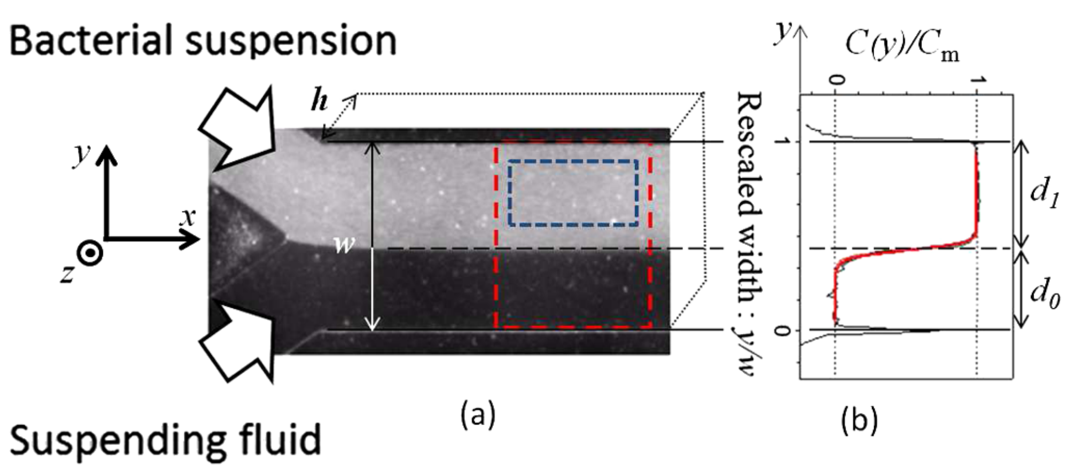
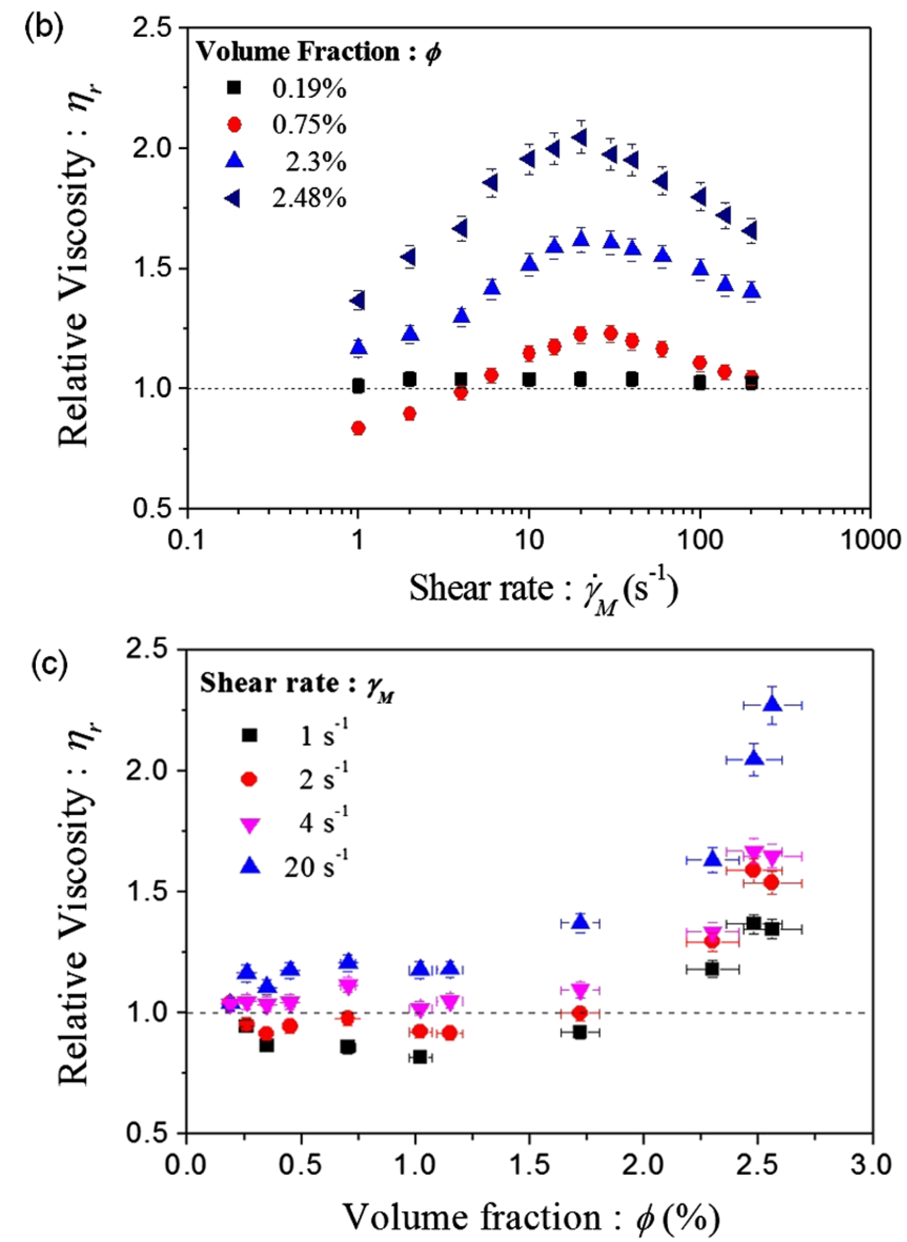


FIG. 1 (color online). Experimental setup. (a) Time-averaged image of the microchannel ($W = 600\ \mu$m) for $Q = 10$ nl/sec in each branch and volume fraction $\phi = 0.35\%$. Bacteria are visualized using a white light microscope. The red and blue frames indicate the measurement areas. (b) Concentration profile $C(y)$ normalized by the maximum concentration C_M (black line) and error function fit used to determine the interface position (red line).



Turning Bacteria Suspensions into Superfluids

Héctor Matías López,[1] Jérémie Gachelin,[2] Carine Douarche,[3] Harold Auradou,[1,*] and Eric Clément[2]
[1]Université Paris-Sud, CNRS, F-91405, Lab FAST, Bâtiment 502, Campus Univ, Orsay F-91405, France
[2]Physique et Mécanique des Milieux Hétérogenes (UMR 7636 ESPCI/CNRS/Université P.M. Curie/Université Paris-Diderot), 10 rue Vauquelin, 75005 Paris, France
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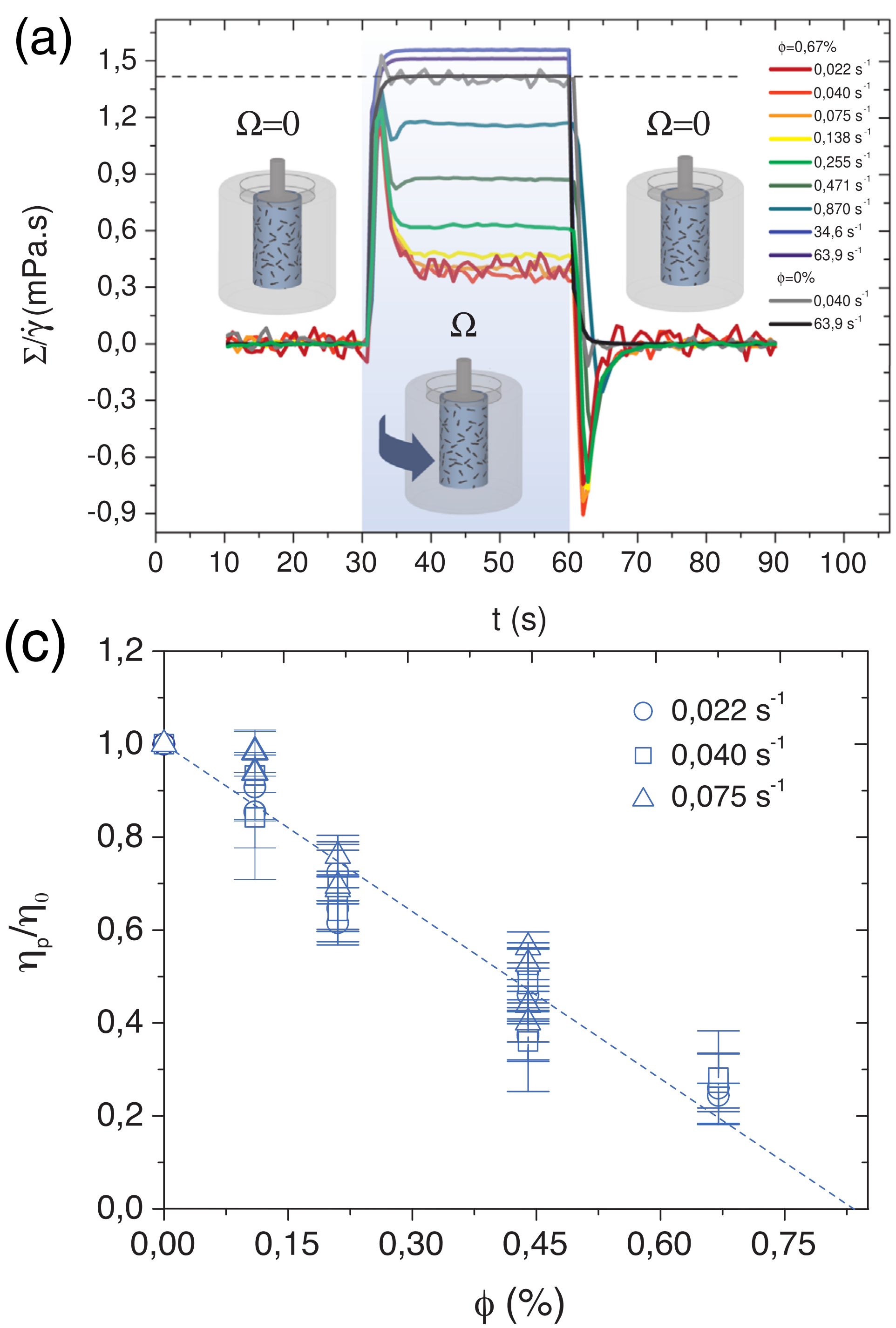
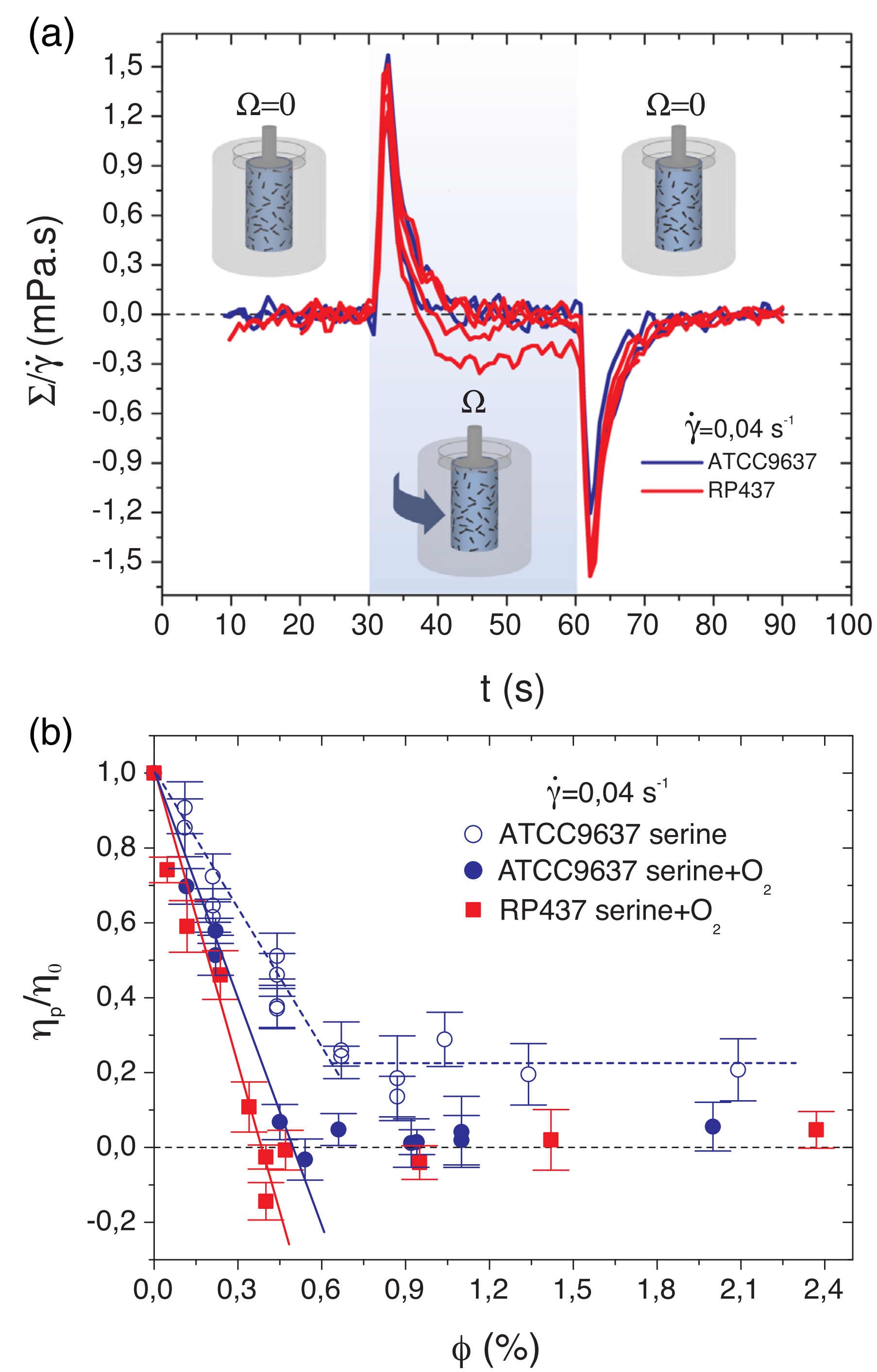
(Received 19 March 2015; revised manuscript received 24 May 2015; published 7 July 2015)





PRL **101,** 068102 (2008) PHYSICAL REVIEW LETTERS week ending 8 AUGUST 2008

Shearing Active Gels Close to the Isotropic-Nematic Transition

M. E. Cates,[1] S. M. Fielding,[2] D. Marenduzzo,[1] E. Orlandini,[3] and J. M. Yeomans[4]

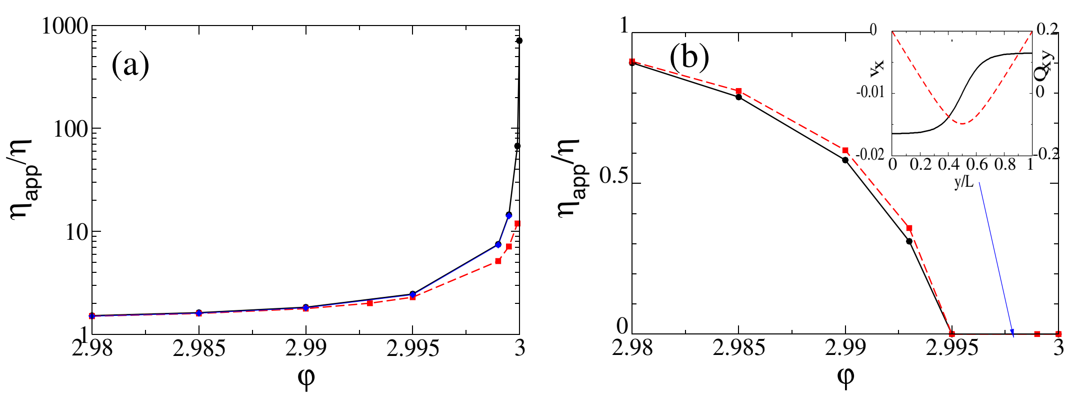


FIG. 2 (color online). (a) Apparent zero shear viscosity for an isotropic contractile gel in a slab under shear. Solid curve(s): free-boundary conditions; HLB data are indistinguishable from those derived from the bulk flow curve [13]. Dashed curve: fixed boundaries (director along flow). (b) Apparent viscosity in a linear regime for an active extensile gel in a slab under shear. Solid and dashed curves correspond to systems with free and fixed boundaries, respectively. The insets show plots of Q_{xy} and u_x (solid and dashed lines) in the $\eta_{\rm app} = 0$ phase.

$$\Pi_{\alpha\beta} = 2\xi\Big(Q_{\alpha\beta} + \frac{1}{3}\delta_{\alpha\beta}\Big)Q_{\gamma\epsilon}H_{\gamma\epsilon} - \xi H_{\alpha\gamma}\Big(Q_{\gamma\beta} + \frac{1}{3}\delta_{\gamma\beta}\Big) - \xi\Big(Q_{\alpha\gamma} + \frac{1}{3}\delta_{\alpha\gamma}\Big)H_{\gamma\beta} - \partial_\alpha Q_{\gamma\nu}\frac{\delta\mathcal{F}}{\delta\partial_\beta Q_{\gamma\nu}} + Q_{\alpha\gamma}H_{\gamma\beta} - H_{\alpha\gamma}Q_{\gamma\beta} - \zeta Q_{\alpha\beta}. \quad (2)$$

$$\eta_{\rm app}(\dot\gamma, L, \ldots) = (\Pi_{xy} + \eta\partial_y u_x)/\dot\gamma.$$

PHYSICAL REVIEW E **81**, 051908 (2010)

Sheared active fluids: Thickening, thinning, and vanishing viscosity

Luca Giomi,[1,2] Tanniemola B. Liverpool,[3] and M. Cristina Marchetti[4]

New Journal of Physics
The open-access journal for physics

The Taylor–Couette motor: spontaneous flows of active polar fluids between two coaxial cylinders

S Fürthauer[1,2], M Neef[3], S W Grill[1,2], K Kruse[3,4] and F Jülicher[1]
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$$\partial_t c = -\nabla[c(\mathbf{v} + c\beta_1 \mathbf{P}) + \Gamma' \mathbf{h} + \Gamma'' \mathbf{f}], \tag{1a}$$

$$[\partial_t + (\mathbf{v} + c\beta_2 \mathbf{P})\nabla]P_i + \omega_{ij}P_j = \lambda u_{ij}P_j + \Gamma h_i + \Gamma' f_i, \tag{1b}$$

with $\omega_{ij} = (\partial_i v_j - \partial_j v_i)/2$ the vorticity tensor, $\mathbf{h} = -\delta F/\delta \mathbf{P}$ the molecular field, and $\mathbf{f} = -\nabla(\delta F/\delta c)$. The flow velocity satisfies the Navier-Stokes equation [27]

$$\rho(\partial_t + \mathbf{v} \cdot \nabla)v_i = \partial_j \sigma_{ij}, \tag{2}$$

$$F = \int_{\mathbf{r}} \left\{ \frac{C}{2}\left(\frac{\delta c}{c_0}\right)^2 + \frac{a_2}{2}|\mathbf{P}|^2 + \frac{a_4}{4}|\mathbf{P}|^4 + \frac{K_1}{2}(\nabla \cdot \mathbf{P})^2 + \frac{K_3}{2}(\nabla \times \mathbf{P})^2 + B_1 \frac{\delta c}{c_0} \nabla \cdot \mathbf{P} + B_2 |\mathbf{P}|^2 \nabla \cdot \mathbf{P} + \frac{B_3}{c_0}|\mathbf{P}|^2 \mathbf{P} \cdot \nabla c \right\},$$

$\sigma_{ij} = 2\eta u_{ij} + \sigma^r_{ij} + \sigma^\alpha_{ij} + \sigma^\beta_{ij}$, with

$$\sigma^\alpha_{ij} = \frac{\alpha c^2}{\Gamma}(P_i P_j + \delta_{ij}),$$

$$\sigma^\beta_{ij} = \frac{\beta_3 c^2}{\Gamma}[\partial_i P_j + \partial_j P_i + \delta_{ij} \nabla \cdot \mathbf{P}]$$

$$\begin{aligned}
\sigma^r_{ij} = &- \delta_{ij}\Pi + \lambda p_i p_j p_k \left[\frac{w}{c_0 \Gamma}\partial_k c + K\nabla^2 p_k \right] \\
&- \frac{\lambda}{2}\left[\frac{w}{c_0\Gamma}(p_i \partial_j c + p_j \partial_i c) + K(p_i \nabla^2 p_j + p_j \nabla^2 p_i) \right] \\
&+ \frac{1}{2}\left[\frac{w}{c_0\Gamma}(p_i \partial_j c - p_j \partial_i c) + K(p_i \nabla^2 p_j - p_j \nabla^2 p_i) \right] \\
&- \lambda \Gamma' \xi p_i p_j (D p_k \partial_k c + w p_k \partial_k \partial_l p_l) + \frac{\lambda^2}{\Gamma} p_i p_j u_{kl} p_k p_l .
\end{aligned}$$

Minimal momentum-conserving model for solvent flow

Jonasz Slomka

Flow equations

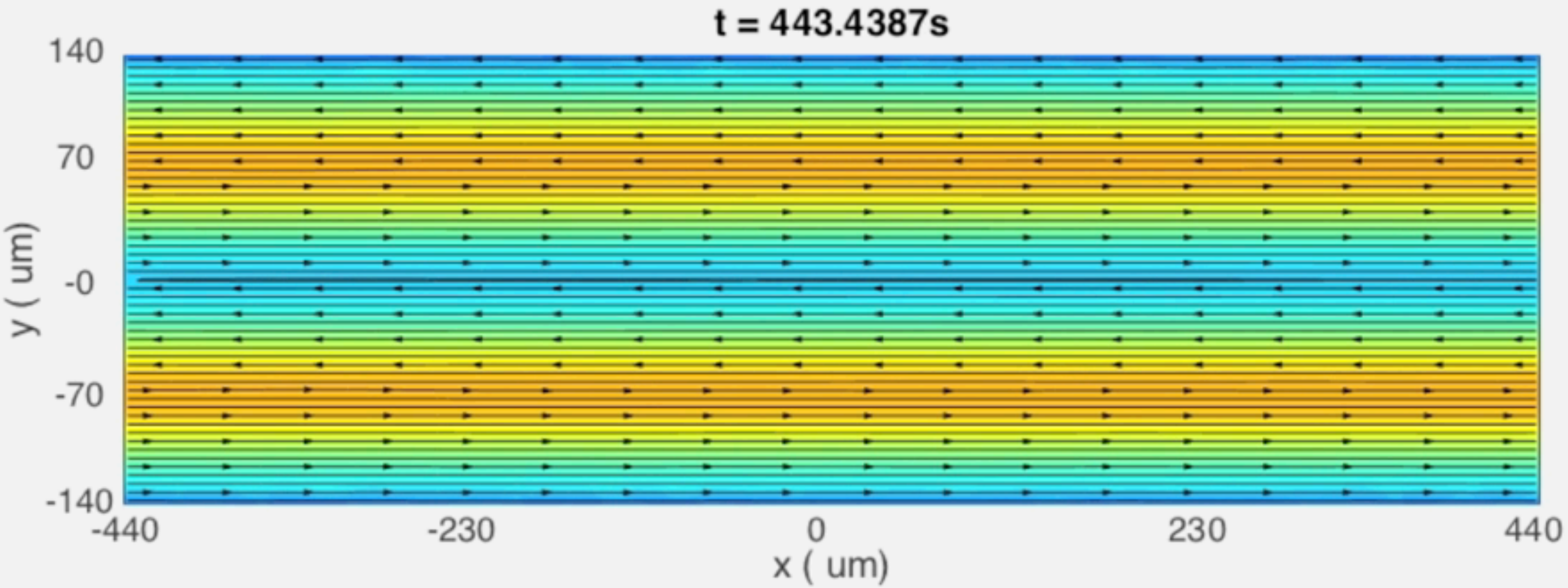
$$
\begin{aligned}
0 &= \nabla \cdot \boldsymbol{v} \\
\partial_t \boldsymbol{v} + (\boldsymbol{v} \cdot \nabla)\boldsymbol{v} &= -\nabla p + \nabla \cdot \boldsymbol{\sigma}
\end{aligned}
$$

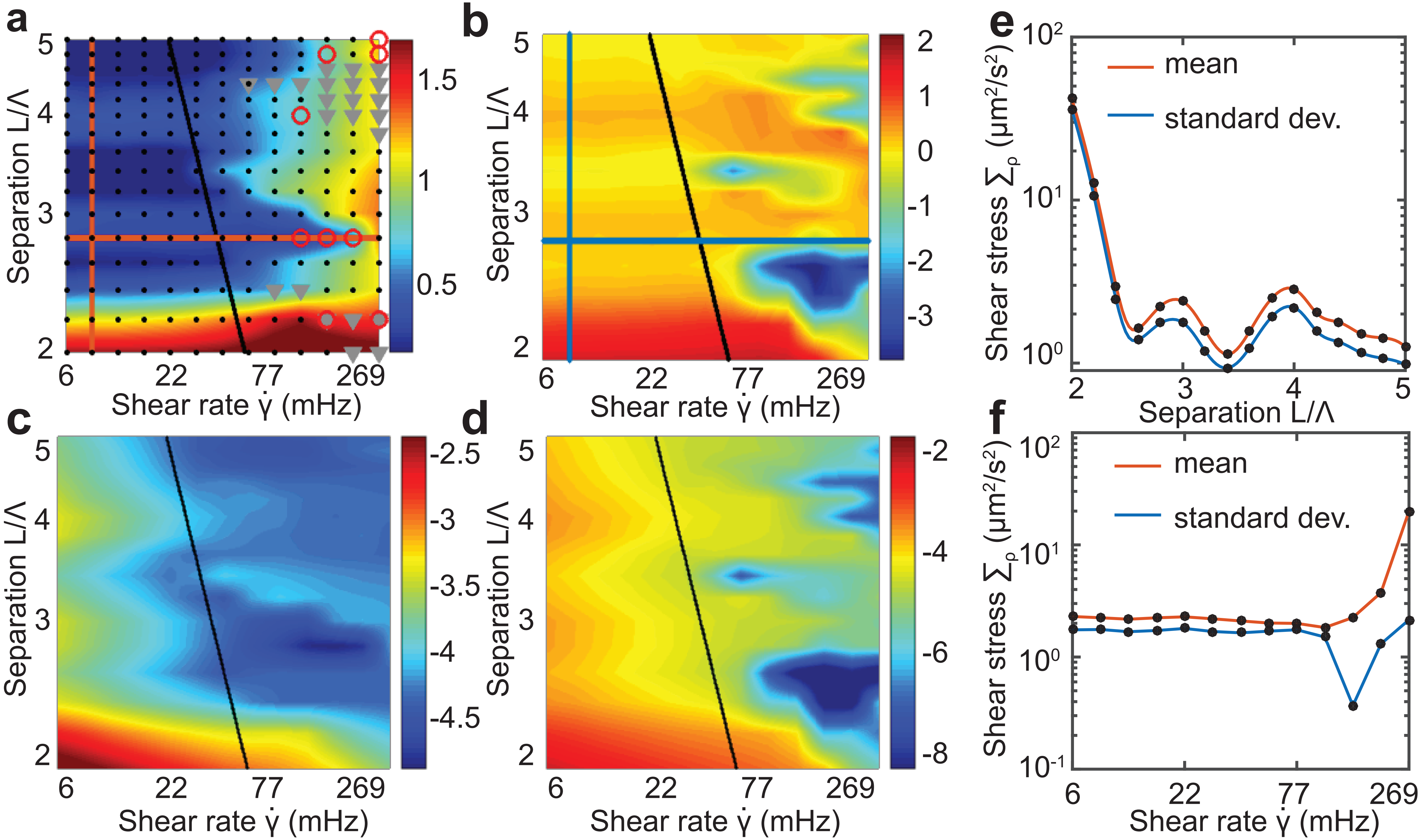
with stress tensor

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

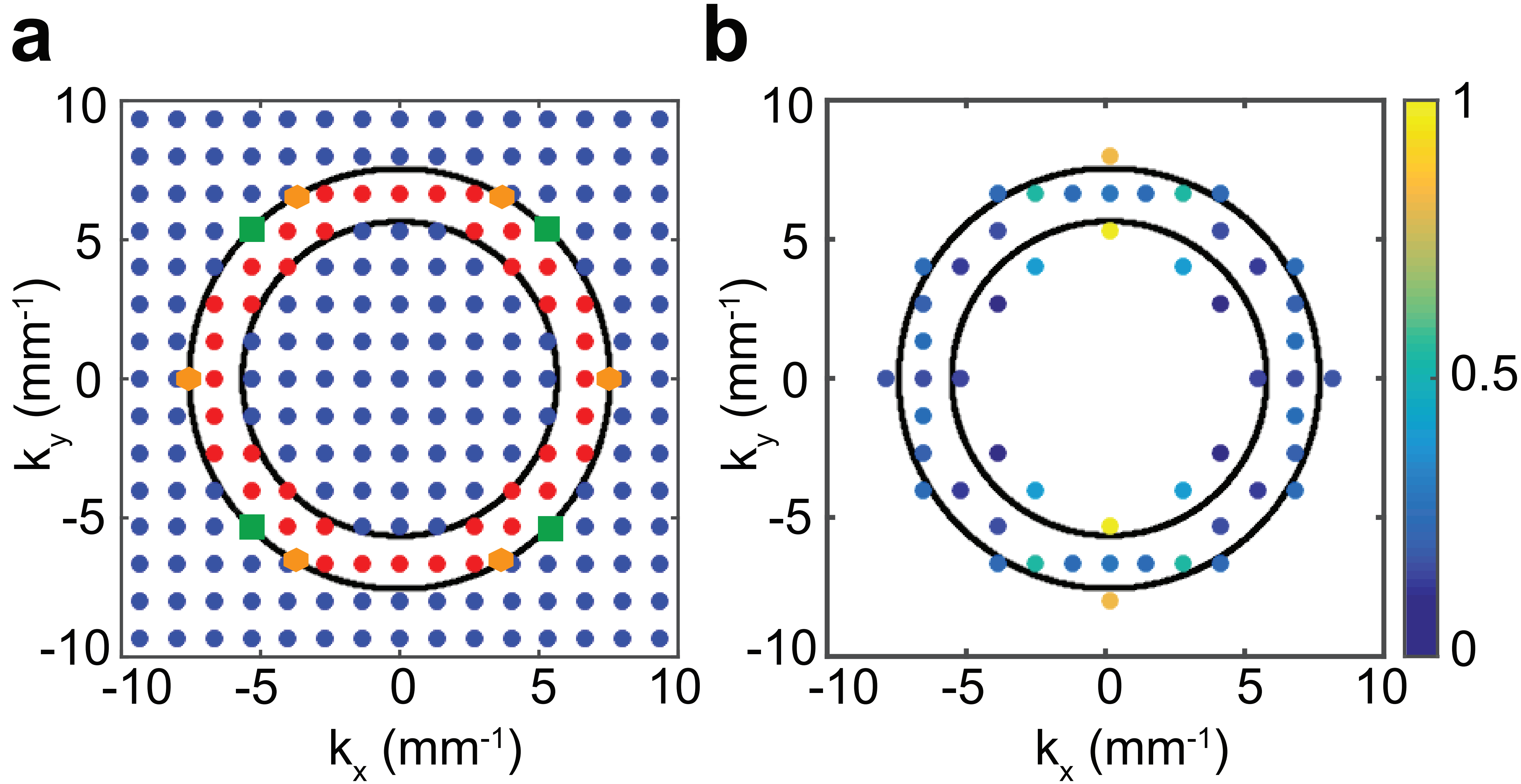
6th order PDE + no-slip +
different types of higher order BC

Preliminary numerical results





a
b
c
d
e
f
Separation L/Λ
Shear rate γ̇ (mHz)
6
22
77
269
2
3
4
5
1.5
1
0.5
2
0
-1
-2
-3
-2.5
-3
-3.5
-4
-4.5
-4
-6
-8
Shear stress Σ_ρ ($\mu m^2/s^2$)
mean
standard dev.
10^2
10^1
10^0
10^{-1}


a
b
10
5
0
-5
-10
-10
-5
0
5
10
k_y (mm^{-1})
k_x (mm^{-1})
1
0.5
0

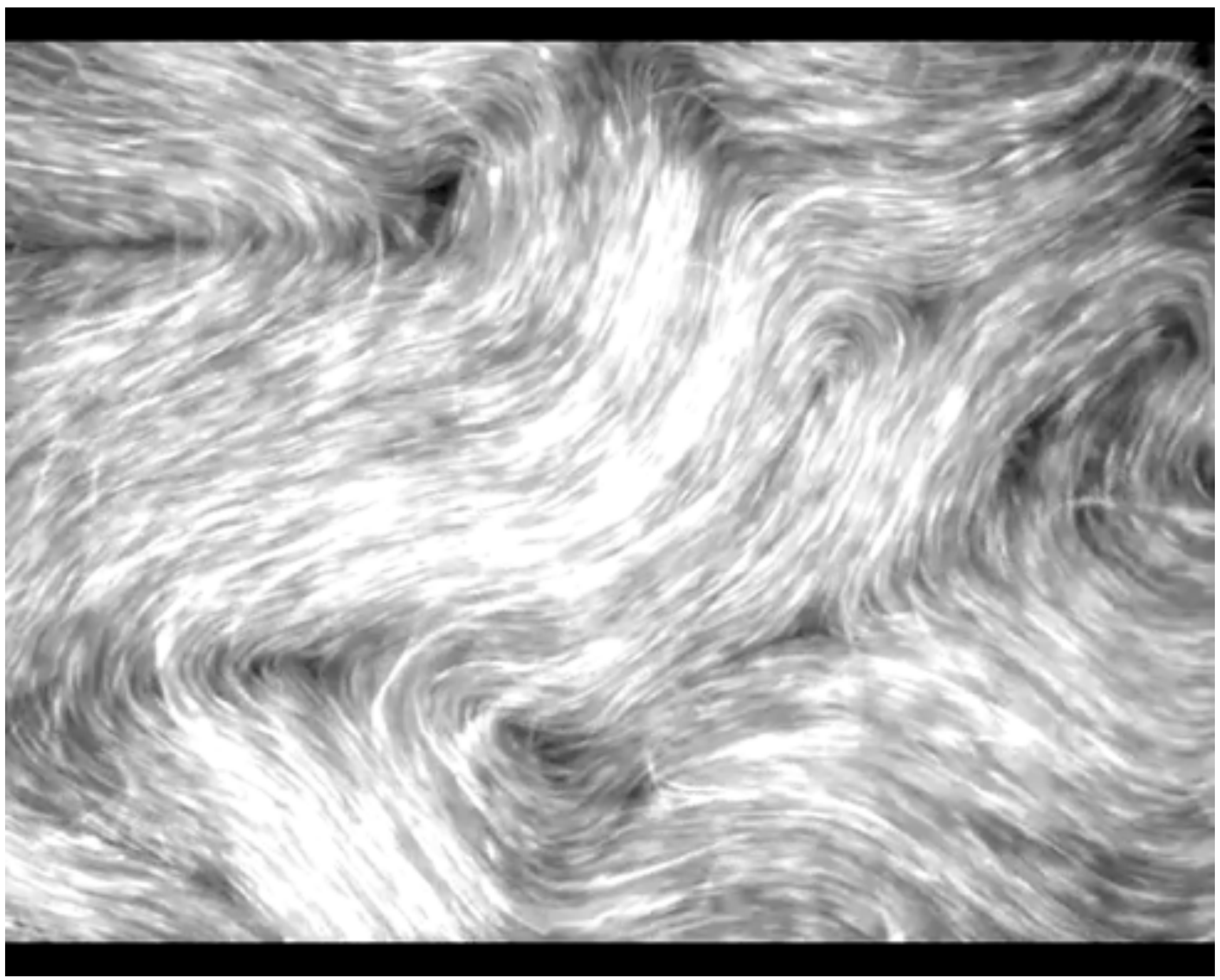
- effects of spatial dimensionality on individual microbial swimming (2D vs. 3D)
- intrinsic vortex scale selection in bacterial suspensions
- confinement & collective dynamics of quasi-2D suspensions (edge currents, magnetic order, quasi-“superfluidity”, etc.)
- defect dynamics and long-range order in 2D planar/curved active nematics

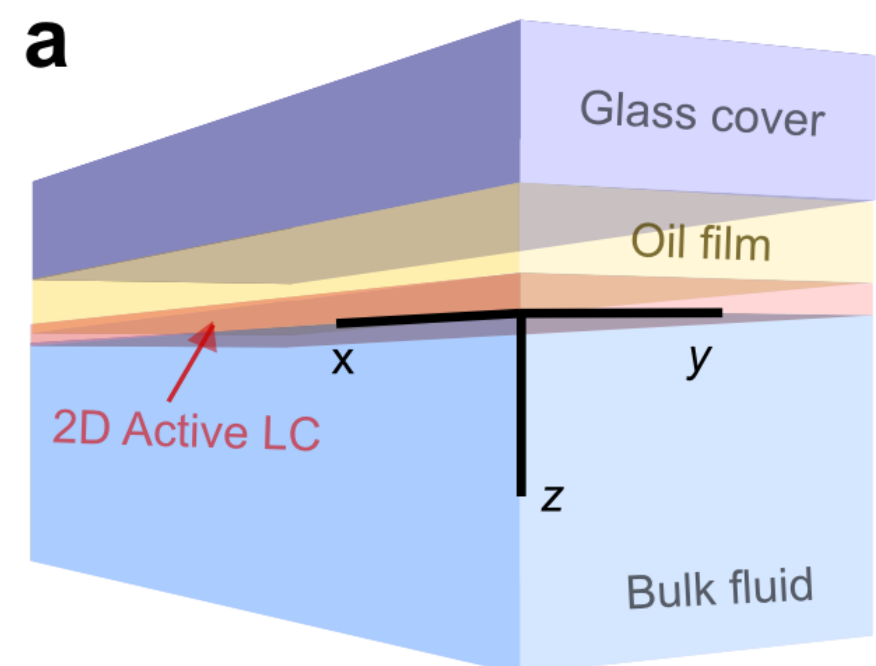
LETTER

doi:10.1038/nature11591

Spontaneous motion in hierarchically assembled active matter

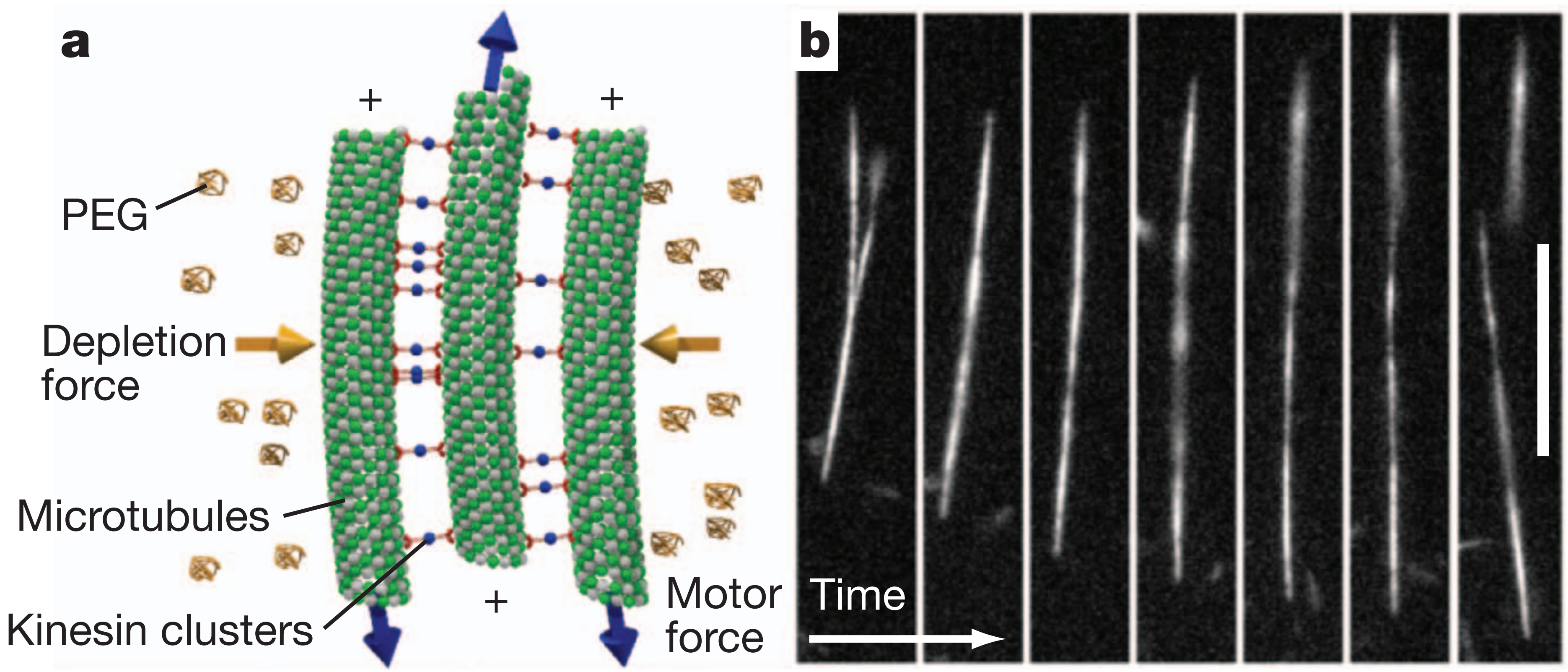
Tim Sanchez[1]*, Daniel T. N. Chen[1]*, Stephen J. DeCamp[1]*, Michael Heymann[1,2] & Zvonimir Dogic[1]





Dogic lab (2012) Nature

Active nematics



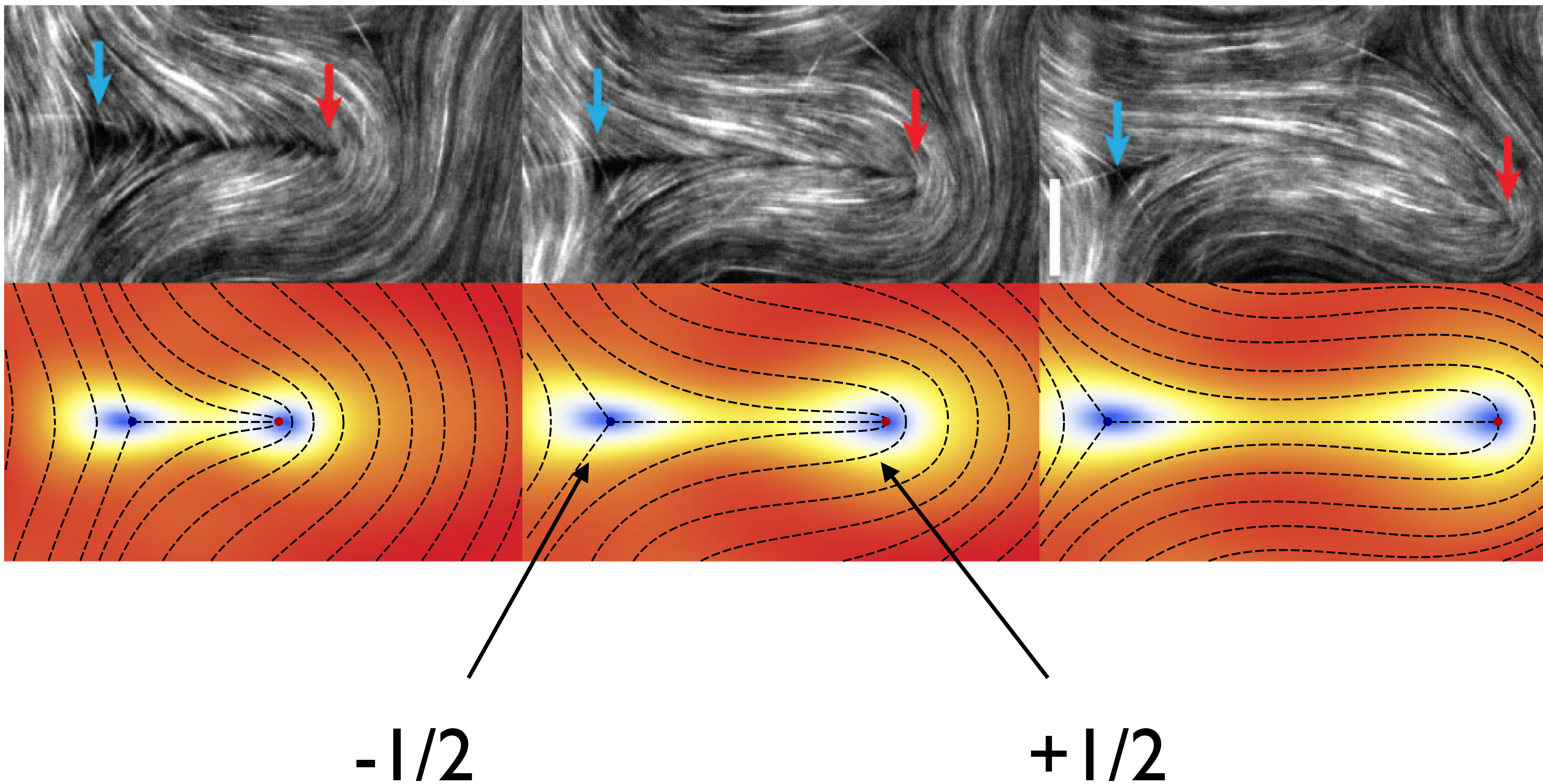
Dogic lab (Brandeis) Nature 2012

no head or tail ⇒ Q-tensor order-parameter

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

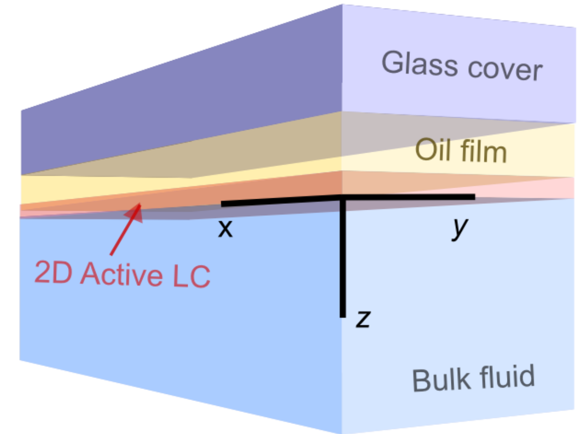
$$\Delta = \sqrt{\lambda^2 + \mu^2}, \qquad \Lambda^{\pm} = \pm \Delta$$

Active nematics



Giomi et al PRL 2012

Active LCs



Anand Oza

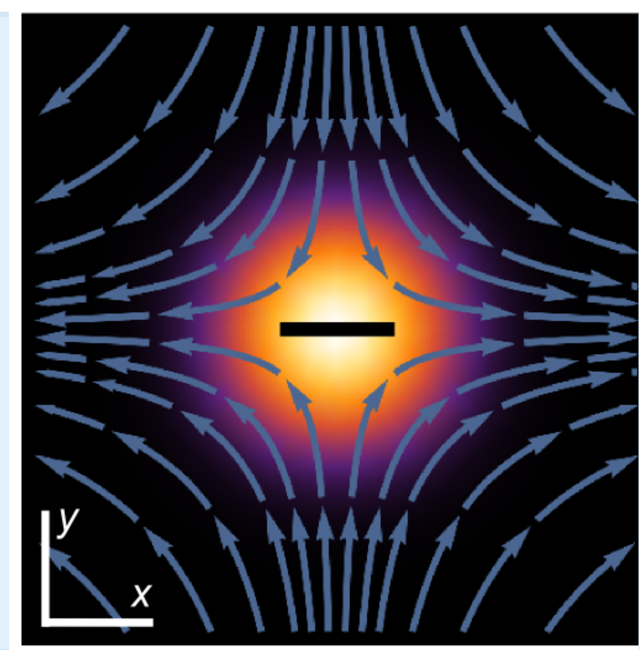
$$\partial_t Q + \boxed{\nabla \cdot (\boldsymbol{v} Q)} = -\frac{\delta \mathcal{F}}{\delta Q}$$

$$F = \mathrm{Tr}\left\{ -\frac{a}{2} Q^2 + \frac{b}{4} Q^4 - \frac{\gamma_2}{2} (\nabla Q)^2 + \frac{\gamma_4}{4} (\nabla \nabla Q)^2 \right\}$$

Non-incompressible overdamped HD

$$-\eta \nabla^2 \boldsymbol{v} + \nu \boldsymbol{v} = -\zeta \nabla \cdot Q$$

$$\boldsymbol{v} = -D \nabla \cdot Q \qquad D = \zeta / \nu$$



arXiv:1507.01055

Complex representation

Generalization of analogy between smectic LCs and Abrikosov vortex
(De Gennes 1972, Renn & Lubensky 1988, Pindak and co-workers 1990)

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

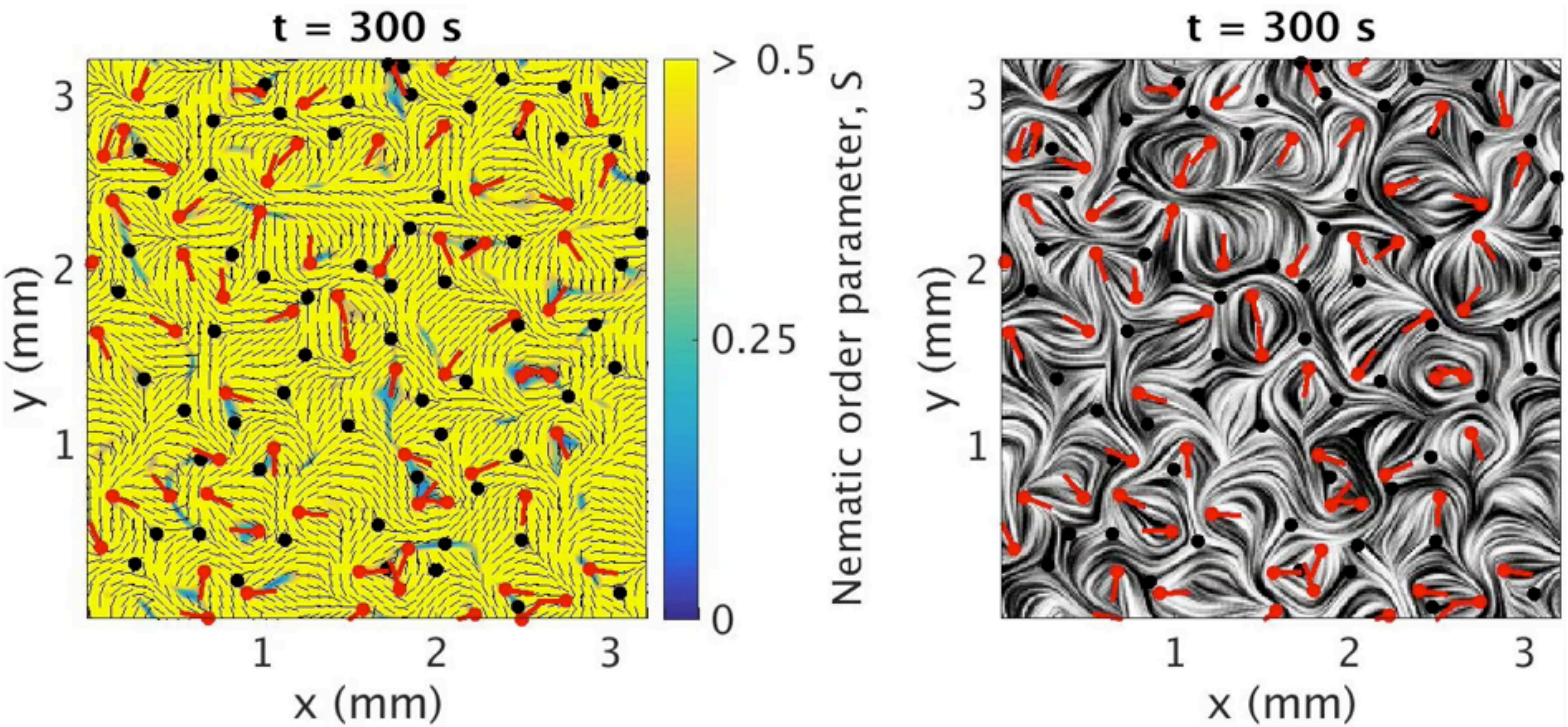
$$Q = \begin{pmatrix} \lambda & \mu \\ \mu & -\lambda \end{pmatrix} \qquad \psi(t,z) = \lambda + i\mu \qquad \partial = \tfrac{1}{2}(\partial_x - i\partial_y)$$

$$\partial_t \psi - 4D\,\Re\{(\partial^2\psi) + (\partial\psi)\partial\}\,\psi = \left(\frac{1}{4} - |\psi|^2\right)\psi - \gamma_2(4\bar{\partial}\partial)\psi - (4\bar{\partial}\partial)^2\psi$$

Generalized Gross-Pitaevski equation
with double-well dispersion

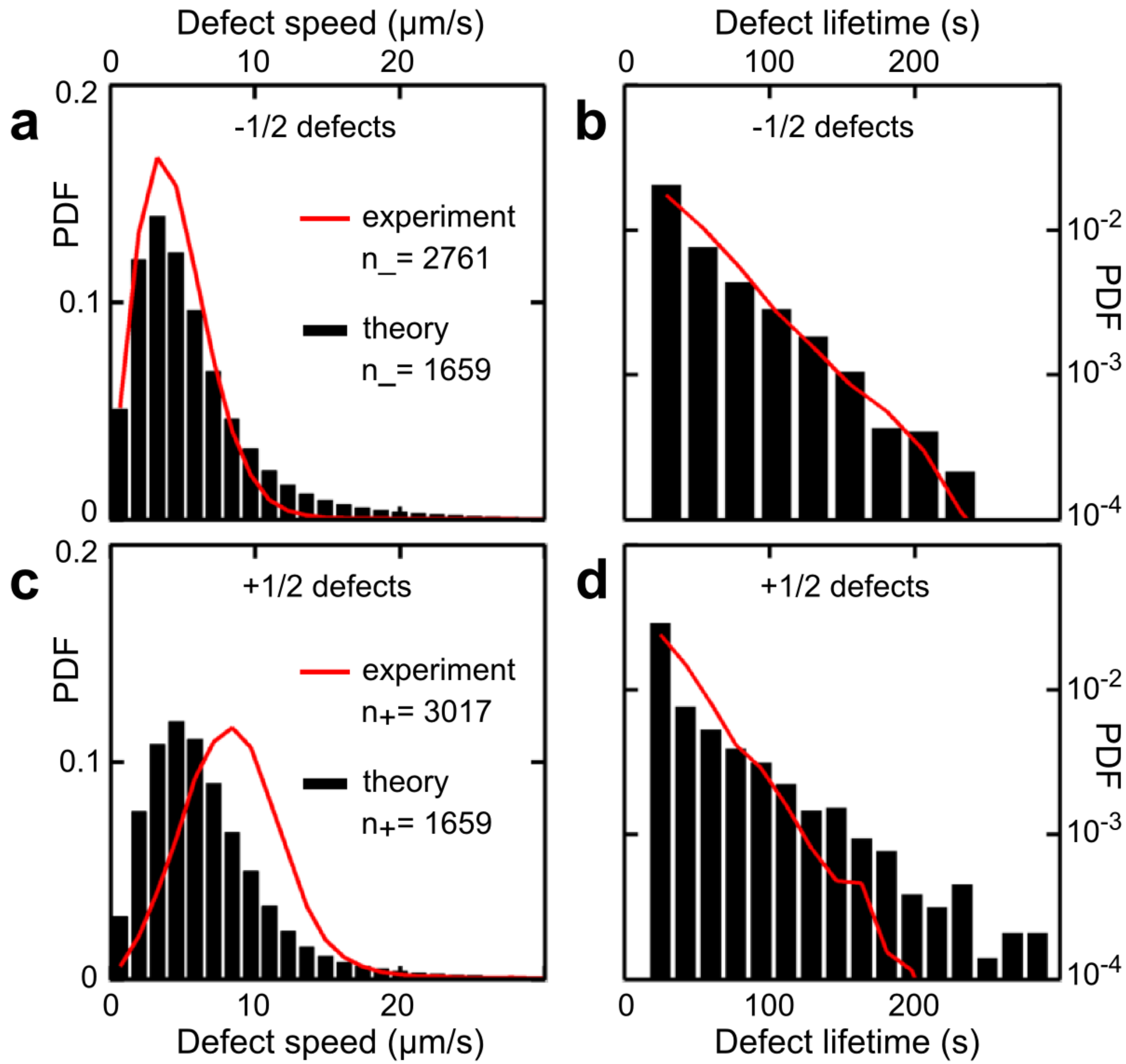
Lin et al Nature 2011 Cheuk et al PRL 2012 Parker et al Nature Phys 2013

Chaotic phase



arXiv:1507.01055

Experiment vs. theory



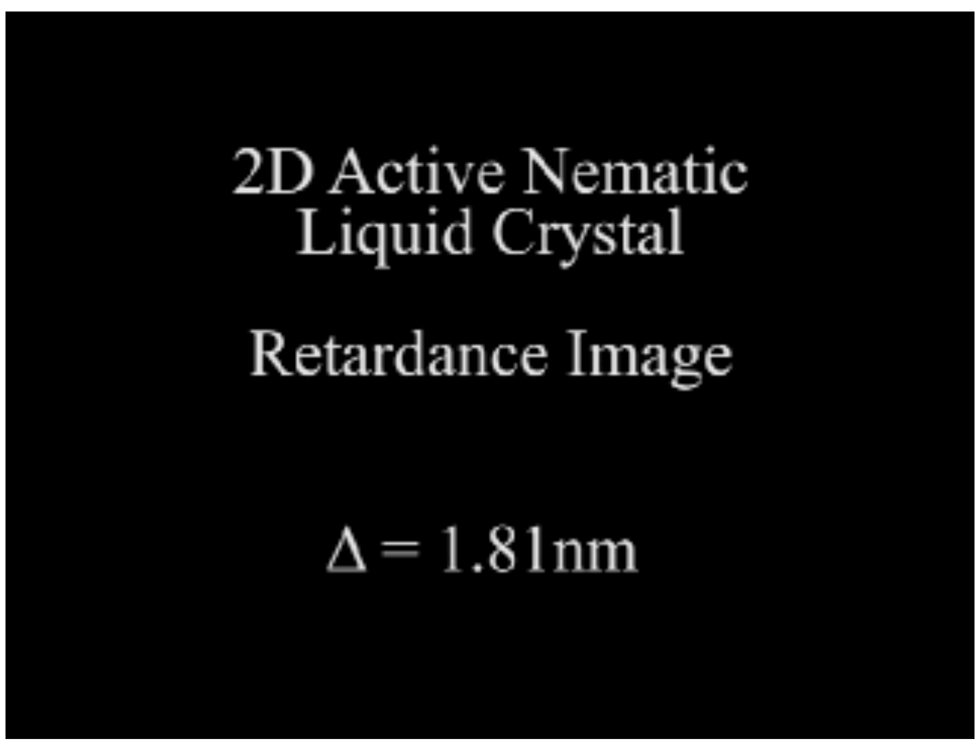
Experimental data kindly provided by Zvonimir Dogic and Steve DeCamp

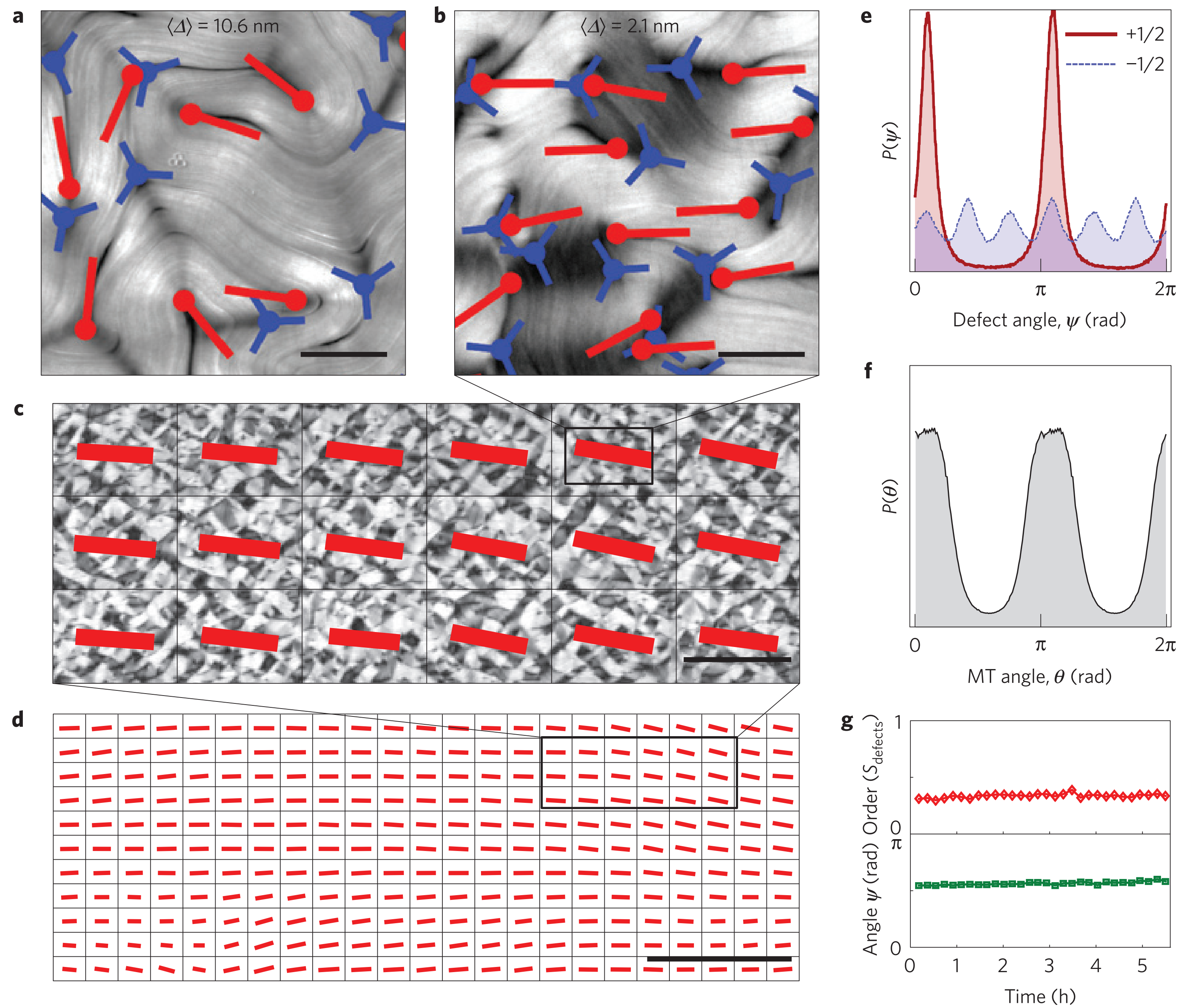
Open problem: longe-range ordering


LETTERS
PUBLISHED ONLINE: 17 AUGUST 2015 | DOI: 10.1038/NMAT4387
nature materials

Orientational order of motile defects in active nematics

Stephen J. DeCamp[†], Gabriel S. Redner[†], Aparna Baskaran, Michael F. Hagan* and Zvonimir Dogic*



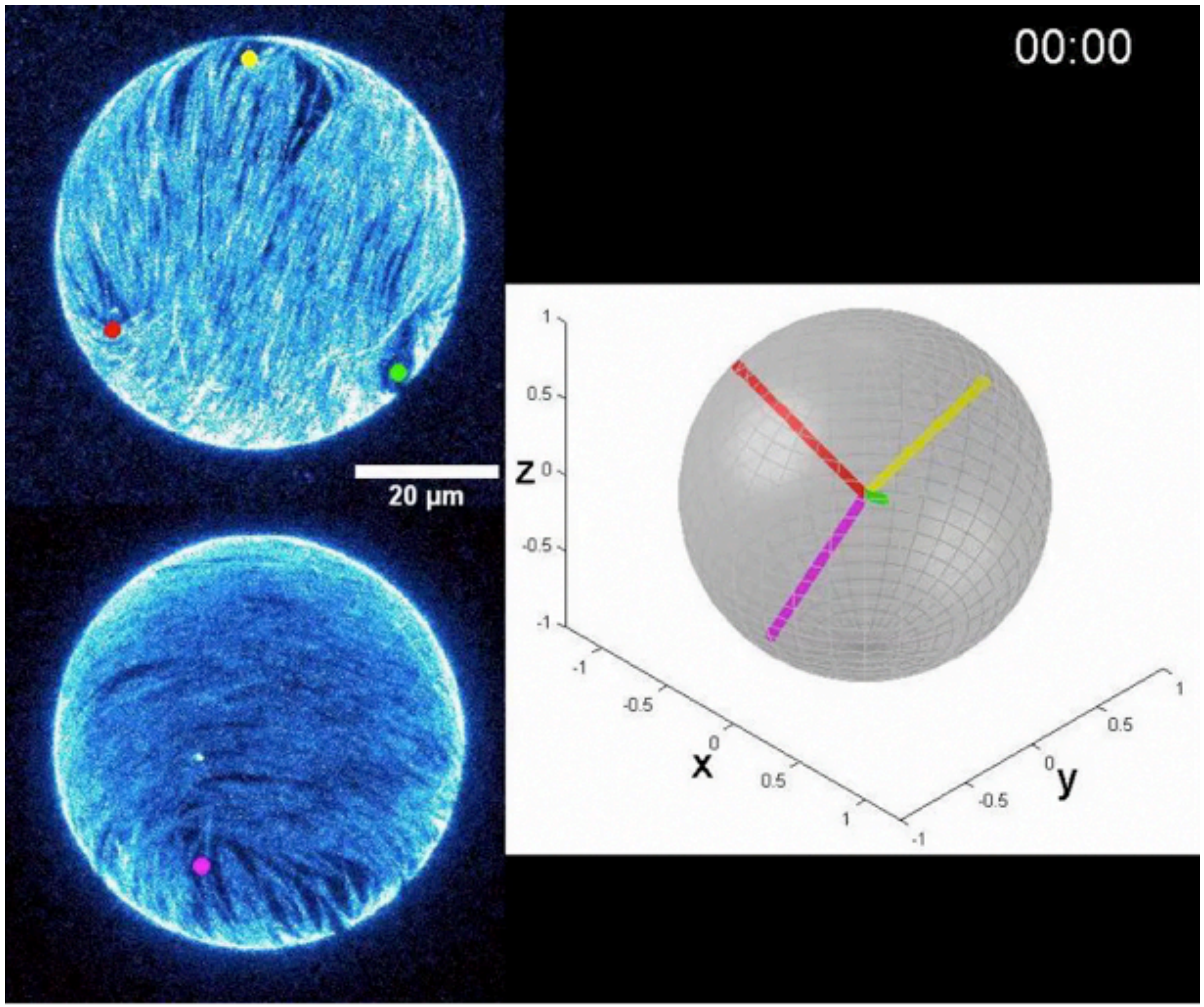


RESEARCH ARTICLES

DYNAMIC ORDERING

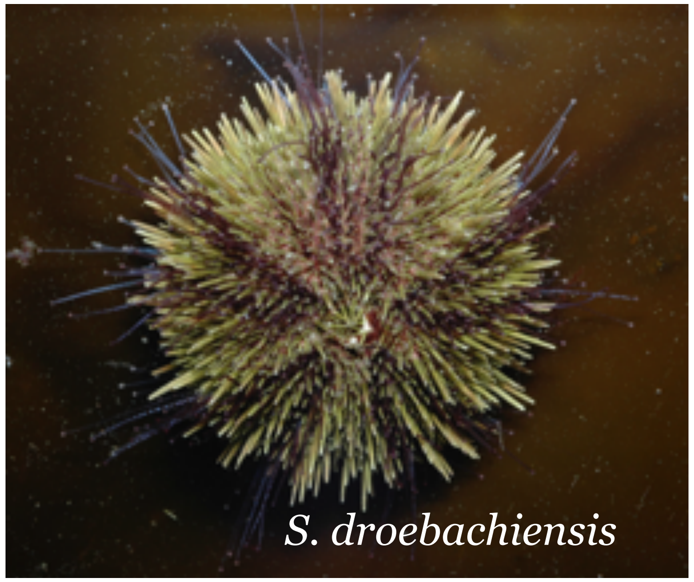
Topology and dynamics of active nematic vesicles

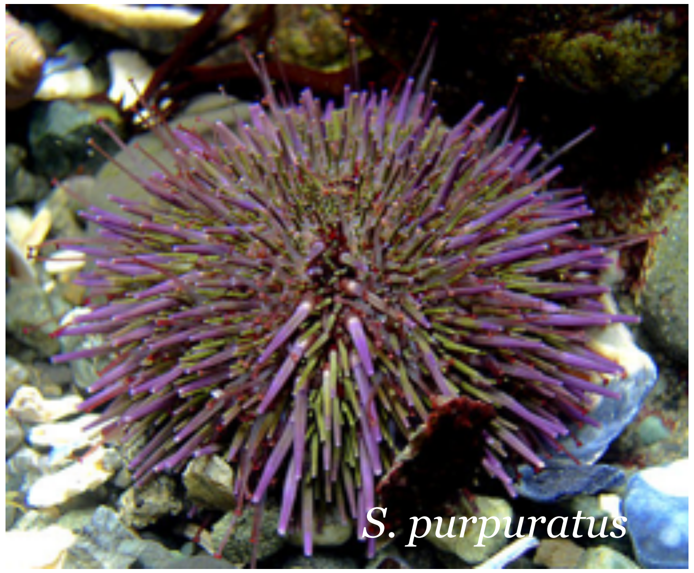
Felix C. Keber,[1,2]* Etienne Loiseau,[1]* Tim Sanchez,[3]* Stephen J. DeCamp,[3] Luca Giomi,[4,5] Mark J. Bowick,[6] M. Cristina Marchetti,[6] Zvonimir Dogic,[2,3] Andreas R. Bausch[1]†

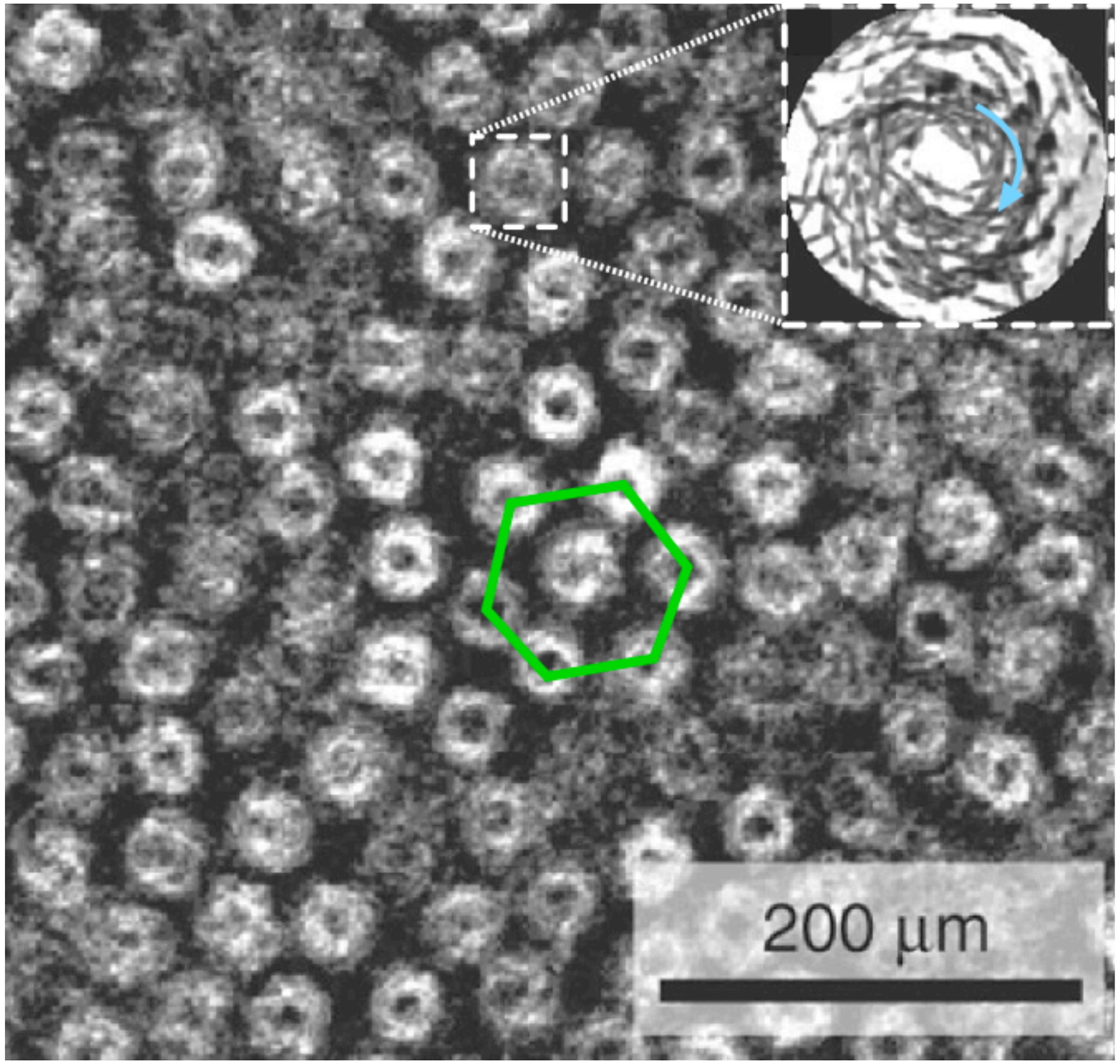


Surface interactions

Sea urchin sperm







Riedel et al (2005) Science