

Control of microbial locomotion by boundaries and flow gradients

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Collaborators

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- Rik Wensink (CNRS Paris)
- Hartmut Loewen (Dusseldorf)

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Hugo Wioland
(Cambridge)

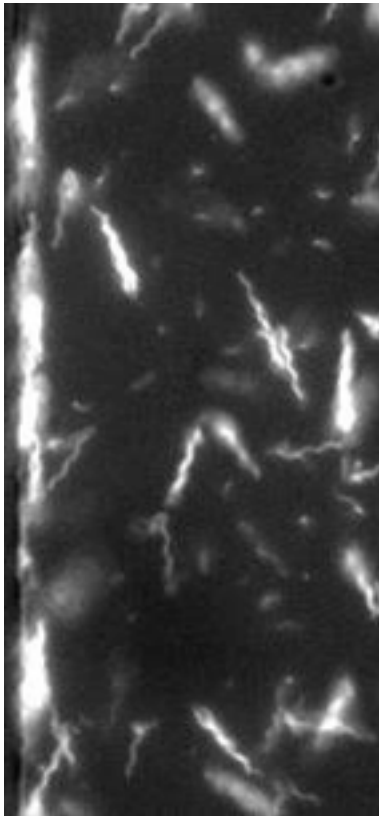


Vasily Kantsler
(Warwick/SkolTech)



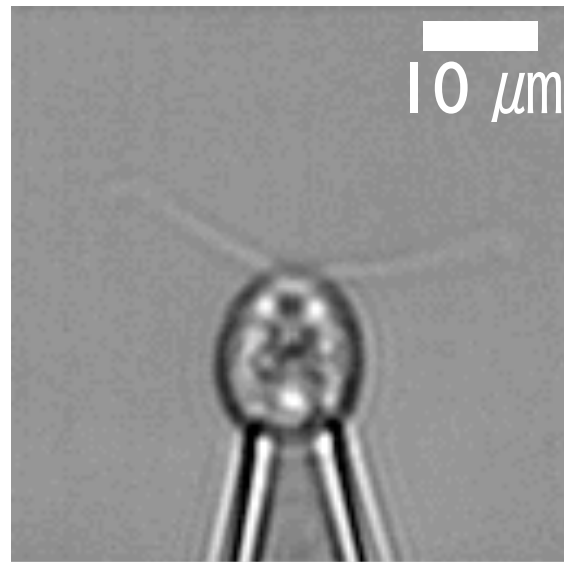
Spatio-temporal control of cell locomotion (swimming)

bacteria



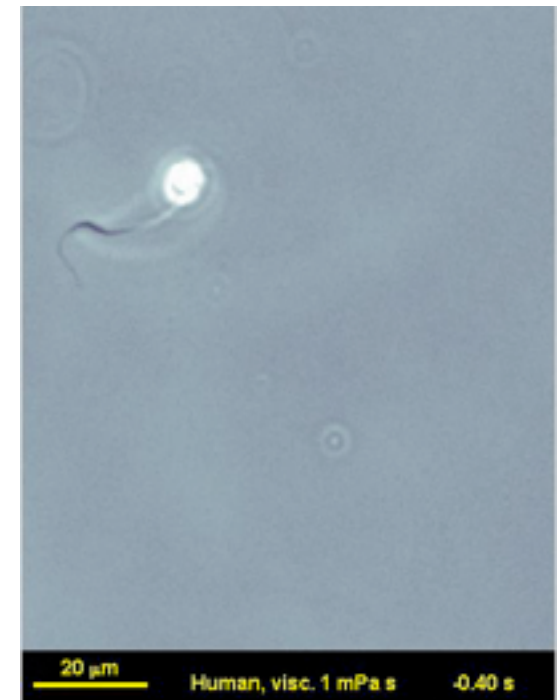
Drescher et al PNAS 2011
Dunkel et al PRL 2013
Wioland et al PRL 2014

algae



Kantsler et al 2013 PNAS

sperm



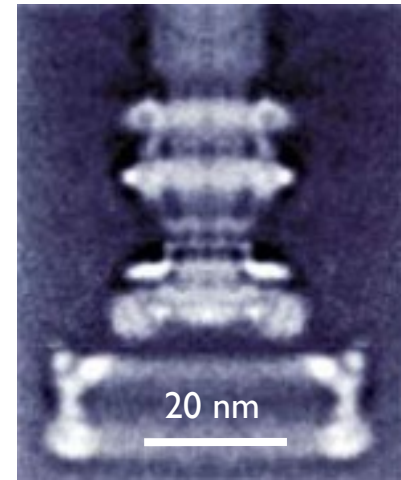
Kantsler et al 2014 (submitted)



Basic questions

✓ Swimming mechanisms ?

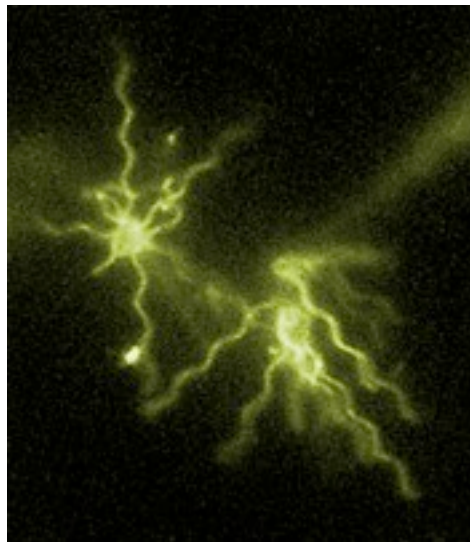
- Flow fields of individual organisms ?
- Collective dynamics ?
- Surface & flow interactions & control ?



Berg (1999) Physics Today

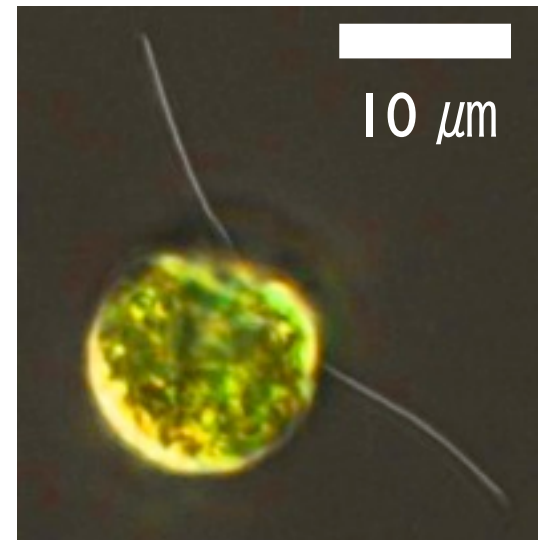
I. Flow fields of individual microorganisms

E coli



Drescher et al PNAS 2011

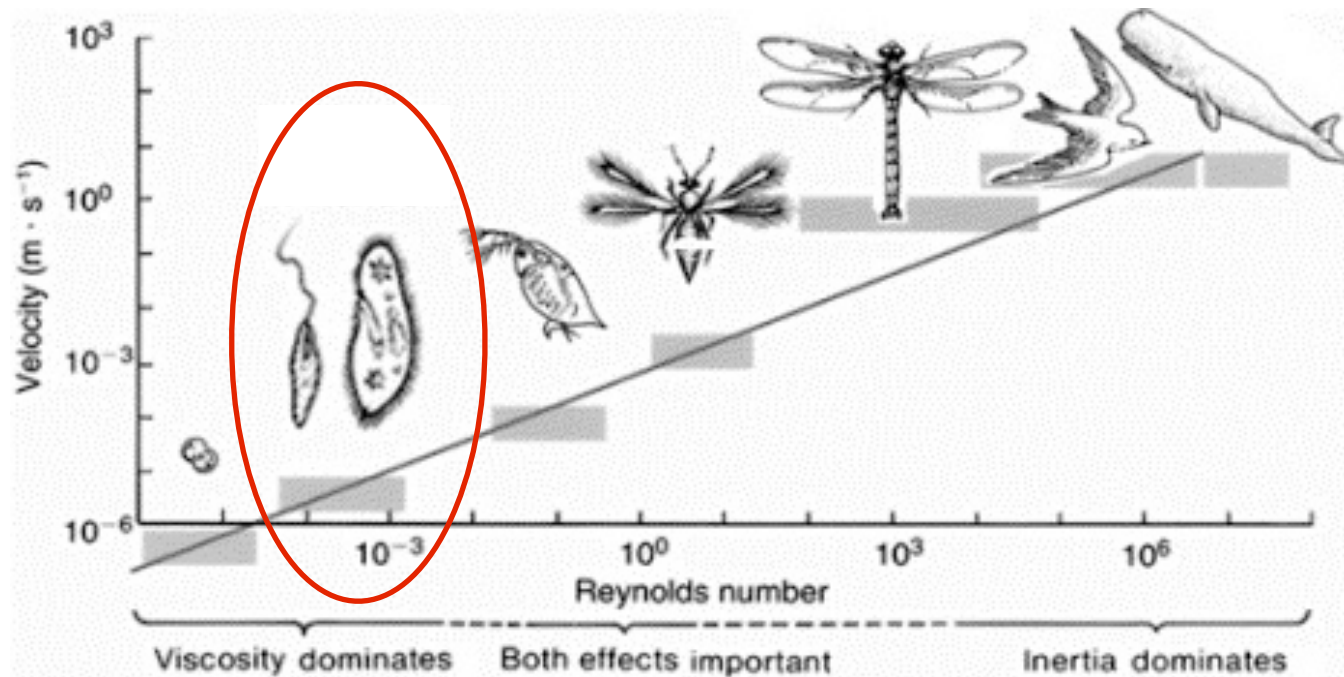
Chlamydomonas



Drescher et al PRL 2010
Guasto et al PRL 2010

Typical Reynolds numbers

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



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 Ingram Taylor



James Lighthill

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

$$0 = \nabla \cdot \mathbf{u}.$$

+ time-dependent BCs



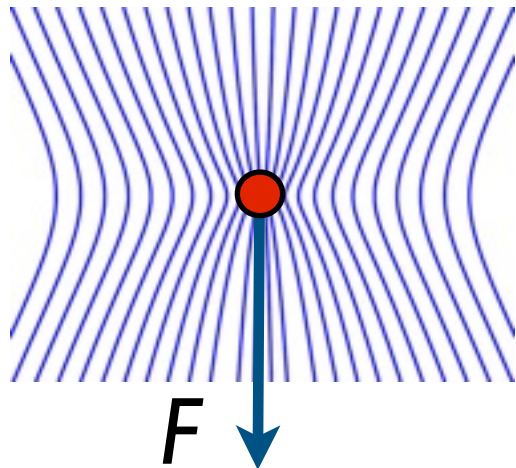
Edward Purcell

Shapere & Wilczek (1987) PRL



Superposition of singularities

stokeslet

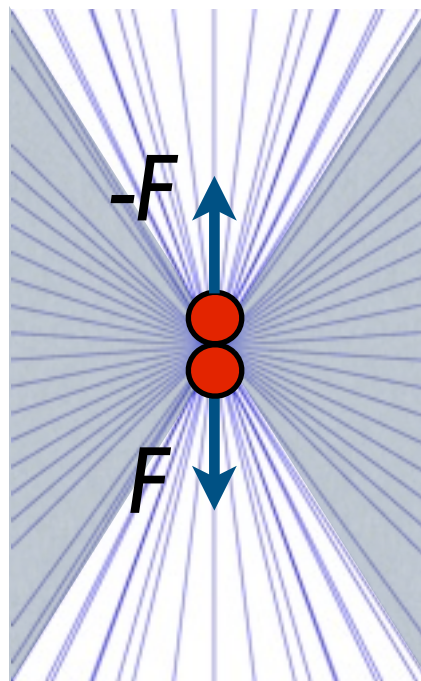


$$p(\mathbf{r}) = \frac{\hat{\mathbf{r}} \cdot \mathbf{F}}{4\pi r^2} + p_0$$

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

flow $\sim r^{-1}$

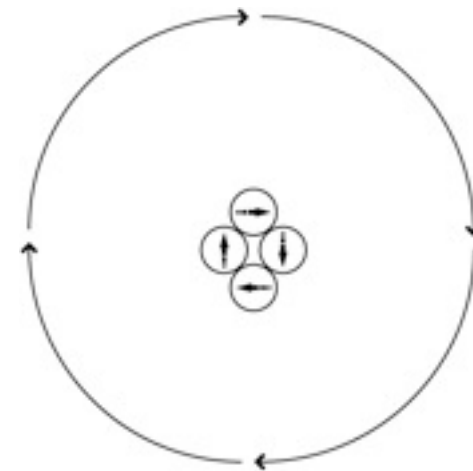
2x stokeslet =
symmetric dipole



r^{-2}

'pusher'

rotlet



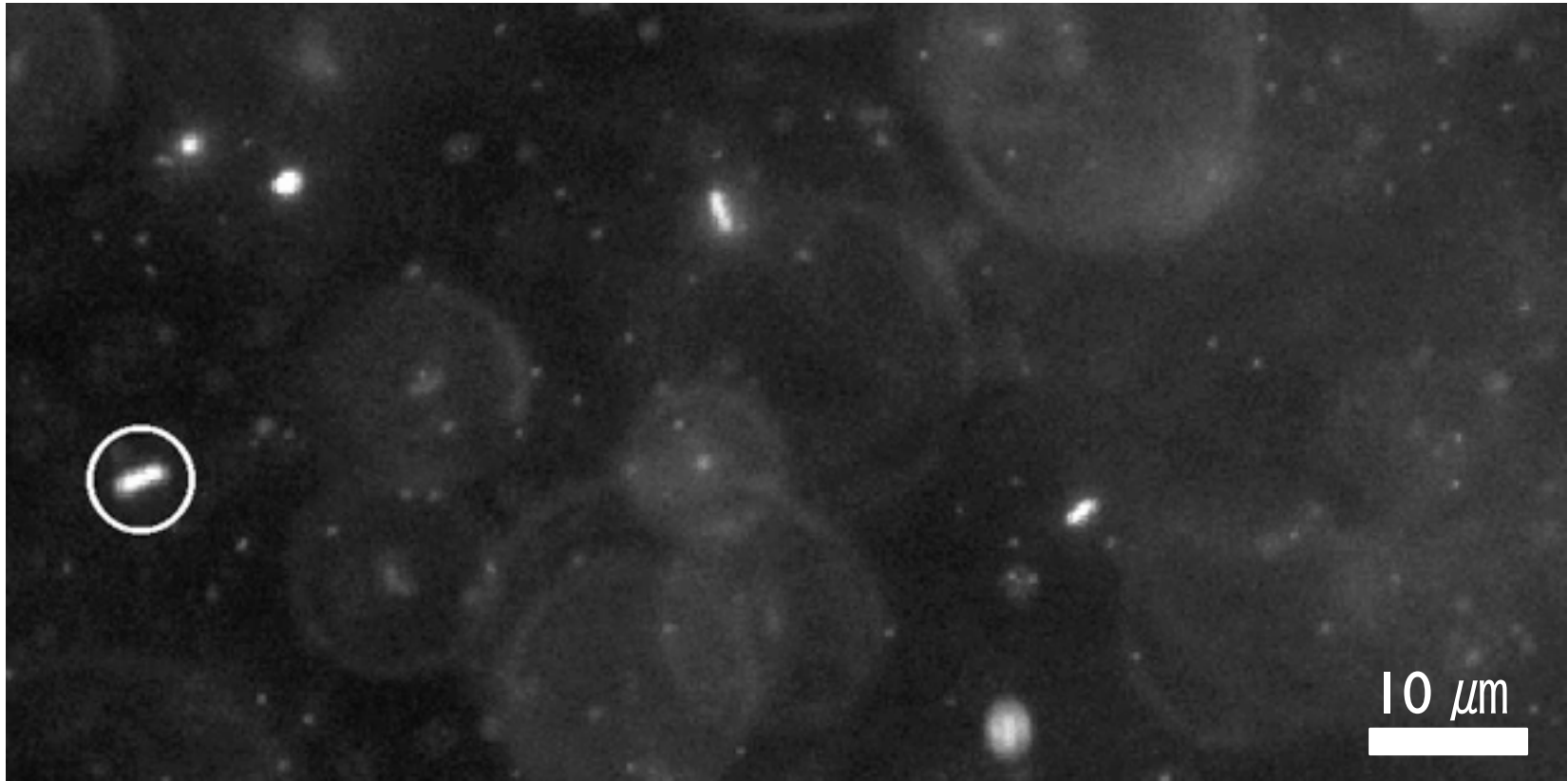
r^{-2}



E. coli (non-tumbling)



non-tumbling HCB 437



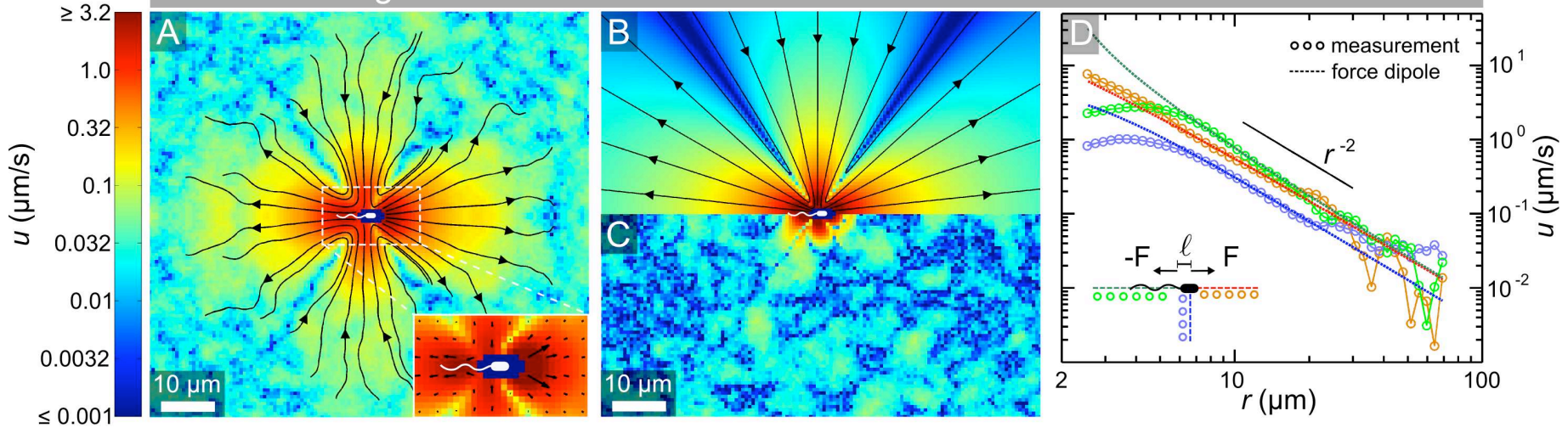
Drescher et al (2011) PNAS



E.coli (non-tumbling HCB 437)



Free swimming



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

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

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

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

'pusher' dipole

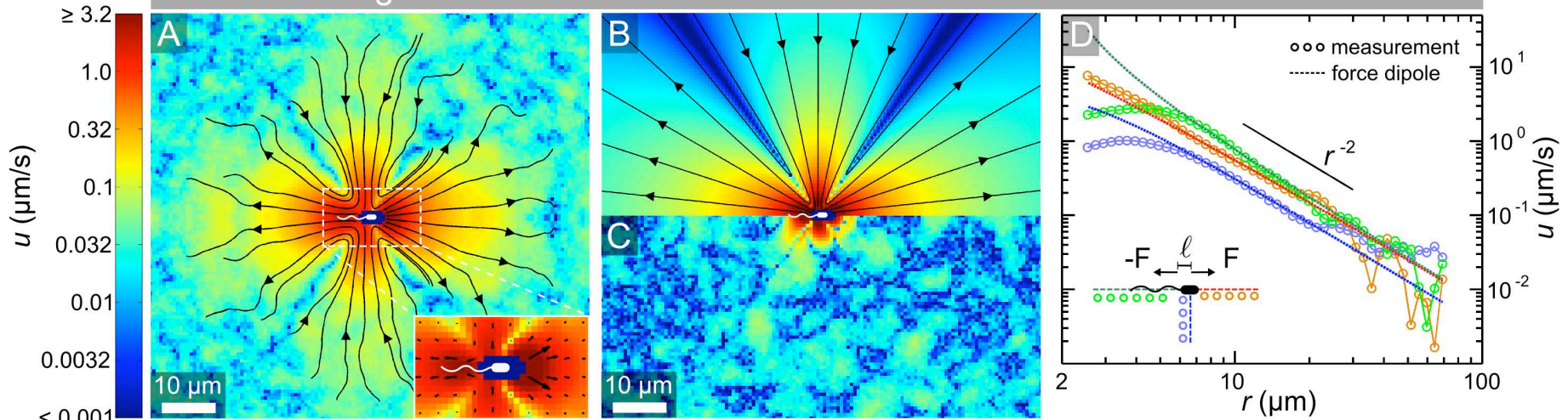
Drescher et al (2011) PNAS



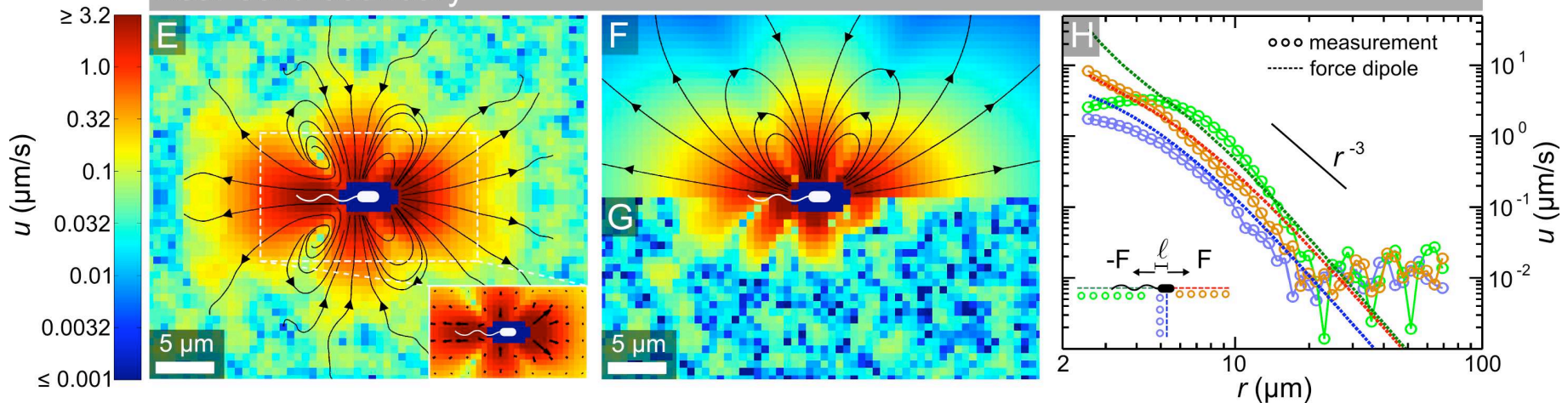
E.coli (non-tumbling HCB 437)



Free swimming



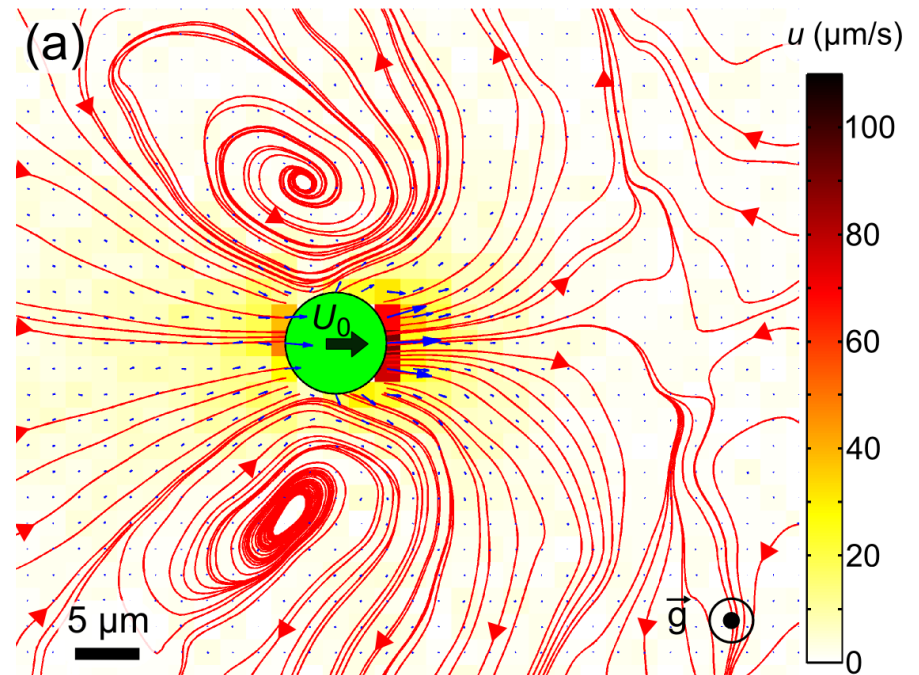
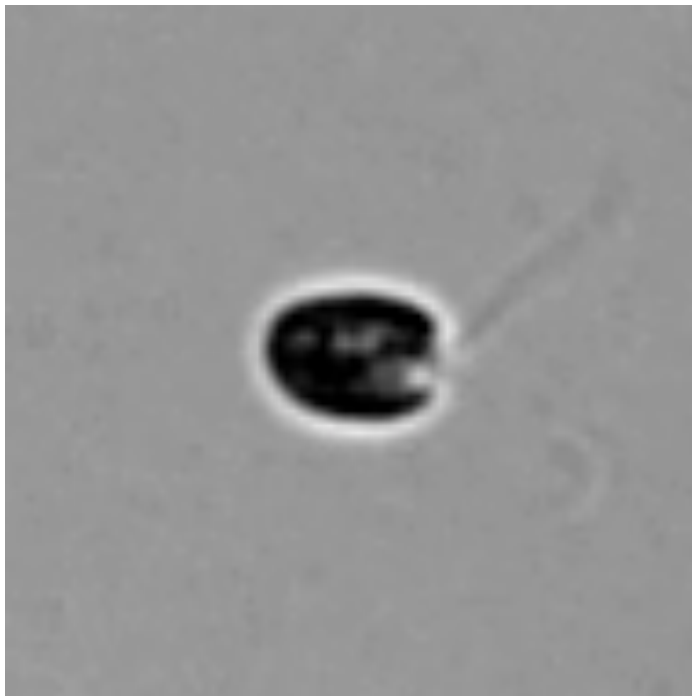
Near solid boundary



Drescher et al (2011) PNAS



Chlamydomonas



Movie: Jeff Guasto (TUFTS)

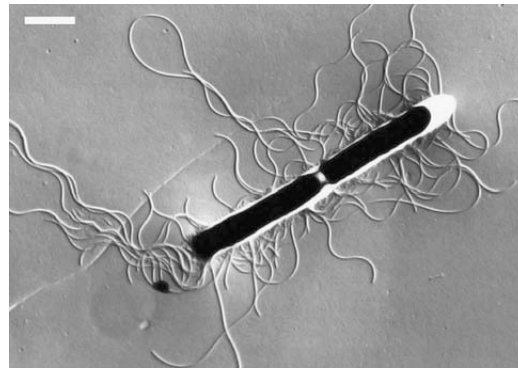
Drescher et al PRL 2010
Guasto et al PRL 2010

‘puller’

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



2. Control of collective bacterial swimming



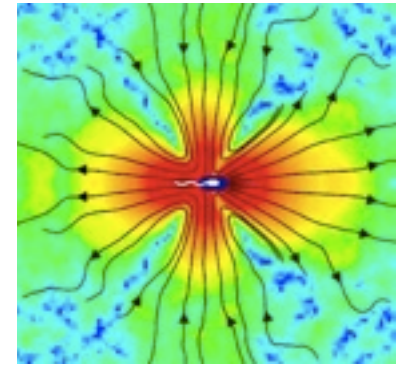
Bacillus subtilis

Cisneros et al (2007) Exp Fluids

Relevant physical mechanisms

✓ hydrodynamic advection

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



✓ steric alignment

• hydrodynamic alignment **less** important

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

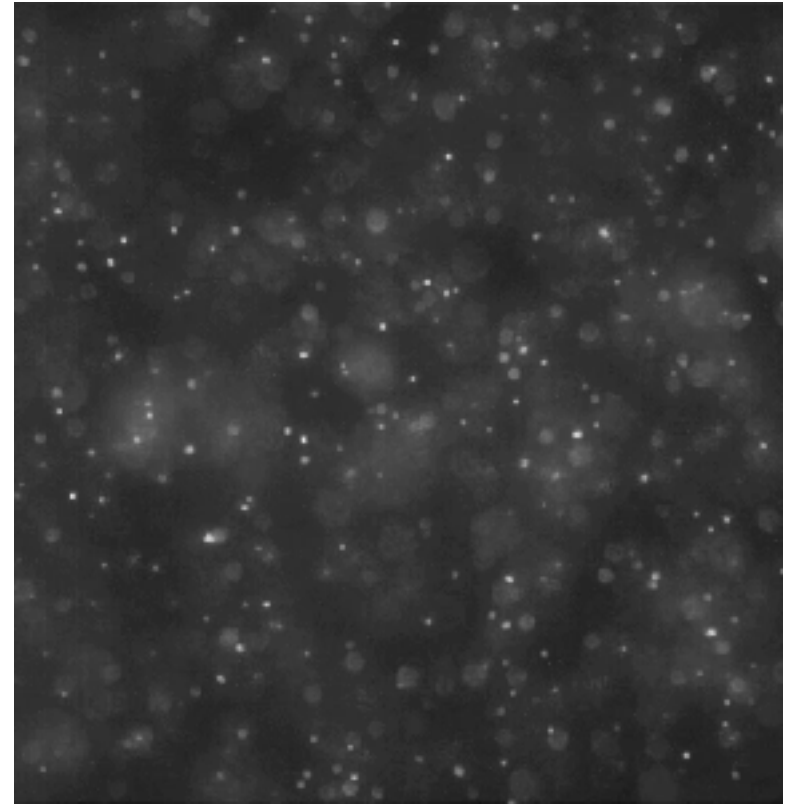
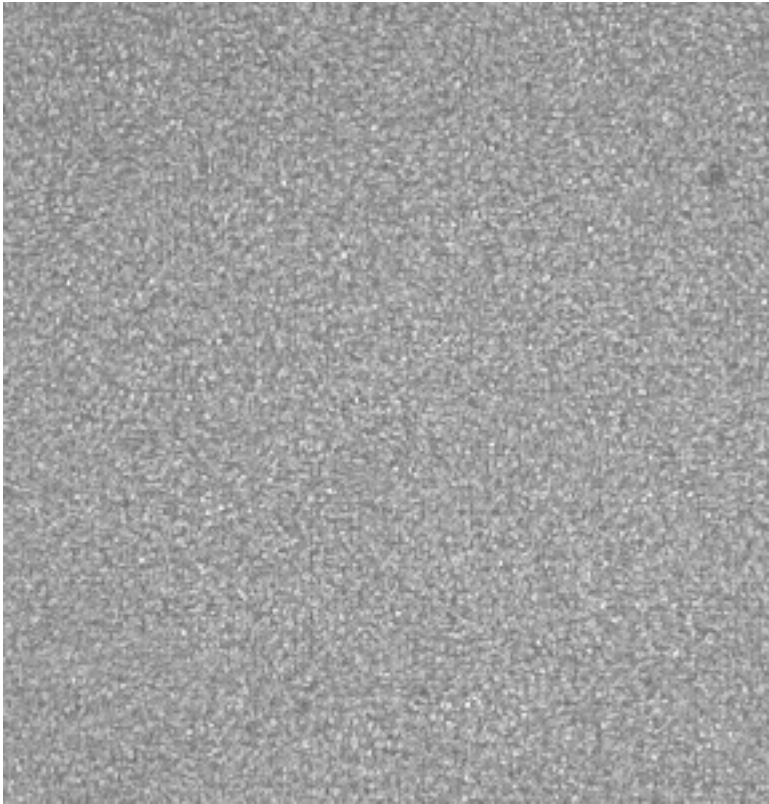
✓ intrinsic rotational noise
much larger than thermal noise

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

Bacterial 'turbulence'

B. subtilis

tracers



bright field

fluorescence

Wensink et al PNAS 2012

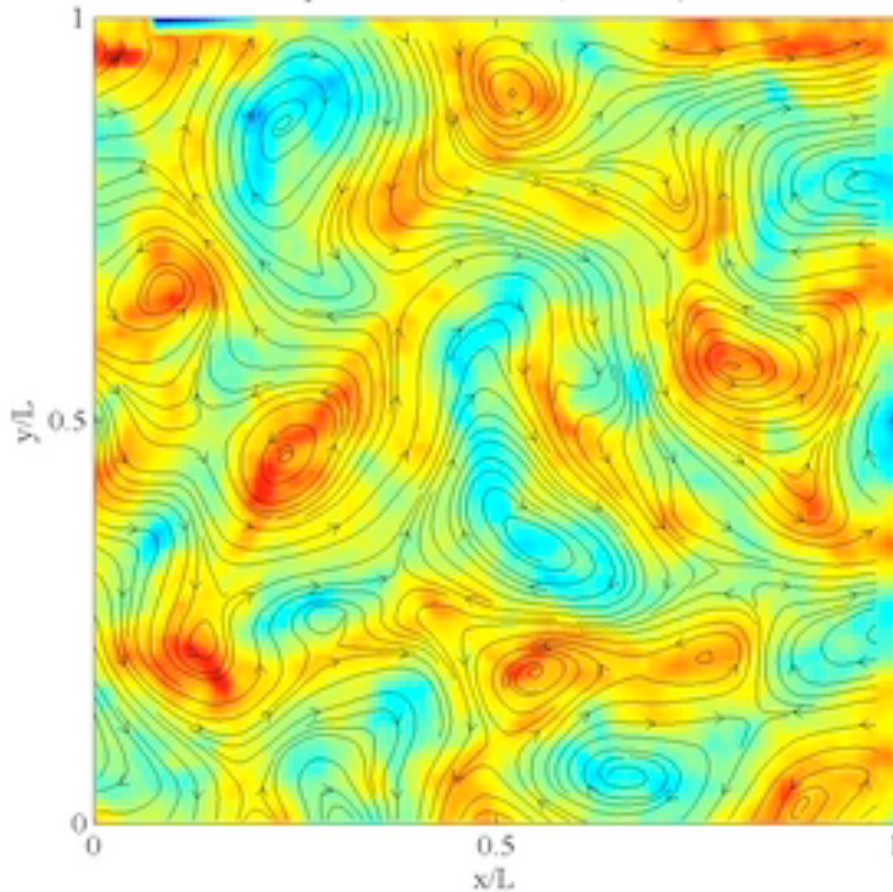
Dunkel et al PRL 2013



Bacterial 'turbulence'

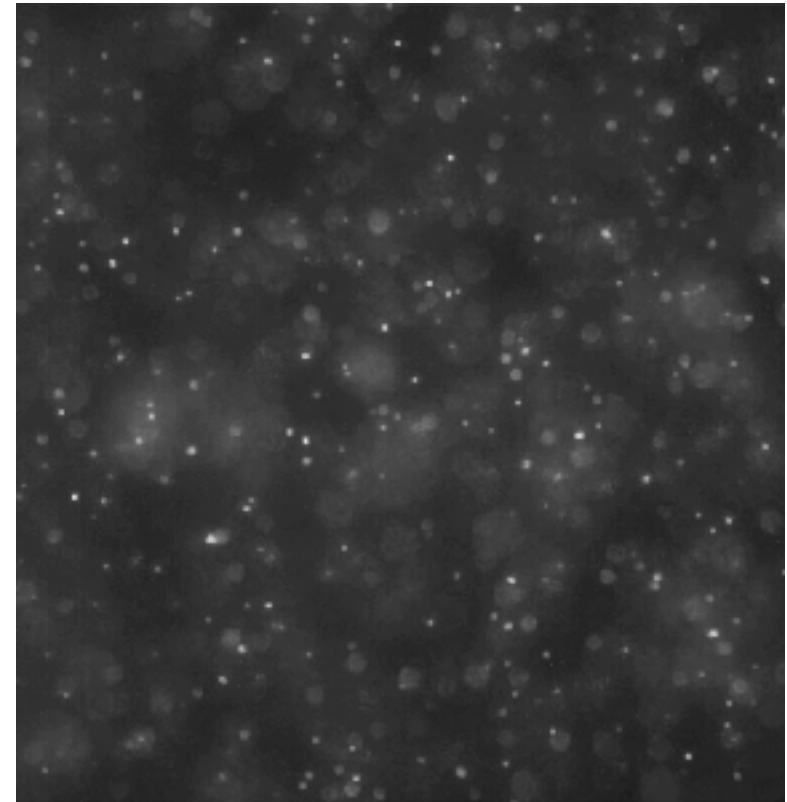
PIV

Experiment: $t = 0.1$ s, $L = 276$ μ m



Vortex diameter ~ 70 μ m
Vortex life time ~ 1 sec

tracers



fluorescence

Dunkel et al PRL 2013



Minimal continuum theory for bacterial velocity field

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

nematic stresses

polar alignment

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

vortices

PNAS 2012

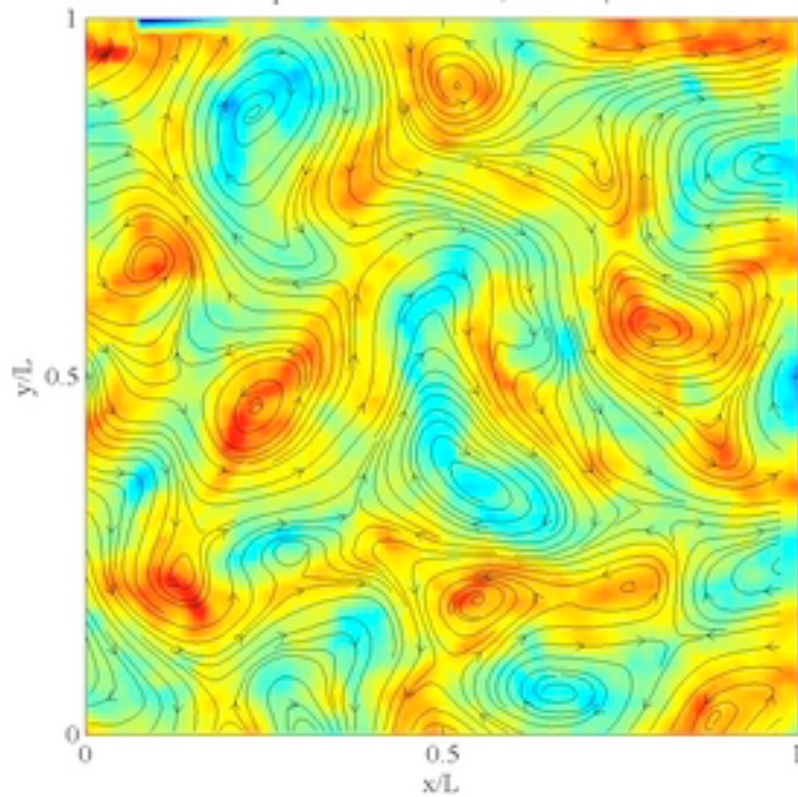
New J Phys 2013

PRL 2013



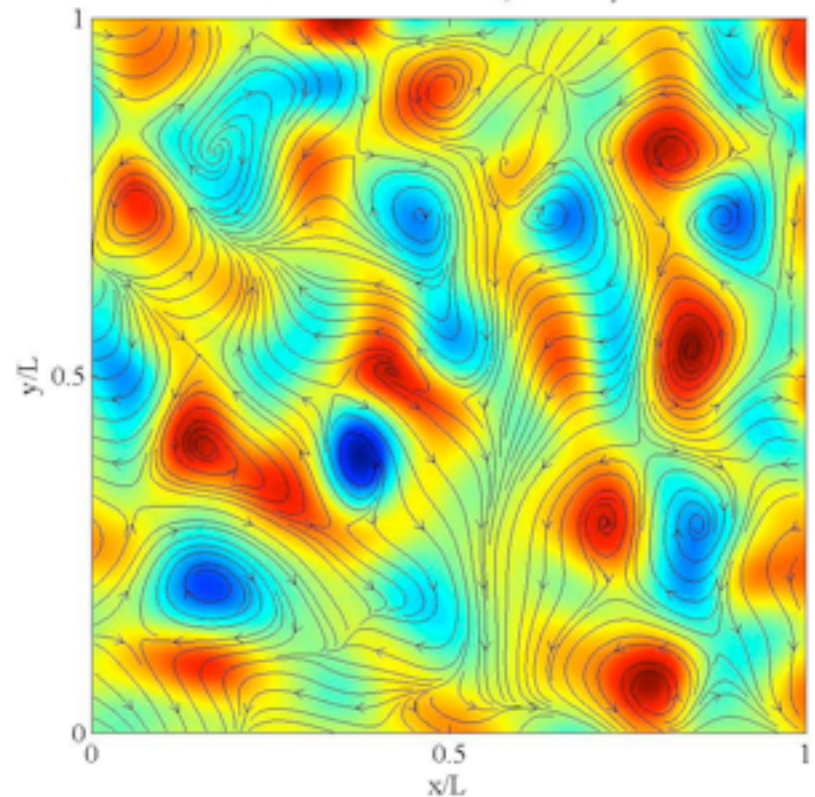
experiment vs. theory

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



quasi-2D slice

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

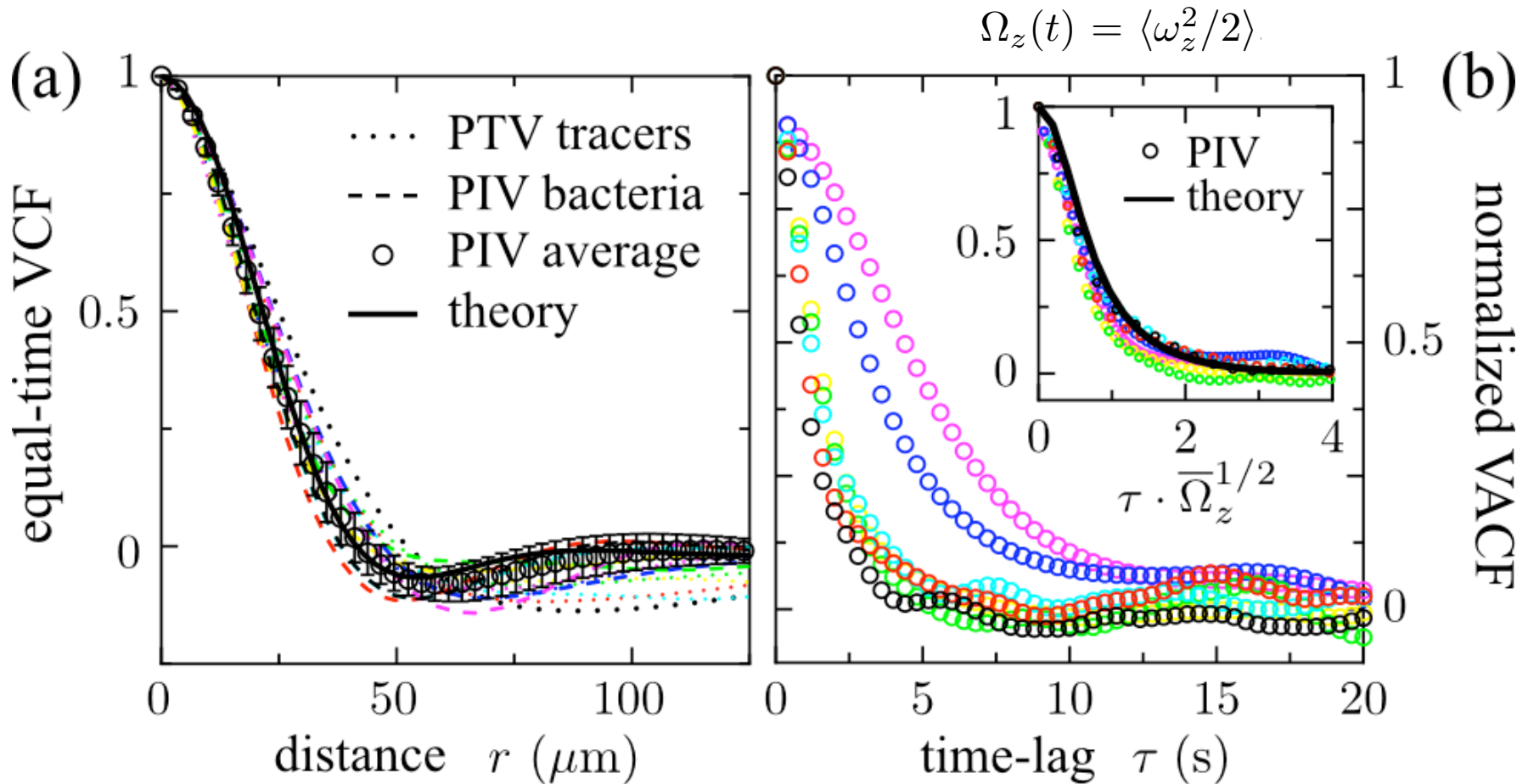


2D slice
from 3D simulation

Dunkel et al PRL 2013



Velocity correlations



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

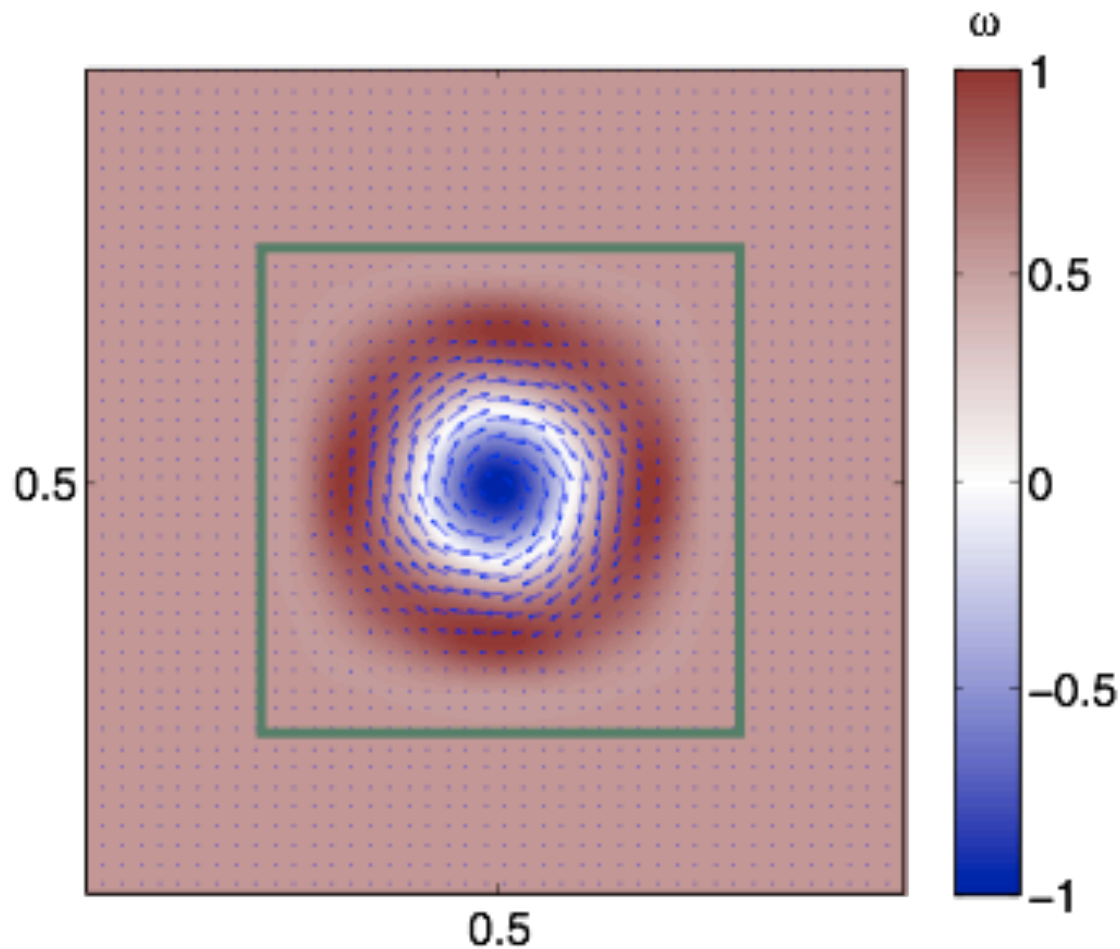
Vortex life time \sim seconds

Dunkel et al PRL 2013

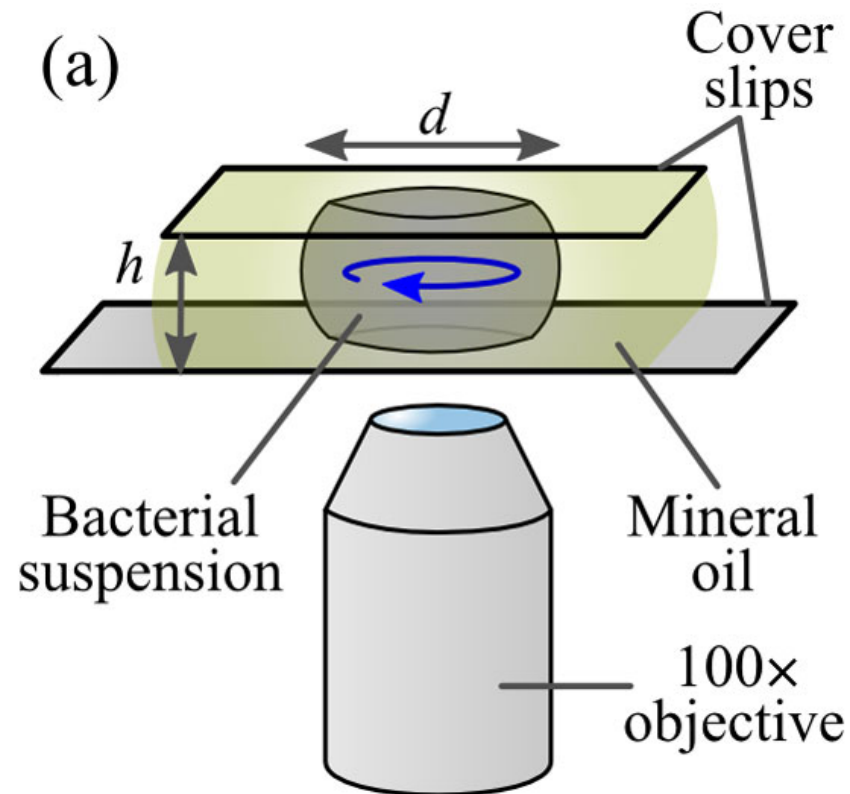


Can we stabilize vortices ?

Theoretical 'prediction' ... of many models



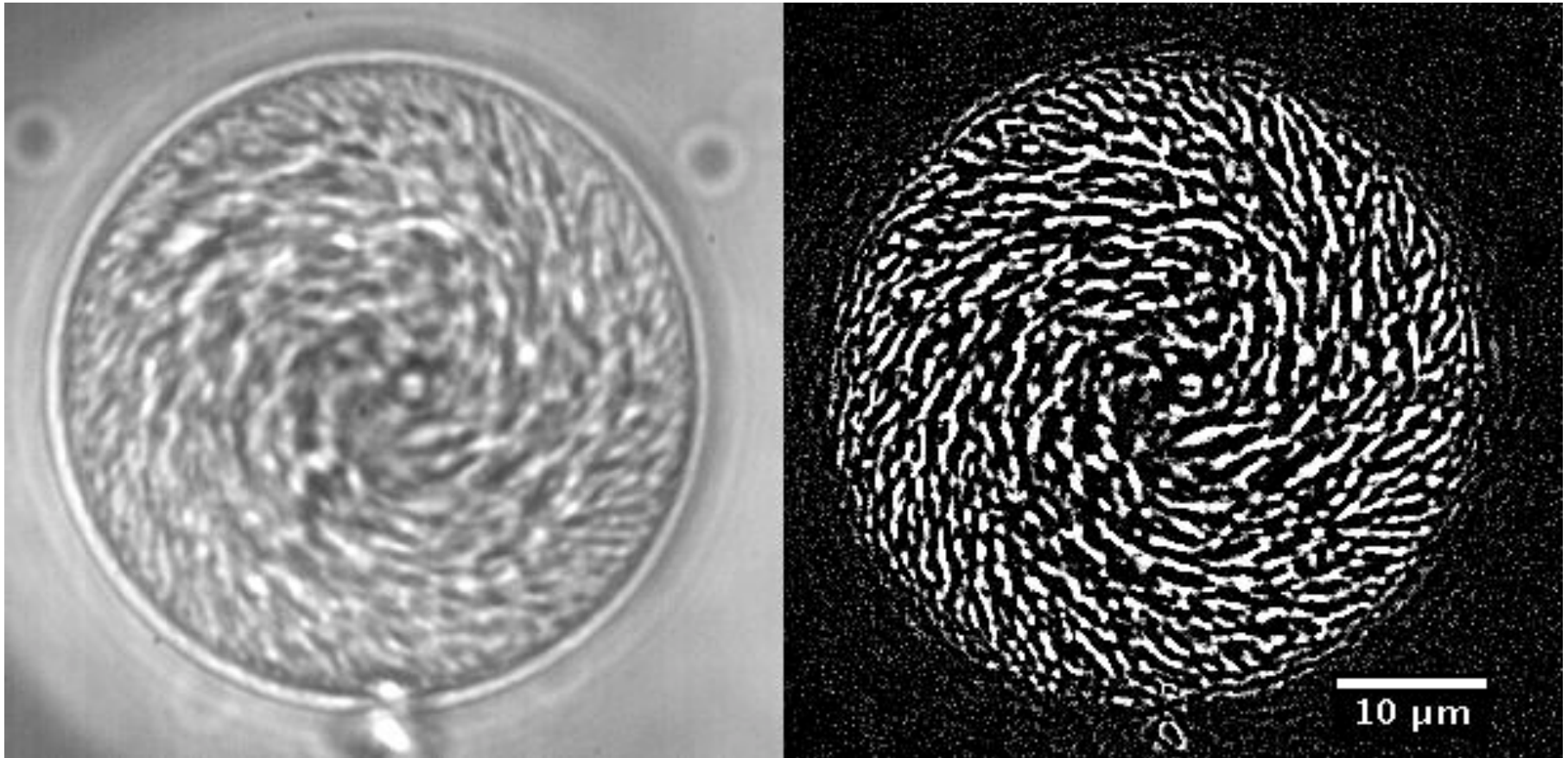
Experiment



Wioland et al (2013) PRL



Stable bacterial spiral vortex



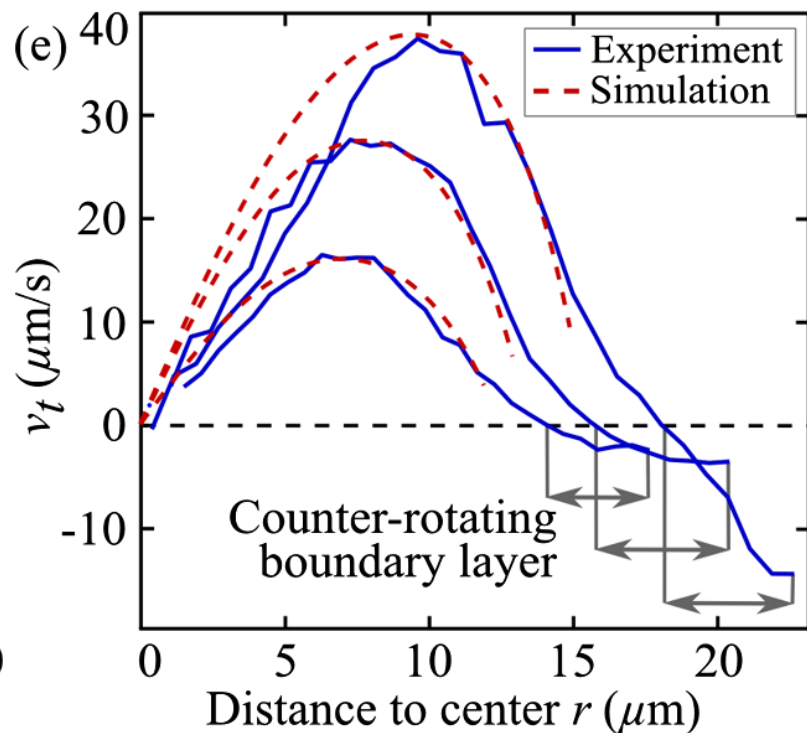
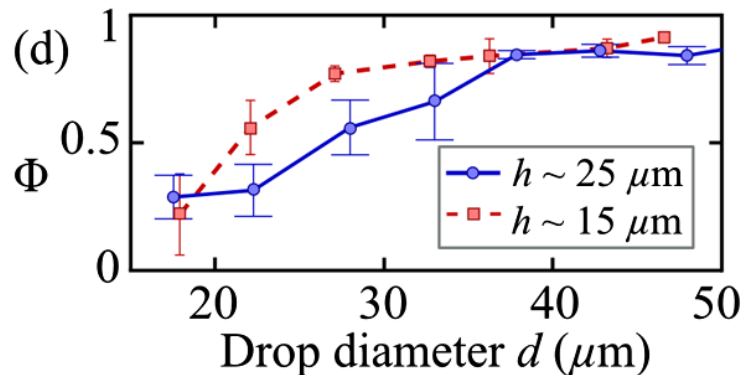
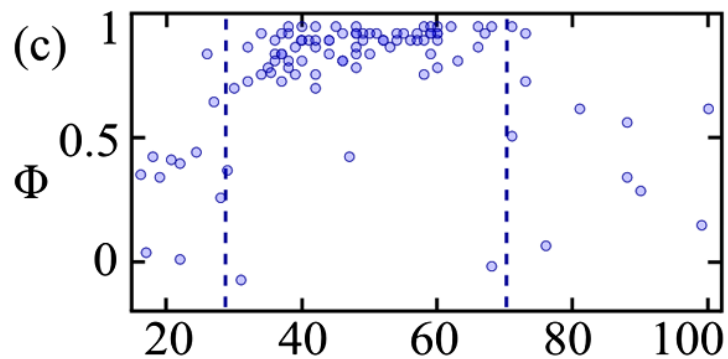
Vortex life time \sim minutes

Wioland et al (2013) PRL



Vortex characterization

$$\Phi = \frac{\sum_i |\mathbf{v}_i \cdot \mathbf{t}_i| / \sum_j \|\mathbf{v}_j\| - 2/\pi}{1 - 2/\pi}$$



... bacteria create their own BCs !

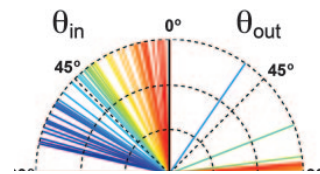
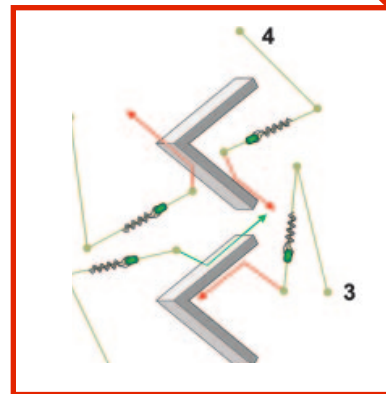
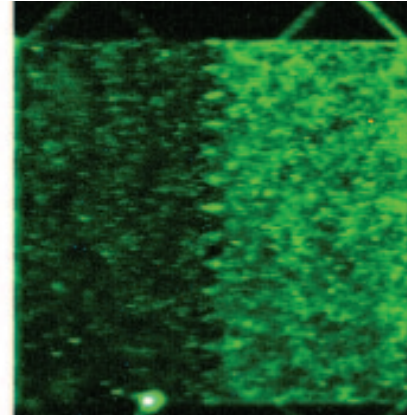
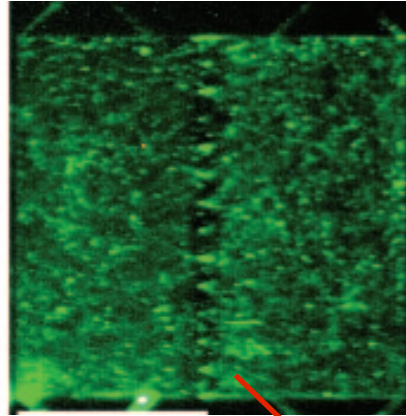


3. Control of eukaryotic locomotion

- rectification of algal swimming
- long distance navigation of sperm cells



Rectification of **prokaryotic** locomotion

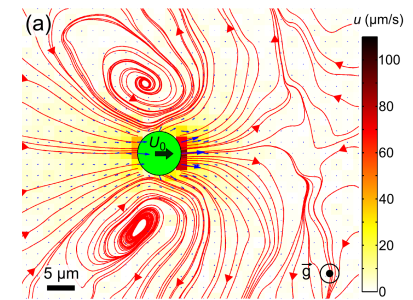
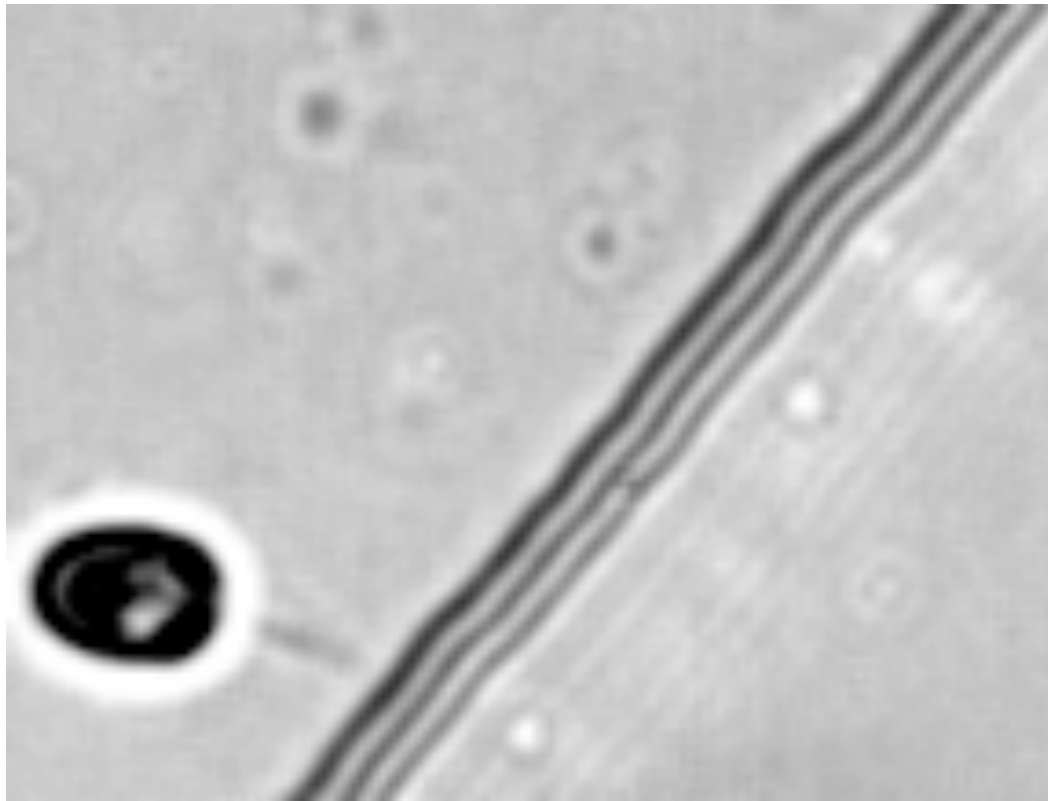


Galadja et al (2009)
J Bacteriology

Austin lab, Princeton, 2009



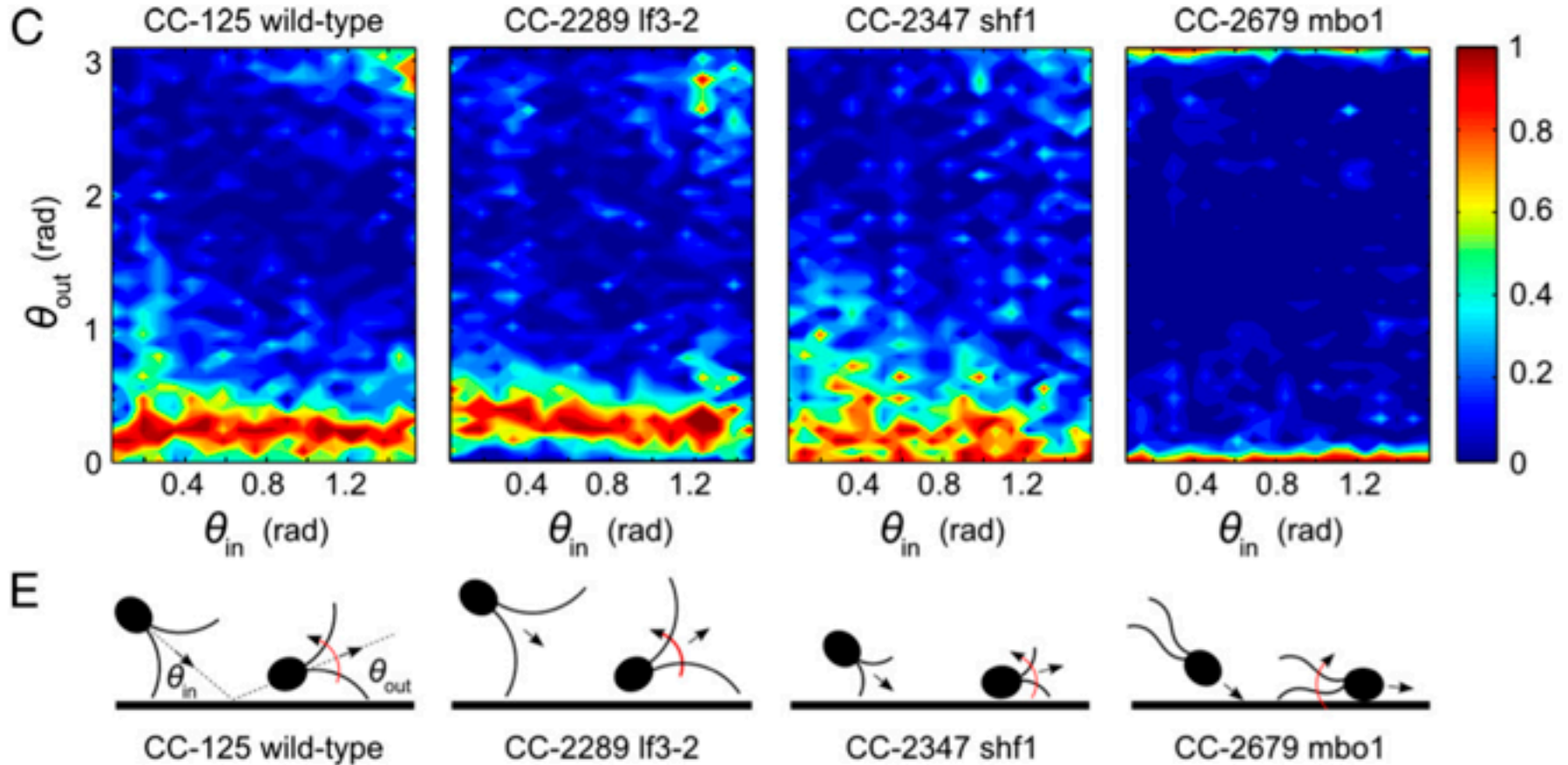
Mechanical control of algal locomotion



Kantsler, Dunkel, Polin, Goldstein (2012) PNAS



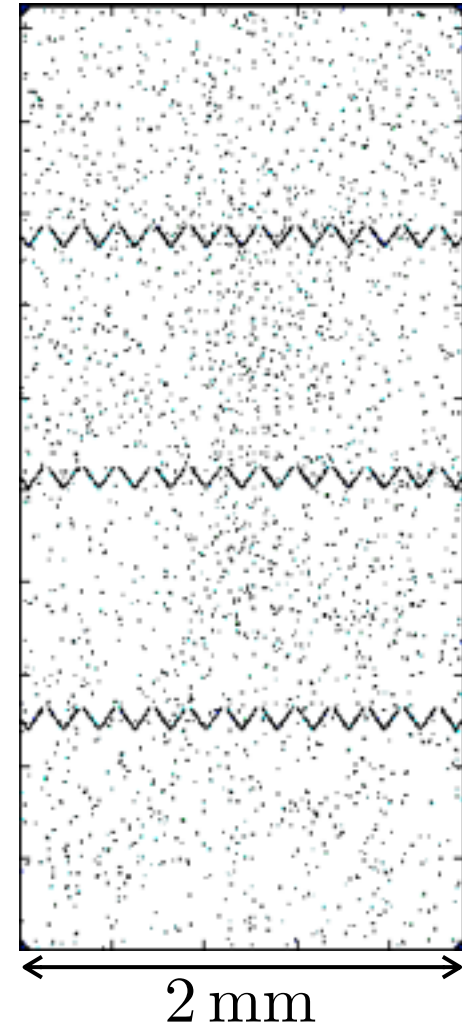
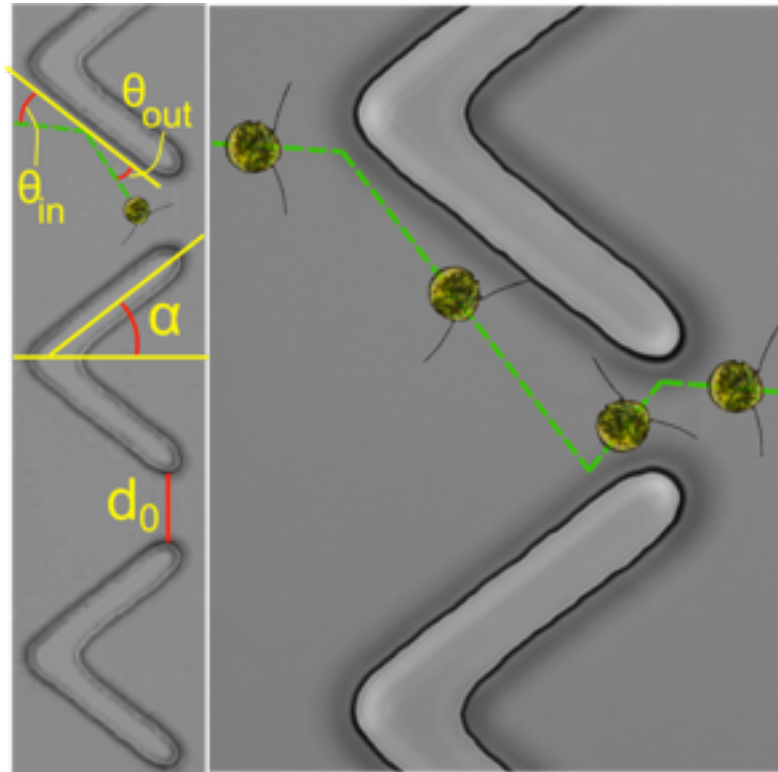
Surface scattering laws



Kantsler, Dunkel, Polin, Goldstein (2012) PNAS



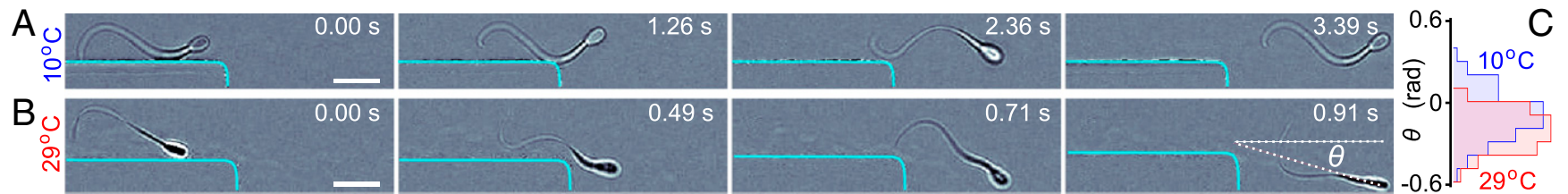
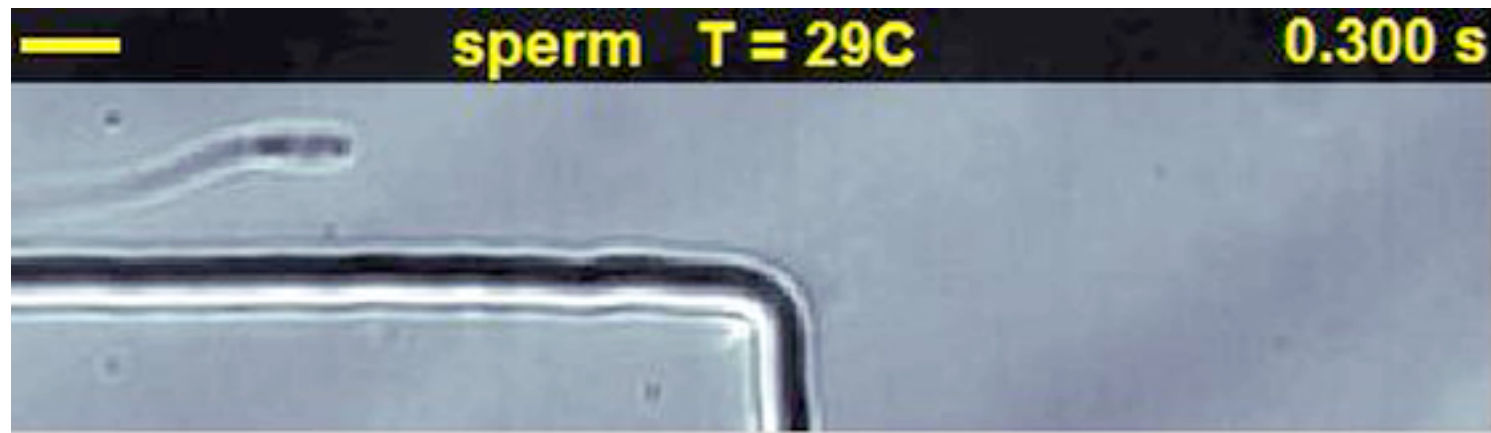
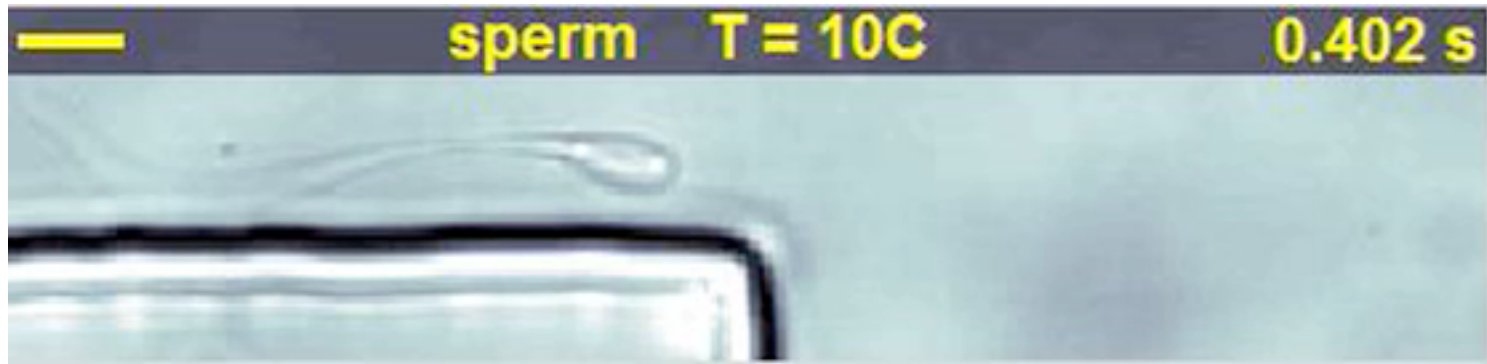
Control of **algal** locomotion



Kantsler, Dunkel, Polin, Goldstein (2012) PNAS



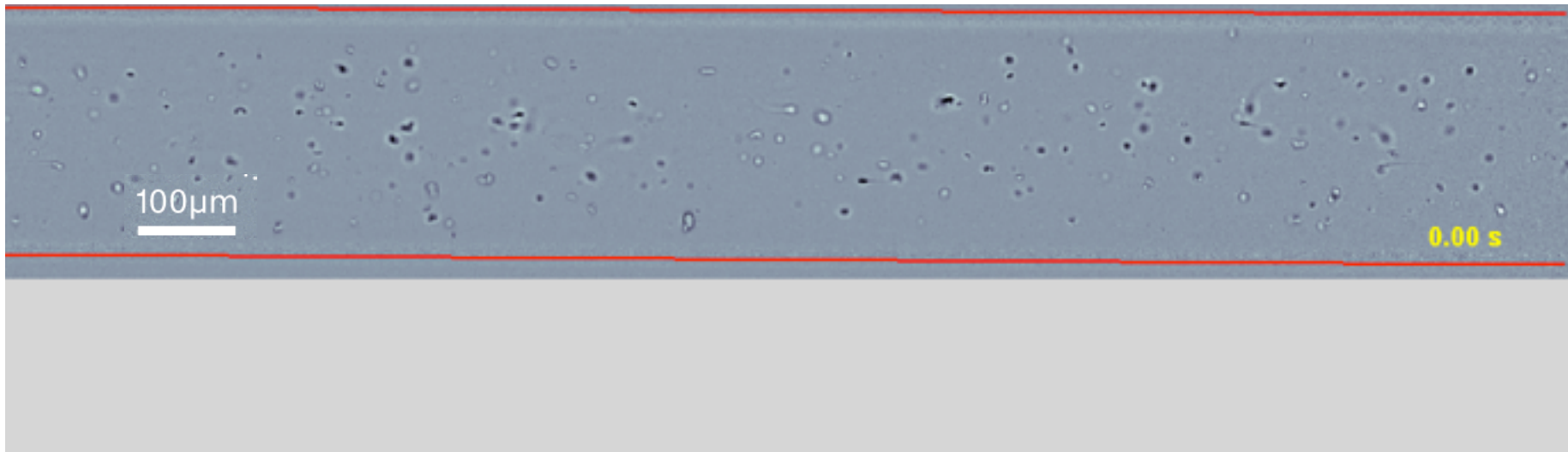
Sperm near surfaces



Kantsler, Dunkel, Polin, Goldstein (2012) PNAS



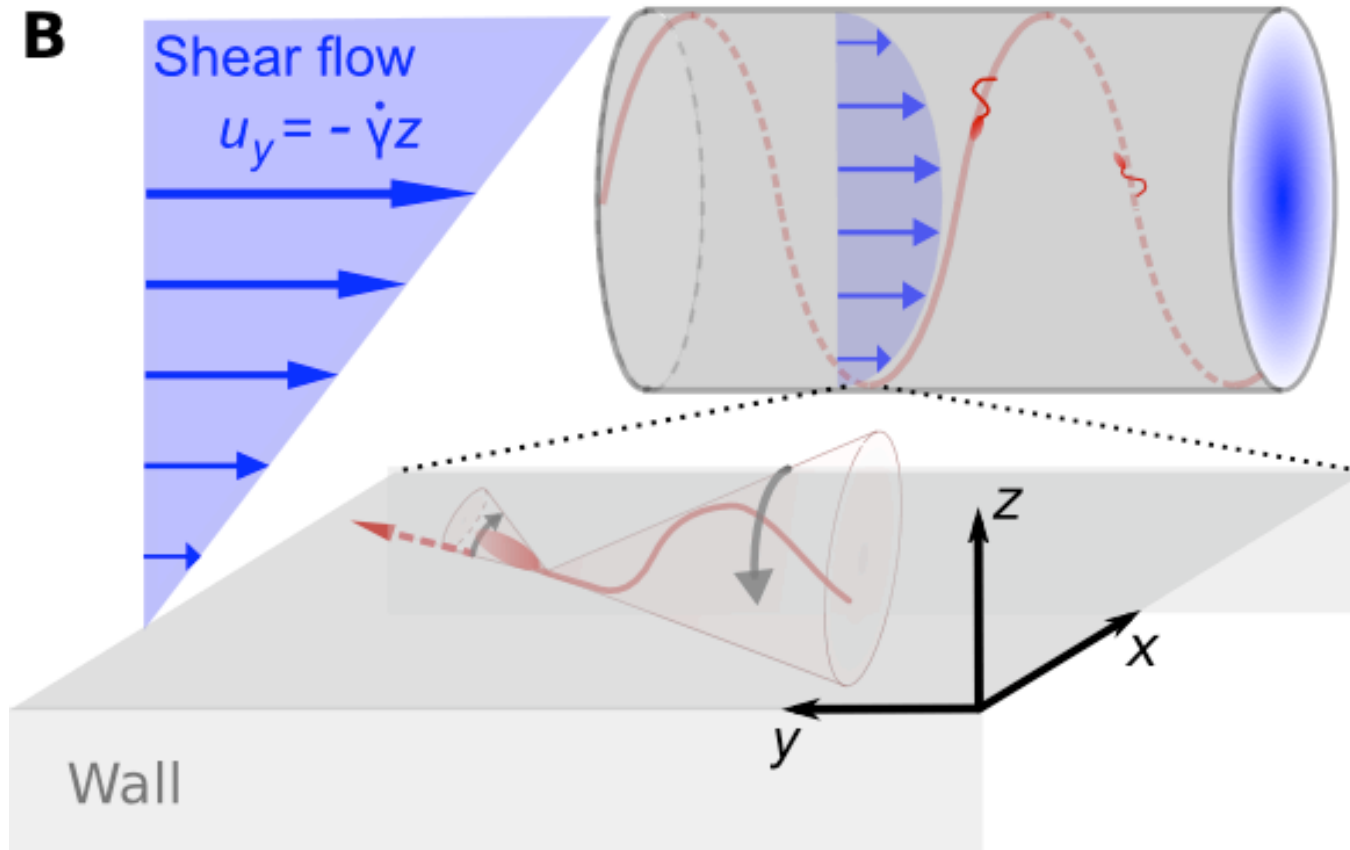
Surface + shear flow



Kantsler et al 2014 (submitted)



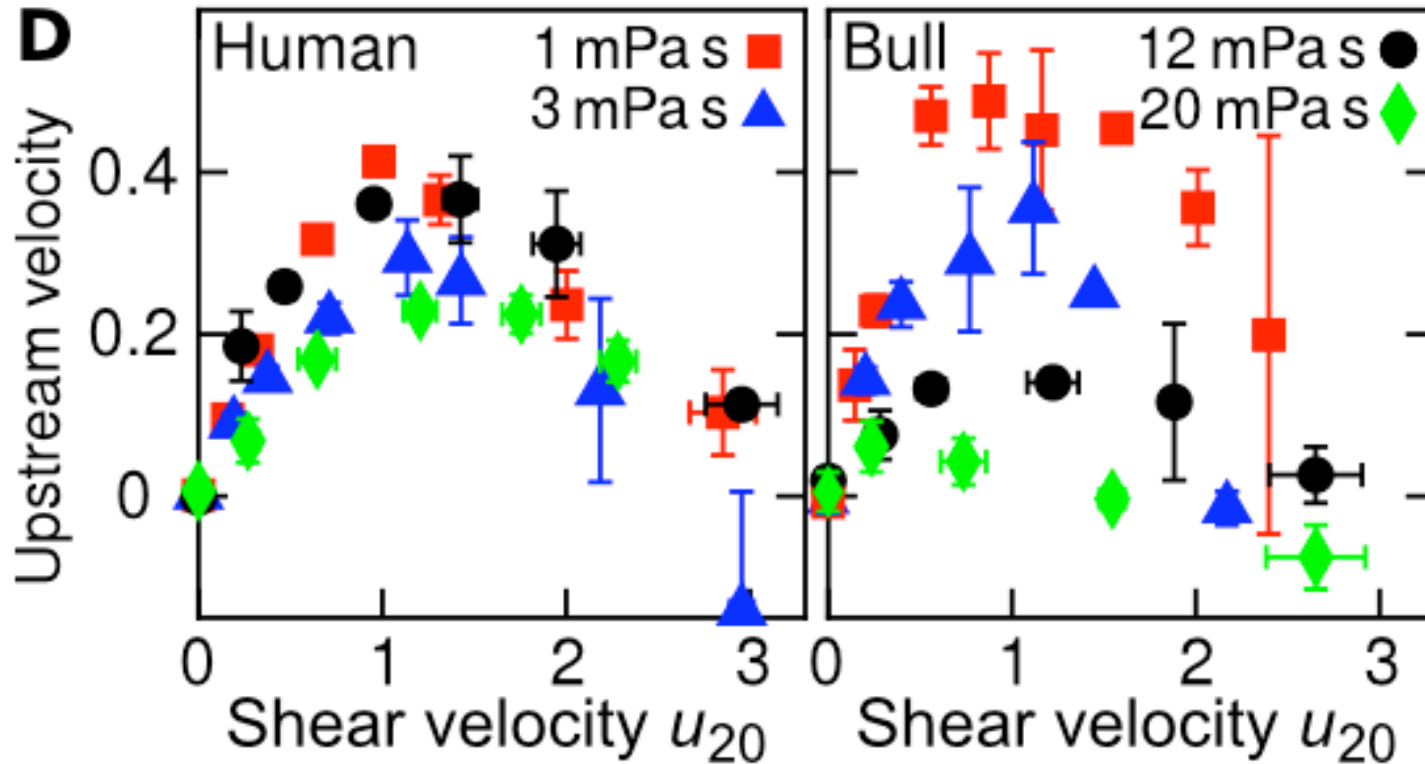
Rheotaxis facilitates upstream navigation



Kantsler et al 2014 (submitted)



Viscosity & shear dependence



long distance navigation by rheotaxis ?



2D minimal model

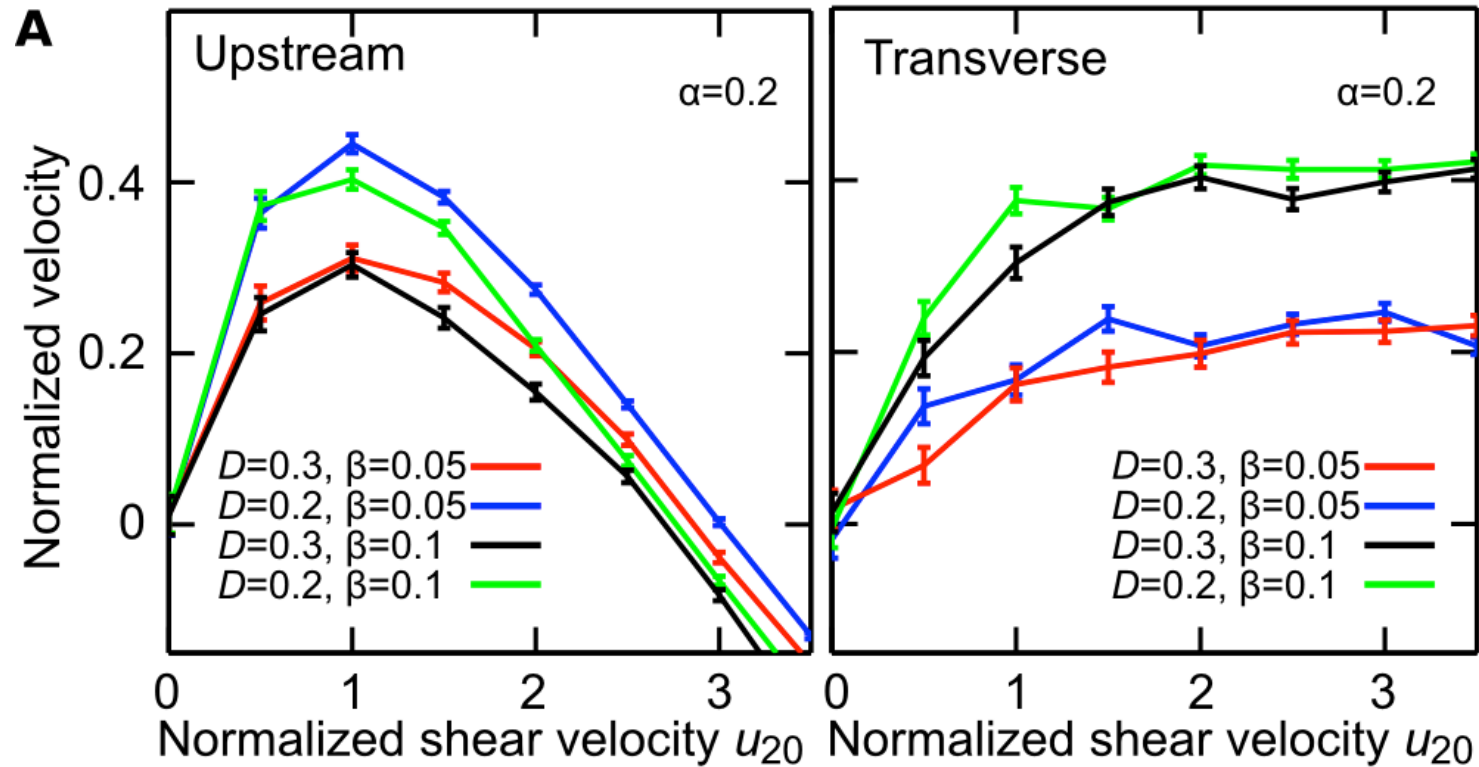
Resistive force theory

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

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

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

2D minimal model

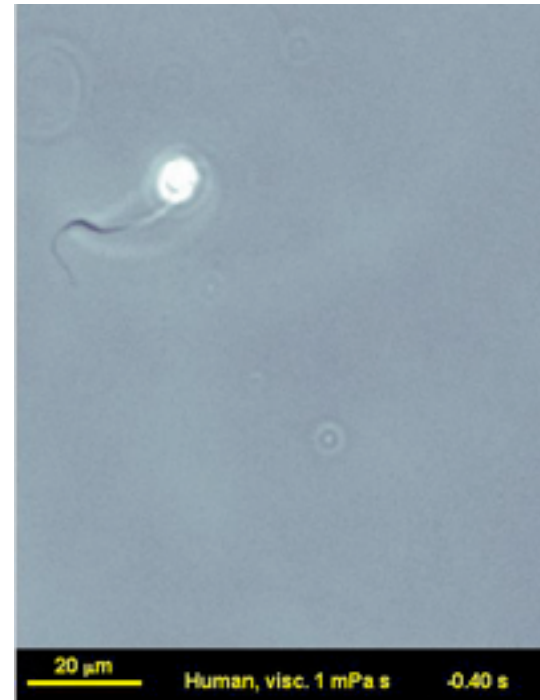
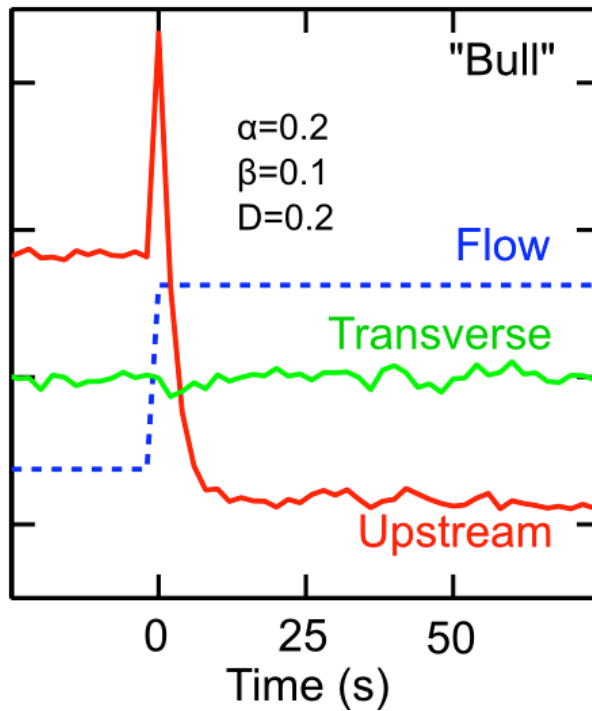


Kantsler et al 2014 (submitted)



Response to flow switch

model

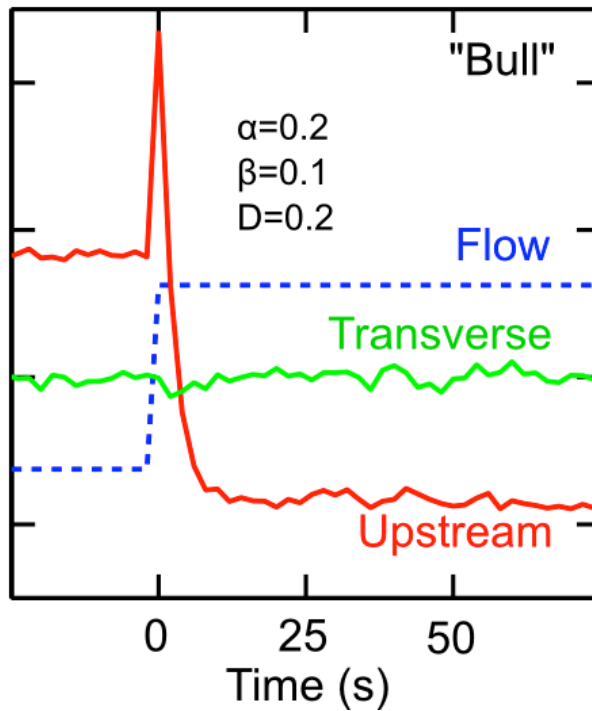


Kantsler et al 2014 (submitted)

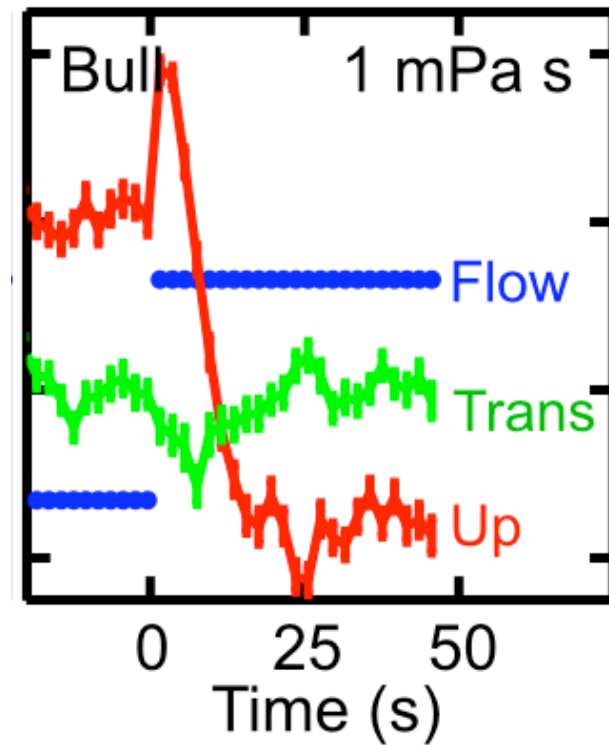


Response to flow switch

model



experiment

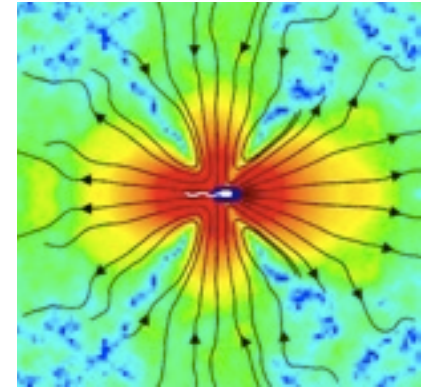


Summary

Bacteria

- weak dipole flows
- vortex stabilization by boundaries

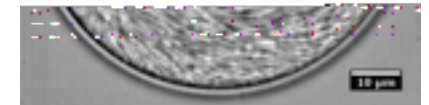
Drescher et al (2011) PNAS
Wensink et al (2012) PNAS
Dunkel et al (2013) PRL
Wioland et al (2013) PRL



Algae

- inelastic 'geometric' scattering
- rectification in ratchets

Kantsler et al (2013) PNAS



Sperm

- boundary interactions & rheotaxis
- swim upstream on spirals

Kantsler et al (2014) submitted

