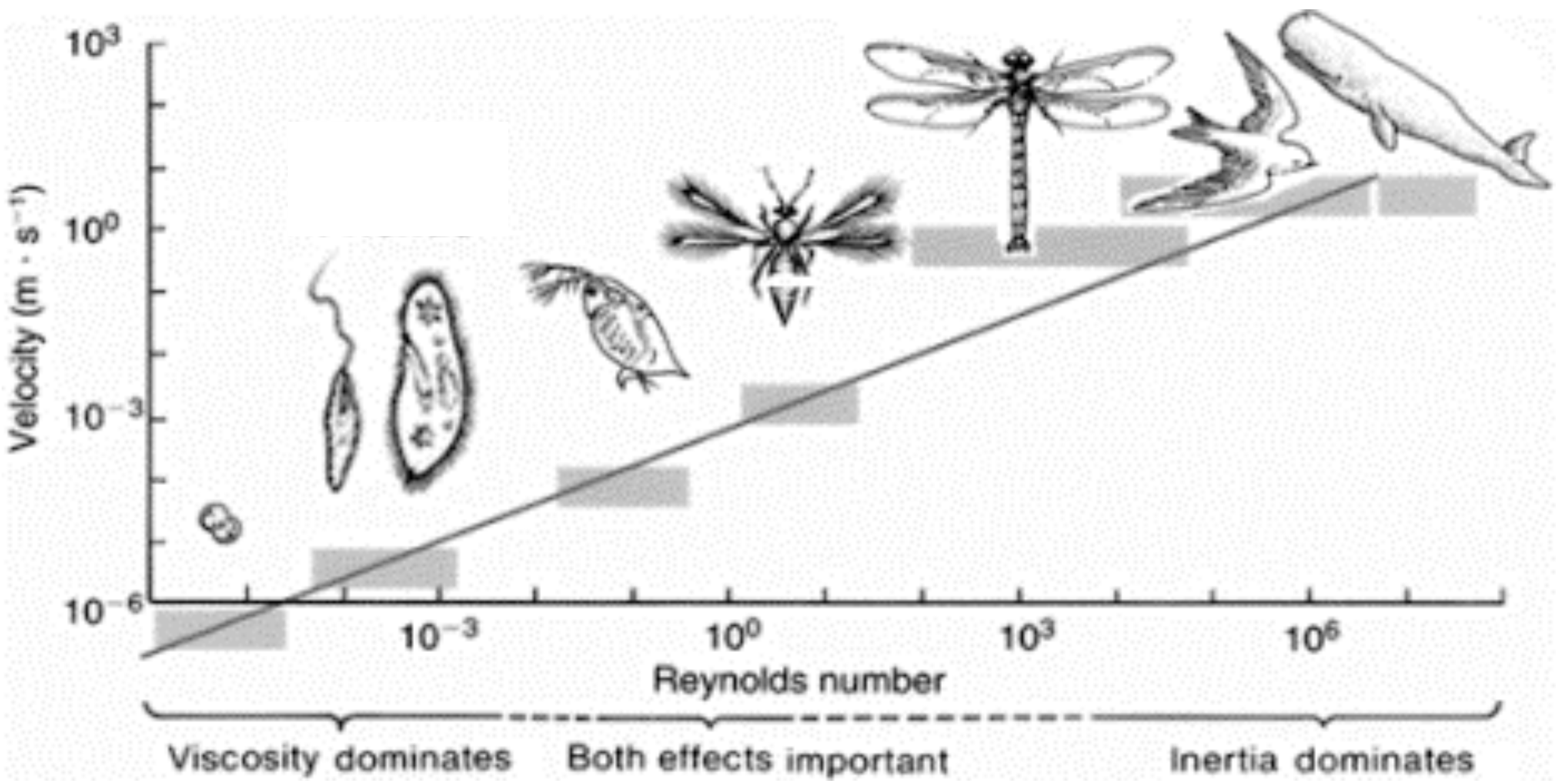
Surface interactions and rheotaxis

18.S995 - L16

dunkel@mit.edu

Reynolds numbers

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



Swimming at low Reynolds number

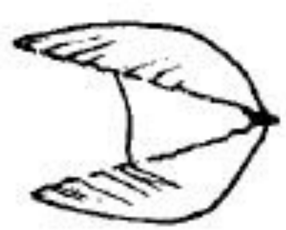
Navier - Stokes:

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

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

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

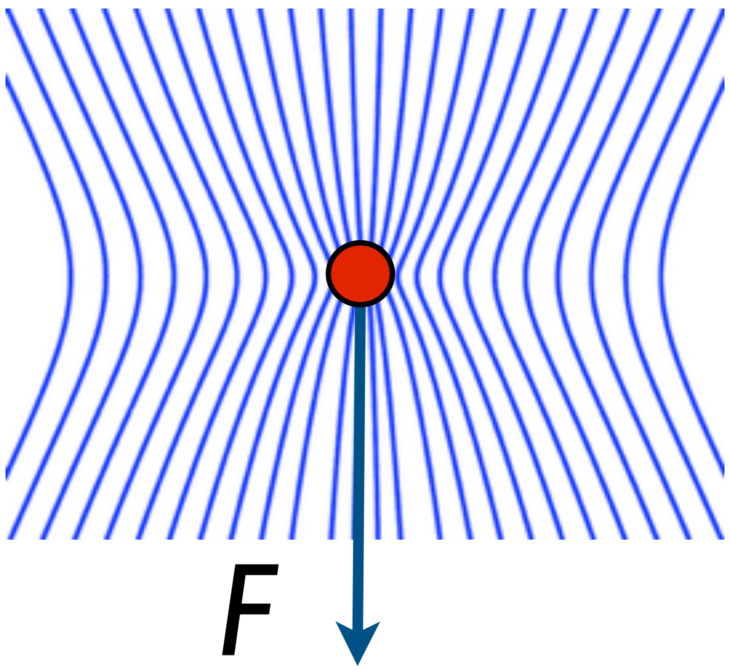
+ time-dependent BCs

Edward Purcell

Shapere & Wilczek (1987) PRL

Superposition of singularities

stokeslet

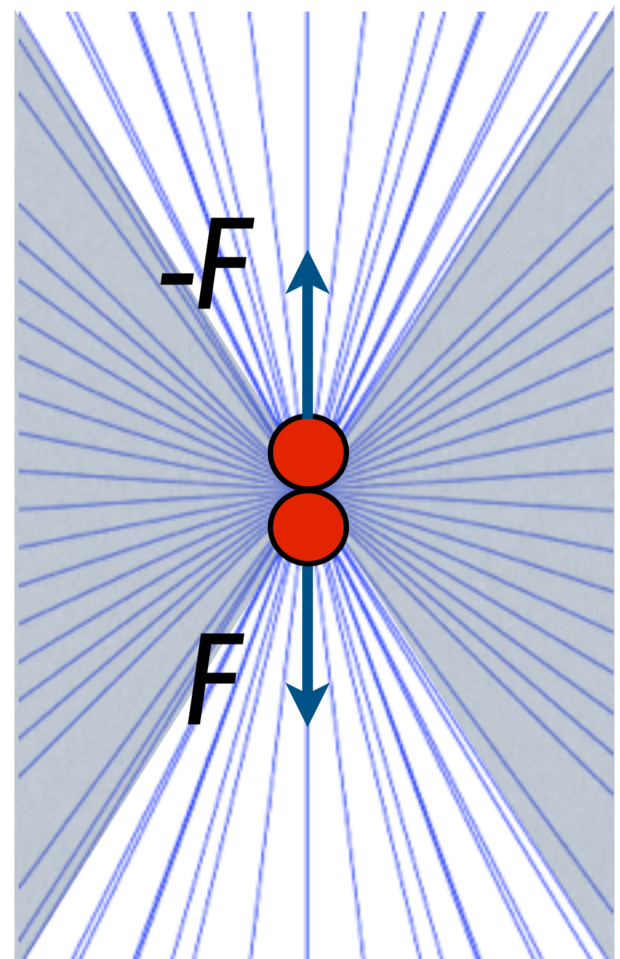


$$p(\boldsymbol{r}) = \frac{\hat{\boldsymbol{r}} \cdot \boldsymbol{F}}{4\pi r^2} + p_0$$

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

flow ~ r^{-1}

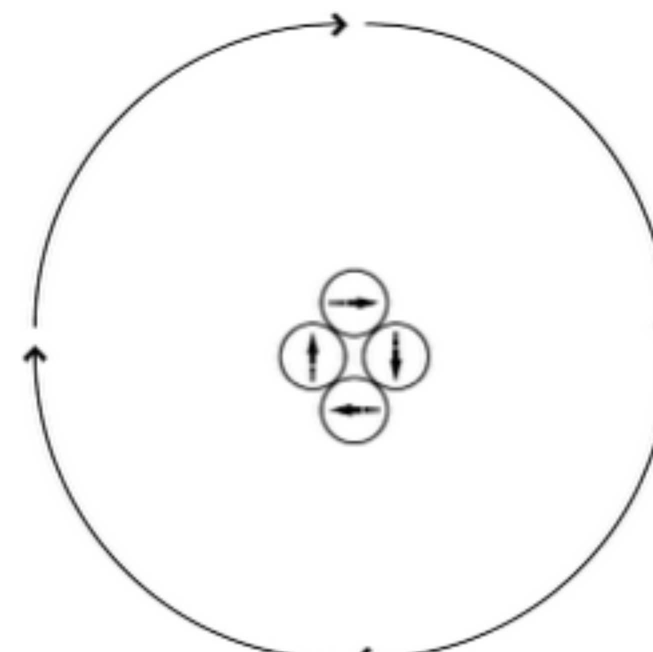
2x stokeslet = symmetric dipole



r^{-2}

'pusher'

rotlet



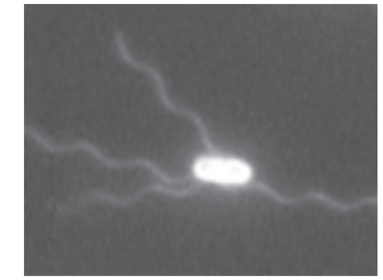
r^{-2}

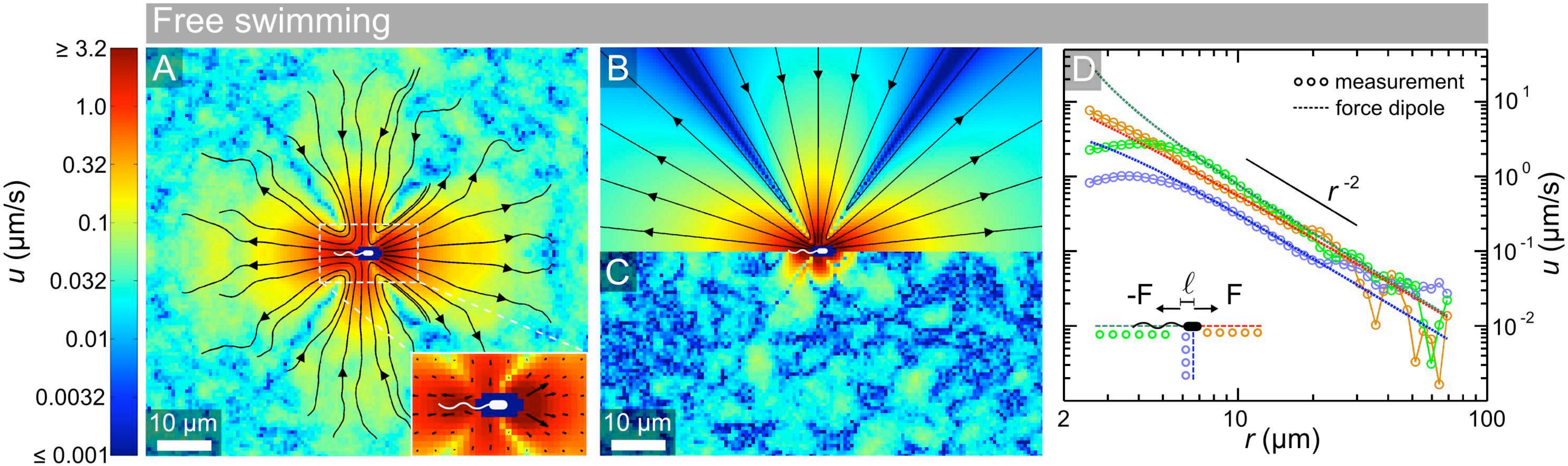
Effect of dimensions

2D: $$\boldsymbol{u}(x) = \frac{F\ell}{2\pi\mu|\boldsymbol{x}|}\left[2(\boldsymbol{n}\cdot\boldsymbol{x})^2 - 1\right]\hat{\boldsymbol{x}}$$

3D: $$\boldsymbol{u}(\boldsymbol{x}) = \frac{F\ell}{4\pi\mu|\boldsymbol{x}|^2}\left[3(\boldsymbol{n}\cdot\boldsymbol{x})^2 - 1\right]\hat{\boldsymbol{x}}.$$

E.coli (non-tumbling HCB 437)





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

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

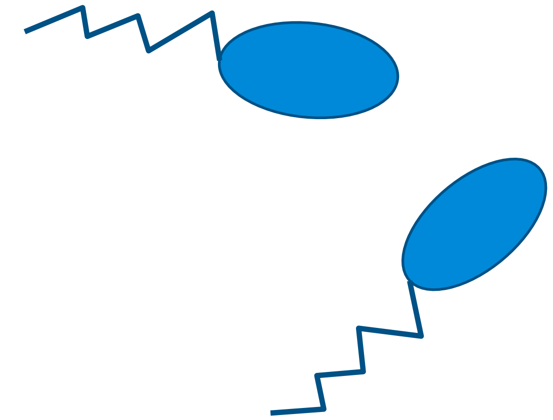
$$\ell = 1.9 \ \mu\text{m}$$

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

weak 'pusher' dipole

Drescher, Dunkel, Ganguly, Cisneros, Goldstein (2011) PNAS

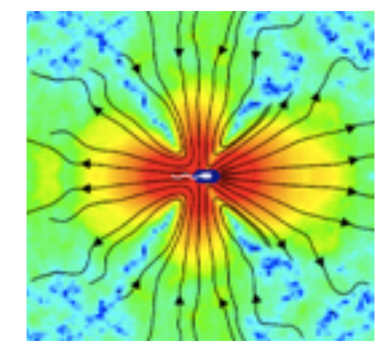
Hydrodynamic pair scattering ?



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

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

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



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

rotational diffusion $$\langle |\Delta\phi|^2 \rangle \sim D_r \tau$$

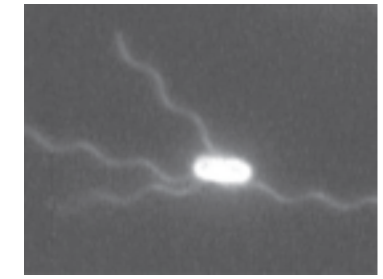
$D_r = 0.057\ \mathrm{rad}^2/\mathrm{s}$

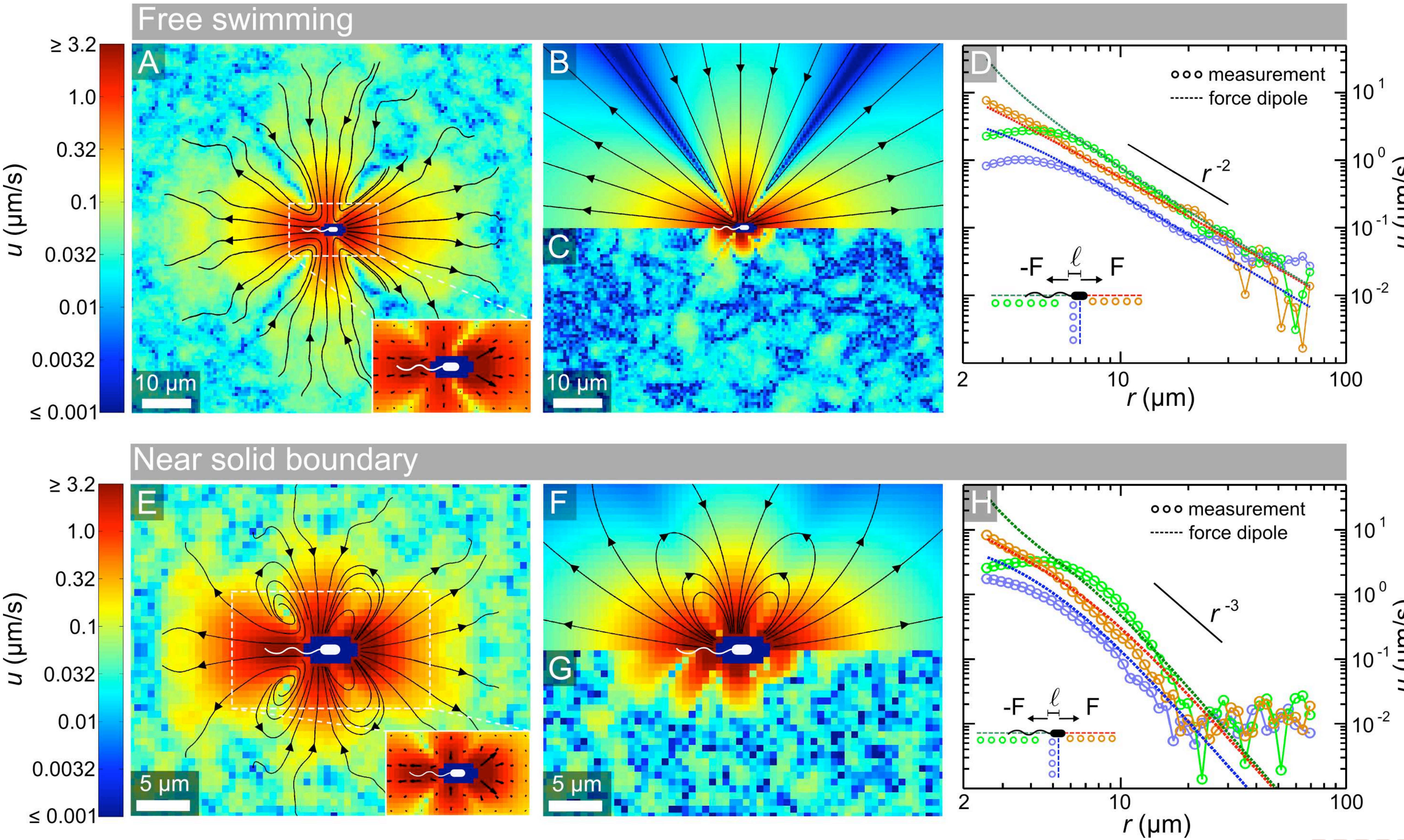
balance $$\boxed{r_H \sim \left(\frac{A^2 \tau}{D_r} \right)^{1/6}}$$

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

Drescher et al (2011) PNAS

E.coli (non-tumbling HCB 437)



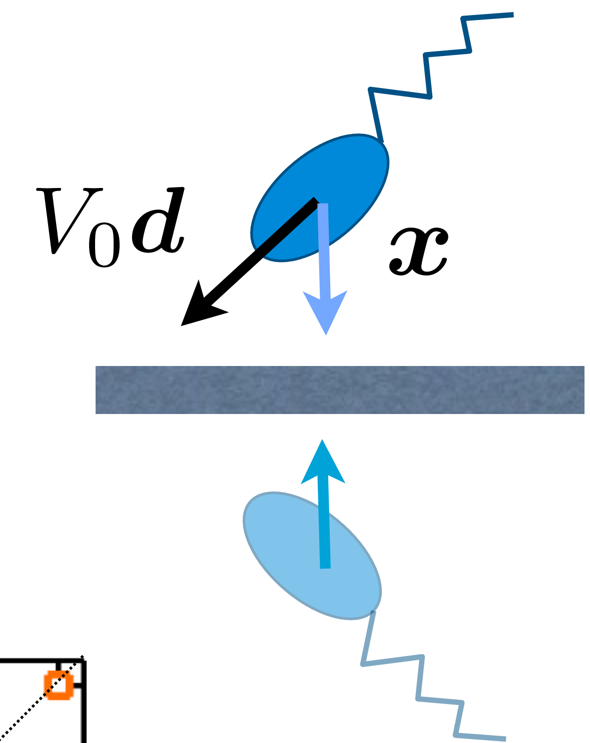


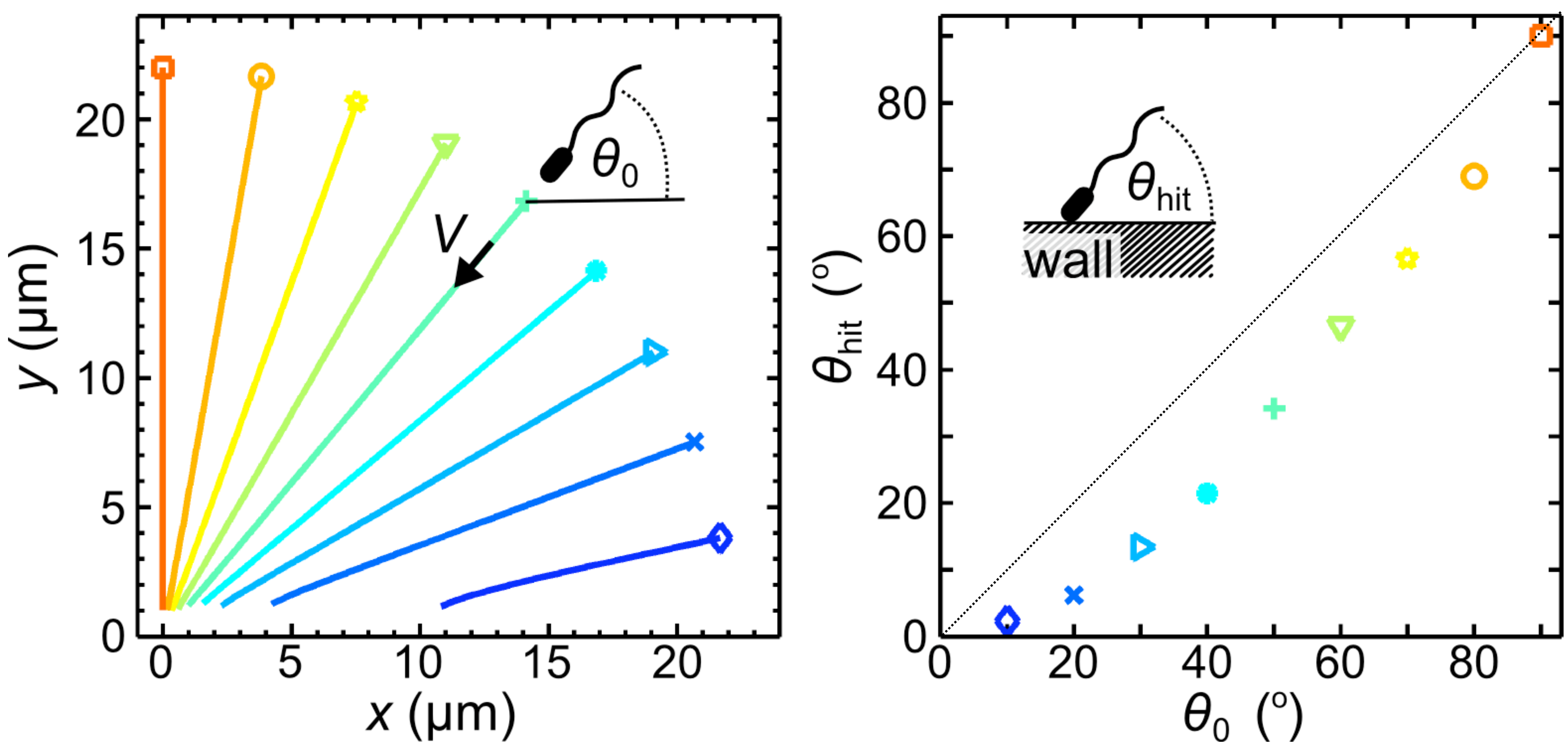
Drescher et al (2011) PNAS

... hitting the wall

$$\dot{\boldsymbol{x}} = V_0 \boldsymbol{d} + \boldsymbol{u}$$

$$\dot{\boldsymbol{d}} = \frac{1}{2}\boldsymbol{\omega} \times \boldsymbol{d} + \Gamma \boldsymbol{d} \cdot \boldsymbol{E} \cdot (\boldsymbol{I} - \boldsymbol{dd})$$





$V_0 = 22 \pm 5\ \mu m/s$

$\ell = 1.9\ \mu m$

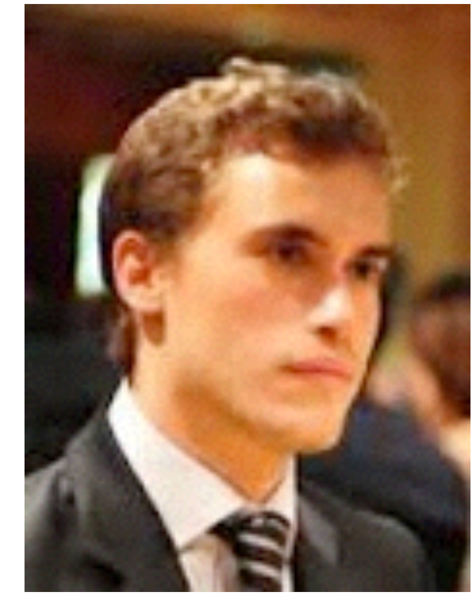
$F = 0.42$ pN

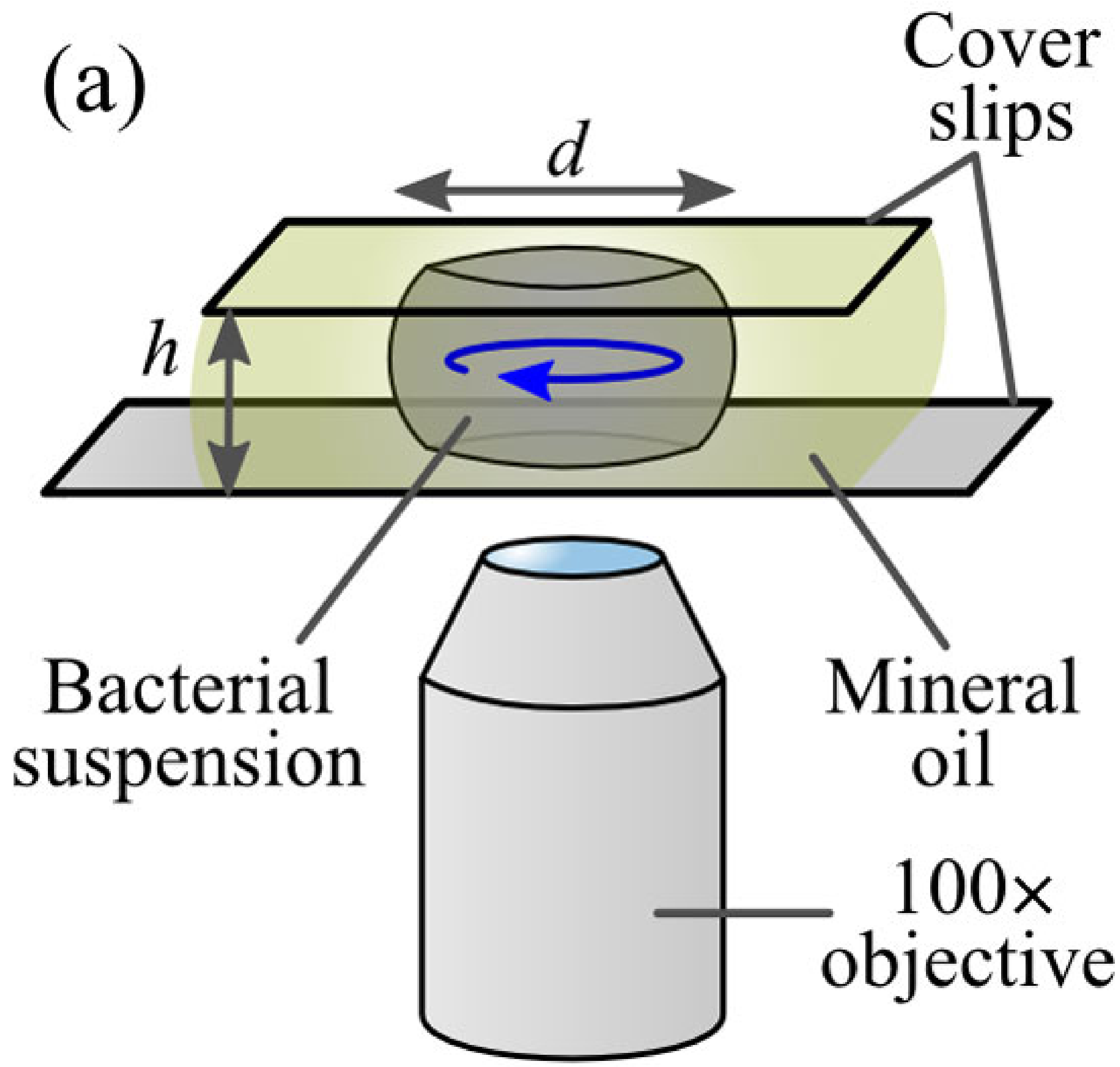
long-range HD <u>not</u> important in bacteria-surface collisions

Drescher, Dunkel, Ganguly, Cisneros, Goldstein (2011) PNAS

UNIVERSITY OF CAMBRIDGE

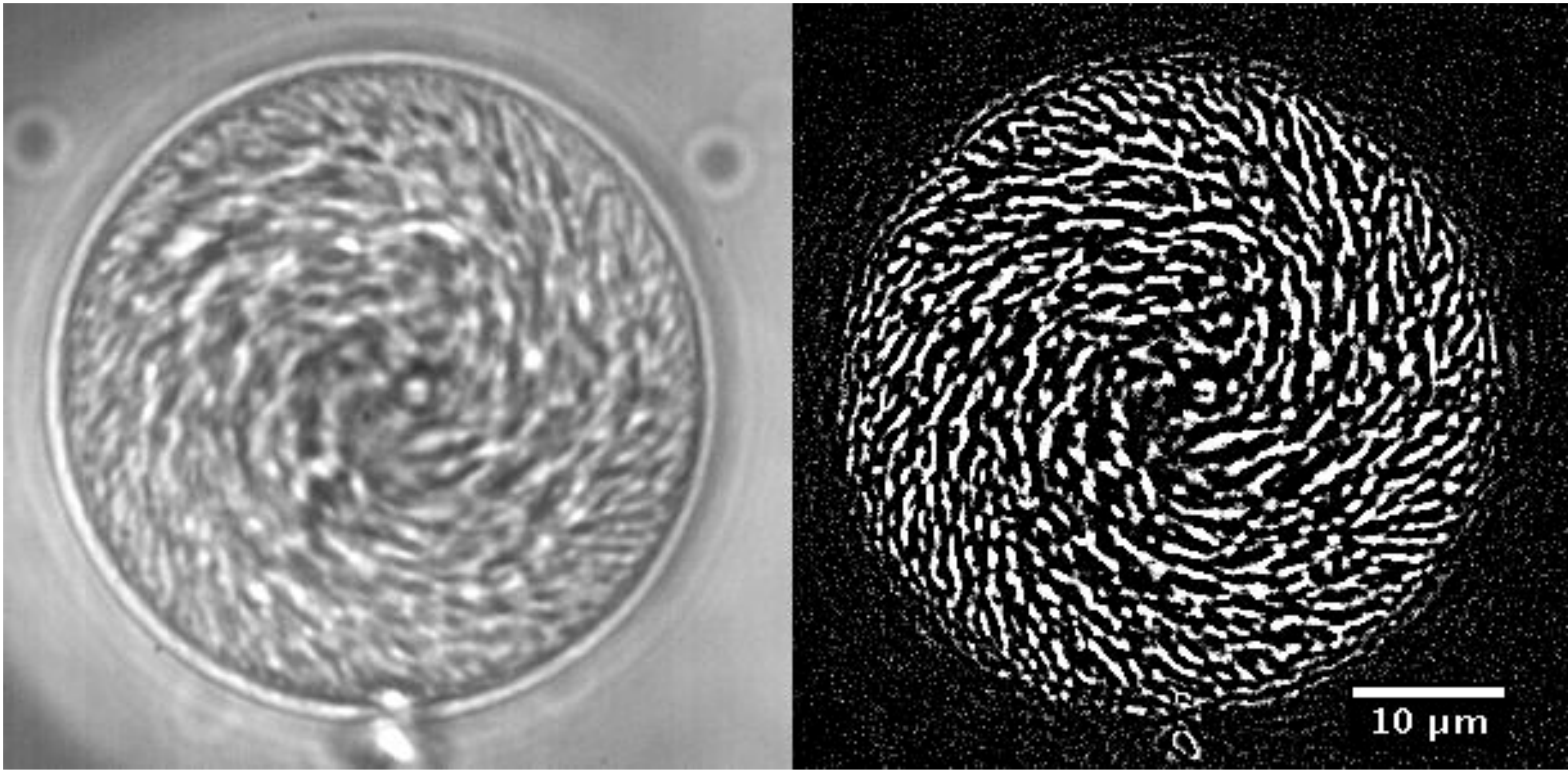
Experiment





Wioland et al (2013) PRL

Stable bacterial spiral vortex



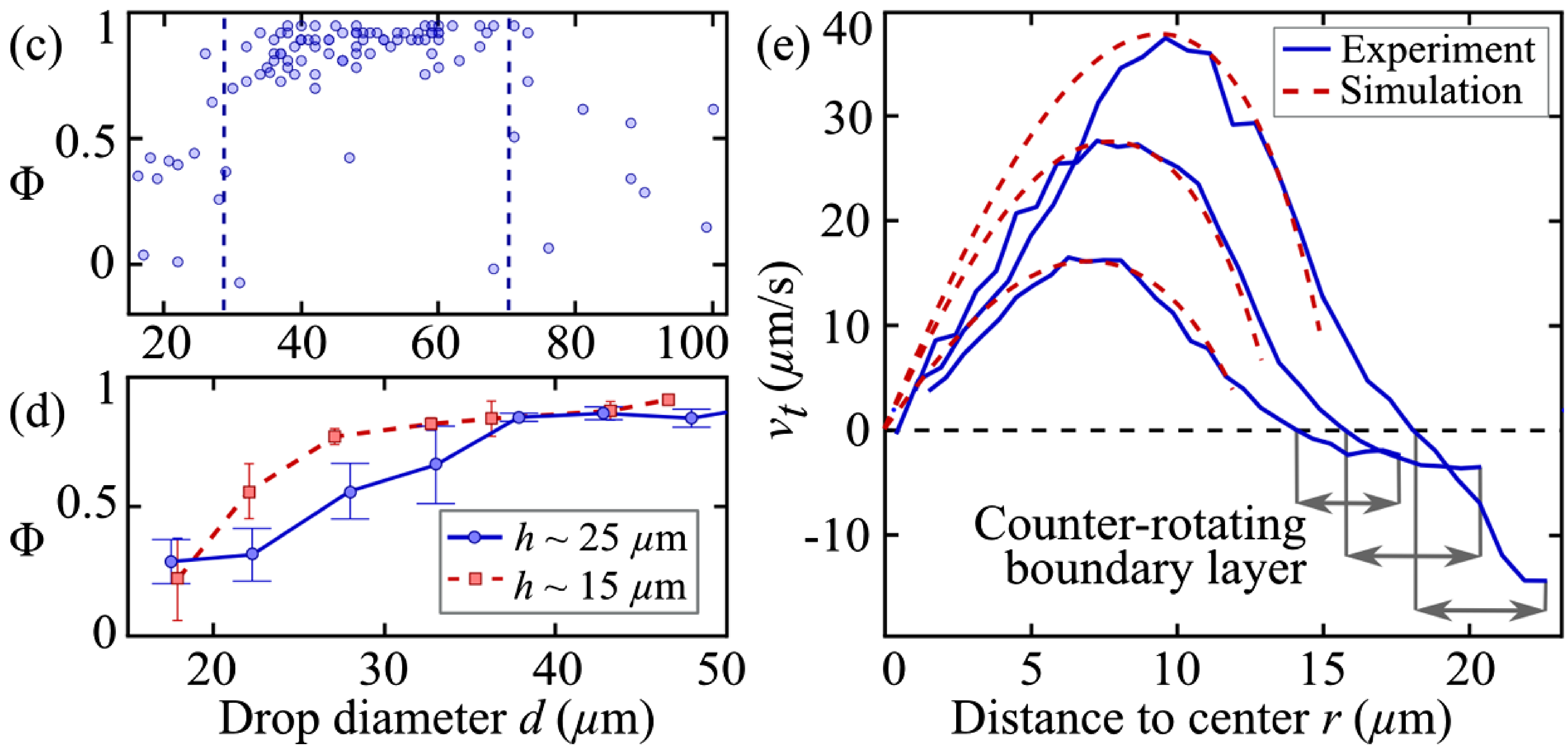
Vortex life time ~ minutes

Wioland et al (2013) PRL

... bacteria create their own BCs !

Vortex characterization

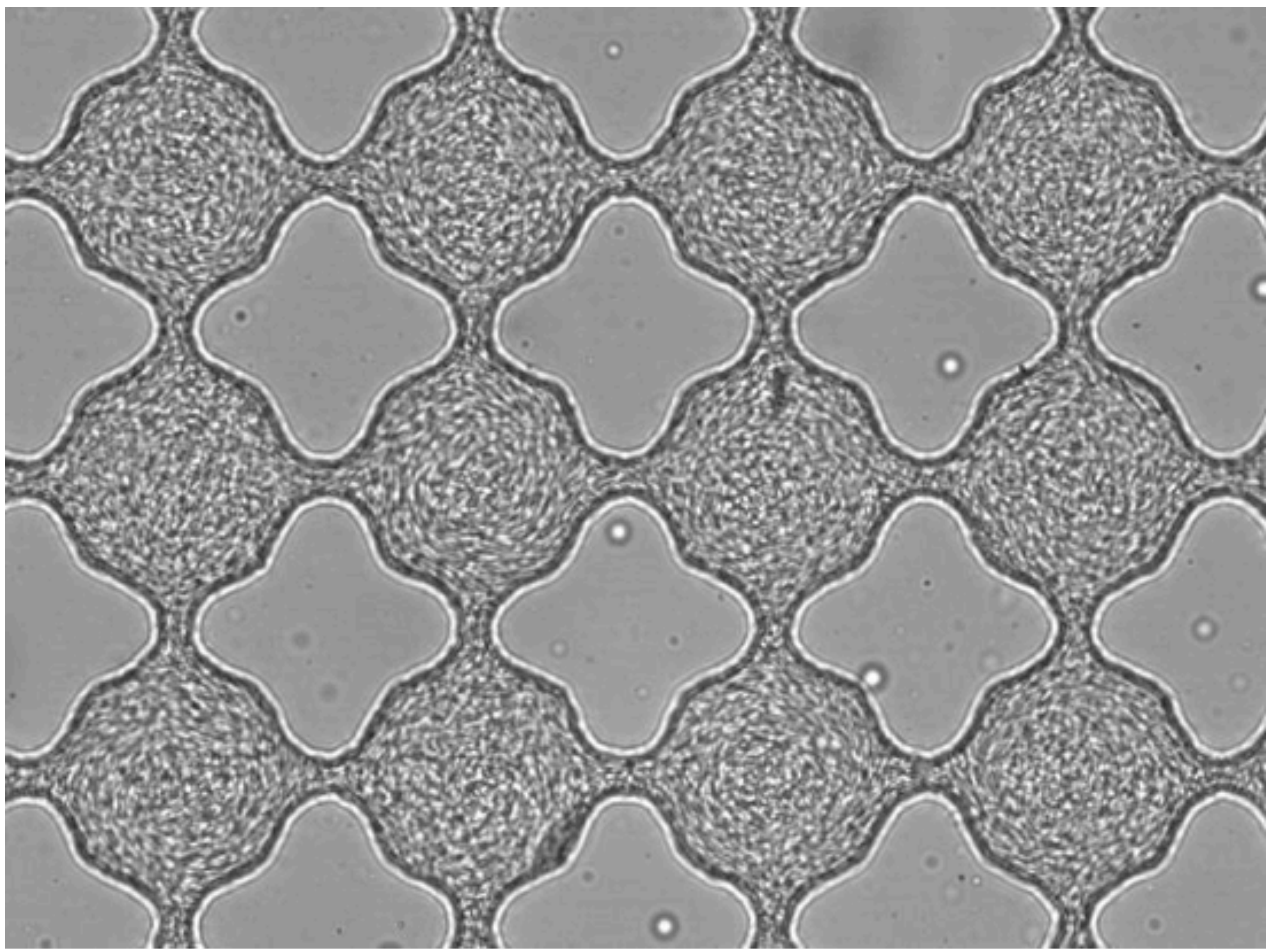
$$\Phi = \frac{\sum_i |\mathbf{v}_i \cdot \mathbf{t}_i| / \sum_j \|\mathbf{v}_j\| - 2/\pi}{1 - 2/\pi}$$

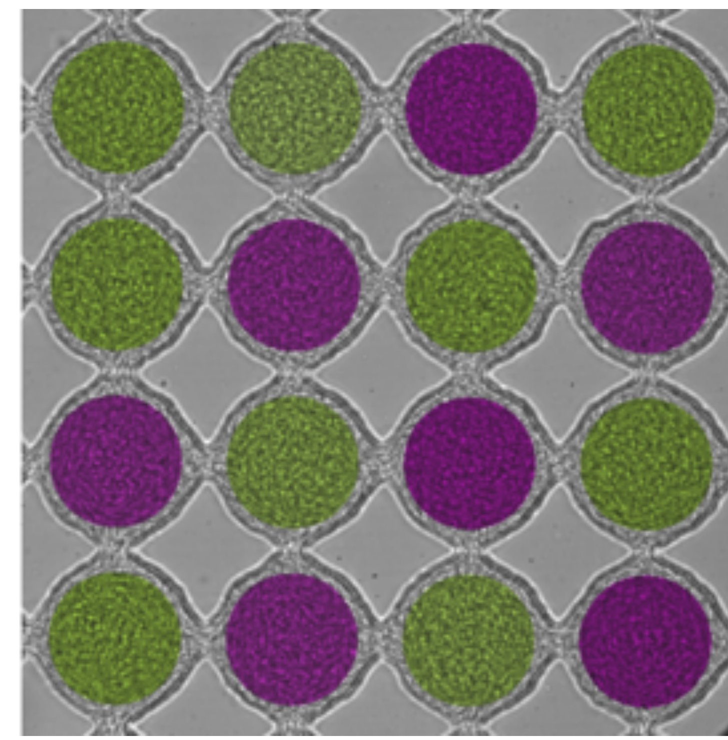


... bacteria create their own BCs !

Wioland et al (2013) PRL

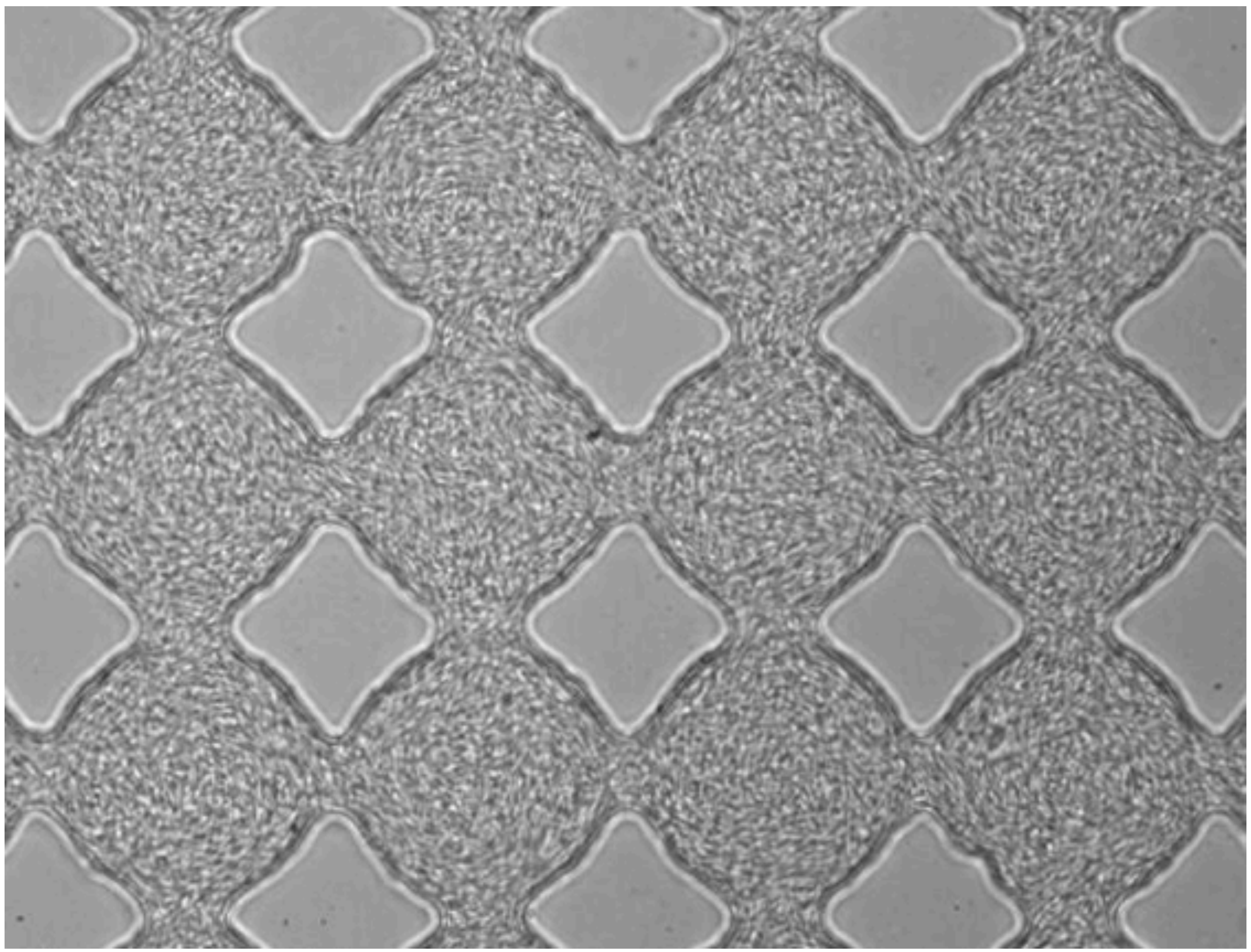
‘Weak’ vortex-coupling: Anti-Ferromagnetic order

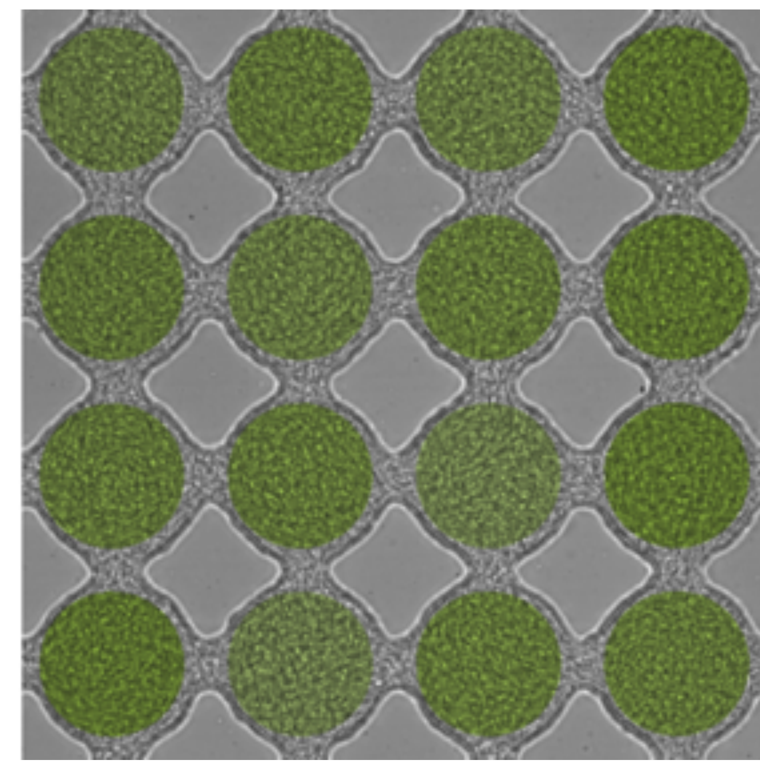




Wioland 2014

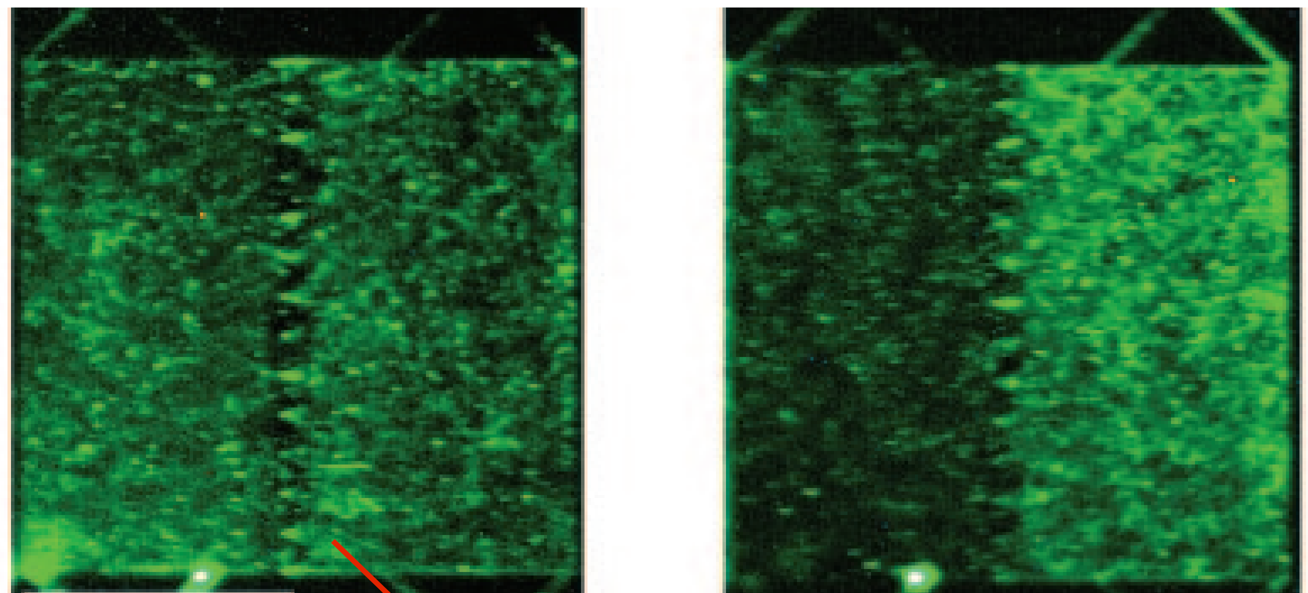
‘Strong’ vortex-coupling: Ferromagnetic order

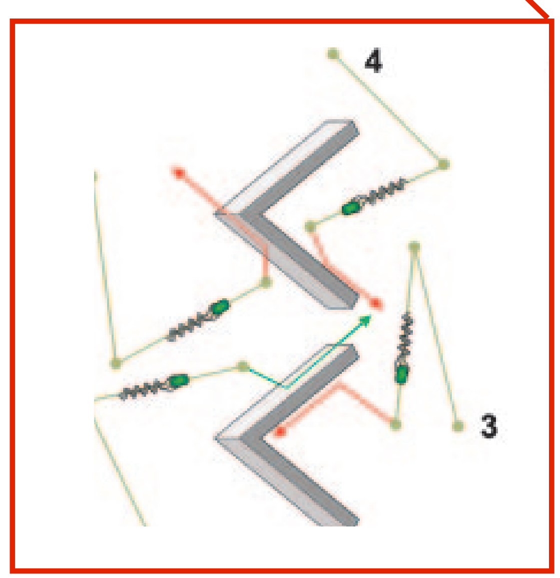


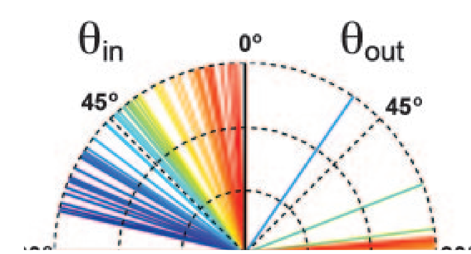


Wioland 2014

Rectification of prokaryotic locomotion





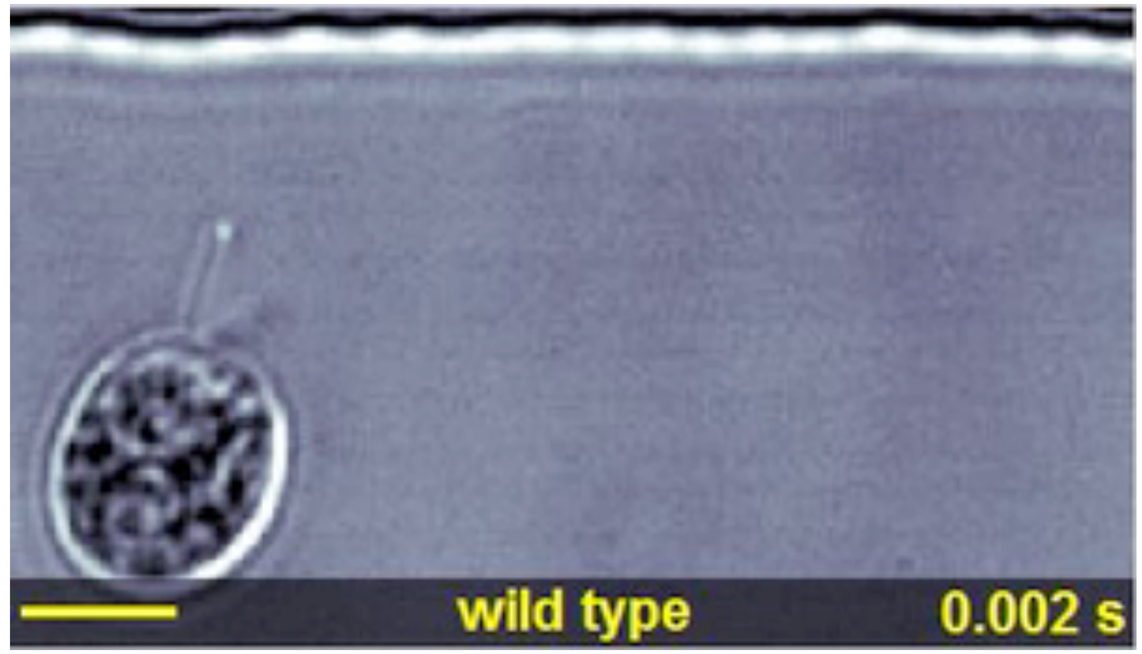


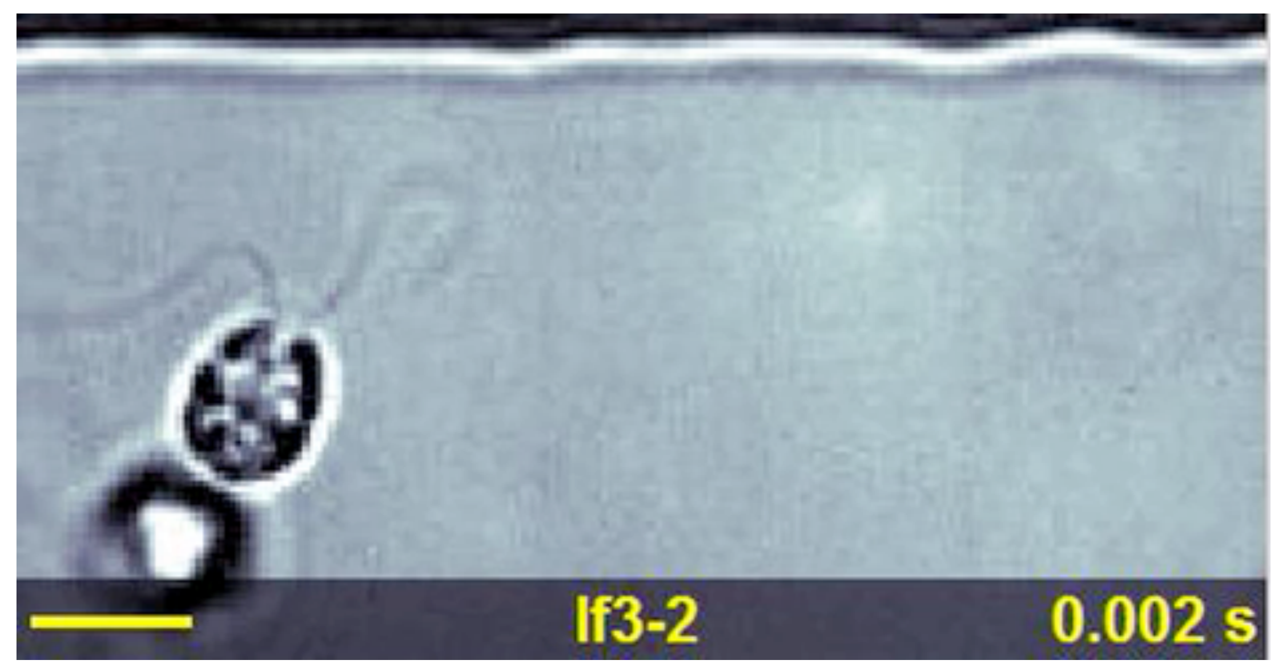
Galadja et al (2009)
J Bacteriology

Austin lab, Princeton, 2009

Swimming near surfaces

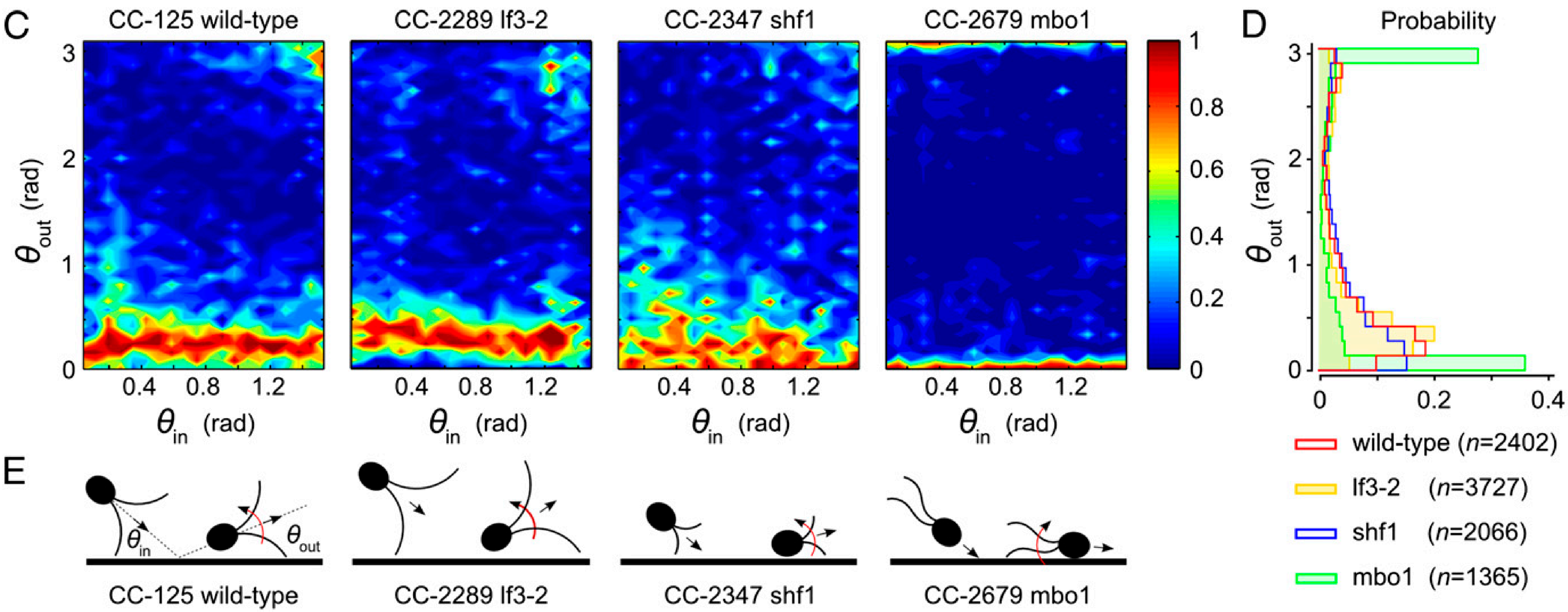
Chlamy





PNAS 2013

Scattering analysis



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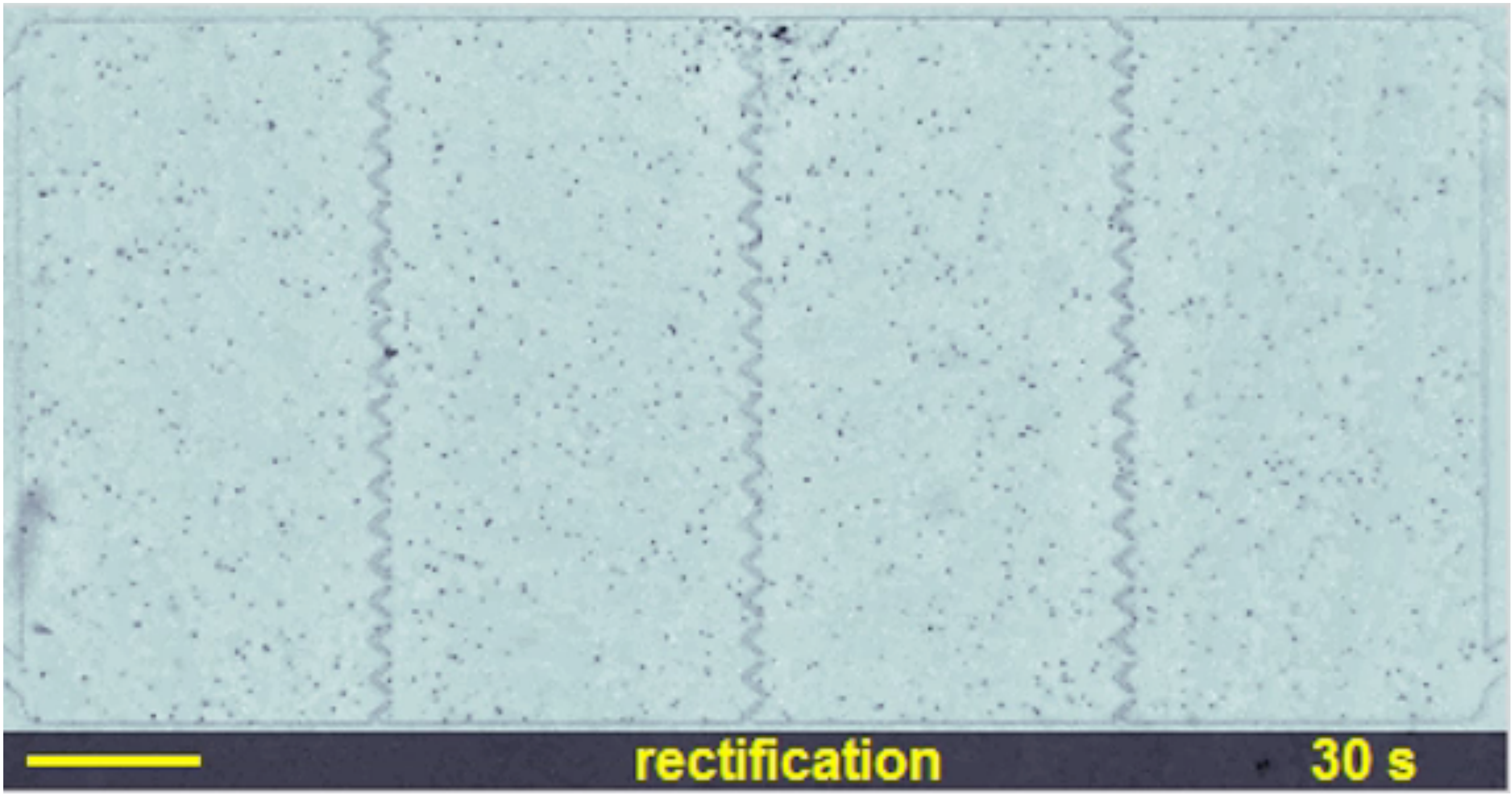
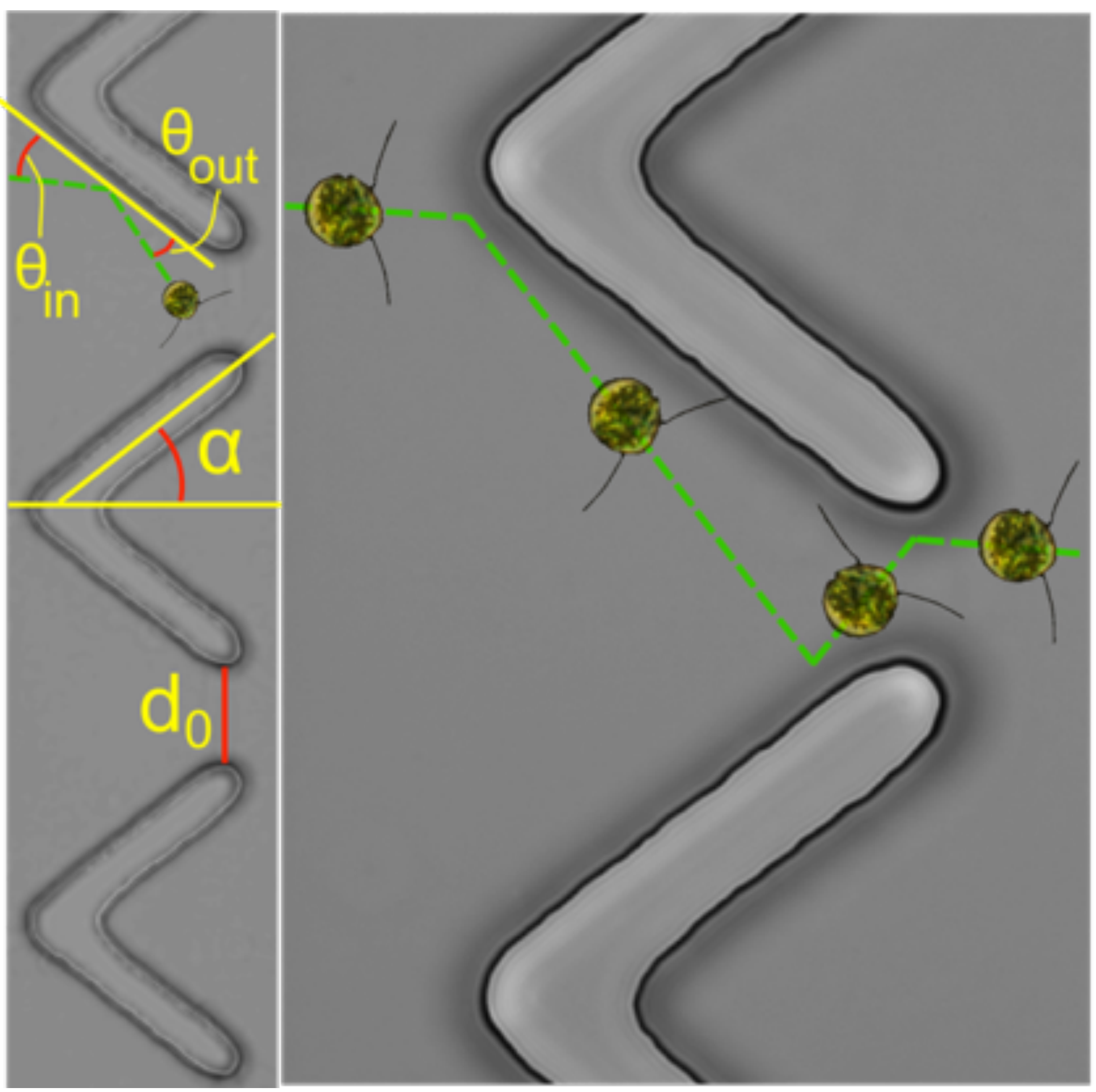
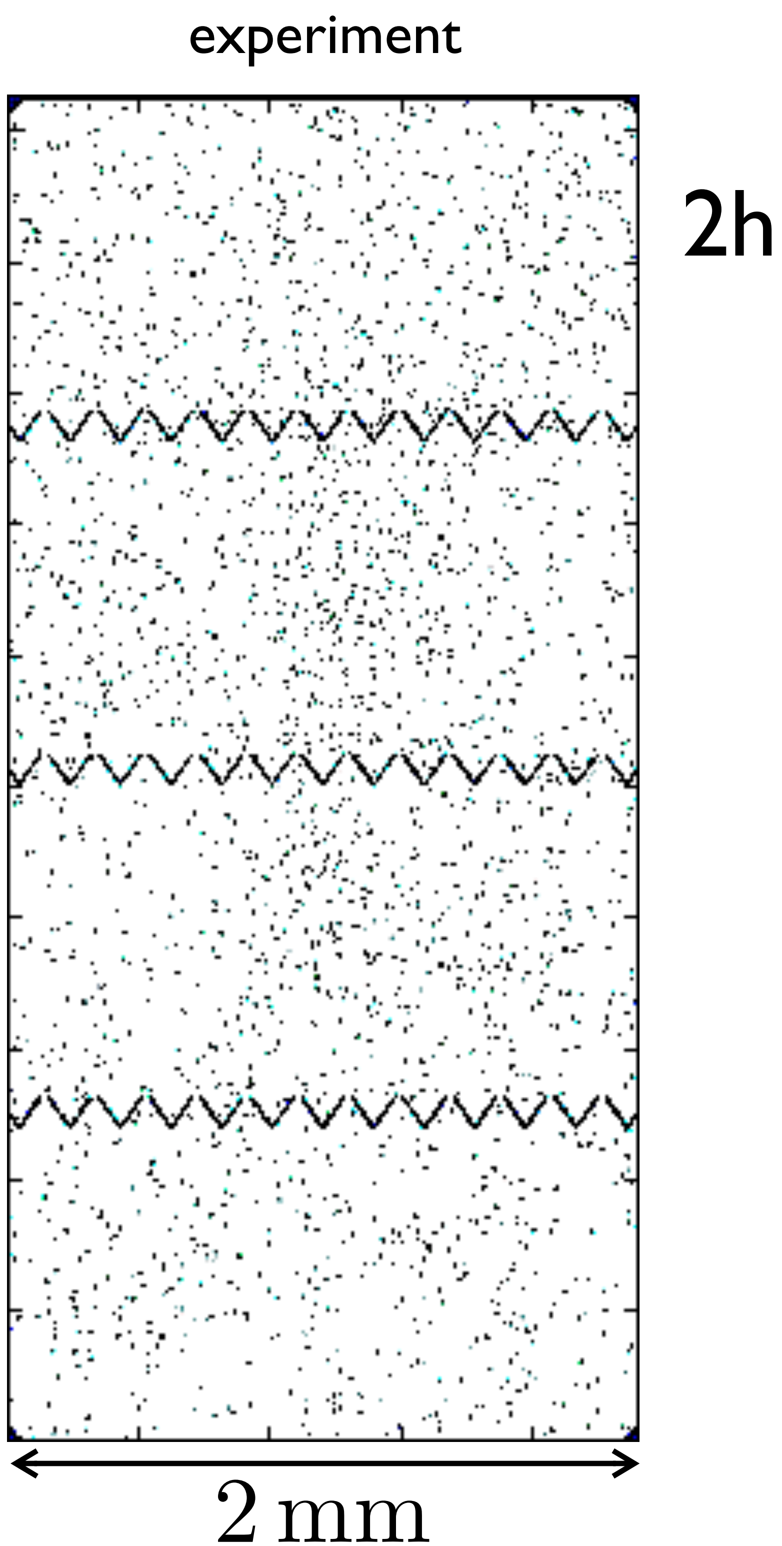
‘Application’



PNAS 2013

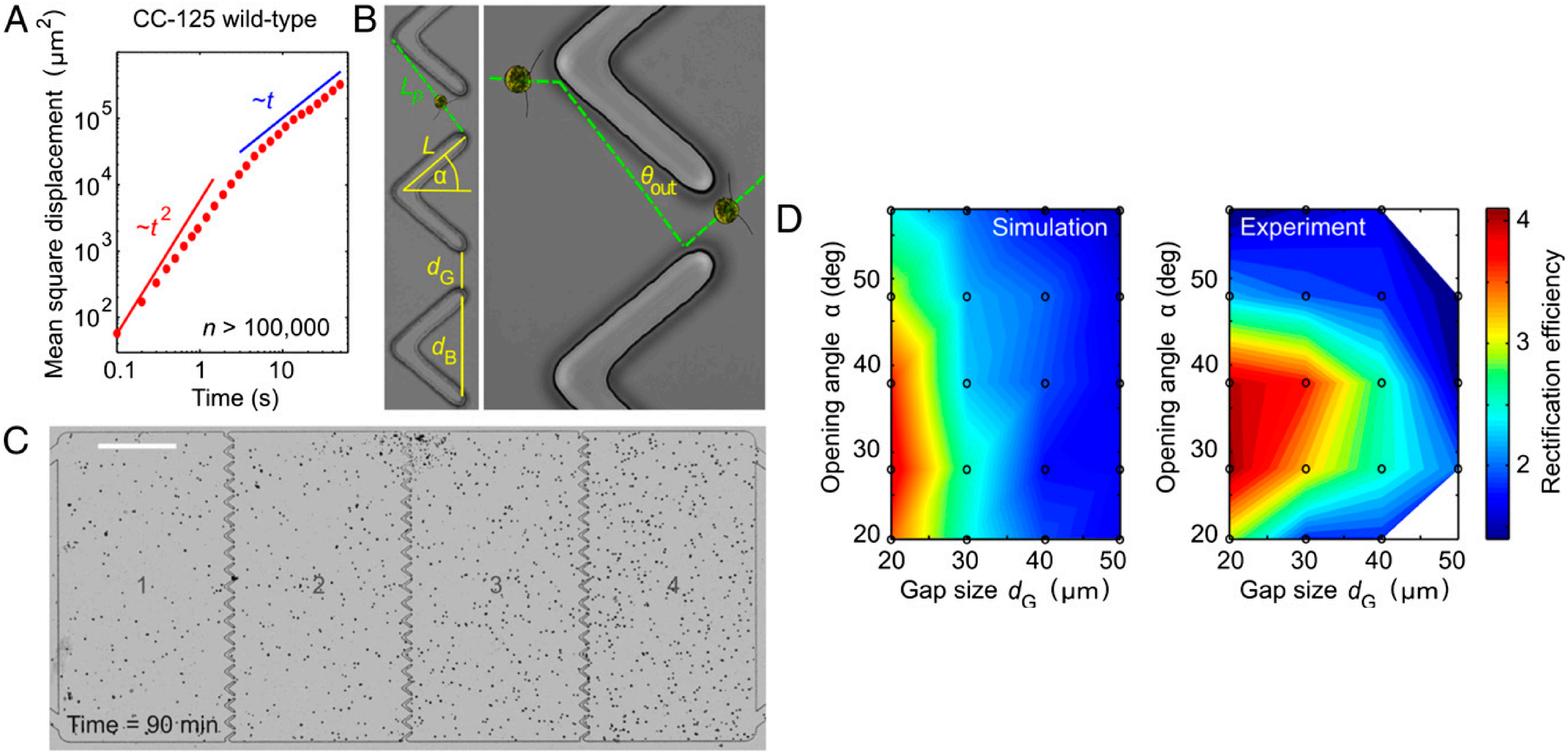
Control of algal locomotion





Kantsler, Dunkel, Polin, Goldstein (2012) PNAS

'Application'

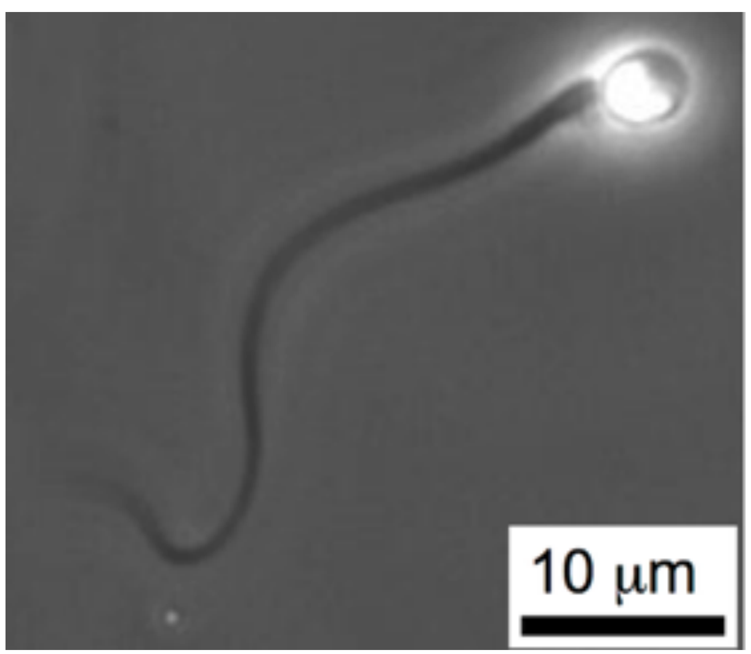


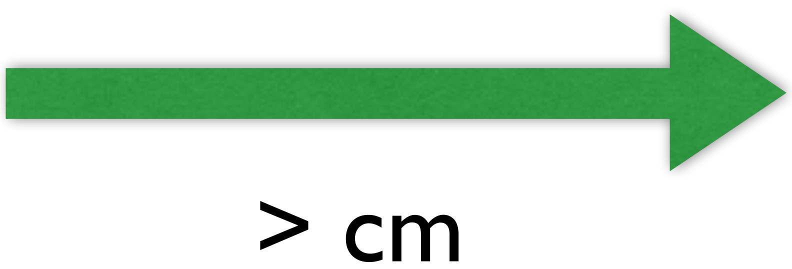
PNAS 2013

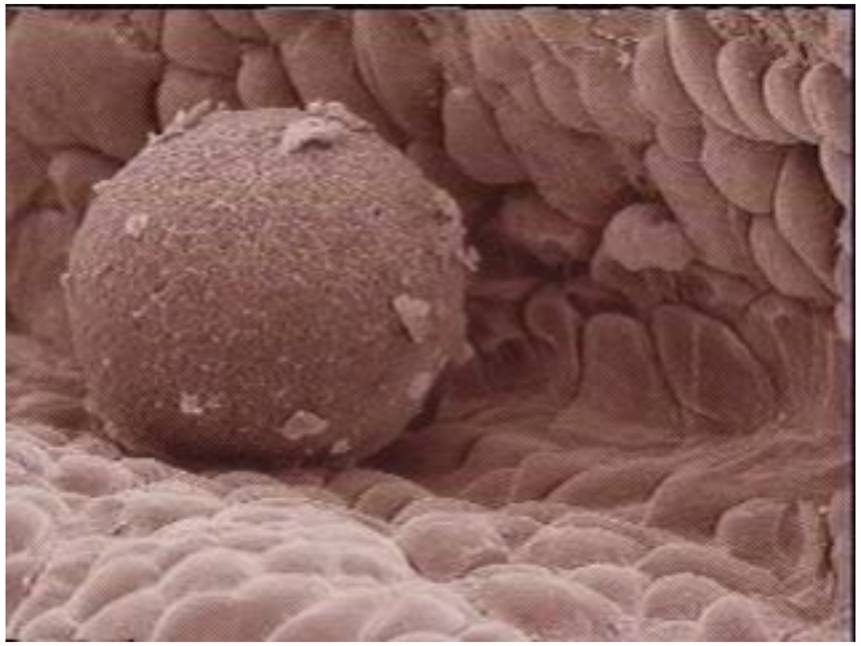
4. Sperm navigation

- chemotaxis ?
- thermotaxis ?
- contractions ?
- rheotaxis ?

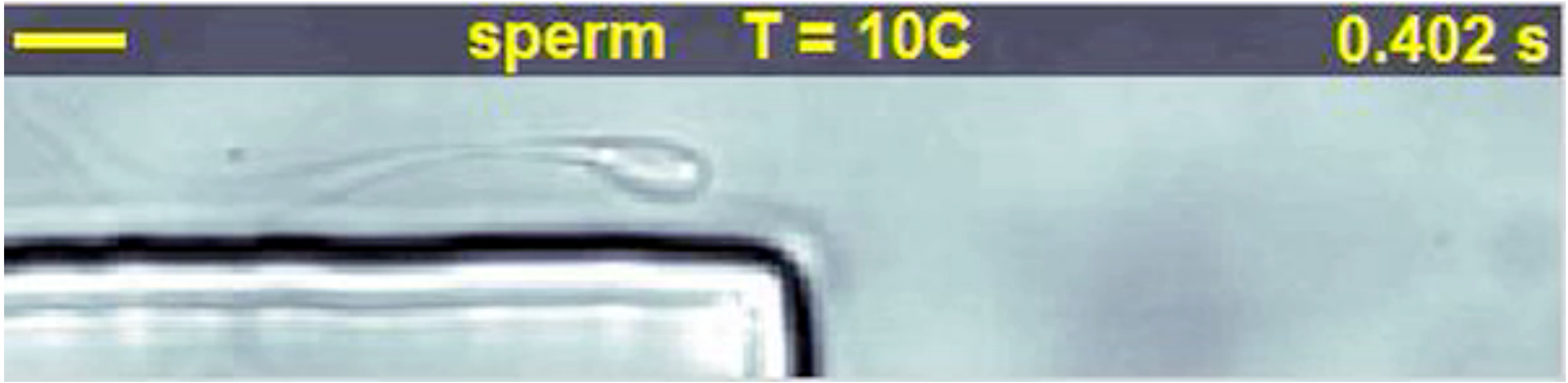
photo credit: Jeff Guasto (Tufts)

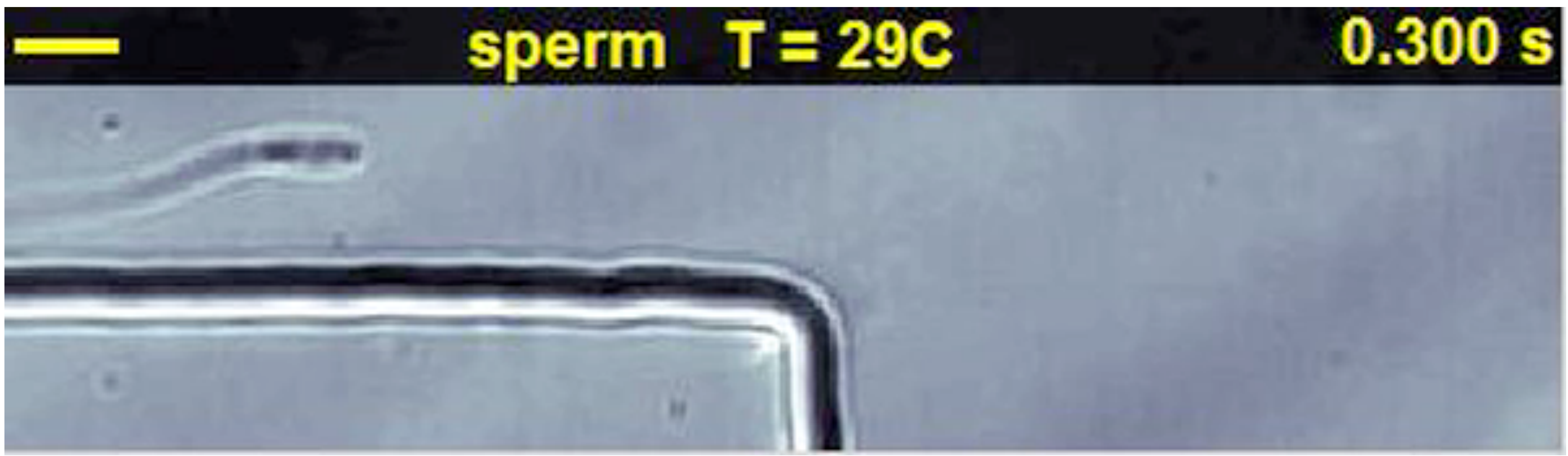


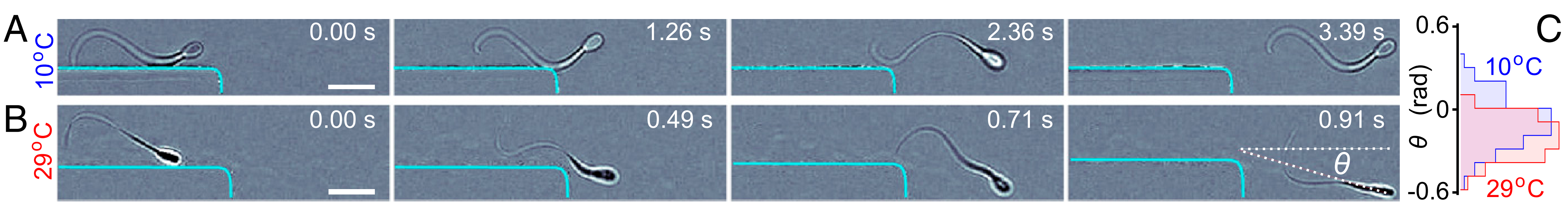




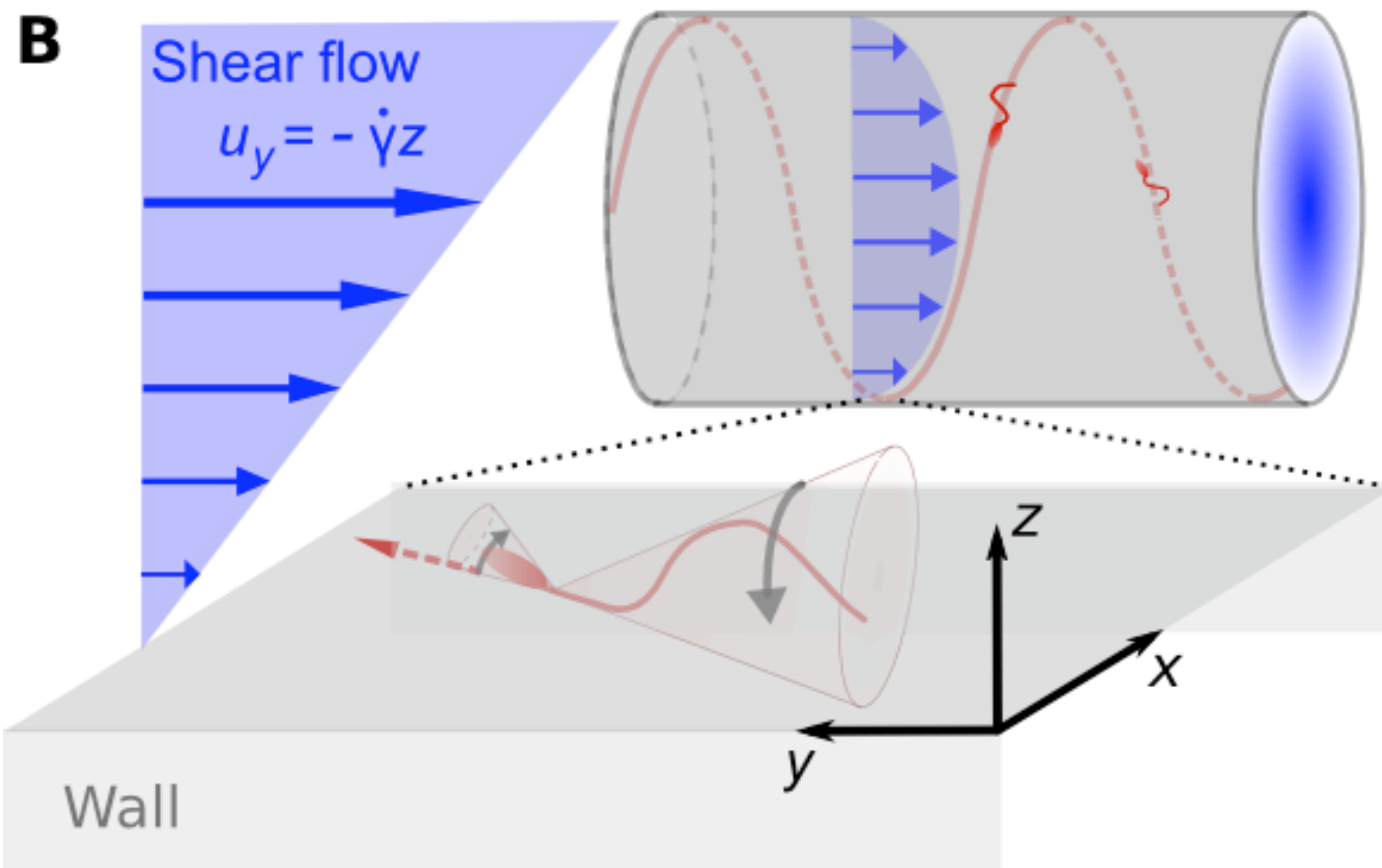
Sperm near surfaces



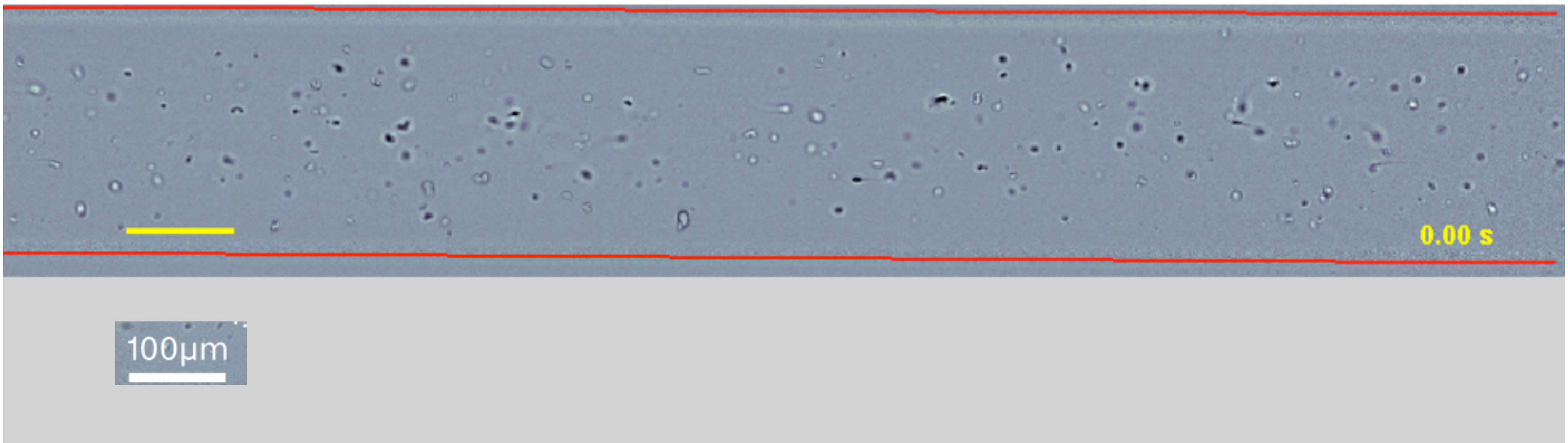




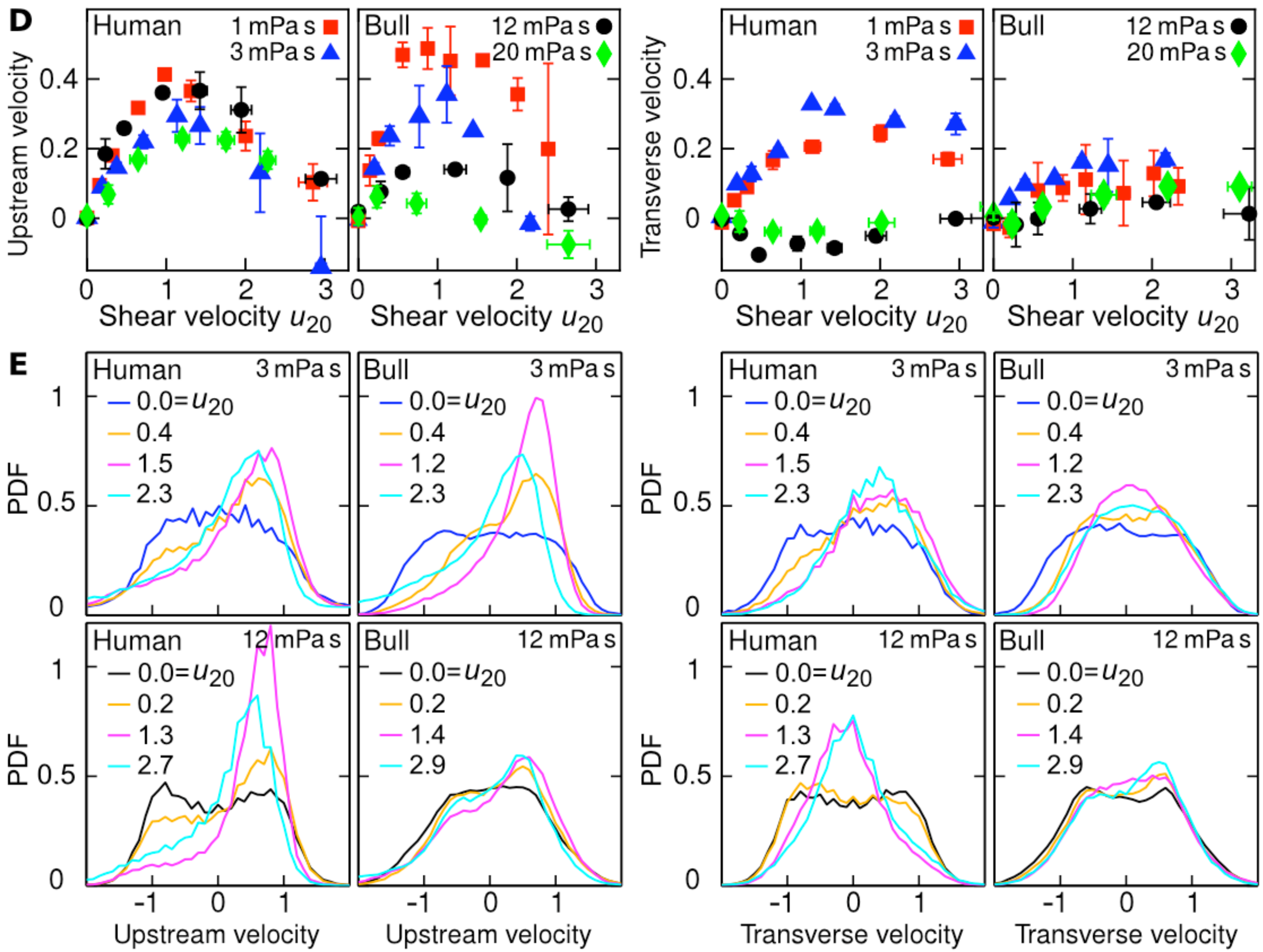
What happens in 3D ?



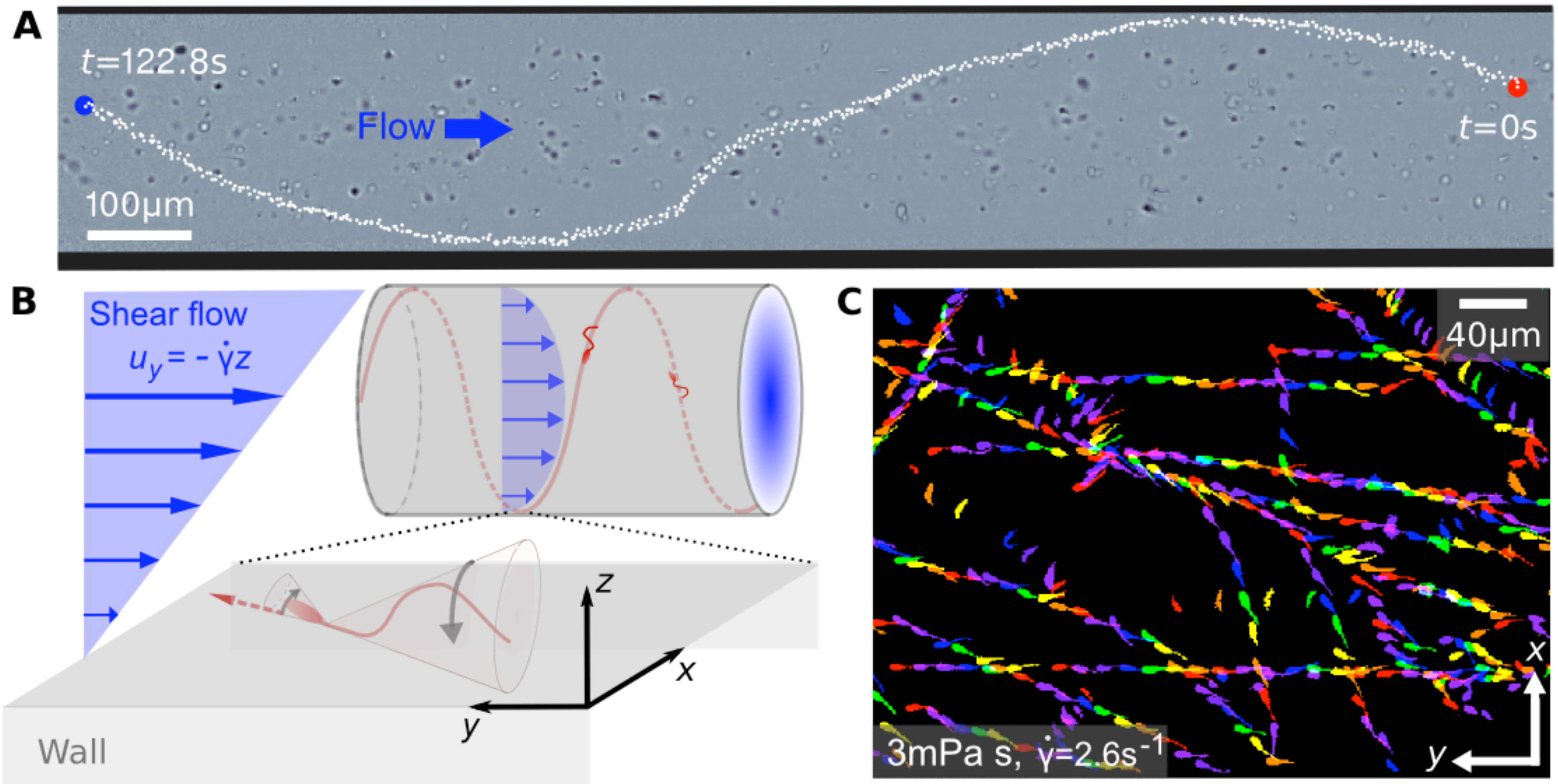
What happens in 3D ?



Viscosity & shear dependence



Rheotaxis



A
t=122.8s
Flow
t=0s
100μm
B
Shear flow
$u_y = -\dot{\gamma}z$
z
x
y
Wall
C
40μm
3mPa s, $\dot{\gamma}$=2.6s^{-1}
x
y

Hagen-Poiseuille flow

$$\frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial u_z}{\partial r}\right) = \frac{1}{\mu}\frac{\partial p}{\partial z}$$

$$u_z = \frac{1}{4\mu}\frac{\partial p}{\partial z}r^2 + c_1 \ln r + c_2$$

$$u_z = -\frac{1}{4\mu}\frac{\partial p}{\partial z}(R^2 - r^2).$$

$$u_{z\,max} = \frac{R^2}{4\mu}\left(-\frac{\partial p}{\partial z}\right).$$

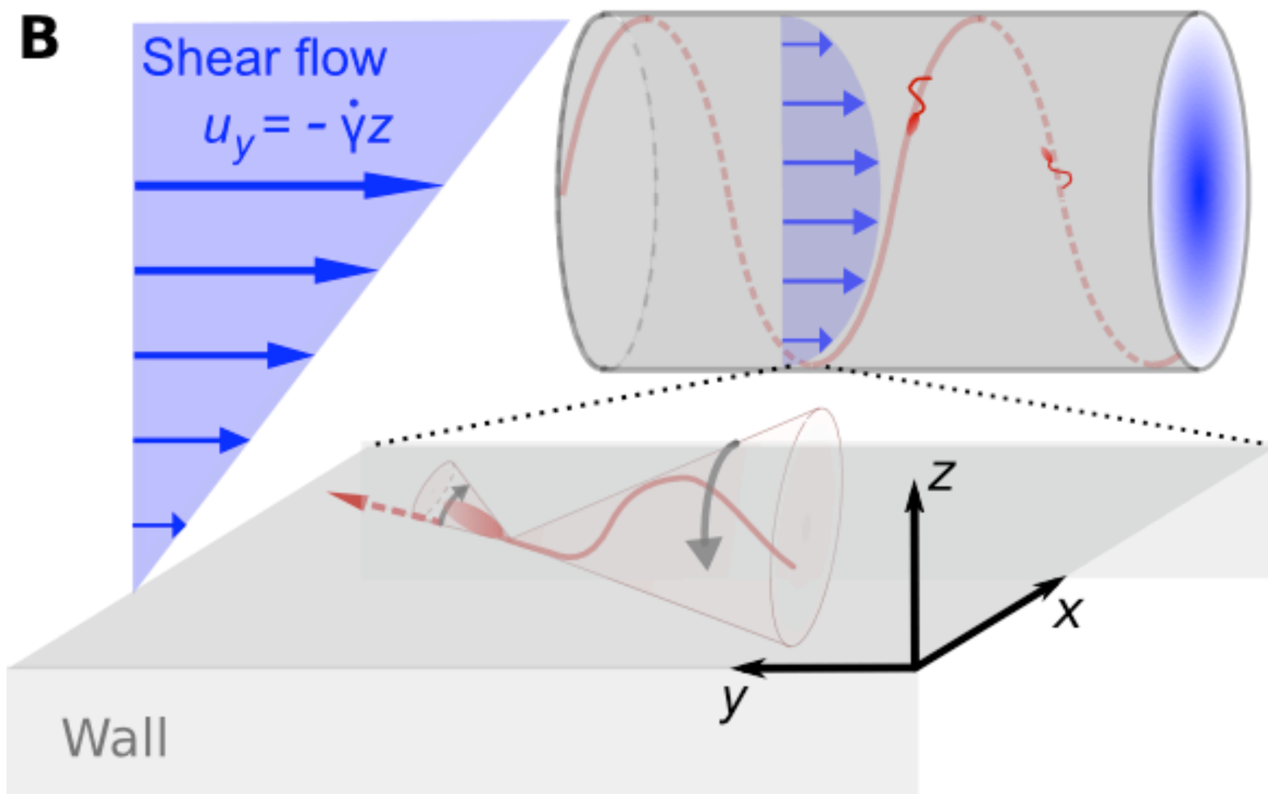
$$u_{z\,\mathrm{avg}} = \frac{1}{\pi R^2}\int_0^R u_z \cdot 2\pi r\,dr = 0.5 u_{z\,\mathrm{max}}.$$

$$-\frac{\partial p}{\partial z} = \frac{\Delta p}{L}$$

or

$$\Delta P = \frac{32\mu L\, u_{z\,\mathrm{avg}}}{D^2}.$$

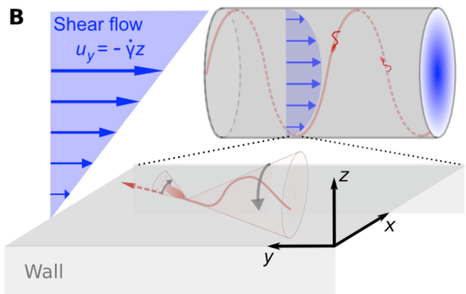
2D minimal model



$$\boldsymbol{u} = \begin{pmatrix} 0 \\ \sigma\dot{\gamma} z \\ 0 \end{pmatrix}$$

$$\boldsymbol{\omega} = \nabla \times \boldsymbol{u} = -\sigma\dot{\gamma}\begin{pmatrix} 1 \\ 0 \\ 0 \end{pmatrix}, \qquad \mathcal{E} = \frac{1}{2}\left(\nabla^{\intercal}\boldsymbol{u} + \nabla\boldsymbol{u}^{\intercal}\right) = \frac{\sigma\dot{\gamma}}{2}\begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 1 \\ 0 & 1 & 0 \end{pmatrix} \qquad \mathcal{P}(\boldsymbol{n}) = \mathcal{I} - \boldsymbol{n}\boldsymbol{n}$$

$$\dot{\boldsymbol{n}} = a\boldsymbol{\omega} \times \boldsymbol{n} + 2b\boldsymbol{n} \cdot \mathcal{E} \cdot \mathcal{P}(\boldsymbol{n})$$



$$\dot{\boldsymbol{n}} = a\boldsymbol{\omega} \times \boldsymbol{n} + 2b\boldsymbol{n} \cdot \mathcal{E} \cdot \mathcal{P}(\boldsymbol{n})$$

$$\begin{aligned} 2\mathcal{W}_{mn} &:= -(\boldsymbol{\omega}\times)_{mn} \\ &= -\epsilon_{min}(\epsilon_{ijk}\partial_j u_k) = \epsilon_{imn}(\epsilon_{ijk}\partial_j u_k) = (\delta_{mj}\delta_{nk} - \delta_{mk}\delta_{nj})\partial_j u_k \\ &= \partial_m u_n - \partial_n u_m, \end{aligned}$$

$$\dot{n}_i = 2a\mathcal{W}_{ij}n_j + 2bn_m\mathcal{E}_{mj}(\delta_{ji} - n_j n_i).$$

For the flow field in (1) we find

$$\dot{\boldsymbol{n}} = -a\sigma\dot{\gamma}\begin{pmatrix} 0 \\ -n_z \\ n_y \end{pmatrix} - b\sigma\dot{\gamma}\begin{pmatrix} 2n_x n_y n_z \\ (2n_y^2 - 1)n_z \\ (2n_z^2 - 1)n_y \end{pmatrix},$$

Steric wall effect

(i) $\dot{n}_z = 0$ and (ii) $n_x^2 + n_y^2 = (1 - n_z^2)$ is conserved

Steric wall effect

(i) $\dot{n}_z = 0$ and (ii) $n_x^2 + n_y^2 = (1 - n_z^2)$ is conserved

$$\begin{pmatrix} \dot{n}_x \\ \dot{n}_y \end{pmatrix} = -a\sigma\dot{\gamma}n_z \begin{pmatrix} 0 \\ -1 \end{pmatrix} - b\sigma\dot{\gamma}n_z \begin{pmatrix} 2n_x n_y \\ 2n_y^2 - 1 \end{pmatrix} + c \begin{pmatrix} n_x \\ n_y \end{pmatrix}. \tag{8}$$

Condition (ii) then gives

$$c = \sigma\dot{\gamma}\frac{n_z[b(1-2n_z^2) - a]}{1 - n_z^2} n_y. \tag{9}$$

Keeping in mind that n_z and $n_x^2 + n_y^2$ are constant, we thus find the reduced 2D equations of motion

$$\begin{pmatrix} \dot{n}_x \\ \dot{n}_y \end{pmatrix} = -\sigma\dot{\gamma}(a+b)\frac{n_z}{n_x^2 + n_y^2} \begin{pmatrix} n_x n_y \\ n_y^2 - (1 - n_z^2). \end{pmatrix} \tag{10}$$

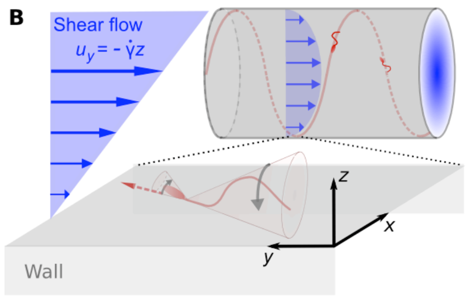
The fixed point criterium $(\dot{n}_x, \dot{n}_y) = 0$ gives

$$n_x = 0, \qquad n_y = \pm\sqrt{1 - n_z^2}, \tag{11}$$

This result implies that, depending on the effective shape parameter

$$\alpha = -(a+b)n_z, \tag{12}$$

Rewrite in terms of 2D orientation



$$\boldsymbol{N} = \begin{pmatrix} N_x \\ N_y \end{pmatrix} = \frac{1}{\sqrt{1-n_z^2}} \begin{pmatrix} n_x \\ n_y \end{pmatrix} \tag{13}$$

as

$$\begin{pmatrix} \dot{N}_x \\ \dot{N}_y \end{pmatrix} = \sigma\dot{\gamma}\alpha \begin{pmatrix} N_x N_y \\ N_y^2 - 1 \end{pmatrix}, \tag{14}$$

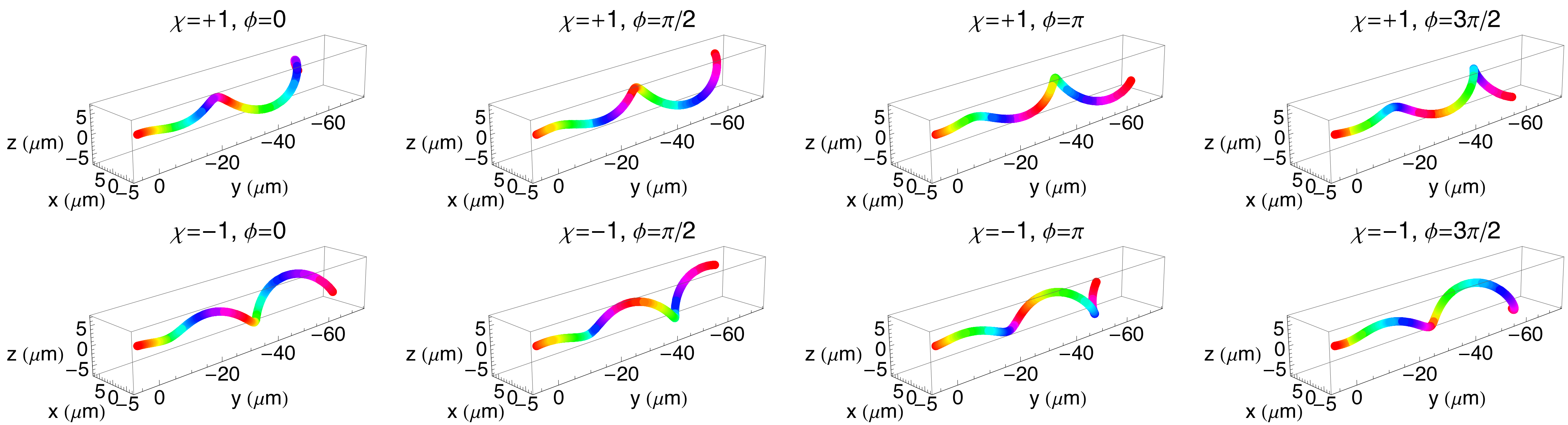
where $\sigma = \pm 1$ accounts for the flow direction and constant geometric prefactors have been absorbed in the 'shape' coefficient

$$\alpha = -(a+b)n_z. \tag{15}$$

Note that α is positive for sperm-type swimmers that point into the surface, for in this case one has $n_z < 0$.

Chirality effects?

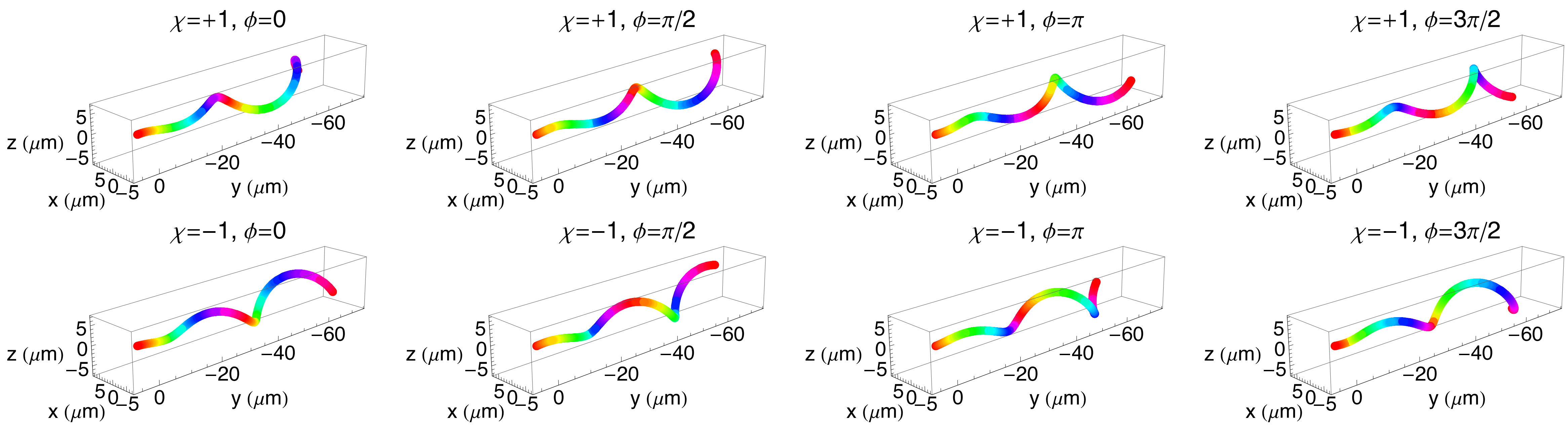
Spiral model



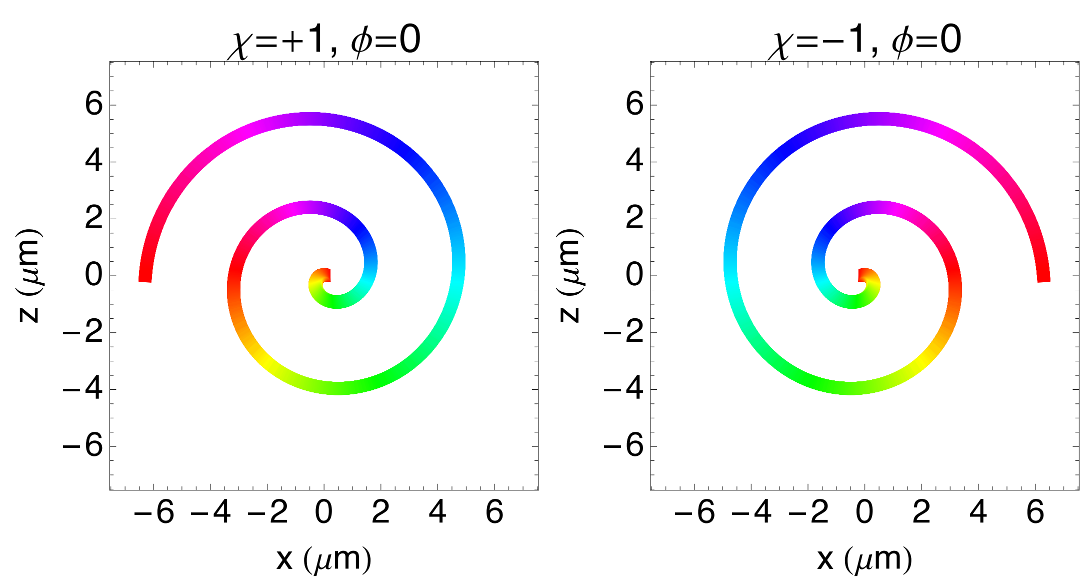
body-centered frame

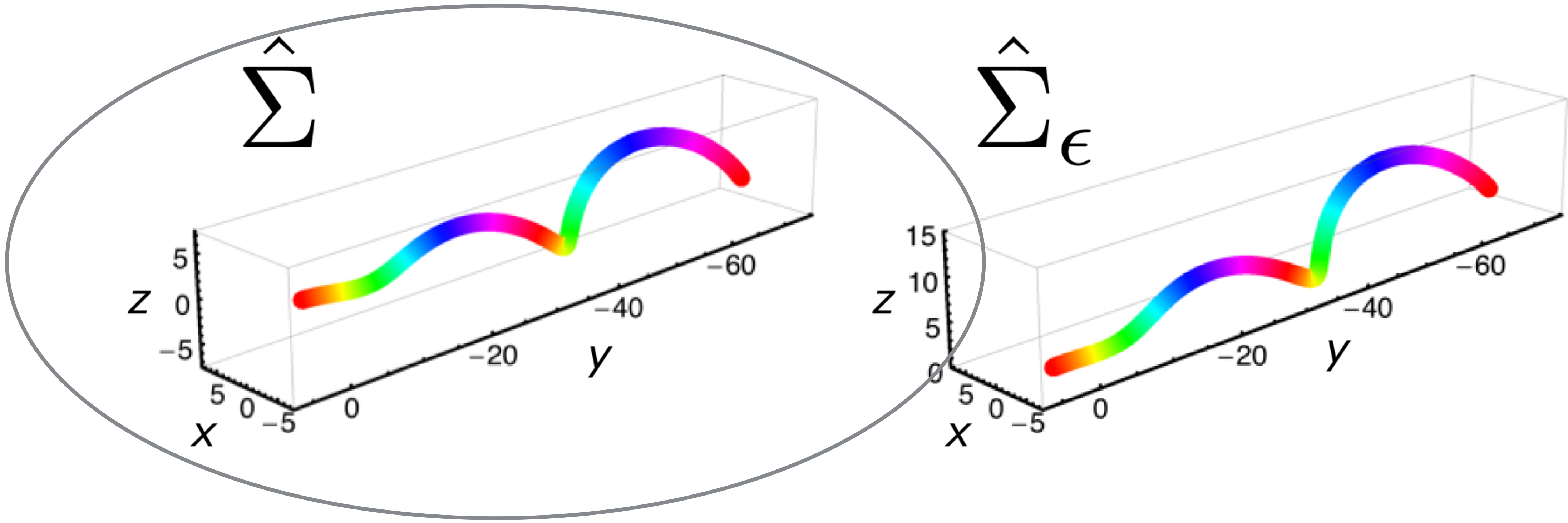
$$\hat{\boldsymbol{C}}(s) = \begin{pmatrix} \hat{X}(s) \\ \hat{Y}(s) \\ \hat{Z}(s) \end{pmatrix} = \lambda s \begin{pmatrix} \chi \epsilon_1 \cos(s-\phi) \\ -1 \\ -\epsilon_2 \sin(s-\phi) \end{pmatrix}, \qquad s \in [0, S].$$

Spiral model



from tip



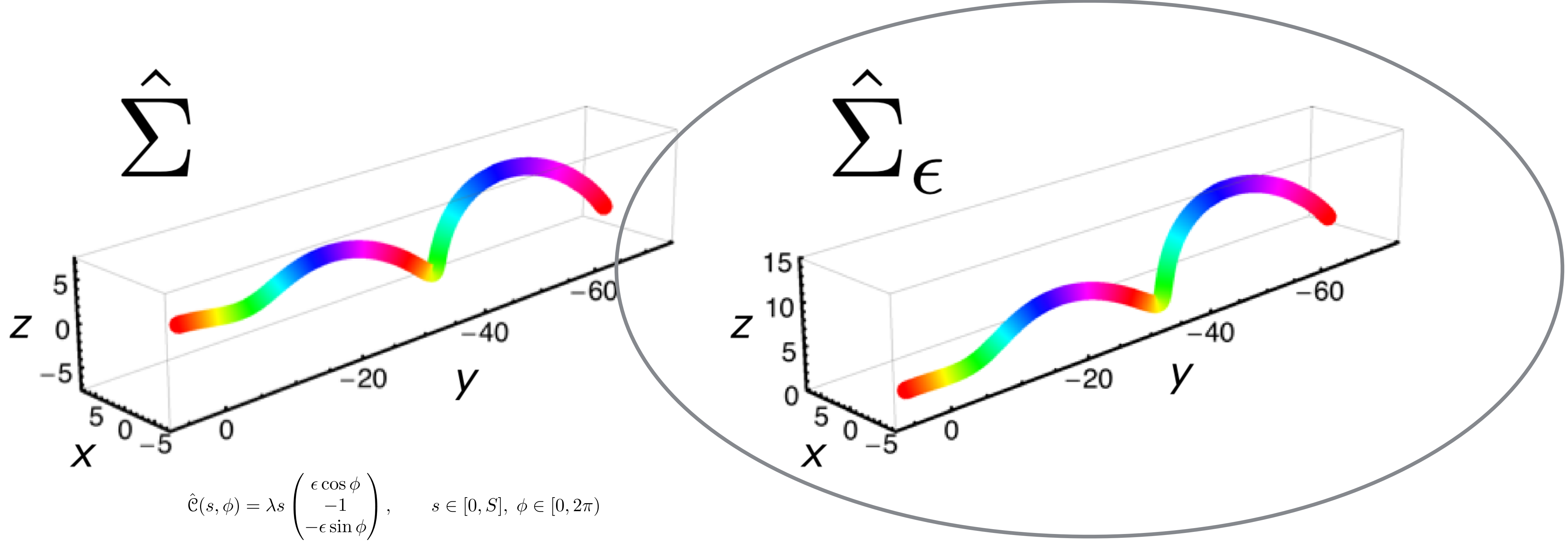


$$\hat{\boldsymbol{C}}(s) = \begin{pmatrix} \hat{X}(s) \\ \hat{Y}(s) \\ \hat{Z}(s) \end{pmatrix} = \lambda s \begin{pmatrix} \chi\epsilon_1 \cos(s-\phi) \\ -1 \\ -\epsilon_2 \sin(s-\phi) \end{pmatrix}, \qquad s \in [0, S].$$

$$\hat{\mathfrak{C}}(s,\phi) = \lambda s \begin{pmatrix} \epsilon \cos\phi \\ -1 \\ -\epsilon \sin\phi \end{pmatrix}, \qquad s \in [0,S],\ \phi \in [0, 2\pi)$$

with half-opening angle

$$\theta_\epsilon = \arctan\epsilon.$$



$$\hat{\boldsymbol{C}}_\epsilon(s) = \mathcal{R}_x(\theta_\epsilon) \cdot \hat{\boldsymbol{C}}(s), \qquad \mathcal{R}_x(\theta_\epsilon) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & \cos\theta_\epsilon & \sin\theta_\epsilon \\ 0 & -\sin\theta_\epsilon & \cos\theta_\epsilon \end{pmatrix}. \tag{19}$$

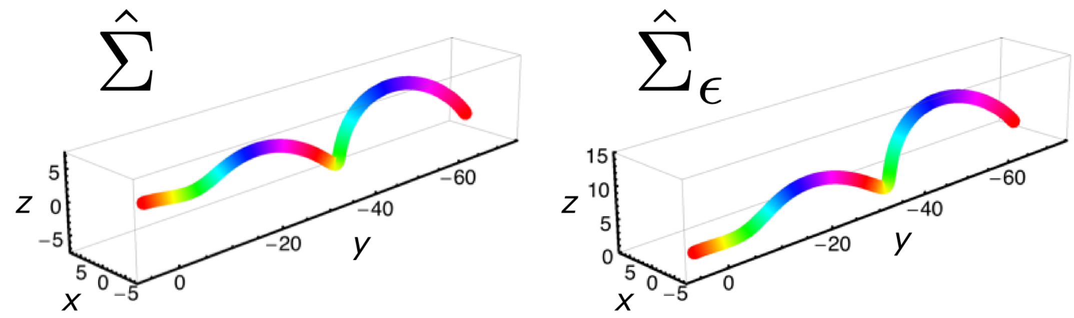
Using $\chi^2 = 1$, the tangent vectors in the body-fixed frame $\hat{\Sigma}$ are found as

$$\begin{aligned} \hat{\boldsymbol{t}}(s) &:= \frac{d\hat{\boldsymbol{C}}(s)/ds}{||d\hat{\boldsymbol{C}}(s)/ds||} \\ &= \frac{1}{\sqrt{1 + (1 + s^2)\,\epsilon^2}} \begin{pmatrix} \epsilon\chi[\cos(s-\phi) - s\sin(s-\phi)] \\ -1 \\ -\epsilon[s\cos(s-\phi) + \sin(s-\phi)] \end{pmatrix}. \end{aligned} \tag{20}$$

and, accordingly, after alignment with the wall in $\hat{\Sigma}_\epsilon$ as

$$\hat{\boldsymbol{t}}_\epsilon(s) = \mathcal{R}_x(\theta_\epsilon) \cdot \hat{\boldsymbol{t}}(s). \tag{21}$$

$$\hat{\mathcal{C}}(s,\phi) = \lambda s \begin{pmatrix} \epsilon\cos\phi \\ -1 \\ -\epsilon\sin\phi \end{pmatrix}, \qquad s\in[0,S],\ \phi\in[0,2\pi)$$



$$\hat{\boldsymbol{C}}_\epsilon(s) = \mathcal{R}_x(\theta_\epsilon)\cdot\hat{\boldsymbol{C}}(s),$$

Due to our chosen parameterisation (16), the tangent vectors point away from the head. The length Λ of the curve $\boldsymbol{C}(s)$ is obtained as

$$\begin{aligned}
\Lambda &= \int_0^S ds \left|\left|\frac{d\hat{\boldsymbol{C}}(s)}{ds}\right|\right| \\
&= \int_0^S ds\,\sqrt{\hat{X}'(s)^2+\hat{Y}'(s)^2+\hat{Z}'(s)^2} \\
&= S\lambda\left[1+\frac{\epsilon^2}{6}(3+S^2)\right]+\mathcal{O}(\epsilon^4). \qquad (22)
\end{aligned}$$

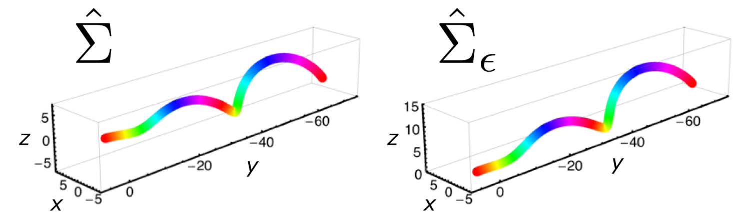
Thus, to leading order, one can identify $\Lambda \simeq S\lambda$ with the length of a flagellum, and $A=\Lambda\epsilon$ with the beat amplitude.

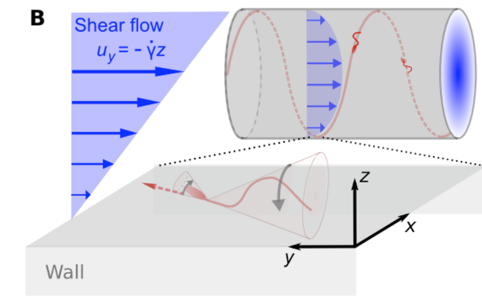
After averaging over all initial conditions ϕ, the mean geometric center of the helix in the body-fixed frame $\hat{\Sigma}_\epsilon$ is found as

$$\begin{aligned}
\hat{\bar{\boldsymbol{C}}}_\epsilon &:= \frac{1}{2\pi}\int_0^{2\pi} d\phi\left[\frac{1}{\Lambda}\int_0^S ds\left|\left|\frac{d\hat{\boldsymbol{C}}(s)}{ds}\right|\right|\,\hat{\boldsymbol{C}}_\epsilon(s)\right] \\
&= \frac{S\lambda}{2}\begin{pmatrix}0\\-1\\\epsilon\end{pmatrix}+\mathcal{O}(\epsilon^2). \qquad (23)
\end{aligned}$$

The orientation $\hat{\boldsymbol{n}}_\epsilon$ in the wall-aligned body-fixed frame $\hat{\Sigma}_\epsilon$ is defined by

$$\hat{\boldsymbol{n}}_\epsilon := -\frac{\hat{\bar{\boldsymbol{C}}}_\epsilon}{||\hat{\bar{\boldsymbol{C}}}_\epsilon||} = \begin{pmatrix}0\\1\\-\epsilon\end{pmatrix}+\mathcal{O}(\epsilon^2), \qquad (24)$$





Let us assume, as before, that the shear fluid flow in the lab frame Σ is along the $\boldsymbol{e}_y$-direction,

$$\boldsymbol{u} = \sigma\dot{\gamma}z\boldsymbol{e}_y, \tag{25}$$

where $\dot{\gamma} > 0$ is the shear rate and $\sigma = \pm 1$ determines the flow direction. Measuring the orientation angle ψ of the swimmer wrt. $\boldsymbol{e}_y$ in counterclockwise direction, we obtain the coordinates $\boldsymbol{C}(t,s)$ of the helix with head position $\boldsymbol{R}(t) = (X(t), Y(t), 0)$ in the lab frame Σ by

$$\boldsymbol{C}(t,s) = \boldsymbol{R}(t) + \mathcal{R}(\psi(t)) \cdot \hat{\boldsymbol{C}}_\epsilon(s), \tag{26}$$

where

$$\mathcal{R}(\psi) = \begin{pmatrix} \cos\psi & -\sin\psi & 0 \\ \sin\psi & \cos\psi & 0 \\ 0 & 0 & 1 \end{pmatrix} \tag{27}$$

represents a rotation about the $\boldsymbol{e}_z$-axis. By applying the rotation matrix $\mathcal{R}(\psi)$ to the orientation vector $\hat{\boldsymbol{n}}_\epsilon$ in $\hat{\Sigma}_\epsilon$, we find that, to leading order in ϵ, the 3D orientation vector $\boldsymbol{n}$ in the lab frame Σ is given by

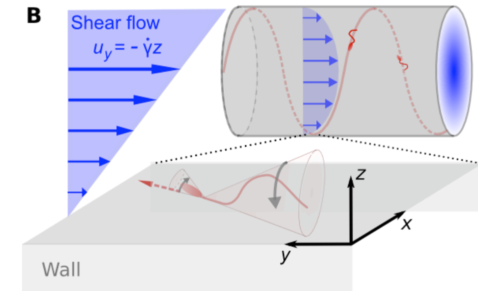
$$\boldsymbol{n} = \begin{pmatrix} \boldsymbol{N} \\ -\epsilon \end{pmatrix} + \mathcal{O}(\epsilon^2), \qquad \boldsymbol{N} = \begin{pmatrix} N_x \\ N_y \end{pmatrix} = \begin{pmatrix} -\sin\psi \\ \cos\psi \end{pmatrix}, \tag{28}$$

where $\boldsymbol{N}$ is the normalised (projected) 2D orientation vector in the (x, y)-plane. This allows us to rewrite the rotation matrix as

$$\mathcal{R}_{\boldsymbol{N}} = \begin{pmatrix} N_y & N_x & 0 \\ -N_x & N_y & 0 \\ 0 & 0 & 1 \end{pmatrix}. \tag{29}$$

Goal: find equation for $\dot{\boldsymbol{R}}(t)$ and $\dot{\boldsymbol{N}}(t)$

Resistive force theory (RFT)



From Eq. (26), the velocity of some point $s \in [0, S]$ on the helix can be decomposed as[1]

$$\dot{\boldsymbol{C}}(s) = \dot{\boldsymbol{R}} + \dot{\mathcal{R}}_{\boldsymbol{N}} \cdot \hat{\boldsymbol{C}}_{\epsilon} = \boldsymbol{U} + \dot{\mathcal{R}}_{\boldsymbol{N}} \cdot \hat{\boldsymbol{C}}_{\epsilon}. \tag{30}$$

Given the shear flow profile $\boldsymbol{u}$, RFT assumes that the force line-density (force per unit length) can be split as

$$\begin{aligned} \boldsymbol{f}(s) \;&=\; \zeta_{||} \left\{ \left[\boldsymbol{u}(\boldsymbol{C}(s)) - \dot{\boldsymbol{C}}(s) \right] \cdot \boldsymbol{t}(s) \right\} \boldsymbol{t}(s) + \\ & \qquad \zeta_{\perp} \left\{ \left[\boldsymbol{u}(\boldsymbol{C}(s)) - \dot{\boldsymbol{C}}(s) \right] \cdot [\boldsymbol{I} - \boldsymbol{t}(s)\boldsymbol{t}(s)] \right\} \end{aligned} \tag{31}$$

where $\zeta_{||}$ and $\zeta_{\perp}$ are tangential and perpendicular drag coefficients. The drag ratio

$$\kappa = \frac{\zeta_{\perp}}{\zeta_{||}}, \tag{32}$$

which equals 2 for rigid rods, takes values $\kappa \simeq 1.4 - 1.7$ for realistic flagella. Combining the RFT ansatz (31) with the zero-force and zero-torque conditions of the over-damped Stokes-regime

$$0 \;=\; F_i = \int_0^S ds \, \left|\left| \frac{d\hat{\boldsymbol{C}}(s)}{ds} \right|\right| f_i(s), \tag{33}$$

$$0 \;=\; \tau_i = \int_0^S ds \, \left|\left| \frac{d\hat{\boldsymbol{C}}(s)}{ds} \right|\right| \epsilon_{ijk}[C_j(s) - X_j^*] f_k(s), \tag{34}$$

Translational motion

$$0 \;=\; F_i = \int_0^S ds \left\| \frac{d\hat{\boldsymbol{C}}(s)}{ds} \right\| f_i(s)$$

$$\begin{aligned} \boldsymbol{f}(s) \;&=\; \zeta_{||} \left\{ \left[\boldsymbol{u}(\boldsymbol{C}(s)) - \dot{\boldsymbol{C}}(s) \right] \cdot \boldsymbol{t}(s) \right\} \boldsymbol{t}(s) + \\ &\quad\; \zeta_{\perp} \left\{ \left[\boldsymbol{u}(\boldsymbol{C}(s)) - \dot{\boldsymbol{C}}(s) \right] \cdot \left[\boldsymbol{I} - \boldsymbol{t}(s)\boldsymbol{t}(s) \right] \right\} \end{aligned}$$

$$\boldsymbol{U} \gg \dot{\mathcal{R}}_{\boldsymbol{N}} \cdot \hat{\boldsymbol{C}} \text{ (translation-dominated regime)}$$

$$\dot{\boldsymbol{C}}(s) = \dot{\boldsymbol{R}} + \dot{\mathcal{R}}_{\boldsymbol{N}} \cdot \hat{\boldsymbol{C}}_{\epsilon} = \boldsymbol{U} + \cancel{\dot{\mathcal{R}}_{\boldsymbol{N}} \cdot} \hat{\boldsymbol{C}}_{\epsilon}$$

To estimate $\boldsymbol{U}$, note that steric interactions between flagellum and channel wall compensate drag forces in vertical directions, so that only the (x, y)-components of the velocity are non-zero. Considering the translation-dominated regime $\boldsymbol{U} \gg \dot{\mathcal{R}}_{\boldsymbol{N}} \cdot \hat{\boldsymbol{C}}$, the zero-force conditions (34) in the (x, y)-directions, $F_1 = 0$ and $F_2 = 0$, can be solved for $\boldsymbol{U} = (U_x, U_y)$. After averaging over ϕ with a uniform angular distribution, we find for $\epsilon \ll 1$ and $\kappa \simeq 1$ to leading order[2]

$$\boldsymbol{U} \simeq \frac{1}{2} \epsilon\, \sigma \dot{\gamma} \lambda S \begin{pmatrix} 0 \\ 1 \end{pmatrix} - \frac{\chi}{3} \epsilon^2 \left(\kappa - 1\right) \sigma \dot{\gamma} \lambda S^2 \begin{pmatrix} 0 \\ N_x N_y \end{pmatrix}, \tag{35}$$

weak chirality dependent advection

$$\boxed{\dot{\boldsymbol{R}} = V\boldsymbol{N} + \boldsymbol{U} = V\boldsymbol{N} + \sigma \dot{\gamma} \epsilon \eta \begin{pmatrix} 0 \\ 1 \end{pmatrix},}$$

Rotational motion

rotation dominated regime, $\boldsymbol{U} \ll \dot{\mathcal{R}}_{\boldsymbol{N}} \cdot \hat{\boldsymbol{C}}$.

$$\dot{\boldsymbol{C}}(s) = \dot{\boldsymbol{R}} + \dot{\mathcal{R}}_{\boldsymbol{N}} \cdot \hat{\boldsymbol{C}}_\epsilon = \cancel{\boldsymbol{U}} + \dot{\mathcal{R}}_{\boldsymbol{N}} \cdot \hat{\boldsymbol{C}}_\epsilon$$

$$0 \;=\; \tau_i = \int_0^S ds \left\| \frac{d\hat{\boldsymbol{C}}(s)}{ds} \right\| \epsilon_{ijk}[C_j(s) - X_j^*] f_k(s).$$

$$\begin{aligned} \boldsymbol{f}(s) \;=\; & \zeta_{||} \left\{ \left[\boldsymbol{u}(\boldsymbol{C}(s)) - \dot{\boldsymbol{C}}(s) \right] \cdot \boldsymbol{t}(s) \right\} \boldsymbol{t}(s) + \\ & \zeta_{\perp} \left\{ \left[\boldsymbol{u}(\boldsymbol{C}(s)) - \dot{\boldsymbol{C}}(s) \right] \cdot [\boldsymbol{I} - \boldsymbol{t}(s)\boldsymbol{t}(s)] \right\} \end{aligned}$$

$$\dot{\psi} = \epsilon\, \dot{\gamma}\sigma \sin\psi + \frac{\chi}{4}\epsilon^2\, \frac{\kappa - 1}{\kappa}\, \dot{\gamma}\sigma\, S \cos\psi. \tag{38}$$

Recalling that $\boldsymbol{N} = (N_x, N_y) = (-\sin\psi, \cos\psi)$, this can be rewritten as

$$\dot{\boldsymbol{N}} = \sigma\dot{\gamma}\epsilon \begin{pmatrix} N_x N_y \\ N_y^2 - 1 \end{pmatrix} + \frac{\chi}{4}\epsilon^2\, \frac{\kappa - 1}{\kappa}\, \dot{\gamma}\sigma\, S \begin{pmatrix} N_x^2 - 1 \\ N_x N_y \end{pmatrix}. \tag{39}$$

$$0 = |\dot{\boldsymbol{N}}|^2 = 2(N_x \dot{N}_x + N_y \dot{N}_y).$$

2D minimal chiral model

Resistive force theory

$$
\begin{aligned}
0 &= F_i = \int_0^S ds \left|\left|\frac{d\hat{C}(s)}{ds}\right|\right| f_i(s), \\
0 &= \tau_i = \int_0^S ds \left|\left|\frac{d\hat{C}(s)}{ds}\right|\right| \epsilon_{ijk}[C_j(s) - X_j^*] f_k(s)
\end{aligned}
$$

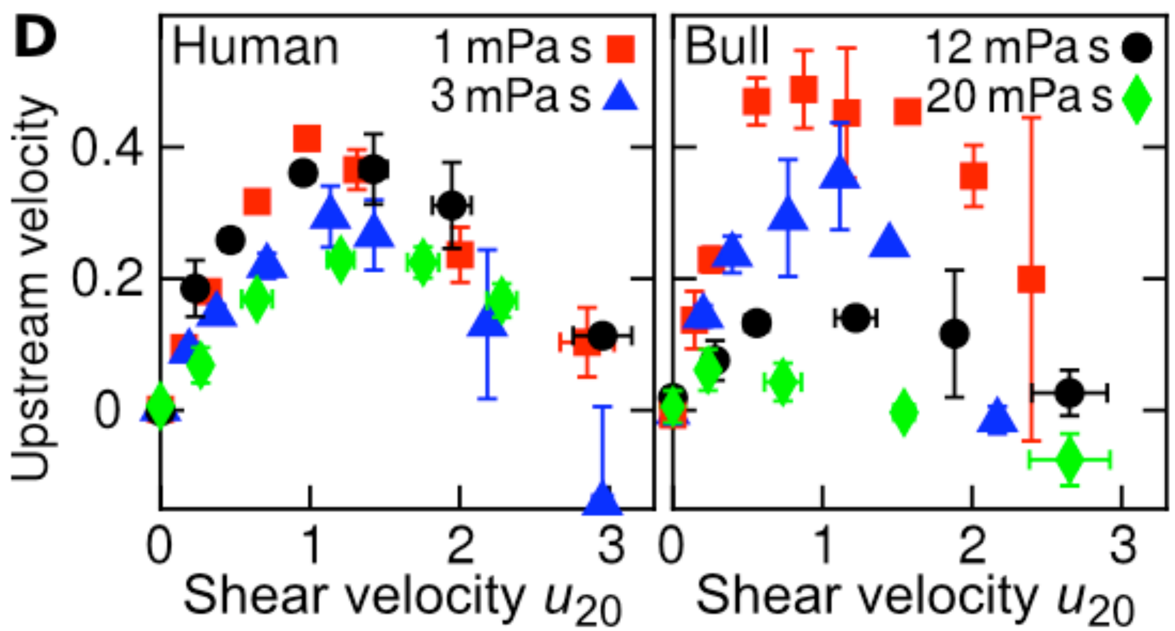
$$
\begin{aligned}
\boldsymbol{f}(s) &= \zeta_{||} \left\{ \left[\boldsymbol{u}(\boldsymbol{C}(s)) - \dot{\boldsymbol{C}}(s) \right] \cdot \boldsymbol{t}(s) \right\} \boldsymbol{t}(s) + \\
&\quad \zeta_{\perp} \left\{ \left[\boldsymbol{u}(\boldsymbol{C}(s)) - \dot{\boldsymbol{C}}(s) \right] \cdot [\boldsymbol{I} - \boldsymbol{t}(s)\boldsymbol{t}(s)] \right\}
\end{aligned}
$$

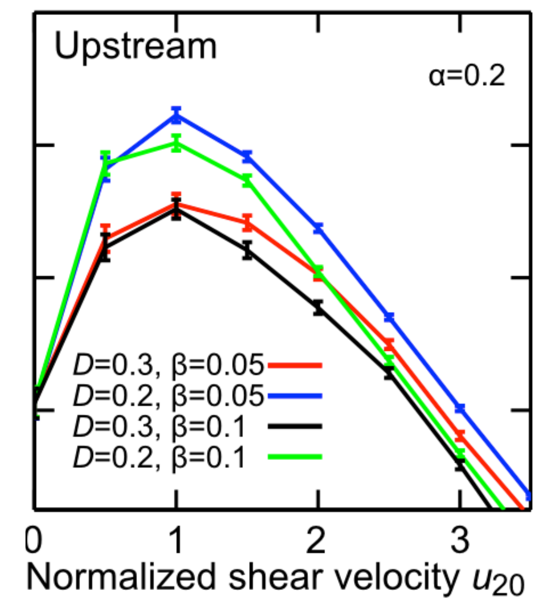
+ some approximations + noise gives to leading order

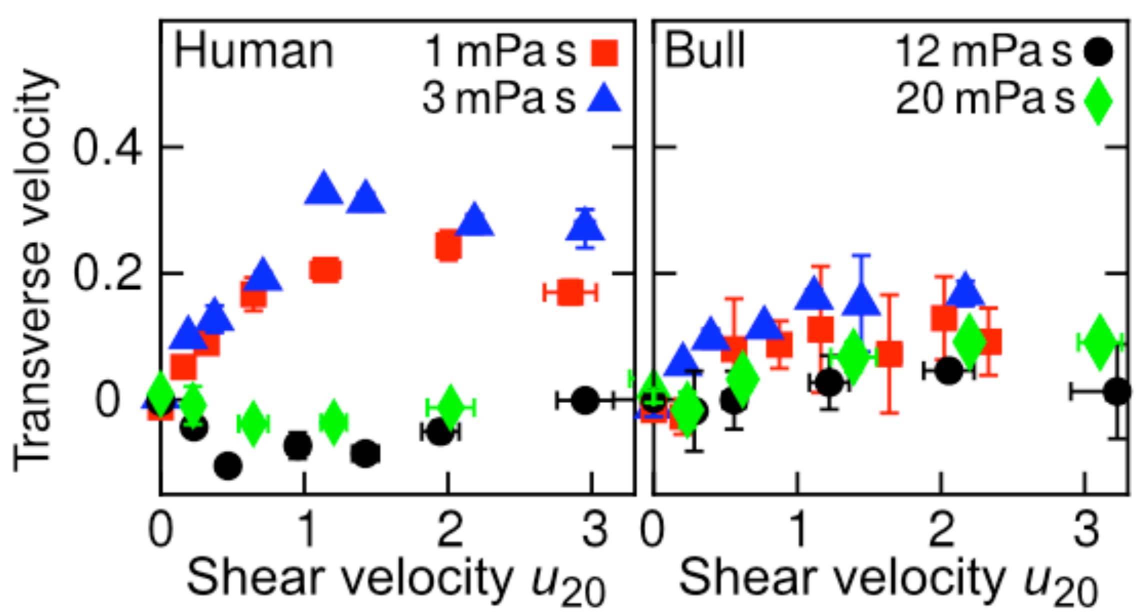
$$
\begin{aligned}
\dot{\boldsymbol{R}} &= V\boldsymbol{N} + \sigma \overline{U} \boldsymbol{e}_y, \\
\dot{\boldsymbol{N}} &= \sigma\dot{\gamma}\alpha \begin{pmatrix} N_x N_y \\ N_y^2 - 1 \end{pmatrix} + \sigma\dot{\gamma}\chi\beta \begin{pmatrix} N_x^2 - 1 \\ N_x N_y \end{pmatrix} + (2D)^{1/2} (\boldsymbol{I}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

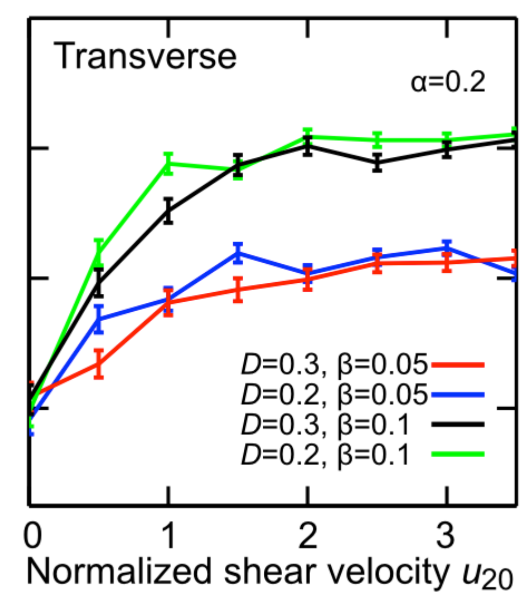
Kantsler et al 2014 (elife)

experiment *vs* theory

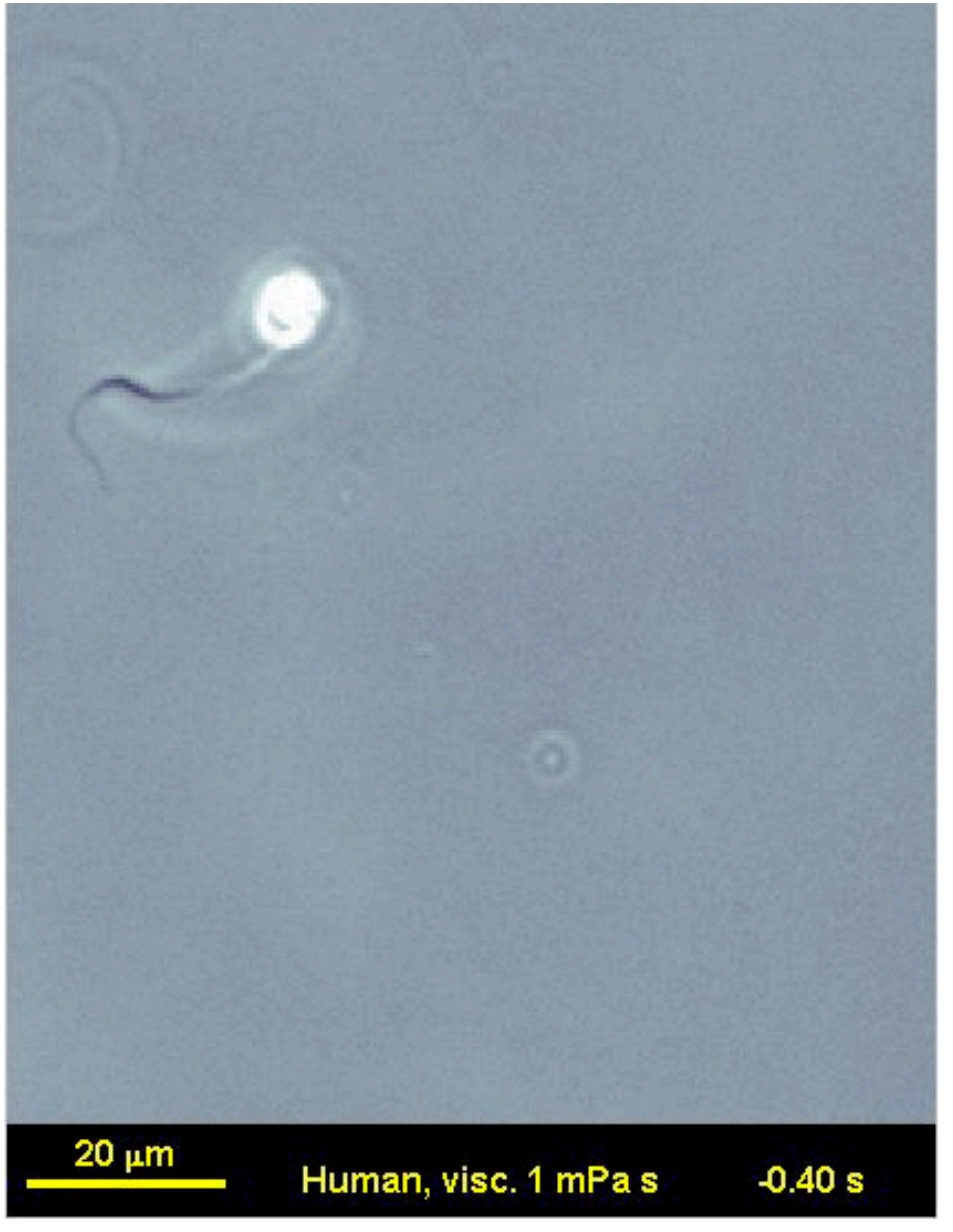






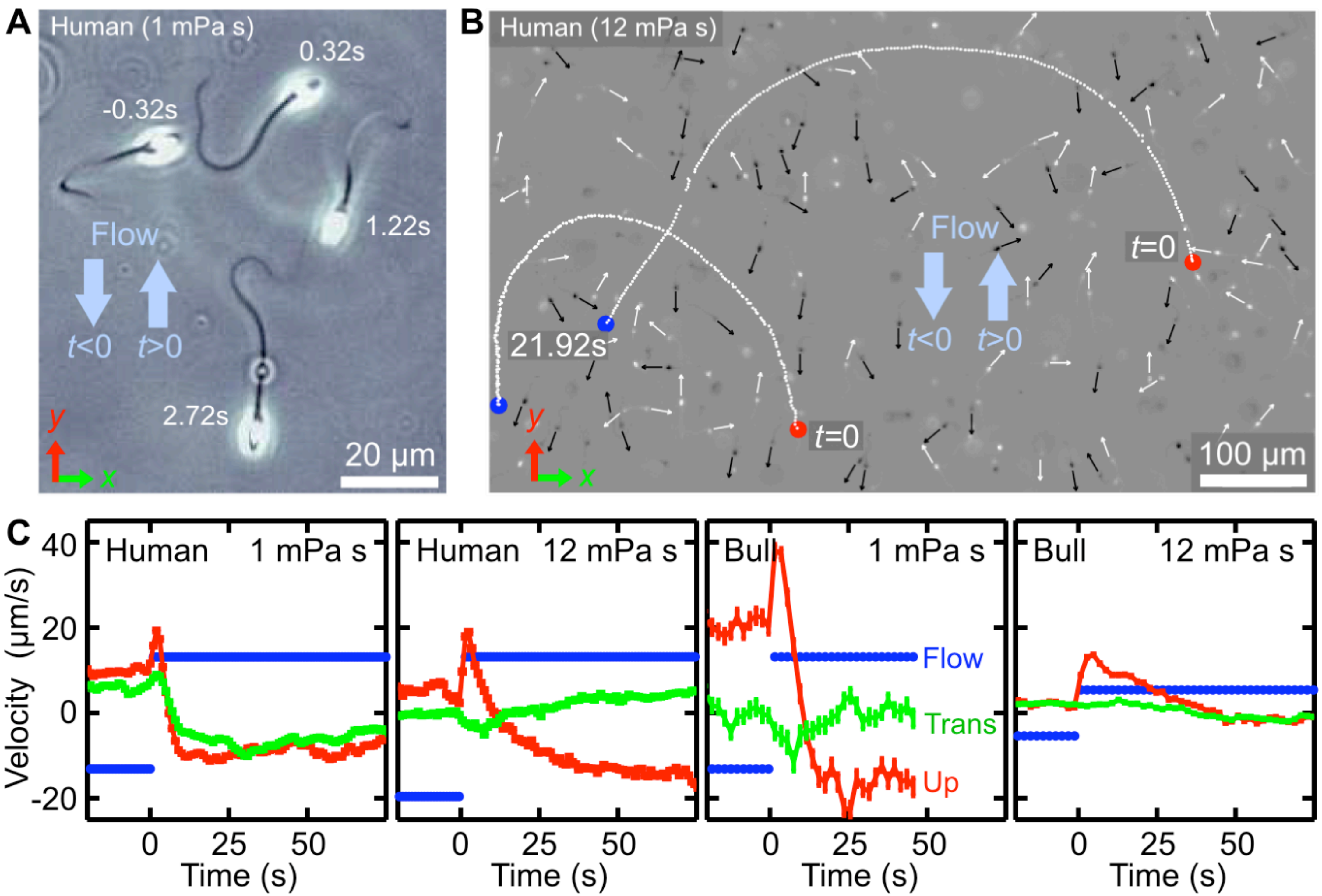


Switch: low viscosity



Switch: high viscosity

Flow switch



A
Human (1 mPa s)
0.32s
-0.32s
1.22s
2.72s
Flow
t<0
t>0
y
x
20 μm
B
Human (12 mPa s)
21.92s
t=0
t=0
Flow
t<0
t>0
100 μm
C
Human 1 mPa s
Human 12 mPa s
Bull 1 mPa s
Bull 12 mPa s
Velocity (μm/s)
40
20
0
-20
0 25 50
Time (s)
Flow
Trans
Up

experiment *vs* theory