Dilute bacterial suspensions

18.S995 - L06 & 07

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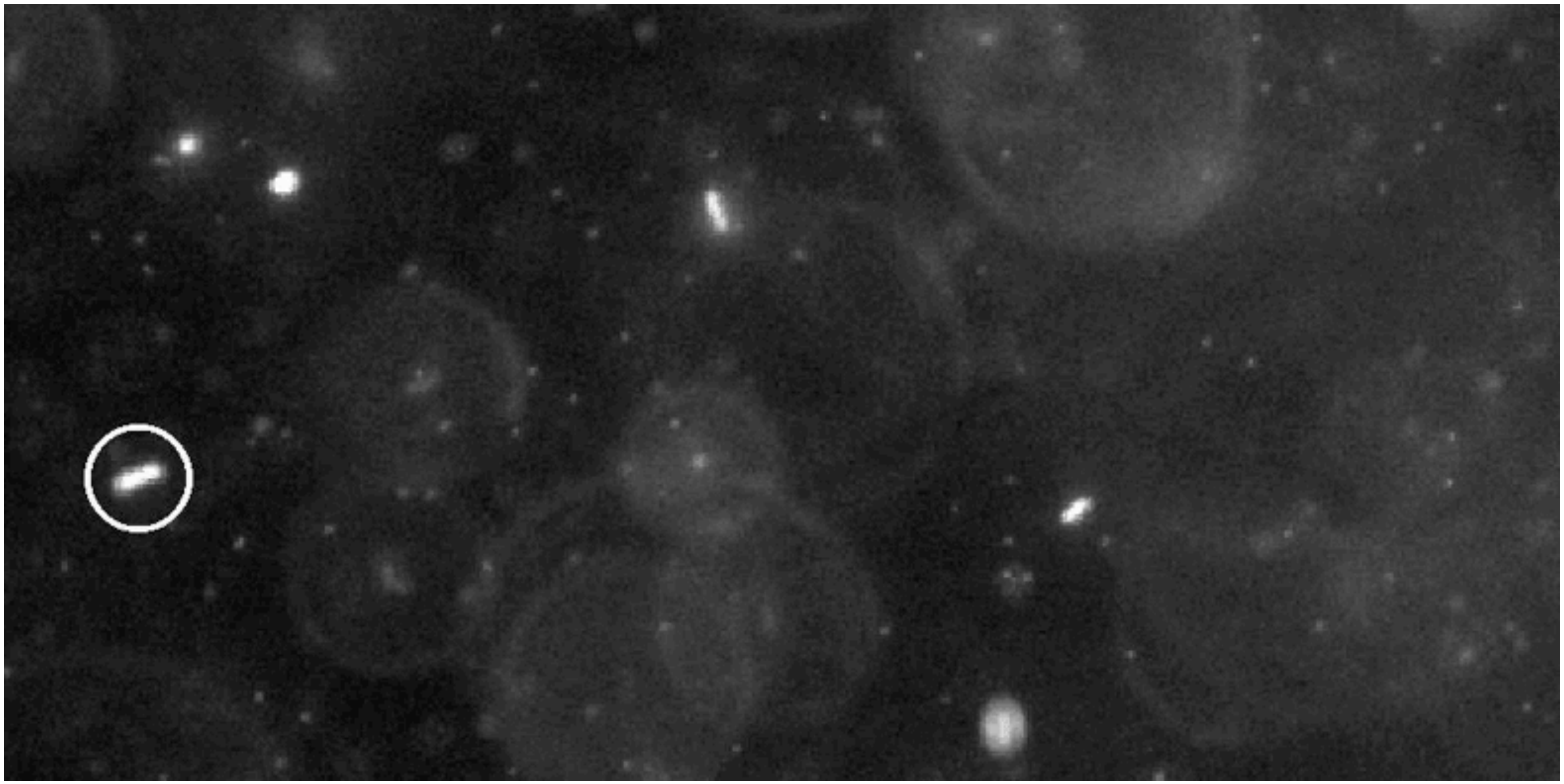
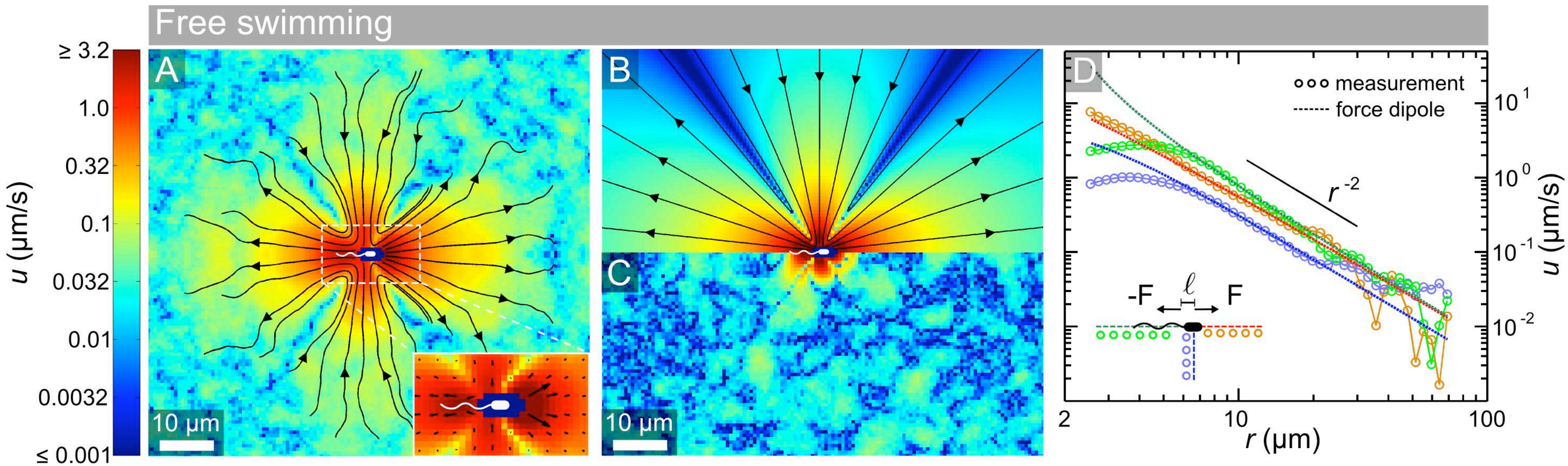
E.coli (non-tumbling HCB 437)



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

E.coli (non-tumbling HCB 437)



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

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

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

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

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

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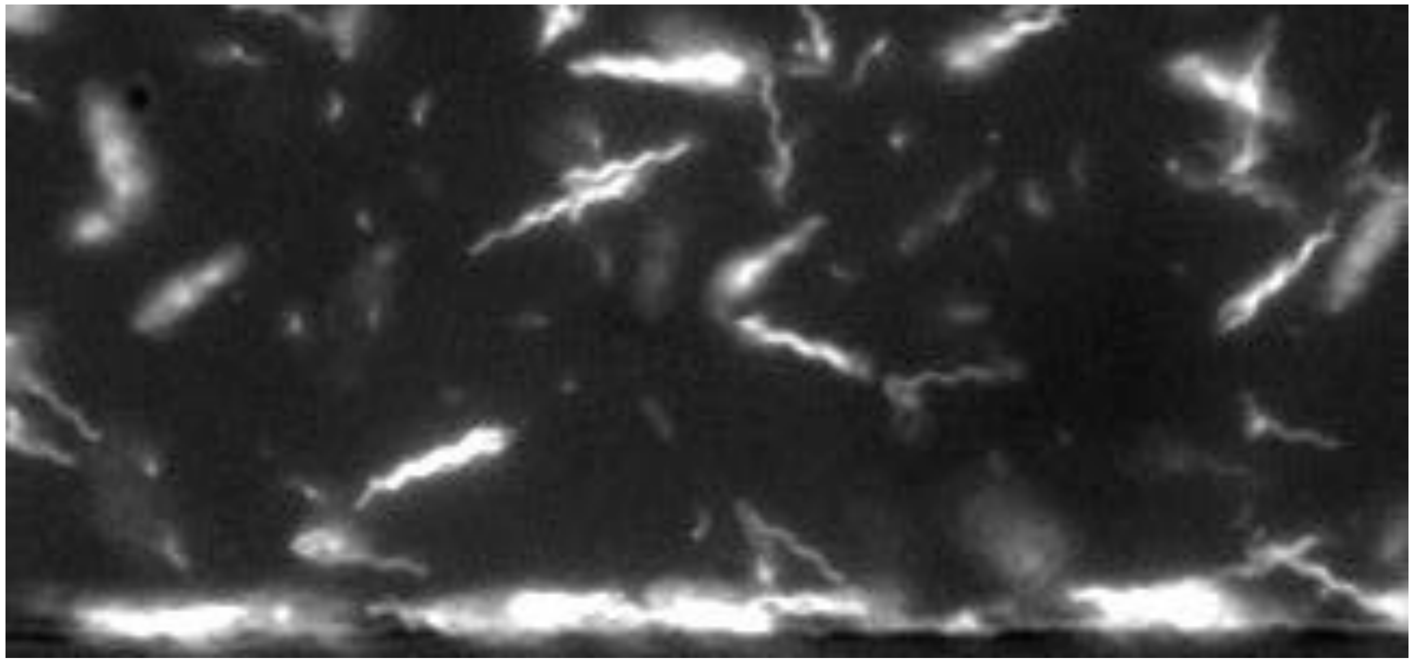
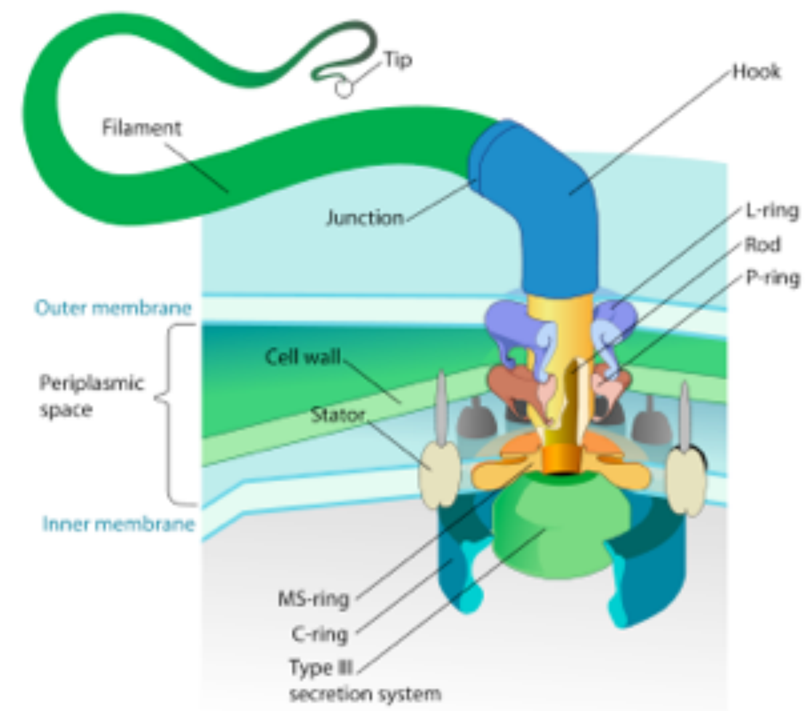
Bacterial run & tumble motion

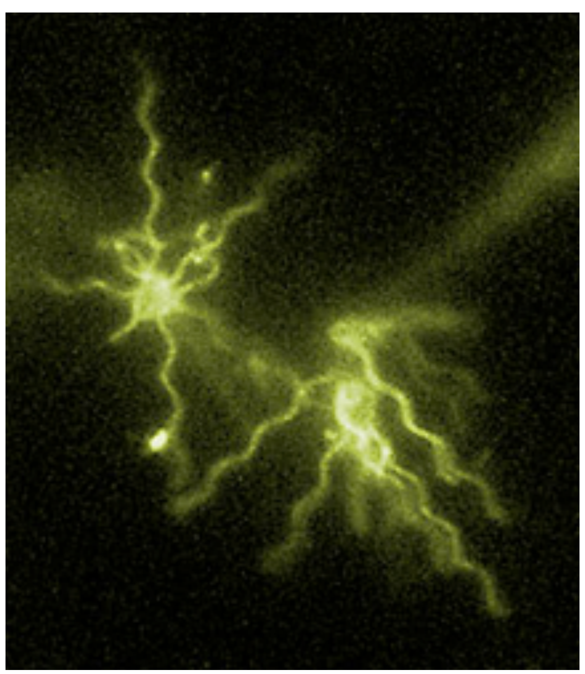
movie: V. Kantsler



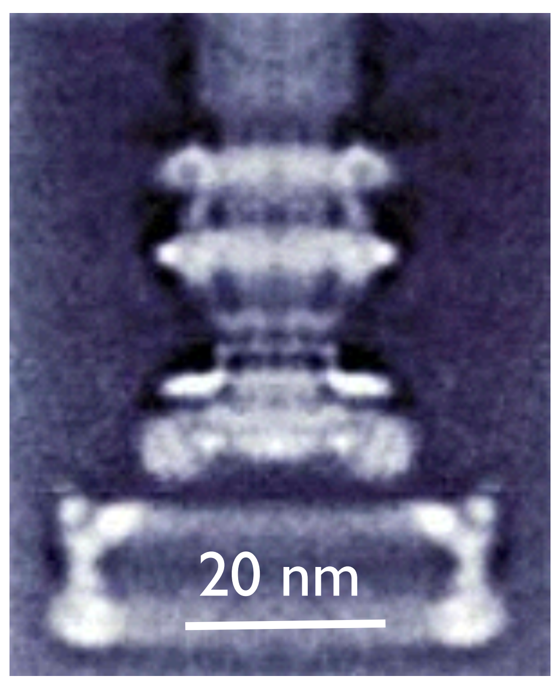
~20 parts



source: wiki

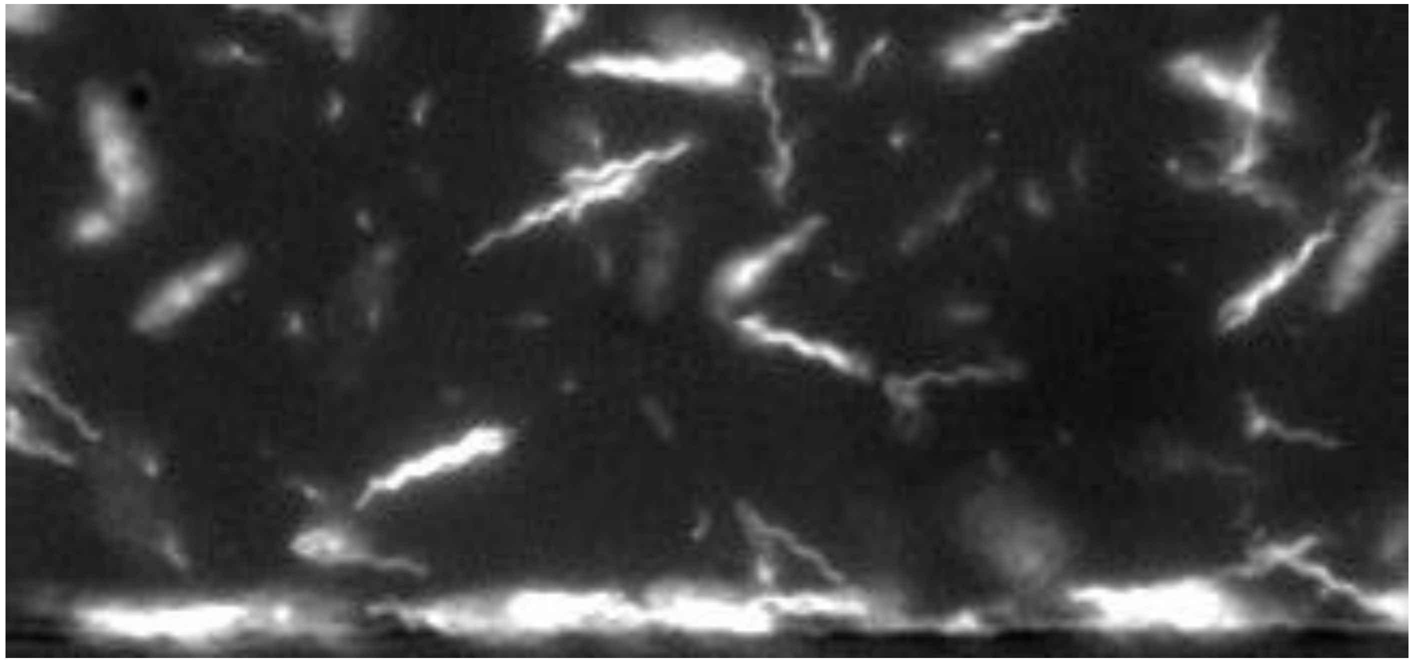


Berg (1999) Physics Today



Chen et al (2011) EMBO Journal

Bacterial run & tumble motion



movie: V. Kantsler

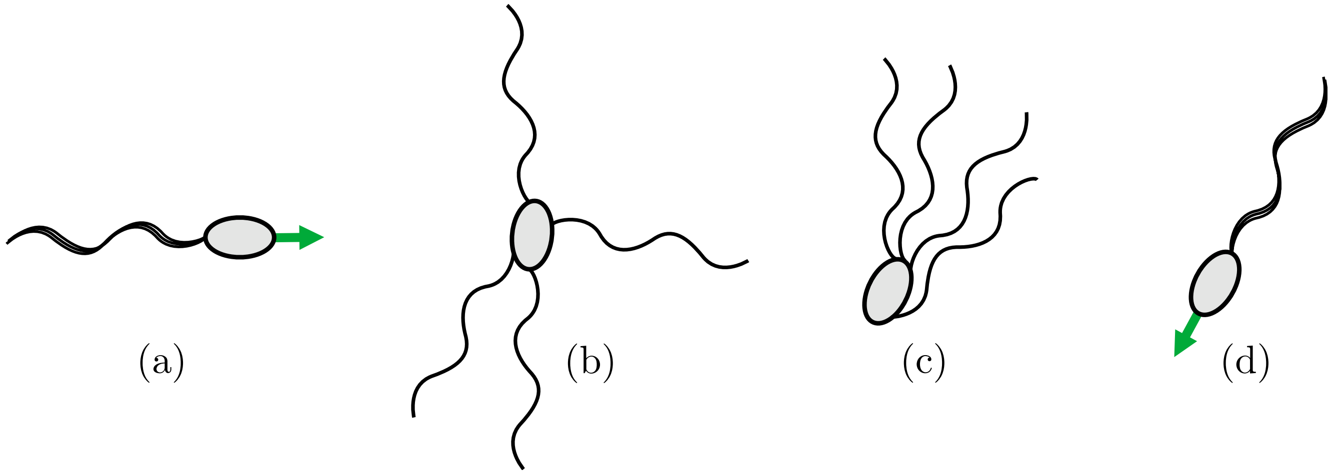


Figure 15. Bundling of bacterial flagella. During swimming, the bacterial flagella are gathered in a tight bundle behind the cell as it moves through the fluid ((*a*) and (*d*)). During a tumbling event, the flagella come out the bundle (*b*), resulting in a random reorientation of the cell before the next swimming event. At the conclusion of the tumbling event, hydrodynamic interactions lead to the relative attraction of the flagella (*c*), and their synchronization to form a perfect bundle (*d*).

for more movies, see also

Howard C. Berg, PI
Bacterial motility and behavior

http://www.rowland.harvard.edu/labs/bacteria/movies/index.php

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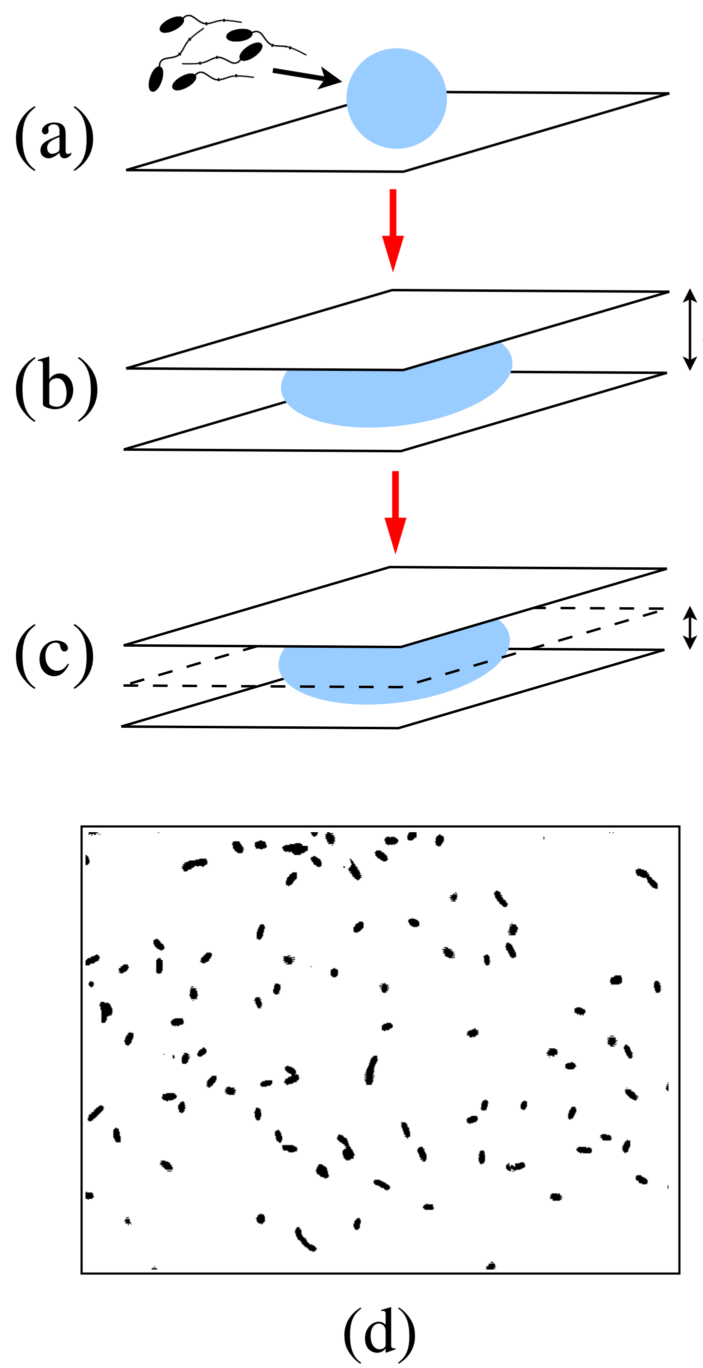
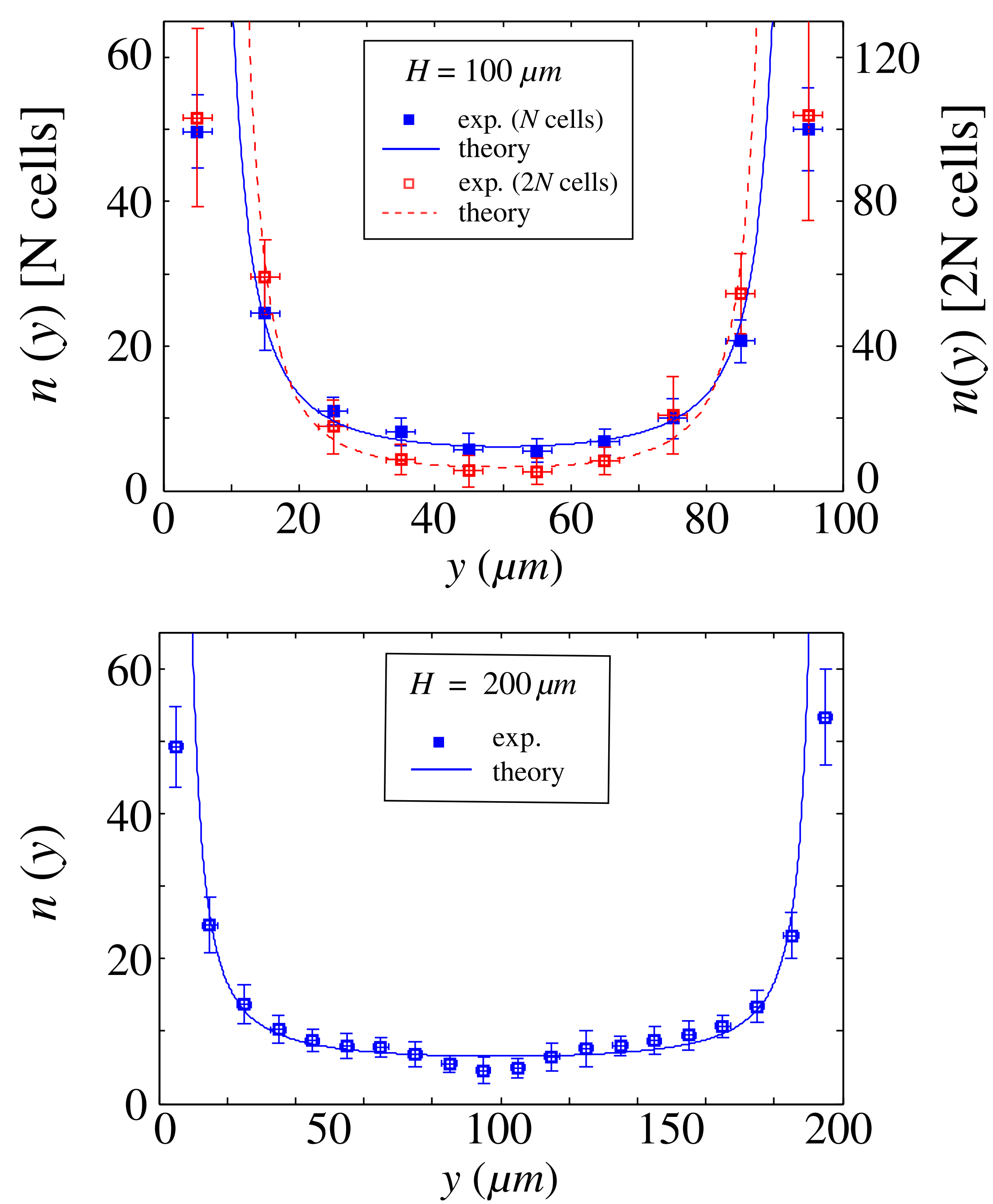
Hydrodynamic Attraction of Swimming Microorganisms by Surfaces

Allison P. Berke,[1] Linda Turner,[2] Howard C. Berg,[2,3] and Eric Lauga[4,*]





Goals

- minimal SDE model for microbial swimming
- wall accumulation & density profile

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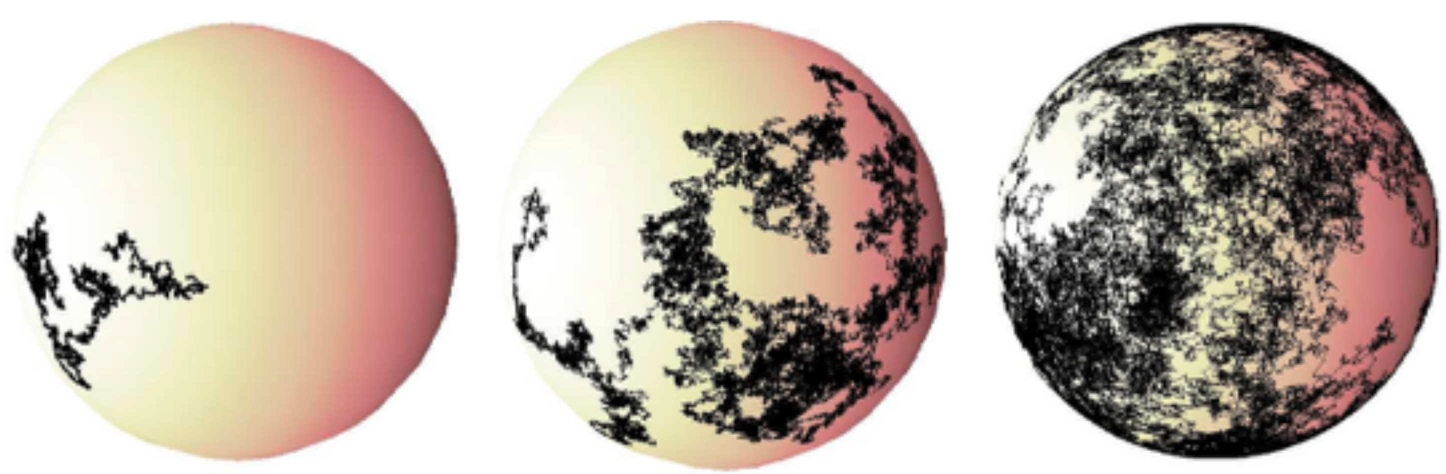
1.3 Dilute microbial suspensions

A minimalist model for the locomotion of an isolated microorganism (e.g., alga or bacterium) with position $\boldsymbol{X}(t)$ and orientation unit vector $\boldsymbol{N}(t)$ is given by the coupled system of Ito SDEs

$$
\begin{aligned}
d\boldsymbol{X} &= V\boldsymbol{N}dt + \sqrt{2D_T} * d\boldsymbol{B}(t), && (1.45a)\\
d\boldsymbol{N} &= (1-d)D_R\boldsymbol{N}\,dt + \sqrt{2D_R}\,(\boldsymbol{I} - \boldsymbol{N}\boldsymbol{N}) * d\boldsymbol{W}(t). && (1.45b)
\end{aligned}
$$

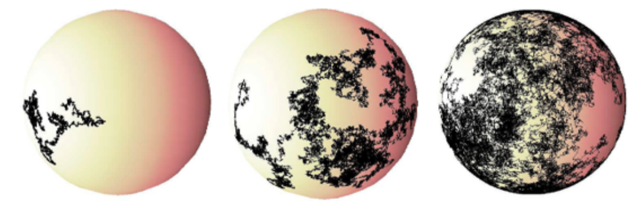
To confirm that Eq. (1.45b) conserves the unit length of the orientation vector, $|\boldsymbol{N}|^2 = 1$ for all t, it is convenient to rewrite Eqs. (1.45) in component form:

$$
\begin{aligned}
dX_i &= VN_i dt + \sqrt{2D_T} * dB_i(t), && (1.46a)\\
dN_j &= (1-d)D_R\,N_j dt + \sqrt{2D_R}\,(\delta_{jk} - N_jN_k) * dW_k(t). && (1.46b)
\end{aligned}
$$



http://www.ploscompbiol.org/article/info%3Adoi%2F10.1371%2Fjournal.pcbi.0020044

BM on the unit sphere



$$dN_j \;=\; (1-d)D_R\, N_j dt + \sqrt{2D_R}\,(\delta_{jk} - N_j N_k) * dW_k(t).$$

For the constraint $|\boldsymbol{N}|^2 = 1$ to be satisfied, we must have $d|\boldsymbol{N}|^2 = 0$. Applying the d-dimensional version of Ito's formula, see Eq. (A.12), to $F(\boldsymbol{N}) = |\boldsymbol{N}|^2$, one finds indeed that

$$\begin{aligned} d|\boldsymbol{N}|^2 &= 2N_j * dN_j + \left(\partial_{N_i}\partial_{N_j} N_k N_k\right)\; D_R(\delta_{ij} - N_i N_j)\, dt \\ &= 2N_j * \left[(1-d)D_R\, N_j\, dt + \sqrt{2D_R}\,(\delta_{jk} - N_j N_k) * dW_k(t)\right] + \\ &\quad\; \partial_{N_i}(\delta_{jk} N_k + N_k \delta_{jk})\; D_R(\delta_{ij} - N_i N_j)\, dt \\ &= 2(1-d)D_R\, dt + \\ &\quad\; (\delta_{jk}\delta_{ik} + \delta_{ik}\delta_{jk})\; D_R(\delta_{ij} - N_i N_j)\, dt \\ &= 0. \end{aligned} \tag{1.47}$$

Orientation correlations

To understand the dynamics (1.46), it is useful to compute the orientation correlation,

$$\langle \boldsymbol{N}(t) \cdot \boldsymbol{N}(0) \rangle = \mathbb{E}[\boldsymbol{N}(t) \cdot \boldsymbol{N}(0)] = \mathbb{E}[N_z(t)], \tag{1.48}$$

where we have assumed (w.l.o.g.) that $\boldsymbol{N}(0) = \boldsymbol{e}_z$. Averaging Eq. (1.46b), we find that

$$\frac{d}{dt}\mathbb{E}[N_z(t)] = (1-d)D_R\,\mathbb{E}[N_z(t)], \tag{1.49}$$

implying that, in this model, the memory loss about the orientation is exponential

$$\langle \boldsymbol{N}(t) \cdot \boldsymbol{N}(0) \rangle = e^{(1-d)D_R t}, \tag{1.50}$$

Mean square displacement

$$\begin{aligned} d|\boldsymbol{X}|^2 &= 2X_j * dX_j + \left(\partial_{X_i}\partial_{X_j} X_k X_k\right)\ D_T \delta_{ij}\, dt \\ &= 2X_j * dX_j + (\delta_{jk}\delta_{ik} + \delta_{ik}\delta_{jk})\ D_T \delta_{ij}\, dt \\ &= 2X_j * dX_j + 2d\, D_T\, dt \\ &= 2X_j[V N_j dt + \sqrt{2D_T} * dB_j(t)] + 2d\, D_T\, dt, \end{aligned} \tag{1.51}$$

averaging and dividing by dt, gives

$$\frac{d}{dt}\mathbb{E}[\boldsymbol{X}^2] = 2V\ \mathbb{E}[\boldsymbol{X}(t)\boldsymbol{N}(t)] + 2d\, D_T. \tag{1.52}$$

The expectation value on the rhs. can be evaluated by making use of Eq. (1.50):

$$\begin{aligned} \mathbb{E}[\boldsymbol{X}(t)\cdot\boldsymbol{N}(t)] &= \mathbb{E}\left[\int_0^t d\boldsymbol{X}(s)\cdot\boldsymbol{N}(t)\right] \\ &= V\,\mathbb{E}\left[\int_0^t ds\ \boldsymbol{N}(s)\cdot\boldsymbol{N}(t)\right] \\ &= V\int_0^t ds\ \langle\boldsymbol{N}(t)\cdot\boldsymbol{N}(s)\rangle \\ &= V\int_0^t ds\ e^{(1-d)D_R(t-s)} \\ &= \frac{V}{(d-1)D_R}\left[1-e^{(1-d)D_R t}\right]. \end{aligned}$$

Mean square displacement

By inserting this expression into Eq. (1.52) and integrating over t, we find

$$\mathbb{E}[\boldsymbol{X}^2] = \frac{2V^2}{(d-1)^2 D_R^2}\left[(d-1)D_R t + e^{(1-d)D_R t} - 1\right] + 2dD_T t. \tag{1.53}$$

If D_T is small, then at short times $t \ll D_R^{-1}$ the motion is ballistic

$$\mathbb{E}[\boldsymbol{X}^2] \simeq V^2 t^2 + 2dD_T t, \tag{1.54}$$

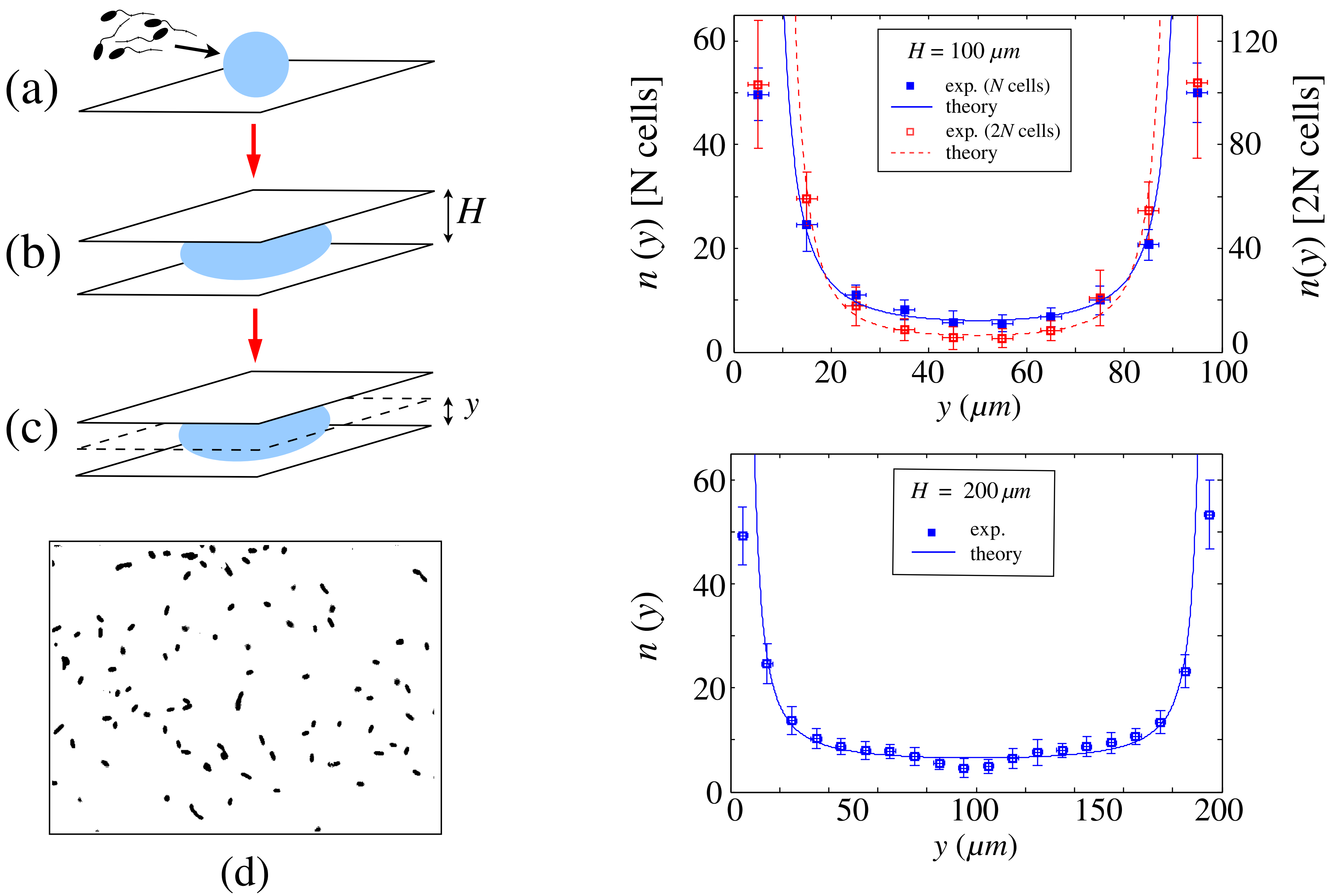
At large times, the motion becomes diffusive, with asymptotic diffusion constant

$$\lim_{t\to\infty} \frac{\mathbb{E}[\boldsymbol{X}^2]}{t} = \frac{2V^2}{(d-1)D_R} + 2dD_T. \tag{1.55}$$

Inserting typical values for bacteria, $V \sim 10\mu\text{m/s}$ and $D_R \sim 0.1/\text{s}$, and comparing with $D_T \sim 0.2\mu\text{m}^2/\text{s}$ for a micron-sized colloids at room temperature, we see that active swimming and orientational diffusion dominate the diffusive dynamics of microorganisms at long times.

Hydrodynamic Attraction of Swimming Microorganisms by Surfaces

Allison P. Berke,[1] Linda Turner,[2] Howard C. Berg,[2,3] and Eric Lauga[4,*]



‘Hydrodynamic’ fields

Concentration profile between two walls An interesting question that is relevant from a medical perspective concerns the spatial distribution of bacteria and other swimming microbes in the presence of confinement. Restricting ourselves to dilute suspensions[10], we may obtain a simple prediction from the model (1.45) by considering the FPE for the associated PDF $p(t, \boldsymbol{x}, \boldsymbol{n})$. Given p and the total number of bacteria N_b in the solutions, we obtain the spatial concentration profile by integrating over all possible orientations

$$c(t, \boldsymbol{x}) = N_b \int_{\mathbb{S}_d} d\boldsymbol{n}\, p(t, \boldsymbol{n}, \boldsymbol{x}). \tag{1.56a}$$

The associated mean orientation field reads

$$\boldsymbol{u}(t, \boldsymbol{x}) = N_b \int_{\mathbb{S}_d} d\boldsymbol{n}\, p(t, \boldsymbol{n}, \boldsymbol{x})\, \boldsymbol{n}. \tag{1.56b}$$

The FPE for the Ito-SDE (1.45) can be written as a conservation law

$$\partial_t p \quad = \quad -(\partial_{x_i} J_i + \partial_{n_i} \Omega_i), \tag{1.57a}$$

where

$$J_i \quad = \quad (V n_i - D_T \partial_{x_i}) p \tag{1.57b}$$

$$\Omega_i \quad = \quad D_R \left\{ (1-d) n_i p - \partial_{n_j} [(\delta_{ij} - n_i n_j) p] \right\}. \tag{1.57c}$$

Concentration field

The FPE for the Ito-SDE (1.45) can be written as a conservation law

$$\partial_t p \quad = \quad -(\partial_{x_i} J_i + \partial_{n_i} \Omega_i), \tag{1.57a}$$

where

$$\begin{aligned} J_i &= (V n_i - D_T \partial_{x_i}) p & (1.57b) \\ \Omega_i &= D_R \left\{ (1-d) n_i p - \partial_{n_j} [(\delta_{ij} - n_i n_j) p] \right\}. & (1.57c) \end{aligned}$$

Focusing on the three-dimensional case, $d = 3$, we are interested in deriving from Eq. (1.57) the stationary concentration profile c of a suspension that is confined by two quasi-infinite parallel walls, which are located $z = \pm H$. That is, we assume that the distance between the walls is much smaller then their spatial extent in the (x, y)-directions, $2H \ll L_x, L_y$. To obtain an evolution equation for c, we multiply Eq. (1.57a) by N_b and integrate over $\boldsymbol{n}$ with

$$\int_{\mathbb{S}_d} d\boldsymbol{n}\, \partial_{n_i} \Omega_i = 0. \tag{1.58}$$

This yields the mass conservation law

$$\partial_t c \quad = \quad -\nabla \cdot (V \boldsymbol{u} - D_T \nabla c). \tag{1.59}$$

Orientation (velocity) field

The FPE for the Ito-SDE (1.45) can be written as a conservation law

$$\partial_t p = -(\partial_{x_i} J_i + \partial_{n_i} \Omega_i), \tag{1.57a}$$

where

$$J_i = (V n_i - D_T \partial_{x_i}) p \tag{1.57b}$$

$$\Omega_i = D_R \left\{ (1-d) n_i p - \partial_{n_j} [(\delta_{ij} - n_i n_j) p] \right\}. \tag{1.57c}$$

To obtain also an evolution equation for $\boldsymbol{u}$, we multiply Eq. (1.57a) by n_k,

$$\partial_t (n_k p) = -\partial_{x_i} (n_k J_i) - n_k \partial_{n_i} \Omega_i. \tag{1.60}$$

and note that

$$n_k \partial_{n_i} \Omega_i = \partial_{n_i} (n_k \Omega_i) - (\partial_{n_i} n_k) \Omega_i = \partial_{n_i} (n_k \Omega_i) - \delta_{ik} \Omega_i. \tag{1.61}$$

Orientation (velocity) field

To obtain also an evolution equation for $\boldsymbol{u}$, we multiply Eq. (1.57a) by n_k,

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and note that

$$n_k \partial_{n_i} \Omega_i = \partial_{n_i}(n_k \Omega_i) - (\partial_{n_i} n_k)\Omega_i = \partial_{n_i}(n_k \Omega_i) - \delta_{ik}\Omega_i. \tag{1.61}$$

This allows us to rewrite (1.60) as

$$\begin{aligned}
\partial_t(n_k p) &= -\partial_{x_i}(n_k J_i) + \Omega_k - \partial_{n_i}(n_k \Omega_i) \\
&= -\partial_{x_i}[V n_k n_i p - D_T \partial_{x_i}(n_k p)] + \\
&\quad D_R \left\{-2n_k p - \partial_{n_j}[(\delta_{kj} - n_k n_j)p]\right\} - \partial_{n_i}(n_k \Omega_i) \\
&= -\partial_{x_i}[V n_k n_i p - D_T \partial_{x_i}(n_k p)] - 2D_R n_k p - \\
&\quad \partial_{n_j}(n_k \Omega_j + (\delta_{kj} - n_k n_j)p).
\end{aligned} \tag{1.62}$$

Orientation (velocity) field

To obtain also an evolution equation for $\boldsymbol{u}$, we multiply Eq. (1.57a) by n_k,

$$\partial_t(n_k p) \;=\; -\partial_{x_i}(n_k J_i) - n_k \partial_{n_i}\Omega_i. \tag{1.60}$$

and note that

$$n_k \partial_{n_i}\Omega_i = \partial_{n_i}(n_k\Omega_i) - (\partial_{n_i} n_k)\Omega_i = \partial_{n_i}(n_k\Omega_i) - \delta_{ik}\Omega_i. \tag{1.61}$$

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&\quad D_R\left\{-2n_k p - \partial_{n_j}[(\delta_{kj} - n_k n_j)p]\right\} - \partial_{n_i}(n_k\Omega_i) \\
&= -\partial_{x_i}[V n_k n_i p - D_T \partial_{x_i}(n_k p)] - 2D_R n_k p - \\
&\quad \partial_{n_j}(n_k\Omega_j + (\delta_{kj} - n_k n_j)p).
\end{aligned} \tag{1.62}$$

Multiplying by N_b and integrating over $\boldsymbol{n}$ with appropriate boundary conditions gives

$$\partial_t u_k \;=\; -\partial_{x_i}[V N_b \langle n_k n_i\rangle p - D_T \partial_{x_i} u_k] - 2D_R u_k,$$

where we have abbreviated

$$\langle n_i n_k \cdots\rangle = \int_{\mathbb{S}_d} d\boldsymbol{n}\; p(t,\boldsymbol{n},\boldsymbol{x})\, n_i n_k \cdots\,. \tag{1.63}$$

To obtain a closed linear system of equations for the fields $(c, \boldsymbol{u})$, we neglect[11] the higher-order moments $N_b\langle n_k n_i\rangle$ in (1.63) and find

$$\partial_t \boldsymbol{u} \;\simeq\; -2D_R\boldsymbol{u} + D_T\nabla^2\boldsymbol{u}. \tag{1.64}$$

Stationary profiles

$$\partial_t \boldsymbol{u} \simeq -2D_R\boldsymbol{u} + D_T\nabla^2\boldsymbol{u}. \tag{1.64}$$

To find the stationary density and orientation profiles, we look for solutions of the form $c = \rho(z)$ and $u_x = u_y = 0, u_z = u(z)$. According to Eqs. (1.59) to (1.63), the functions ρ and u_z must satisfy

$$0 = Vu - D_Tc', \tag{1.65}$$

$$0 = -2D_Ru + D_Tu'', \tag{1.66}$$

and it is physically plausible that they also fulfill the symmetry[12] requirements $\rho(z) = \rho(-z)$ and $u(z) = -u(-z)$. Hence, solution takes the form

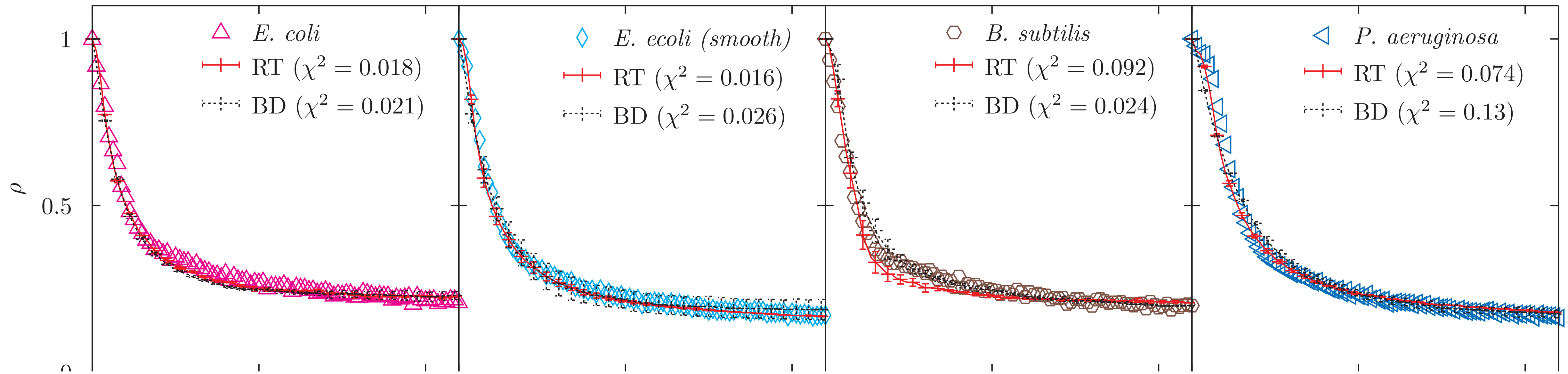
$$u(z) = A\sinh(z/\Lambda), \tag{1.67a}$$

$$\rho(z) = A\frac{V\Lambda}{D_T}[\cosh(z/\Lambda) - 1] + \rho_0, \tag{1.67b}$$

where $\Lambda = \sqrt{D_\perp/(2D_R)}$.

The cosh-profile (1.67b) agrees qualitatively with experimental measurements for dilute bacterial suspensions [BTBL08, LT09].

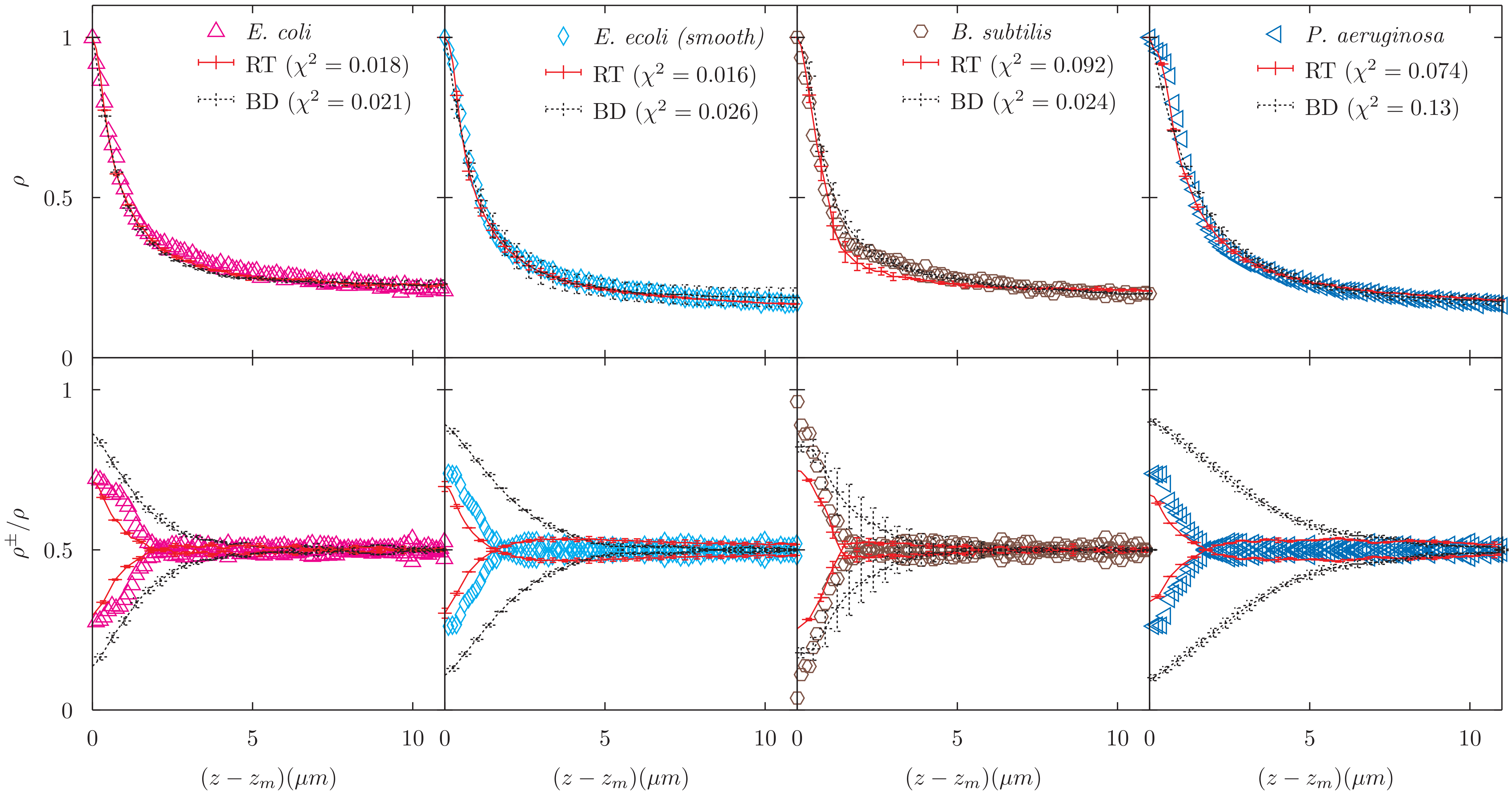
But …



Density profiles seem ok … what about fluxes?

joint work with Peter Lu, Rik Wensink & Jeff Guasto

But …



E. coli
RT ($\chi^2 = 0.018$)
BD ($\chi^2 = 0.021$)
E. ecoli (smooth)
RT ($\chi^2 = 0.016$)
BD ($\chi^2 = 0.026$)
B. subtilis
RT ($\chi^2 = 0.092$)
BD ($\chi^2 = 0.024$)
P. aeruginosa
RT ($\chi^2 = 0.074$)
BD ($\chi^2 = 0.13$)
ρ
$\rho^{\pm}/\rho$
1
0.5
0
0
5
10
$(z - z_m)(\mu m)$

Need to include run & tumbling

BD:

$$\delta \mathbf{r} = \mathbf{D_T} \cdot \mathbf{F}_{bw} \delta t + v_0 \hat{\mathbf{u}} \delta t + \sqrt{2\delta t D_T}\, \delta \mathbf{r}_G$$

$$\delta \hat{\mathbf{u}} = D_R (\mathbf{T}_{bw} \times \hat{\mathbf{u}}) \delta t + \sqrt{2 \delta t D_R}\, \delta \hat{\mathbf{u}}_G$$

(SF-SDE)

$P_T^{-1} = D_T / v_0 \tilde{\ell}$ and $P_R^{-1} = D_R \ell / v_0$

RT:

$$\ell^{-1} \delta \mathbf{r} = \frac{\mathbf{F}_{\mathrm{bw}}}{F_a} \delta \tau$$

$$\delta \hat{\mathbf{u}} = \xi \left(\frac{\mathbf{T}_{\mathrm{bw}}}{F_a \ell} \times \hat{\mathbf{u}} \right) \delta \tau + \left[\left(\hat{\mathbf{u}} \times \frac{\Delta \hat{\mathbf{u}}}{\Delta \tau_{\mathrm{tumble}}} \right) \times \hat{\mathbf{u}} \right] \delta \tau$$

TABLE I: Main bacterial parameters used for the fit.

culture	ℓ (μm)	a (a_{eff})	v_0 $(\mu m/s)$	θ_T	$\Delta t_{\mathrm{tumble}}$ (s)	Δt_{run} (s)
E. coli	~ 3	$\sim 2(5.6)$	~ 20	68°	~ 0.1	~ 1
E. coli (smooth)	~ 3	$\sim 2(5.6)$	~ 20	0°	0	∞
B. subtilis	~ 5	$\sim 6(11.5)$	~ 50	$\sim 40^\circ$	~ 0.1	~ 0.5
P. aeruginosa	~ 2	$\sim 4(9.8)$	~ 40	$\sim 110^\circ$	~ 0.1	~ 0.5

	RT		BD	
	rotation P_R^{-1}	translation P_T^{-1}	rotation P_R^{-1}	translation P_T^{-1}
E. coli	0.04 ± 0.005	0.1 ± 0.01	0.11 ± 0.005	0.31 ± 0.005
E. coli (smooth)	0.02 ± 0.005	0.07 ± 0.005	0.07 ± 0.001	0.34 ± 0.001
B. subtilis	0.14 ± 0.05	0.02 ± 0.005	0.10 ± 0.001	0.09 ± 0.001
P. aeruginosa	0.02 ± 0.005	0.08 ± 0.005	0.04 ± 0.001	0.49 ± 0.005

Need to include run & tumbling