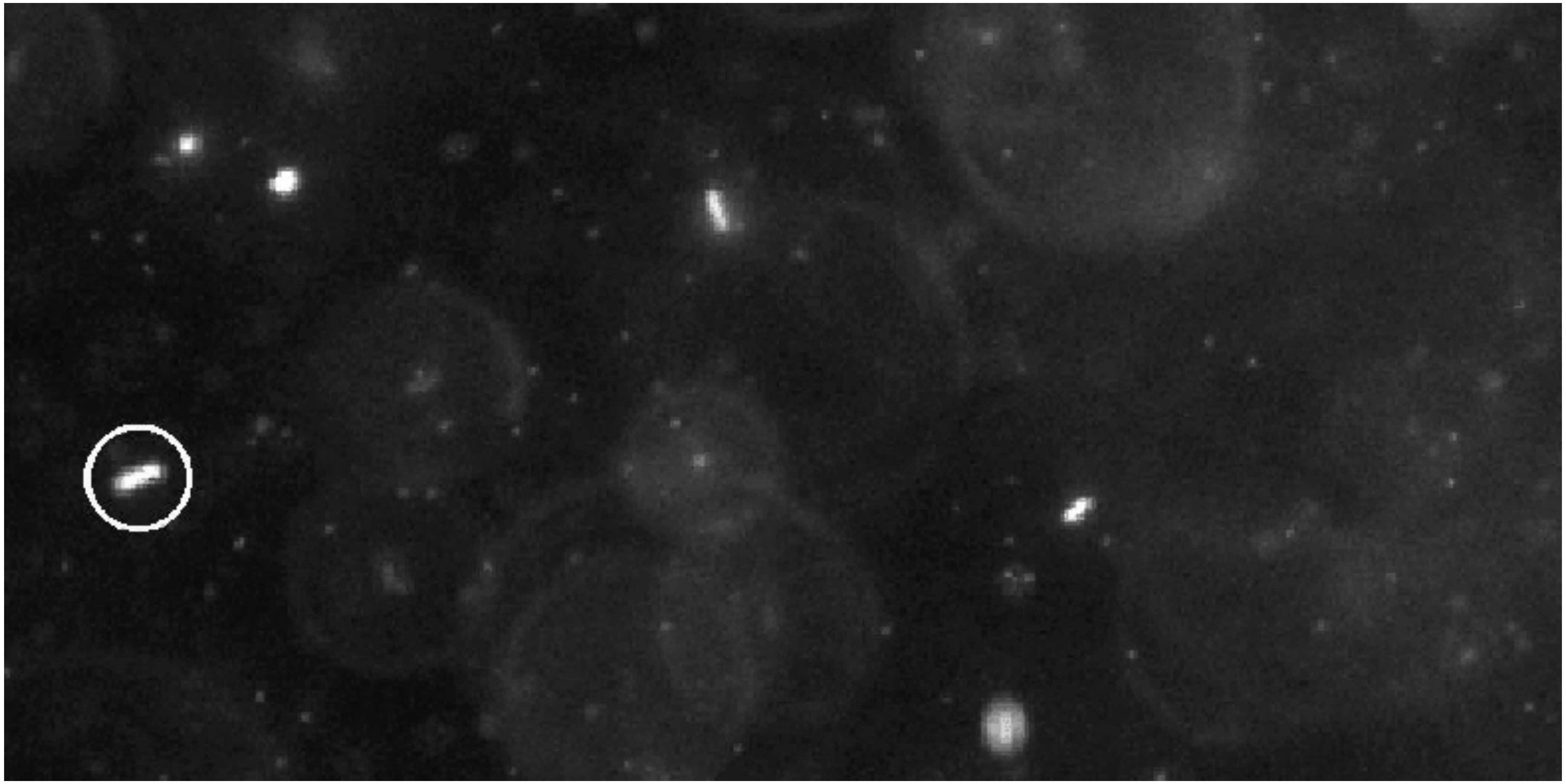
Dilute bacterial suspensions

18.S995 - L06 & 07

dunkel@mit.edu

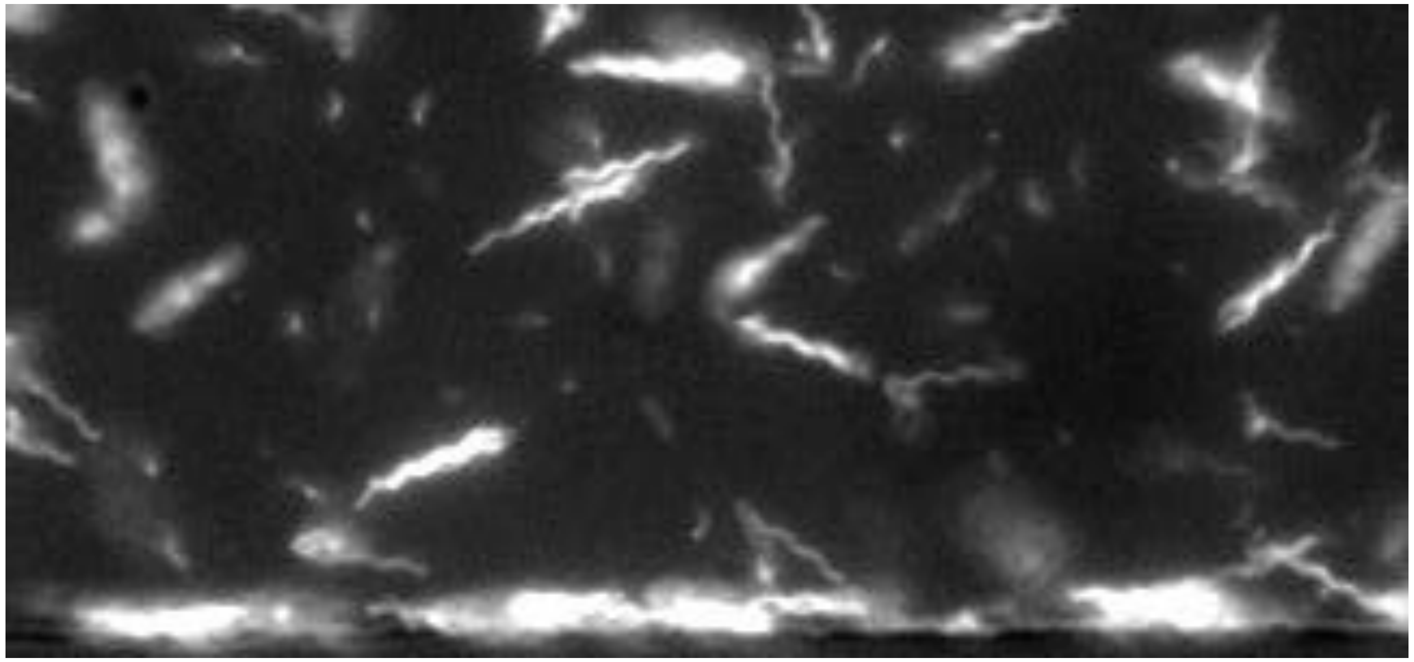
E.coli (non-tumbling HCB 437)



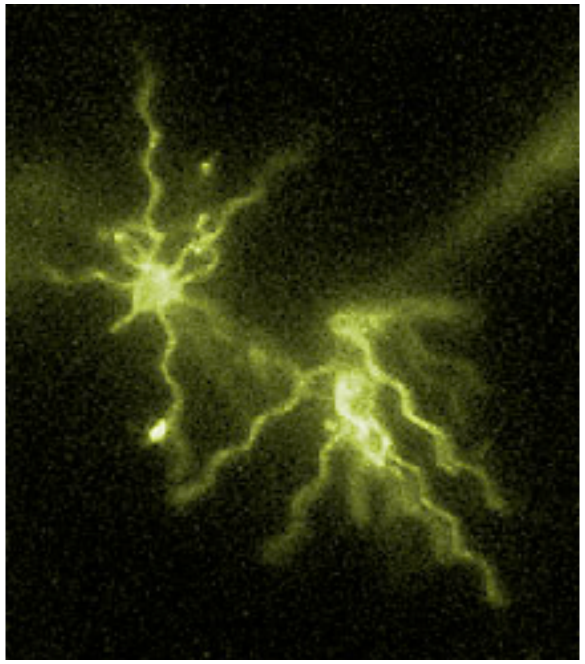
Drescher, Dunkel, Ganguly, Cisneros, Goldstein (2011) PNAS

dunkel@math.mit.edu

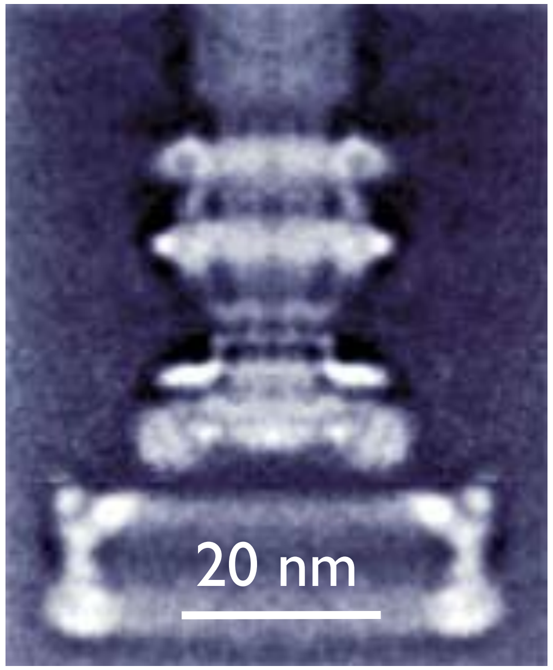
Bacterial run & tumble motion



movie: V. Kantsler

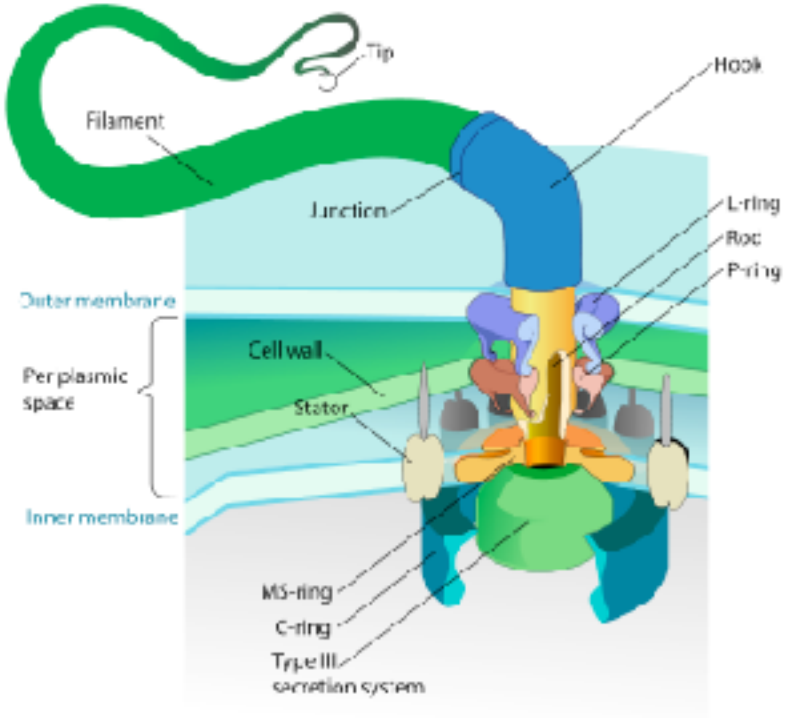


Berg (1999) Physics Today



Chen et al (2011) EMBO Journal

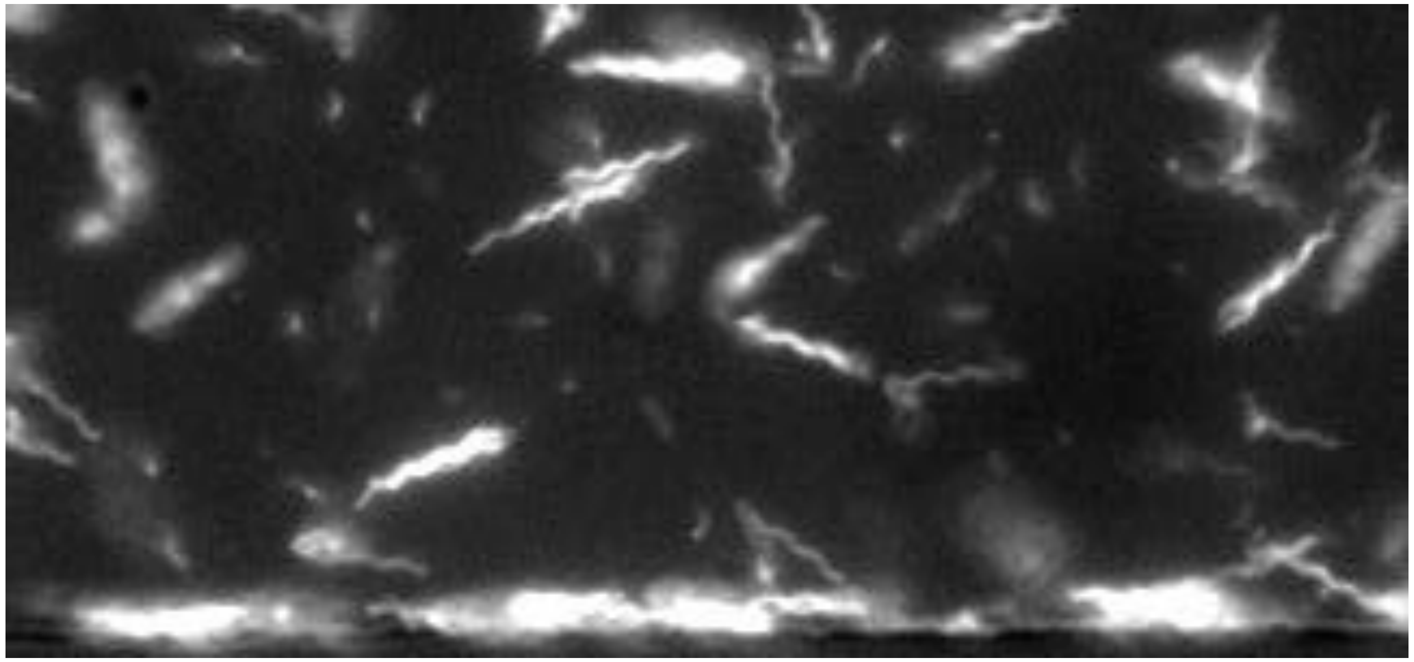
~20 parts



source: wiki

Bacterial run & tumble motion

movie: V. Kantsler



Rep. Prog. Phys. **72** (2009) 096601 E Lauga and T R Powers

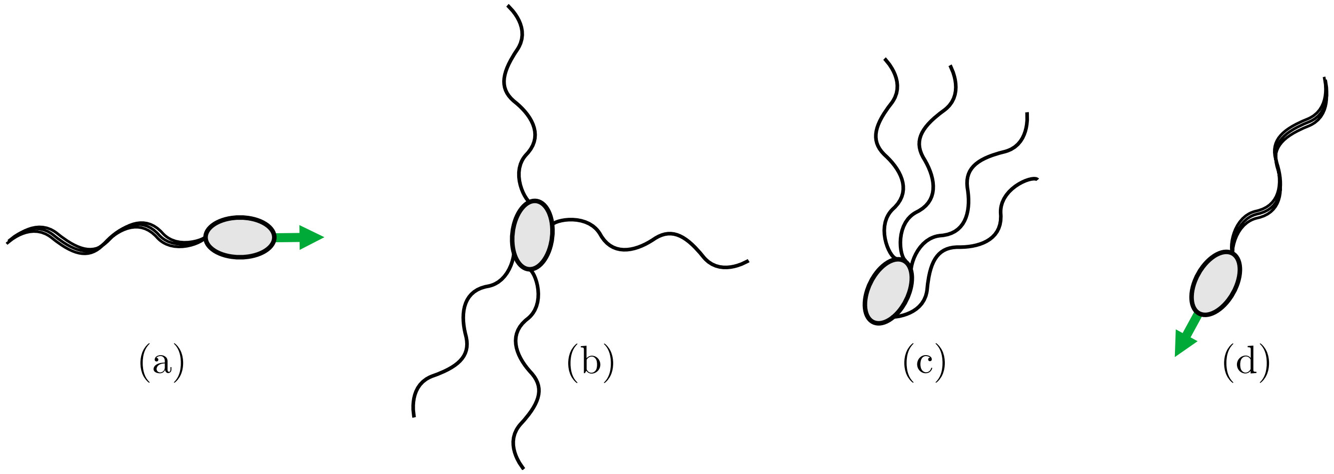


Figure 15. Bundling of bacterial flagella. During swimming, the bacterial flagella are gathered in a tight bundle behind the cell as it moves through the fluid ((*a*) and (*d*)). During a tumbling event, the flagella come out the bundle (*b*), resulting in a random reorientation of the cell before the 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*).

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

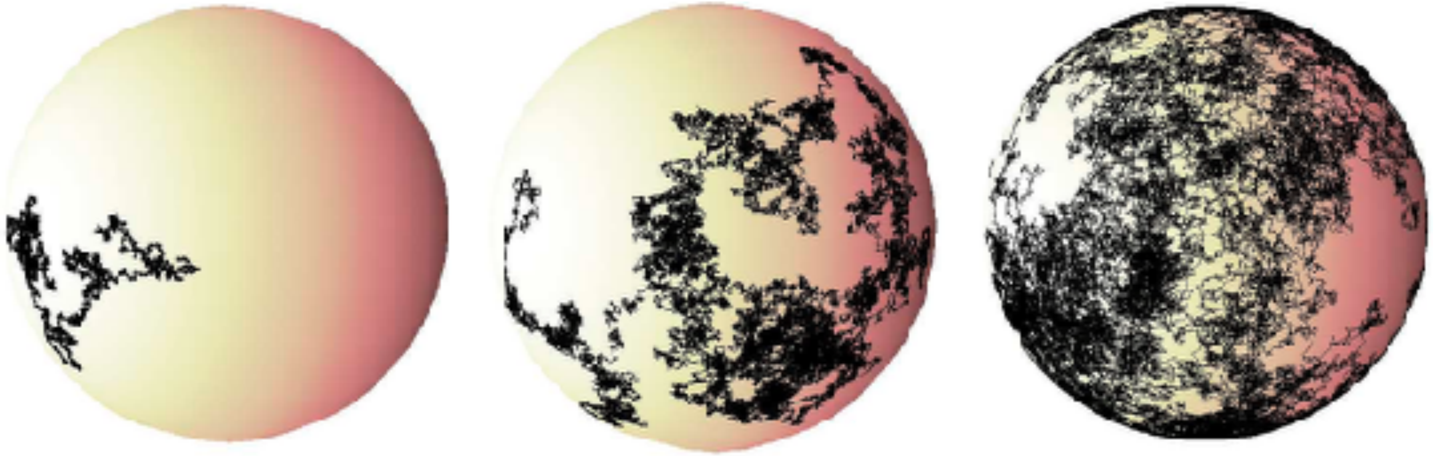
$$d\boldsymbol{X} = V\boldsymbol{N}dt + \sqrt{2D_T} * d\boldsymbol{B}(t), \tag{1.45a}$$

$$d\boldsymbol{N} = (1-d)D_R\boldsymbol{N}\,dt + \sqrt{2D_R}\,(\boldsymbol{I} - \boldsymbol{N}\boldsymbol{N}) * d\boldsymbol{W}(t). \tag{1.45b}$$

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:

$$dX_i = VN_i dt + \sqrt{2D_T} * dB_i(t), \tag{1.46a}$$

$$dN_j = (1-d)D_R\,N_j dt + \sqrt{2D_R}\,(\delta_{jk} - N_j N_k) * dW_k(t). \tag{1.46b}$$



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

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

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

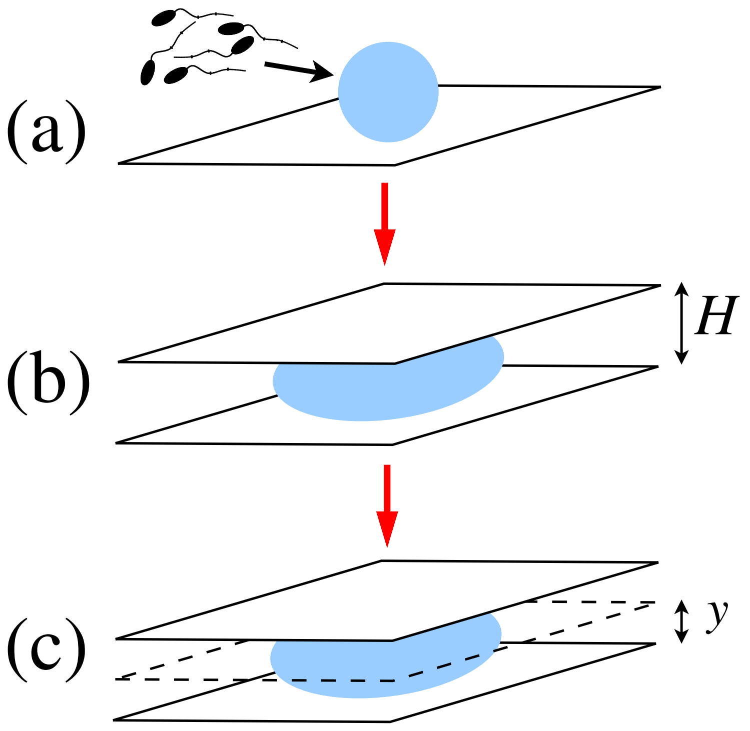
$$\lim_{t\to\infty} \frac{\mathbb{E}[\boldsymbol{X}^2]}{t} = \frac{2V^2}{(d-1)D_R} + 2dD_T. \tag{1.55}$$

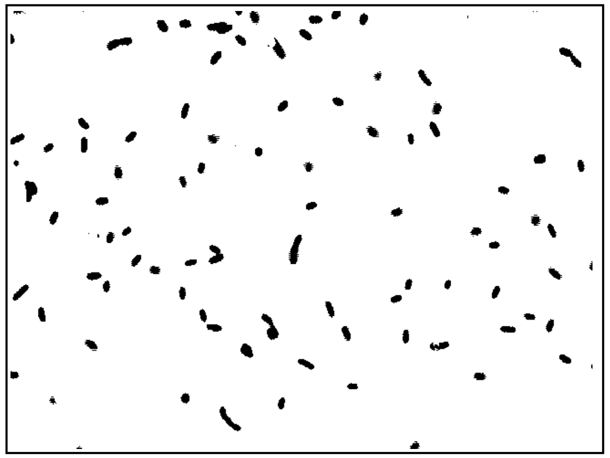
Inserting typical values for bacteria, $V \sim 10\mu\text{m/s}$ and $D_R \sim 0.1/\text{s}$, and comparing with $D_T \sim 0.2\mu\text{m}^2/\text{s}$ for a micron-sized colloids at room temperature, we see that active swimming and orientational diffusion dominate the diffusive dynamics of microorganisms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

PRL **101,** 038102 (2008) PHYSICAL REVIEW LETTERS week ending 18 JULY 2008

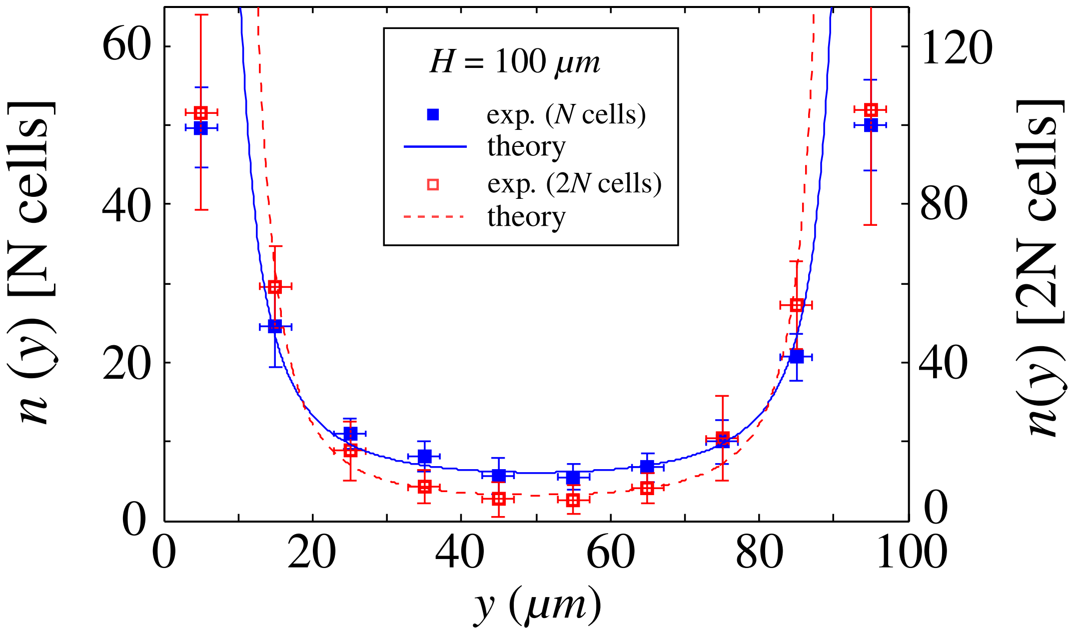
Hydrodynamic Attraction of Swimming Microorganisms by Surfaces

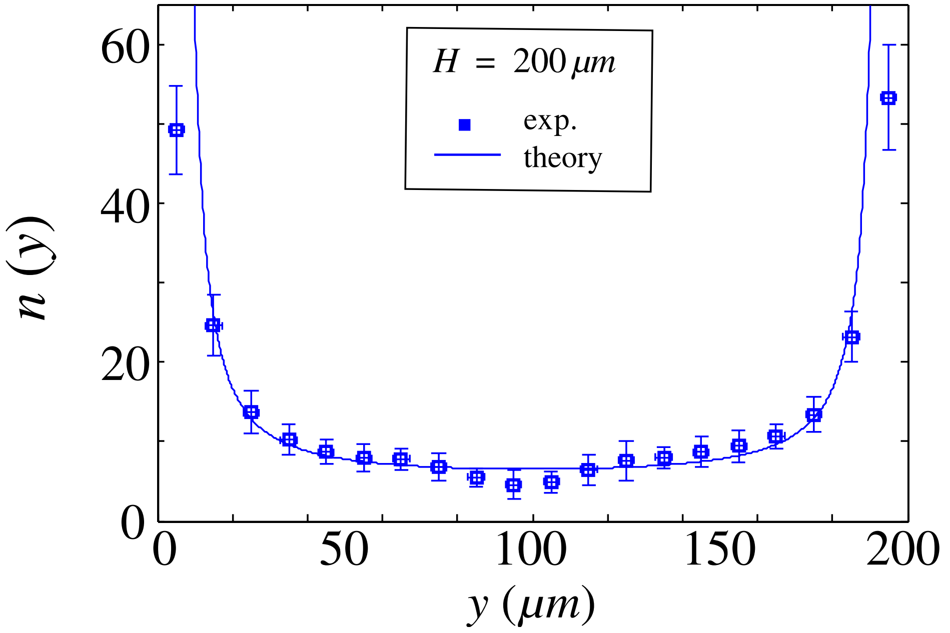
Allison P. Berke,[1] Linda Turner,[2] Howard C. Berg,[2,3] and Eric Lauga[4,*]





(d)





‘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

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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

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

Orientation (velocity) field

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

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

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

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

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,

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

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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,

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

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This allows us to rewrite (1.60) as

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

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

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

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

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

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

$$0 \;=\; Vu - D_T c', \tag{1.65}$$

$$0 \;=\; -2D_R u + D_T u'', \tag{1.66}$$

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

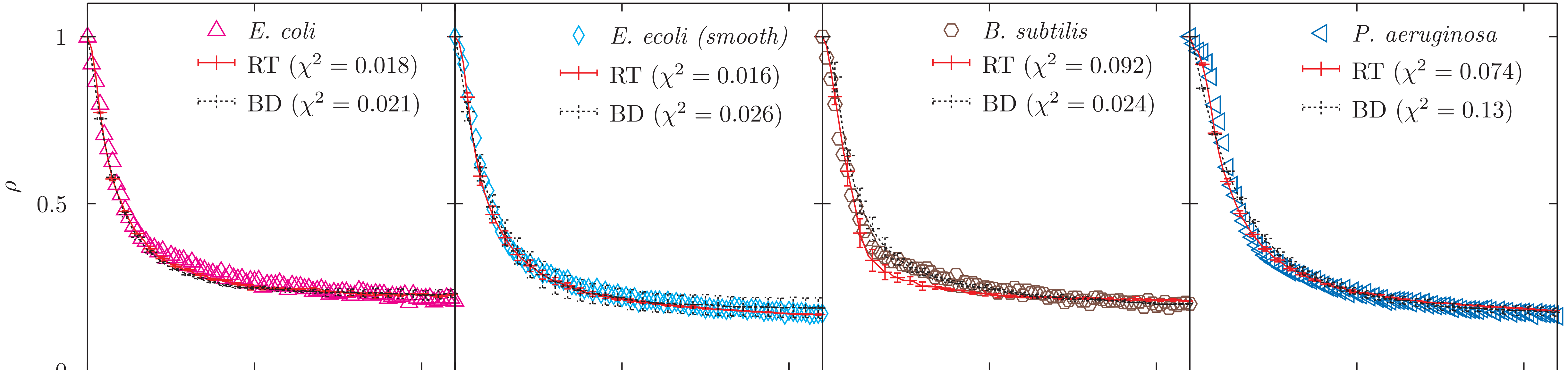
$$u(z) \;=\; A \sinh(z/\Lambda), \tag{1.67a}$$

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

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

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

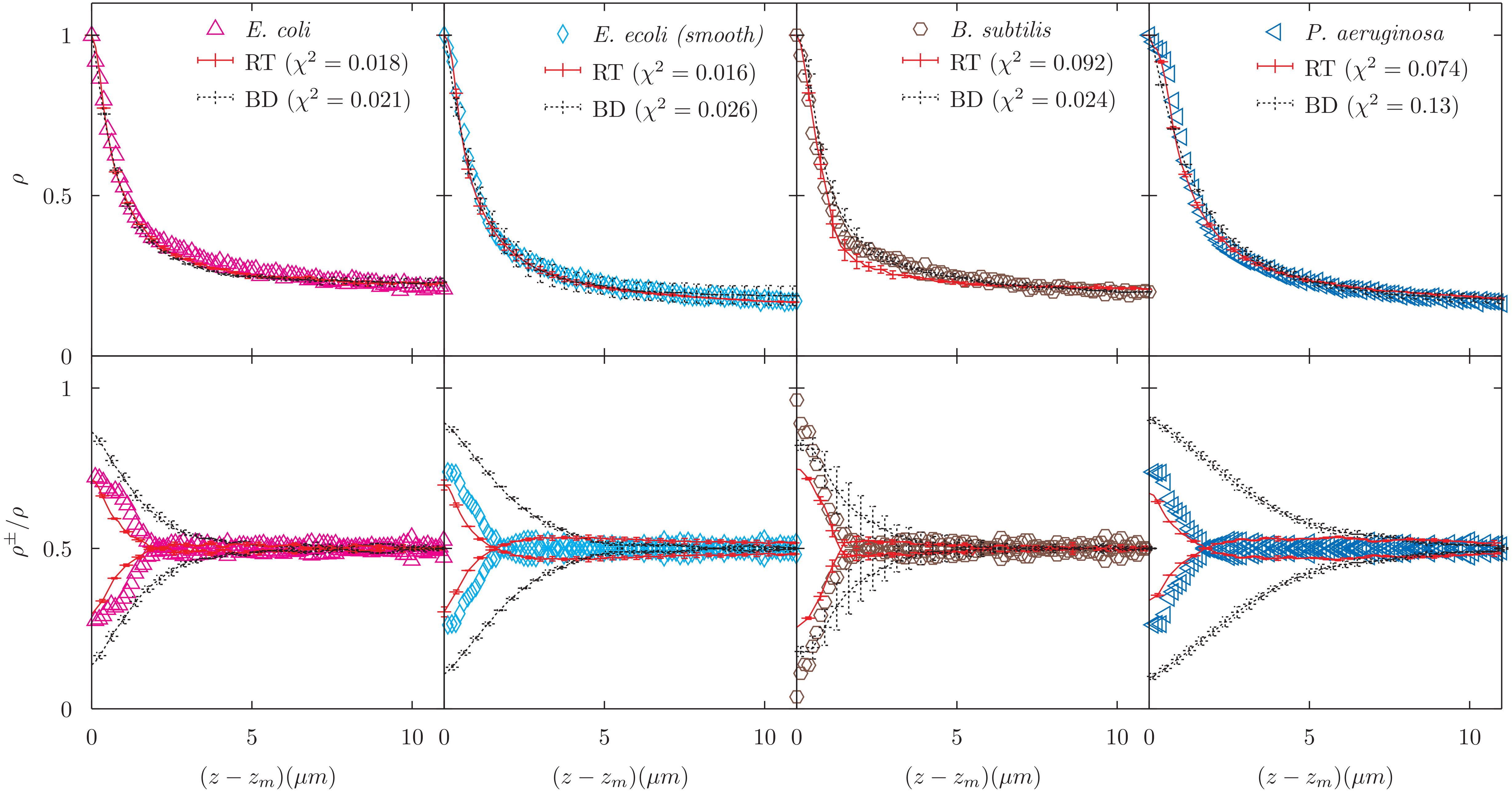
But …



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)

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

RT:

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

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

TABLE I: Main bacterial parameters used for the fit.

culture	ℓ (μm)	a (a_{eff})	v_0 ($\mu m/s$)	θ_T	Δt_{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