Swimming at low Reynolds numbers

Experiments
Part 2

Wilson Poon

School of Physics & Astronomy
The University of Edinburgh

EPSRC
Engineering and Physical Sciences Research Council

erc
European Research Council

By popular vote ...

1. *E. coli* in polymer solutions

2. Artificial Janus swimmers

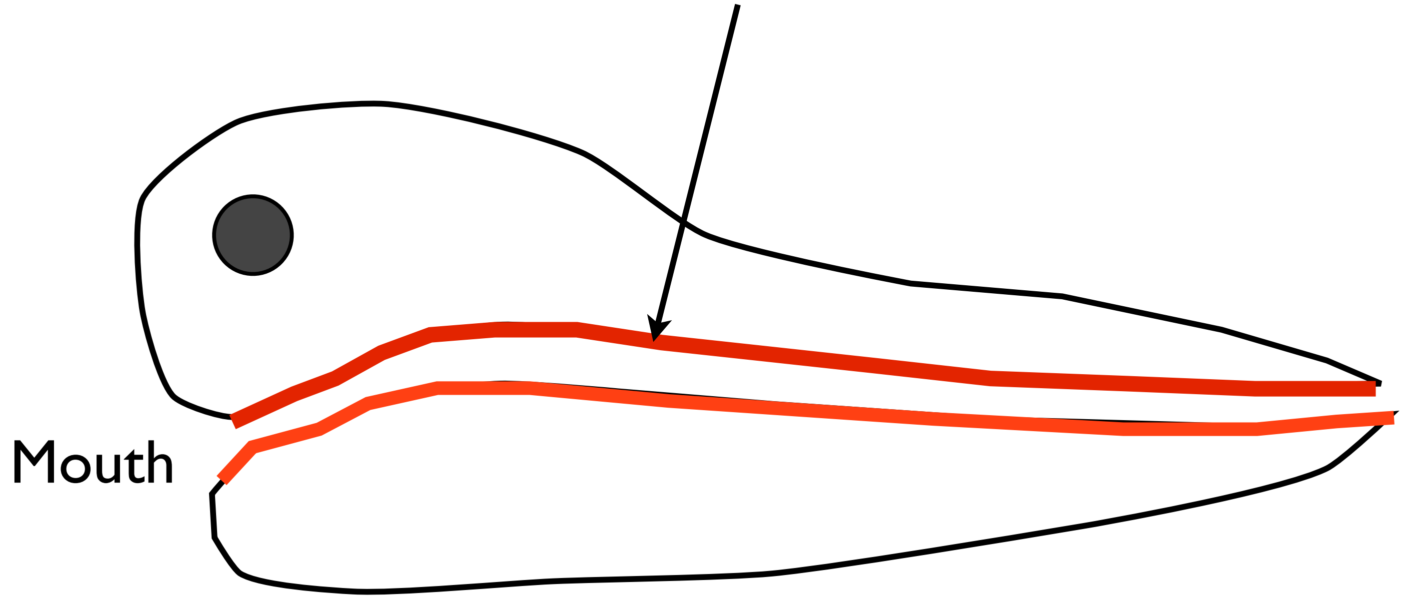
3. Bacterial colony

1. Bacterial swimming in polymer solutions

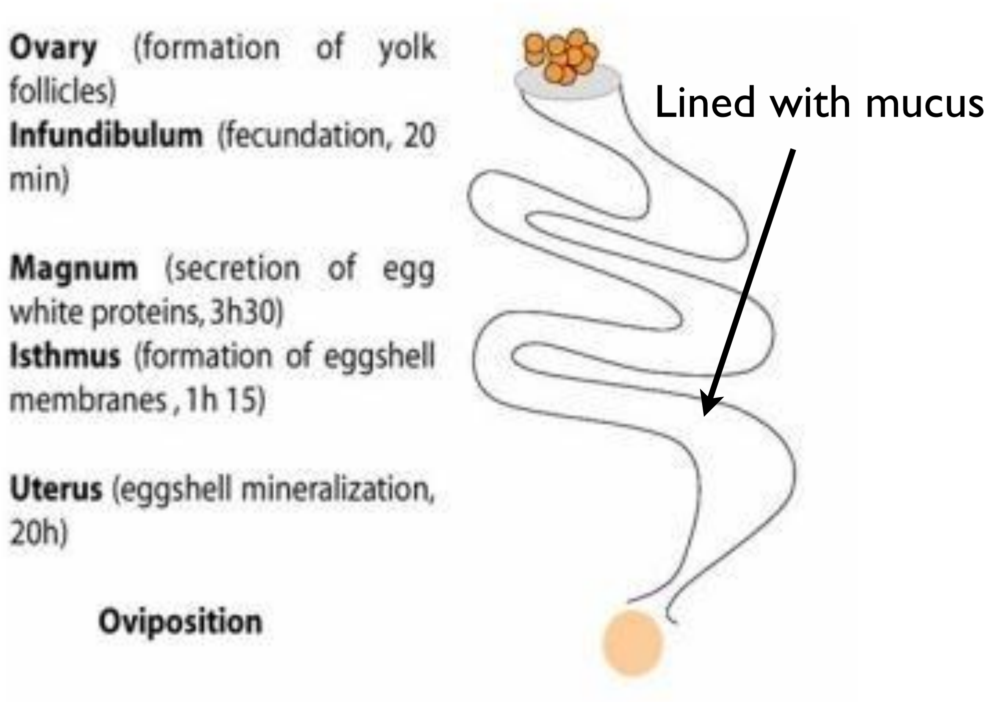
Vincent Martinez
Jana Schwarz-Linek
Mathias Reufer
Lawrence Wilson
Alexander Morozov

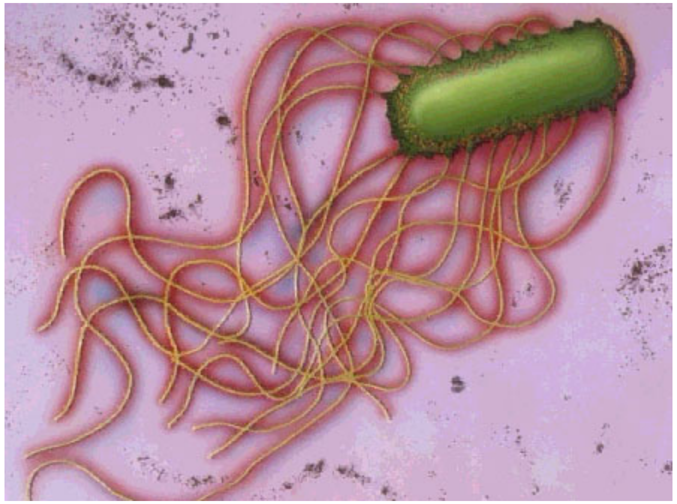
Biomedical motivation

Mucus (high M_w polymers) lining to stop pathogen invasion

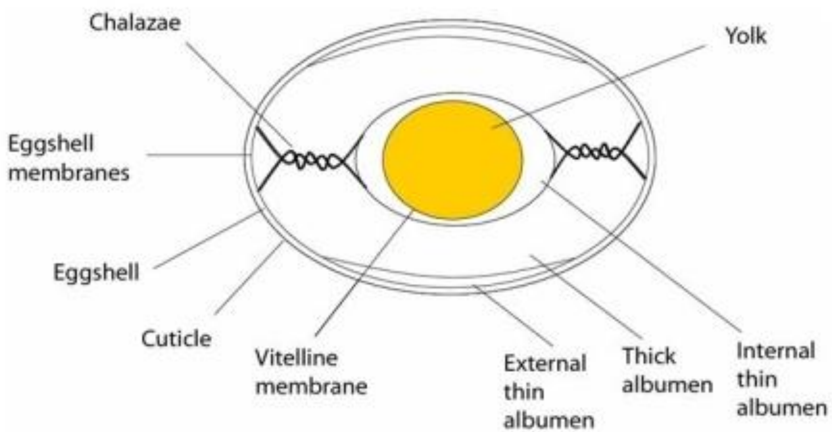


- Highly conserved amongst all metazoans (higher animals)
- Covers gastrointestinal *and* respiratory tracks
- Some very dangerous bacteria can penetrate mucus

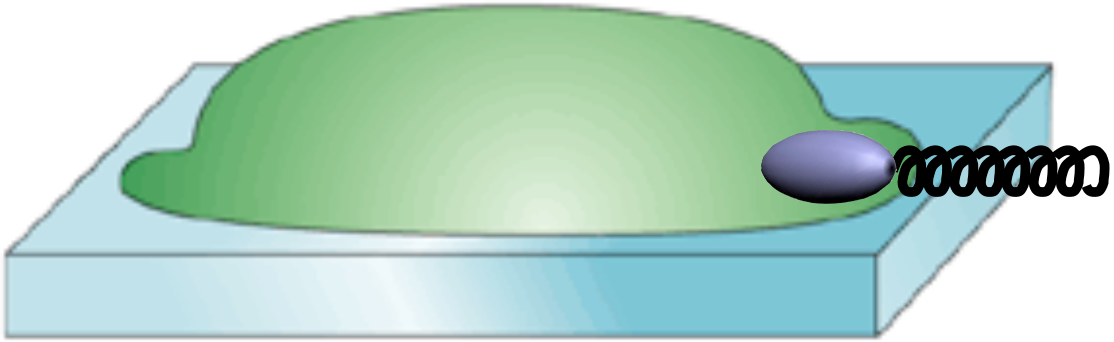

Ovary (formation of yolk follicles)
Infundibulum (fecundation, 20 min)
Magnum (secretion of egg white proteins, 3h30)
Isthmus (formation of eggshell membranes, 1h 15)
Uterus (eggshell mineralization, 20h)
Oviposition
Lined with mucus



Salmonella


Chalazae
Yolk
Eggshell membranes
Eggshell
Cuticle
Vitelline membrane
External thin albumen
Thick albumen
Internal thin albumen

Biofilm - covered in thick exopolysaccharide solution



Bacterial swimmers that infiltrate and take over the biofilm matrix

Ali Houry[a,b], Michel Gohar[a,b], Julien Deschamps[a,b], Ekaterina Tischenko[a,b], Stéphane Aymerich[a,b], Alexandra Gruss[a,b], and Romain Briandet[a,b,1]

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13088–13093 | PNAS | **August 7, 2012** | vol. 109 | no. 32

The Standard Model of Bugs in Goo

Experiments

Schneider & Doetsch
1974

J. Bacteriol. **117** 696

Concept

Berg & Turner
1979

Nature **278** 349

Theory

Magariyama & Kudo
2003

Biophys. J. **83** 733

"The speed has a peak."

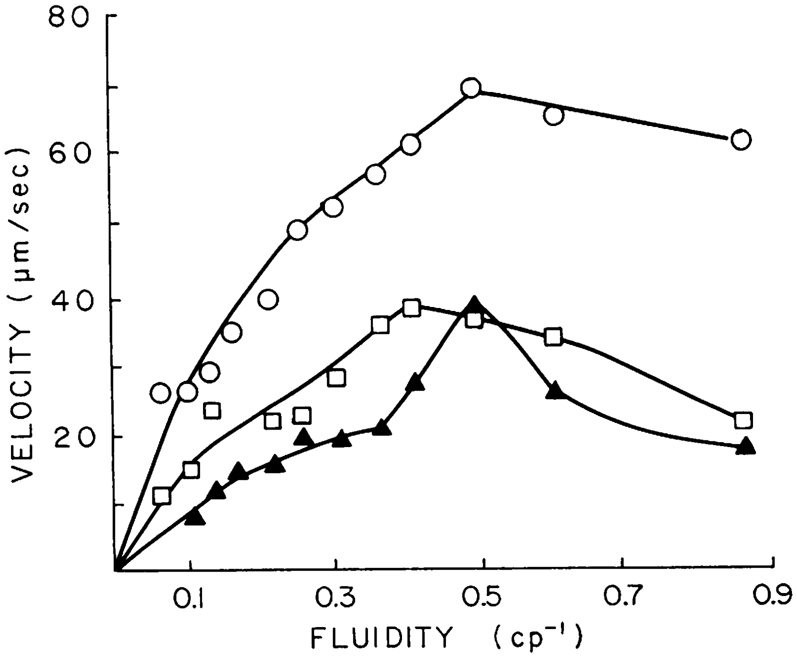
JOURNAL OF BACTERIOLOGY, Feb. 1974, p. 696–701
Vol. 117, No. 2

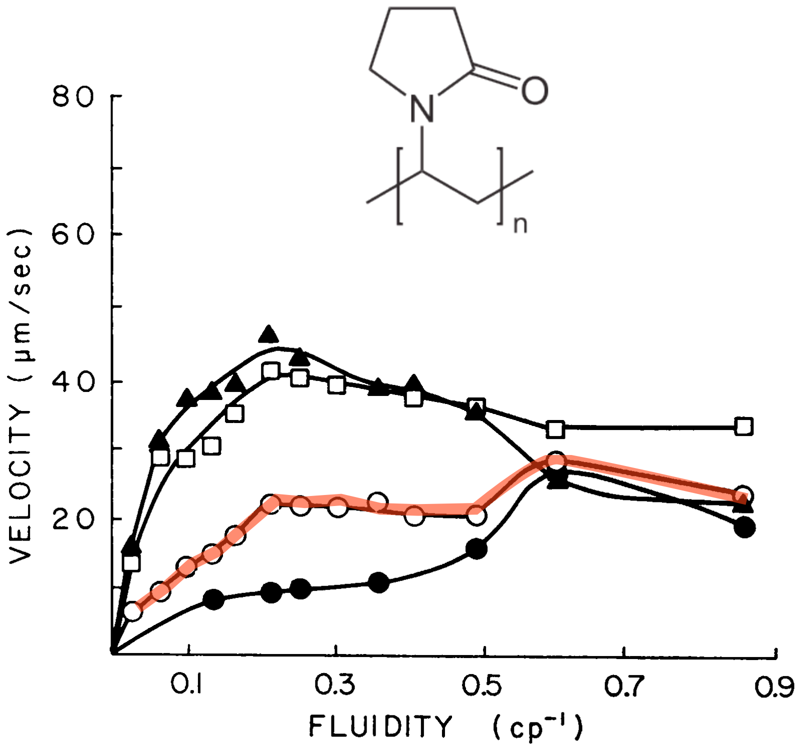
Effect of Viscosity on Bacterial Motility

W. R. SCHNEIDER AND R. N. DOETSCH

"All showed an increase in velocity in more viscous solutions."

360k PVP





Fluidity = (viscosity)$^{-1}$, 1 cp^{-1} = water

The qualitative explanation ...

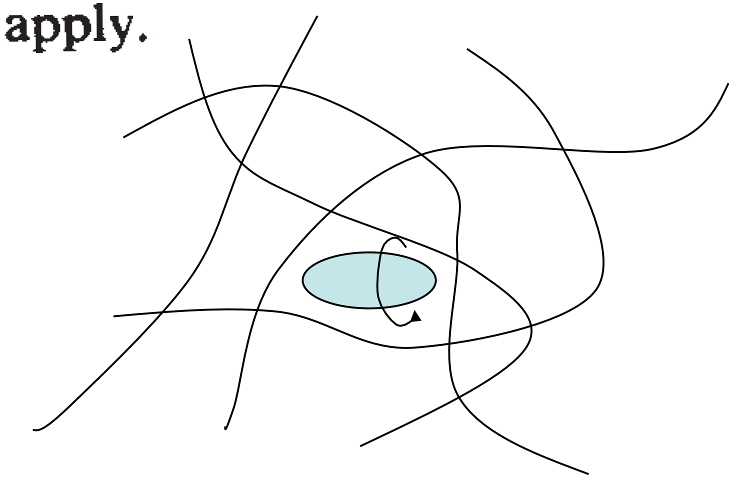
Nature Vol. 278 22 March 1979

Movement of microorganisms in viscous environments

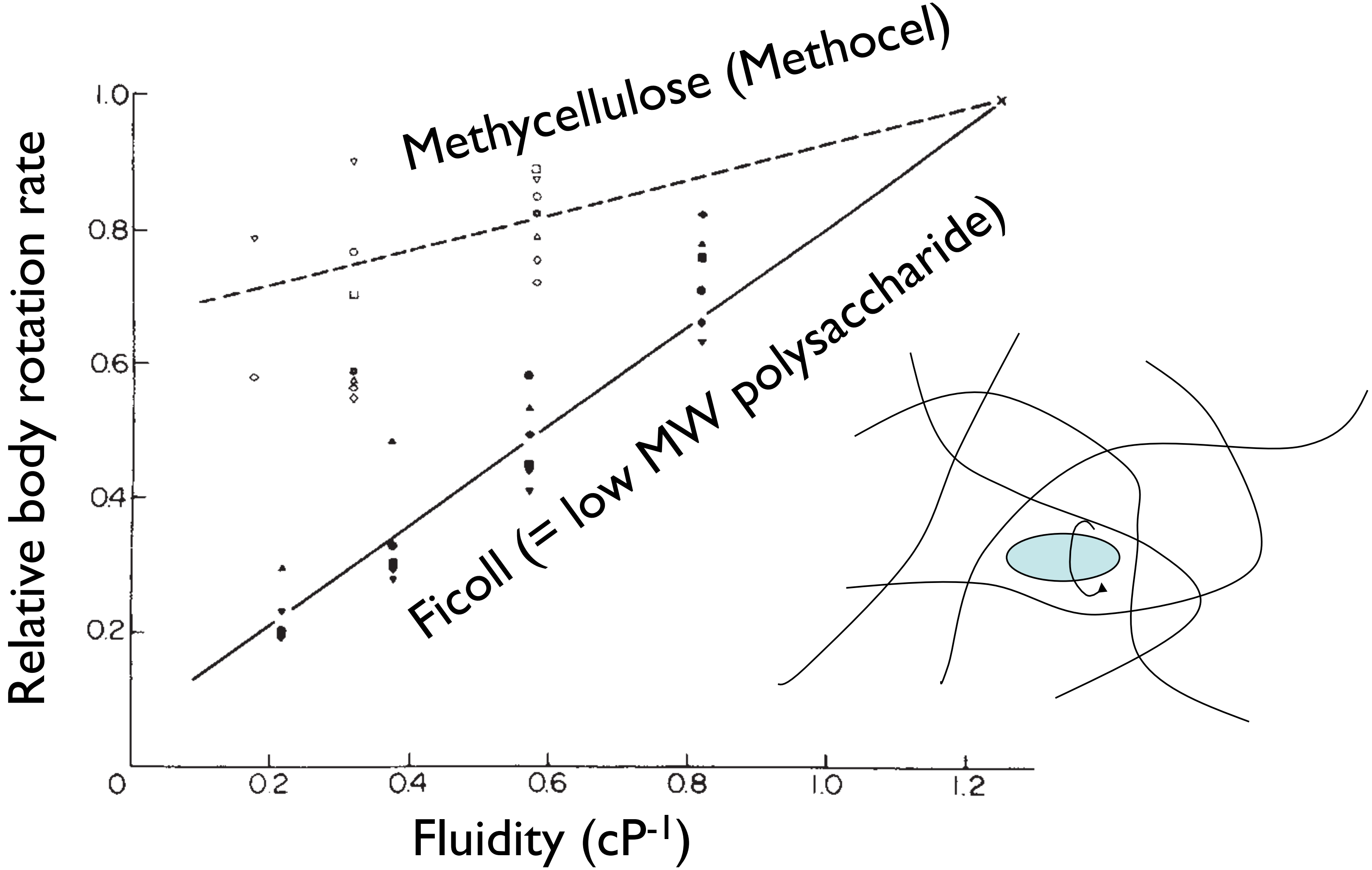
Howard C. Berg*
Linda Turner
Department of Molecular, Cellular and Developmental Biology, University of Colorado, Boulder, Colorado 80309

Many kinds of bacteria swim more rapidly in dilute solutions of viscous agents (viscosities of the order of 2 cP) than they do in ordinary media[1,2,6]

The solute forms a loose quasi-rigid network easily penetrated by particles of microscopic size. The network can exert forces normal to a segment of the body of a slender cell even when that segment does not possess a component of velocity in the normal direction; hydrodynamic treatments of the motion of micro-organisms (or of cilia and flagella) do not apply.



Solutions of Methocel perturbed the motion of *E. coli* less than did solutions of Ficoll of the same apparent viscosity; evidently, the cells were able to push the chains of methylcellulose out of the way and to move more as they would in pure solvent.



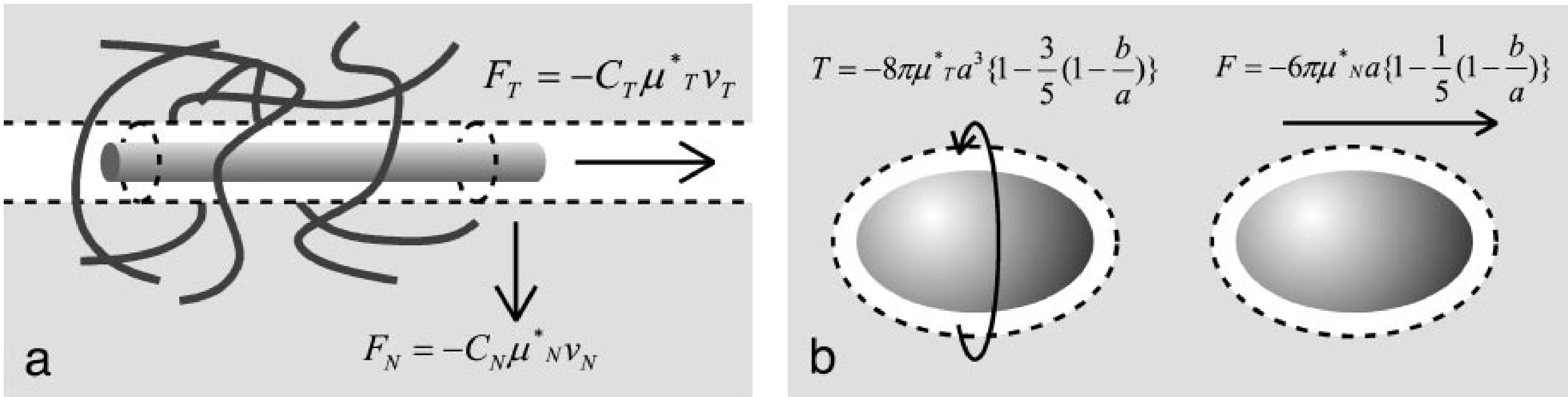
And finally, a theory ...

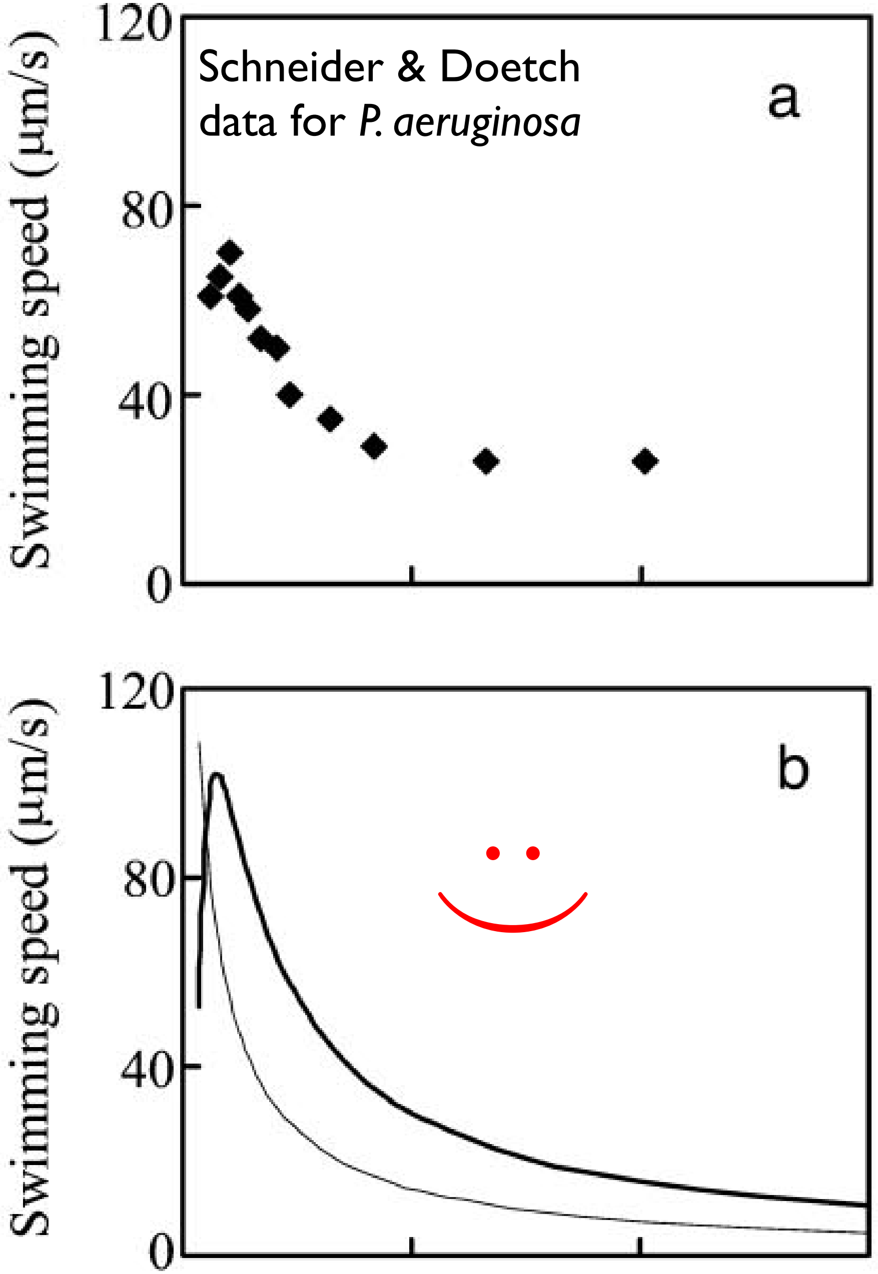
Biophysical Journal Volume 83 August 2002 733–739 733

A Mathematical Explanation of an Increase in Bacterial Swimming Speed with Viscosity in Linear-Polymer Solutions

Yukio Magariyama* and Seishi Kudo†

In this study we interpreted the suggestion by Berg and Turner and mathematically developed it with regard to the motion of a single-polar-flagellated bacterium .




Swimming speed (μm/s)
120
80
40
0
Schneider & Doetch
data for *P. aeruginosa*
a
Swimming speed (μm/s)
120
80
40
0
b

But there are *a priori* reasons not to believe the Standard model!

Experiments

Schneider & Doetsch
1974

J. Bacteriol. **117** 696

Concept

Berg & Turner
1979

Nature **278** 349

Theory

Magariyama & Kudo
2003

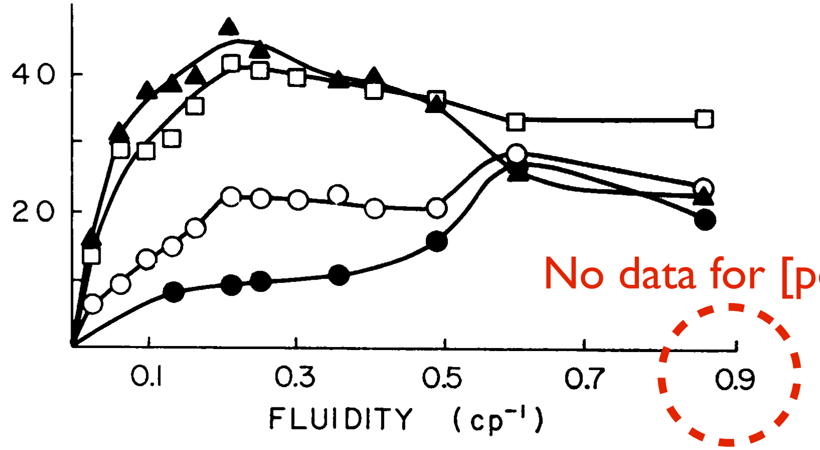
Biophys. J. **83** 733

Experiments

Schneider & Doetsch
1974

J. Bacteriol. **117** 696

Statistics was awful!



No data for [polymer] = 0!

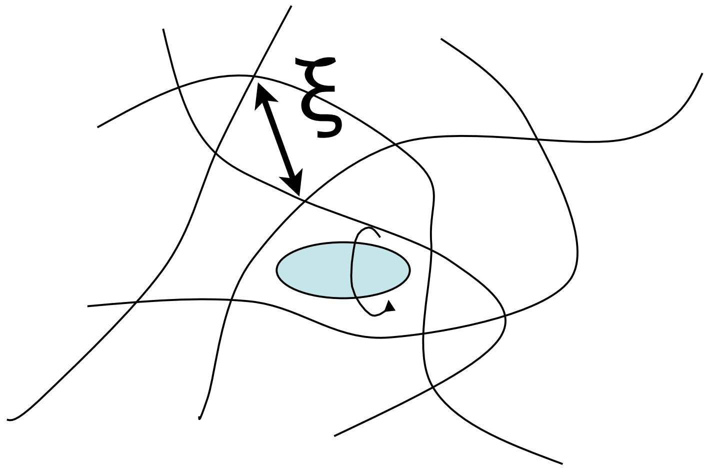
Motility measurements. Unless noted in the text, velocity data were obtained by using a 1-inch (2.54-cm) video tape recorder (Panasonic NV-504) coupled to a television camera (Concord MTC-21) attached to a Zeiss II photomicroscope, incorporating a "phase 2" system (×40 Neofluar objective lens and a ×10 eyepiece), and illuminated by a 12-V 60-W incandescent lamp. The tape was played back on a monitor (Electrohome EMV-23AG), and paths of individual bacteria traced on a transparent plastic sheet were measured with a calibrated planimeter and replayed and timed with a 1/100-s stopwatch. The 10 greatest velocities were used to calculate the average velocity.

Concept

Berg & Turner
1979

Nature **278** 349

360k PVP, r_g ~ 60 nm << coli size



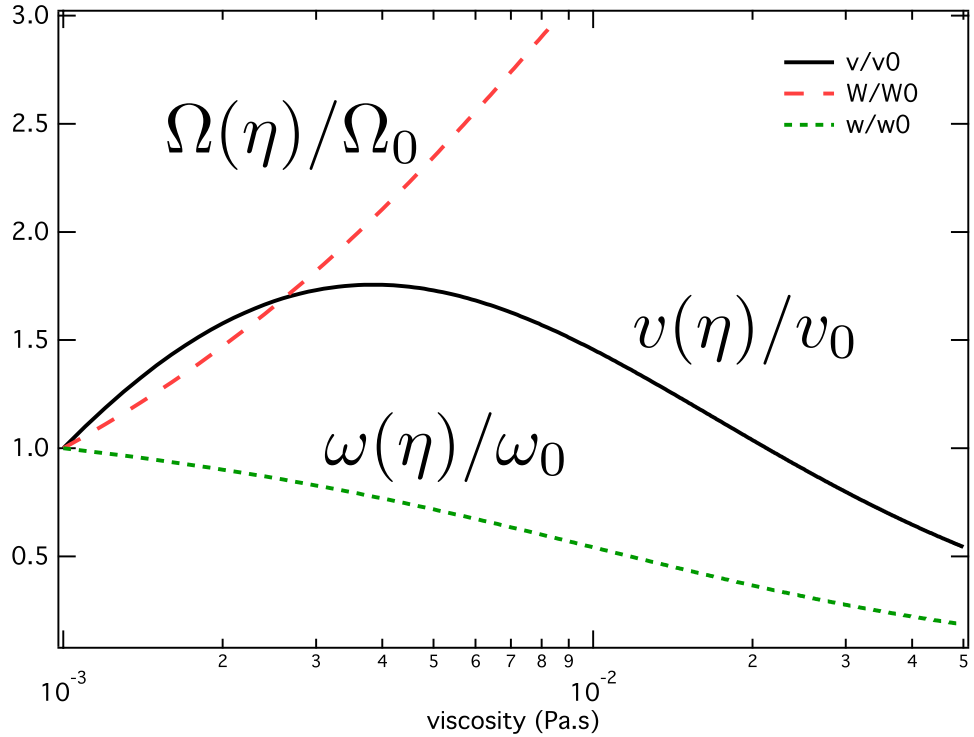
Polymer solutions do have ‘holes’ …
… but only a valid picture at ‘overlap’ …
… where $\xi \sim r_g$ of coils

Theory

Magariyama & Kudo 2003

Biophys. J. **83** 733

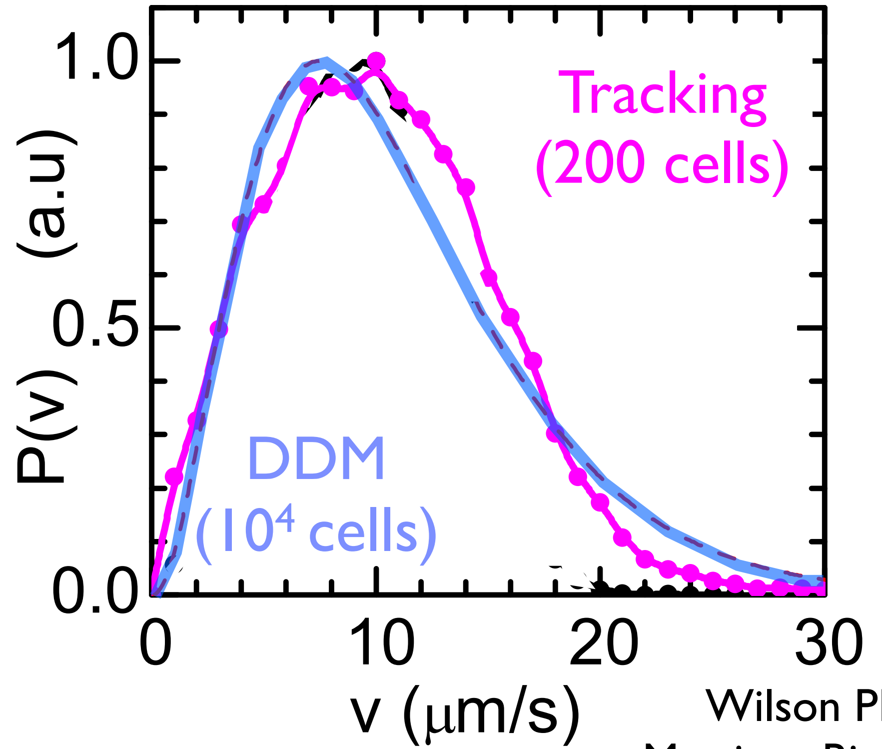
$$\mu_{\text{peak}} = \{1.5 \times 10^{190} T_0 + 3.8 \times 10^{169} \omega_0 + 7.6 \times 10^{172} \times (2.7 \times 10^{36} T_0^2 + 7.5 \times 10^{15} T_0 \omega_0 + 7.9 \times 10^{-7} \omega_0^2)^{1/2}\} \times (3.3 \times 10^{193} T_0 + 8.7 \times 10^{172} \omega_0)^{-1} \quad (28)$$



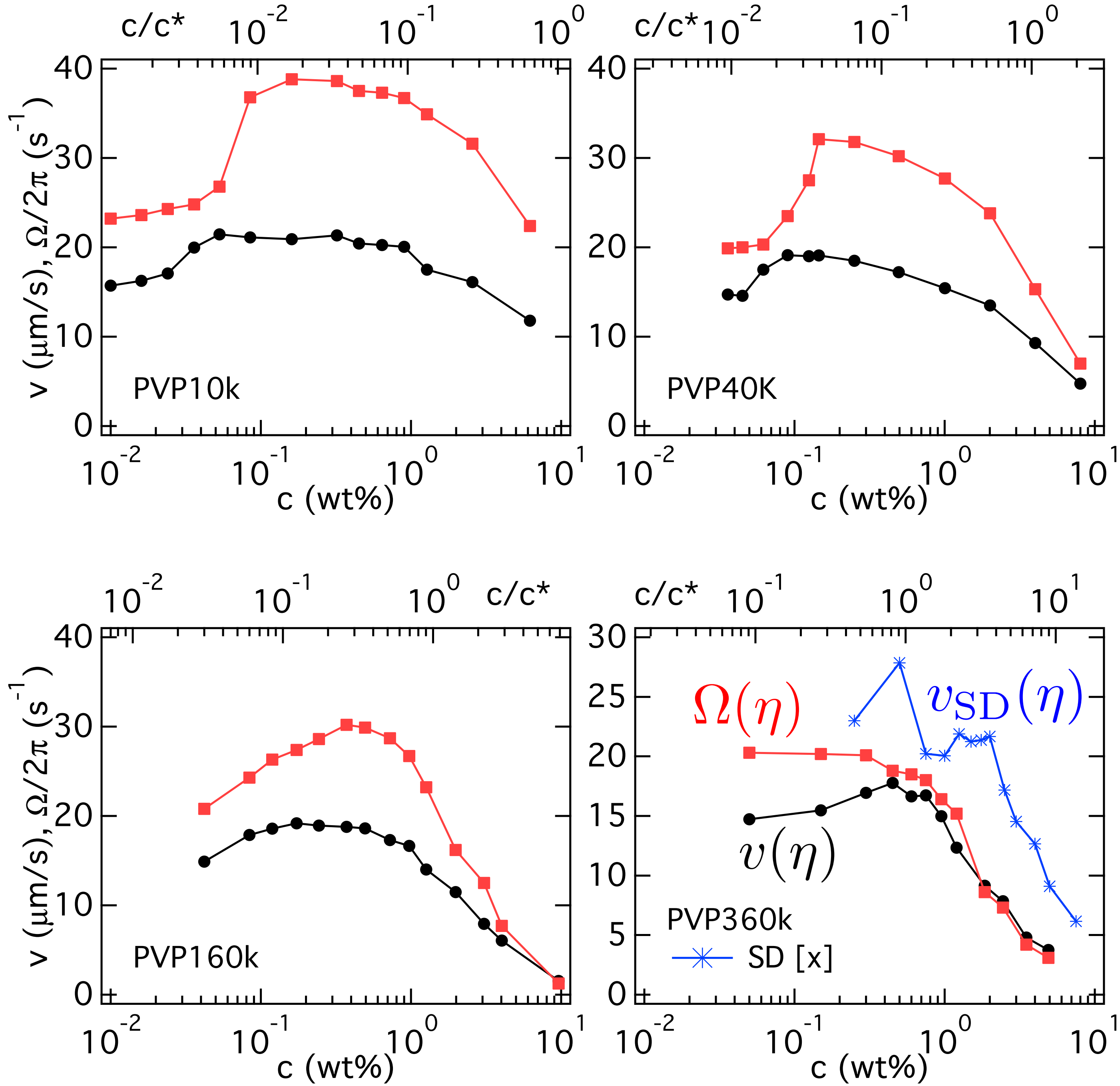
Repeat experiments using new high-throughput techniques

Differential dynamic microscopy (DDM) → *v*
Dark-field fluctuation microscopy → Ω

Schneider & Doetsch: average over 10 cells in 2D
We average over ~ 10^4 cells in 3D 2 mins

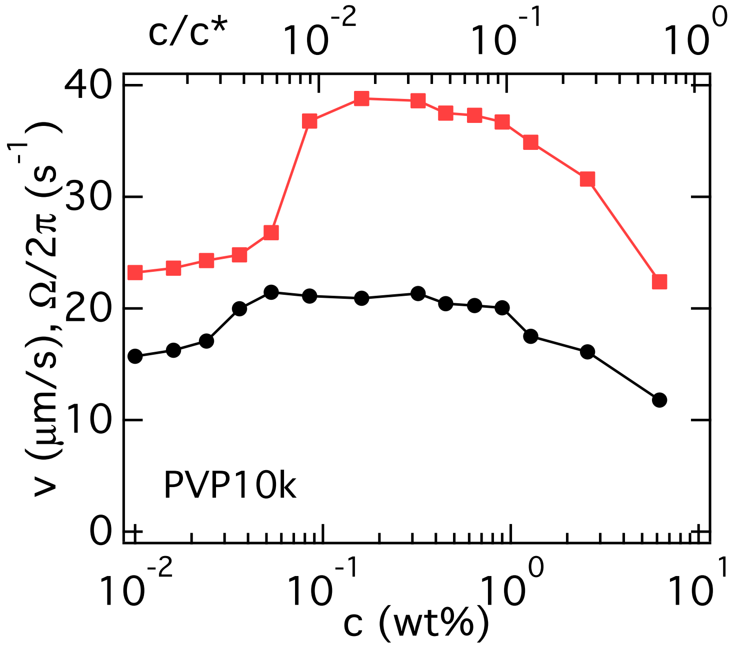


Wilson PRL (2011)
Martinez Biophys J (2012)

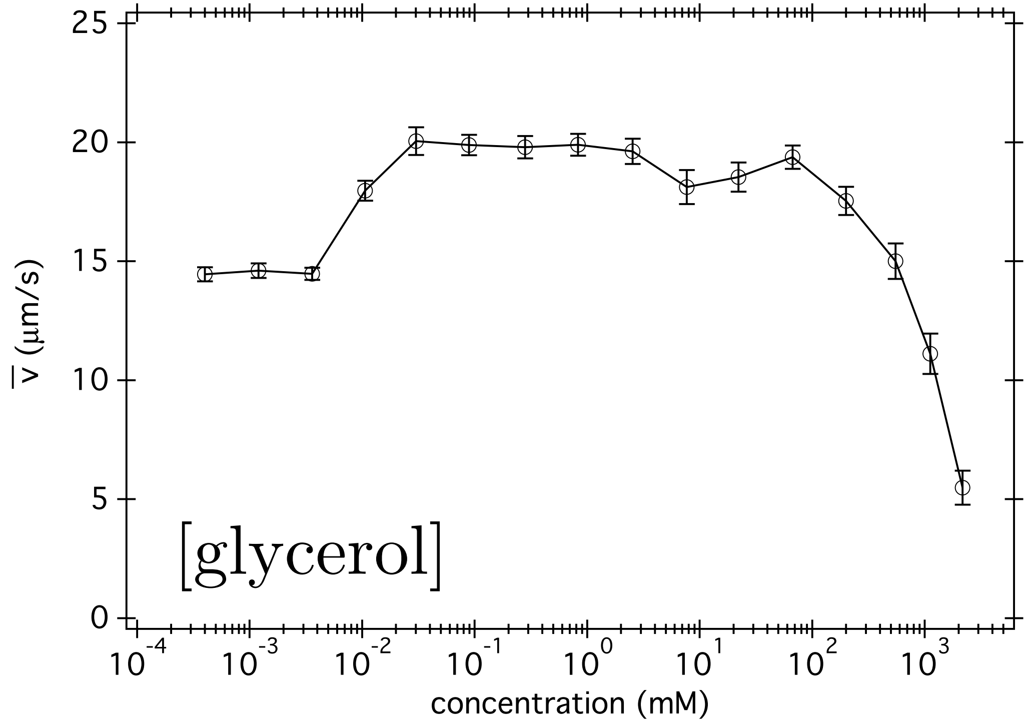


c/c*
PVP10k
PVP40K
PVP160k
PVP360k
v (μm/s), Ω/2π (s^-1)
c (wt%)
Ω(η)
v_SD(η)
v(η)
SD [x]

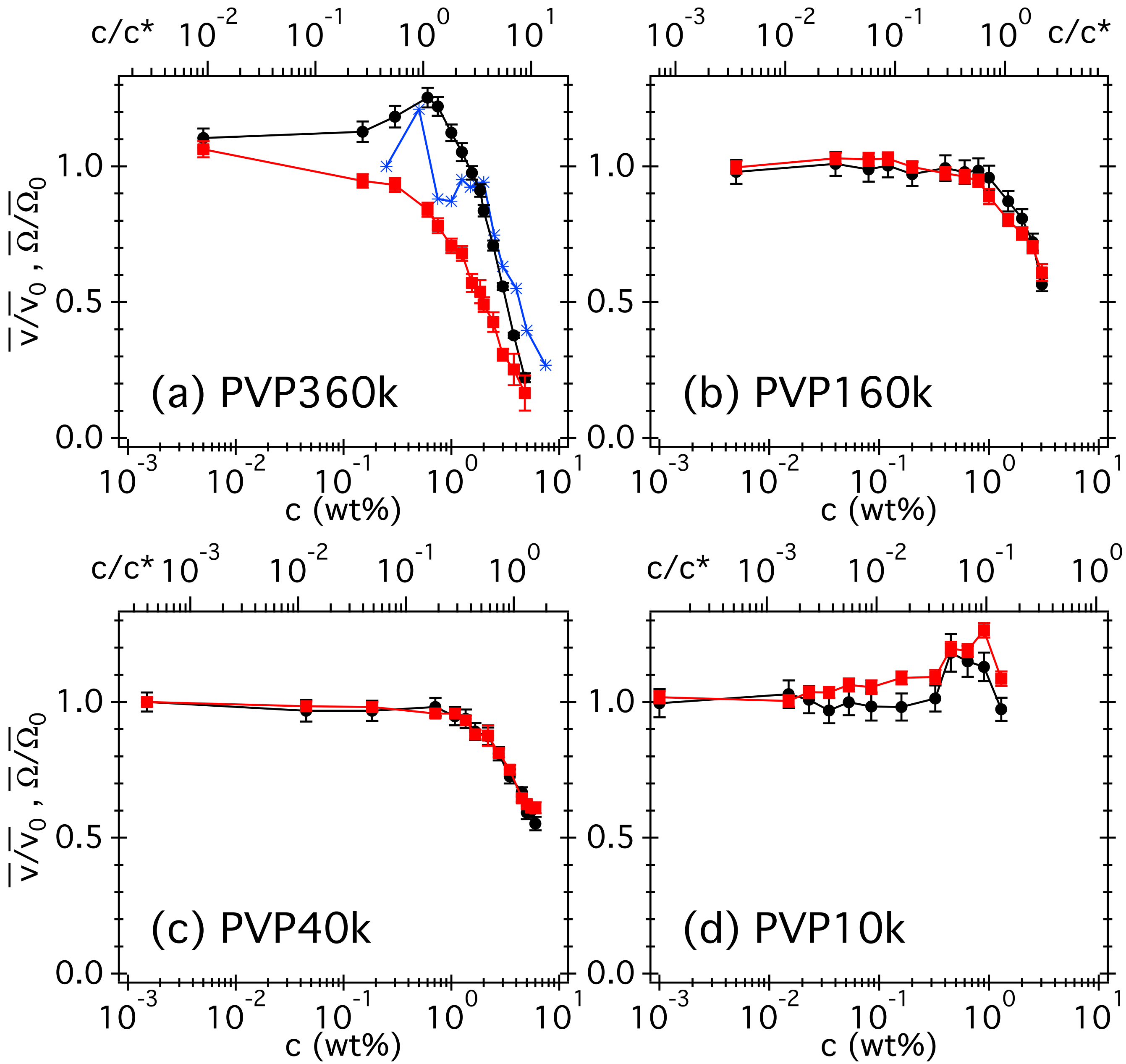
Maybe there are edible impurities



Can remove by dialysis!



Polymers purified by dialysis

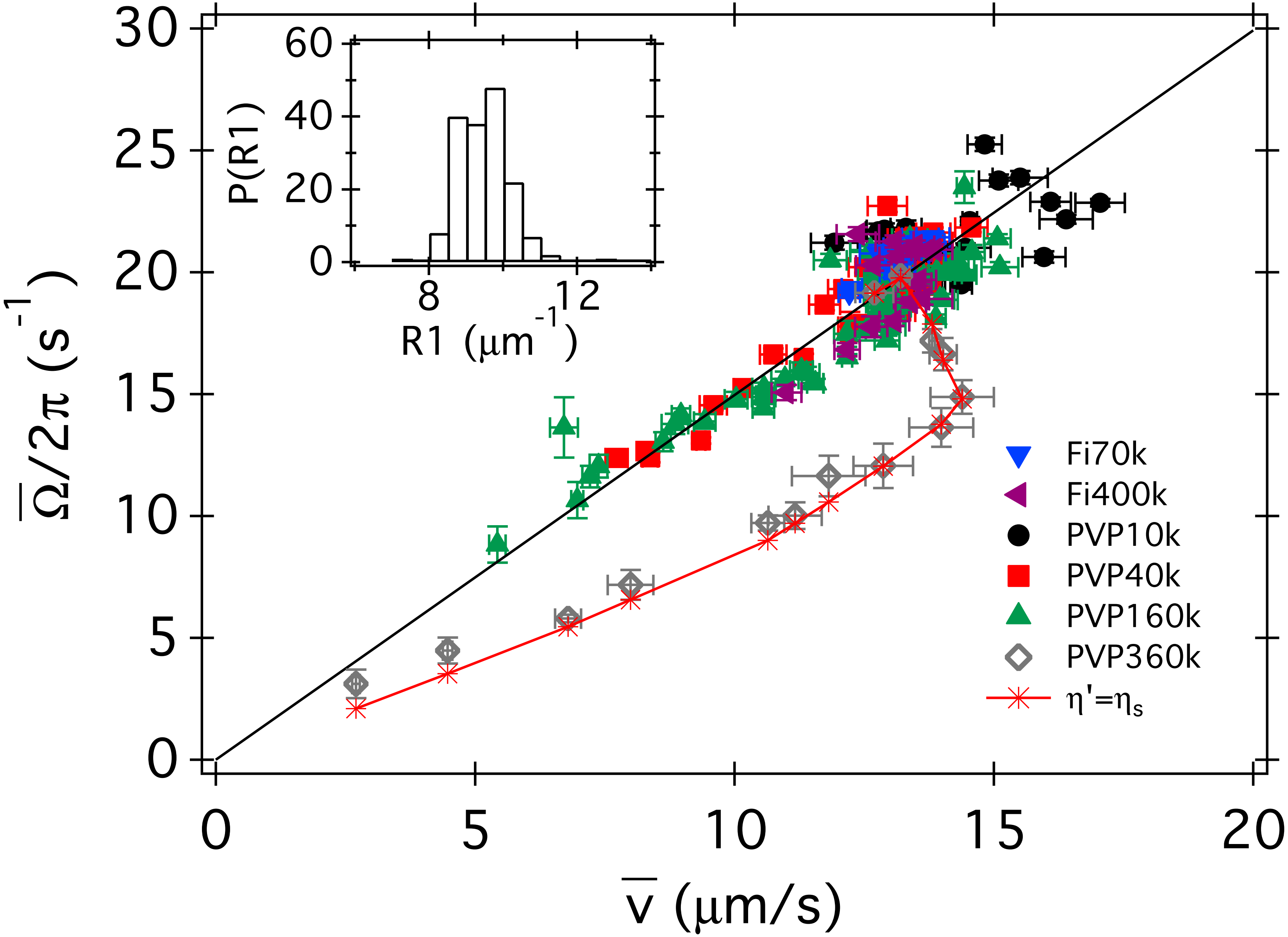


$$\frac{\Omega}{\Omega_0} = \frac{v}{v_0}$$

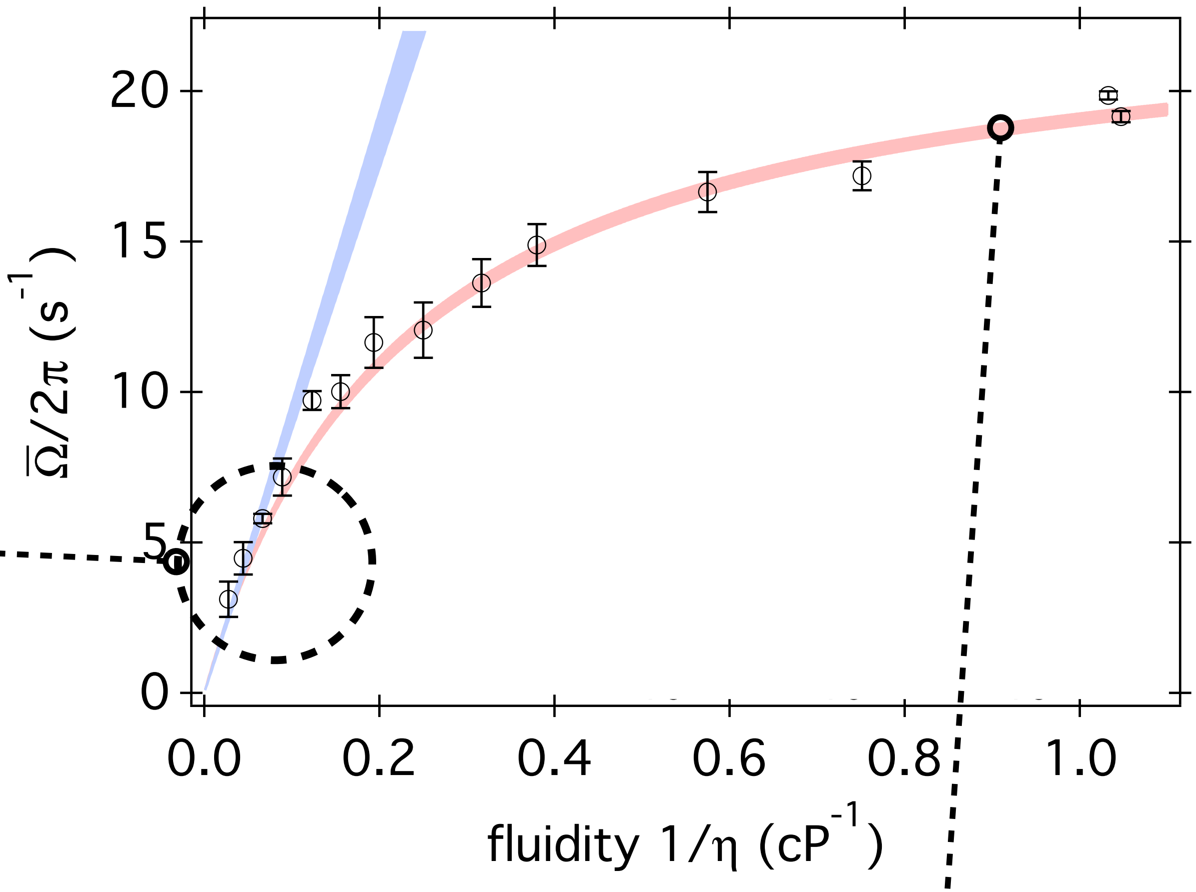
except @ 360k

η drops out!

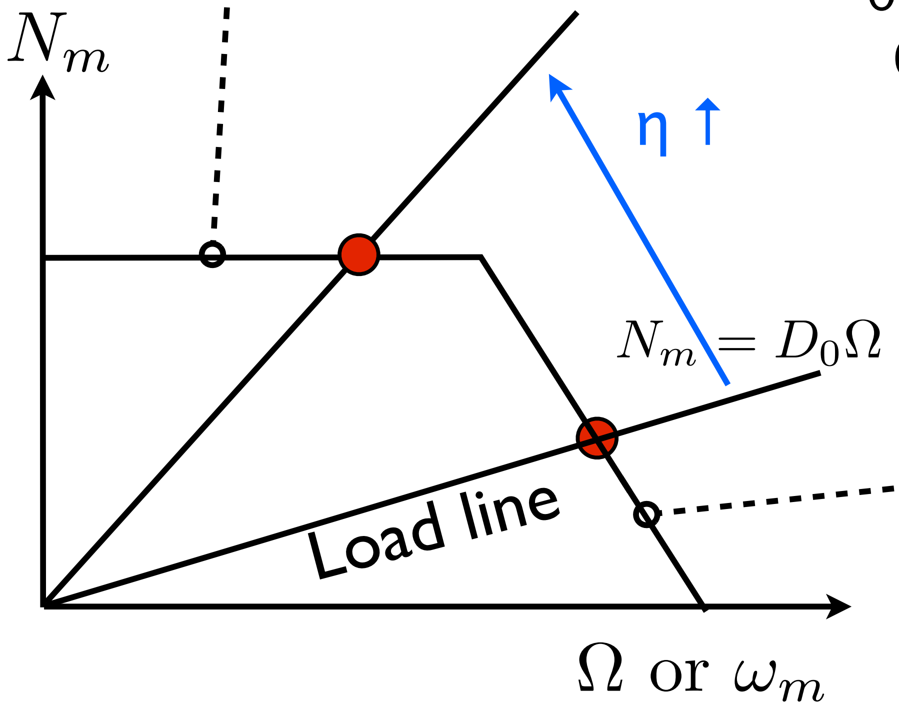
Stokes flow: $\Omega = R_1 v$, with R_1 independent of η



Calculate $D_0 \rightarrow N_{max}$
Consistent with lit. values

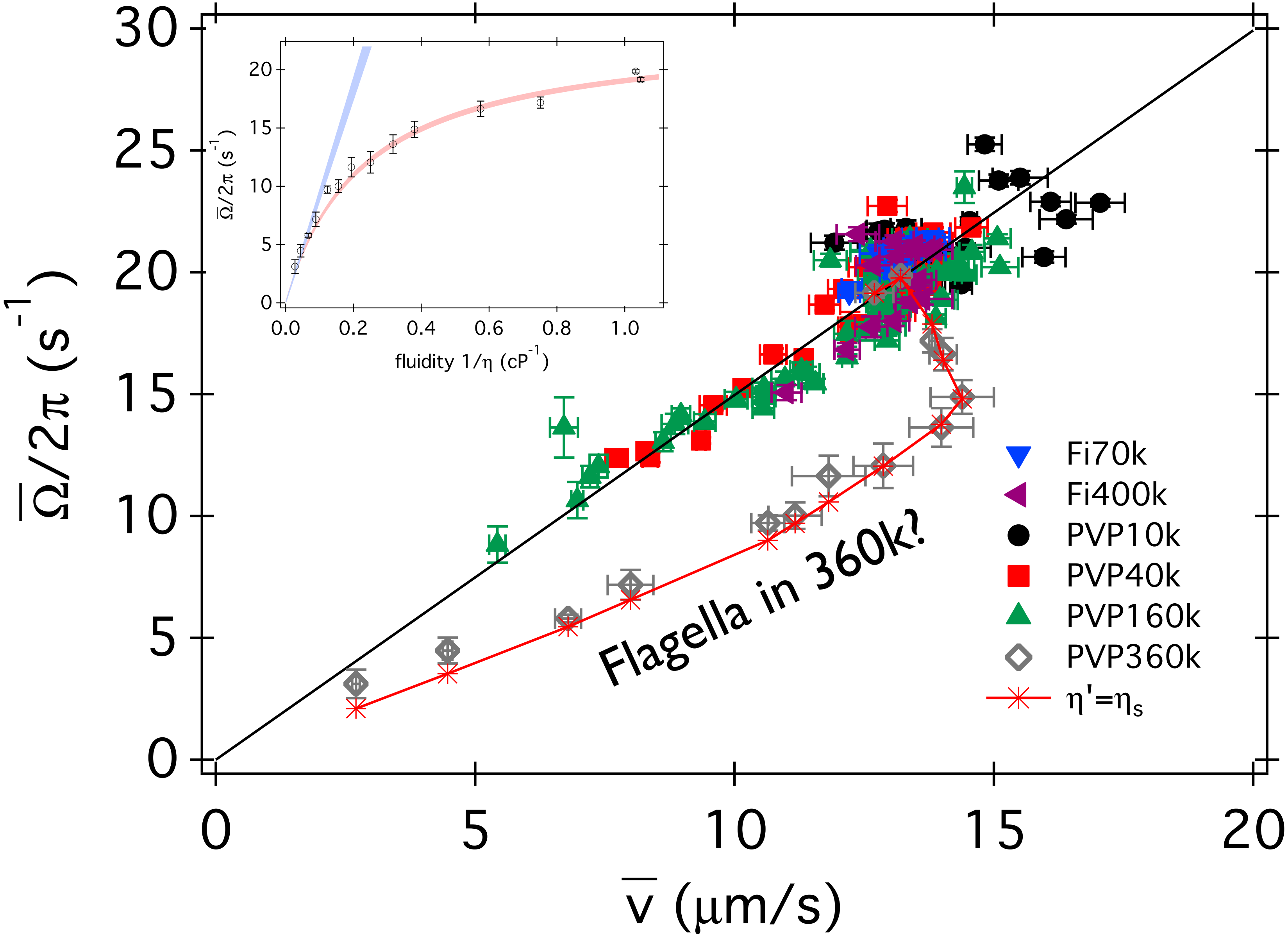


$N_m = \text{constant}$
$\Rightarrow \Omega \propto D_0^{-1} \propto \eta^{-1}$



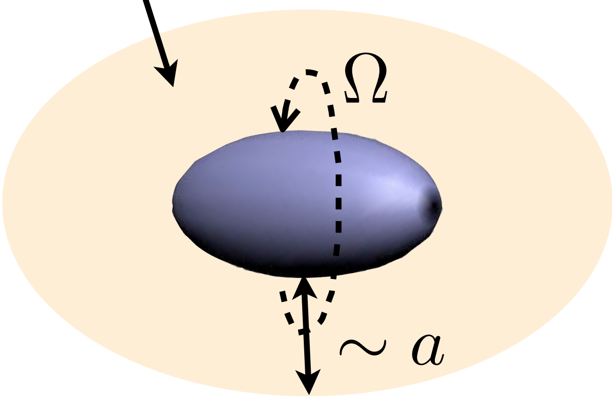
A more complex $\Omega(\eta^{-1})$

All motion for 10k, 40k, 160k and body rotation for 360k: Newtonian Stokes flow



Shear rate $\sim \Omega a/a \sim \Omega$

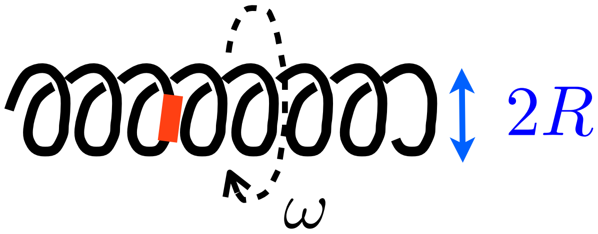
$\Omega \sim 20\pi \text{ s}^{-1} \lesssim 10^2 \text{ s}^{-1}$



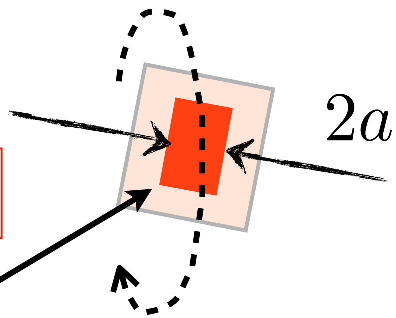
$\sim 10\lambda, 10^2$ Hz

Goes $\sim 10\lambda/\text{s}$

~ 10 turns per λ



Each bit is essentially going round circle (radius R) at ω at speed ωR

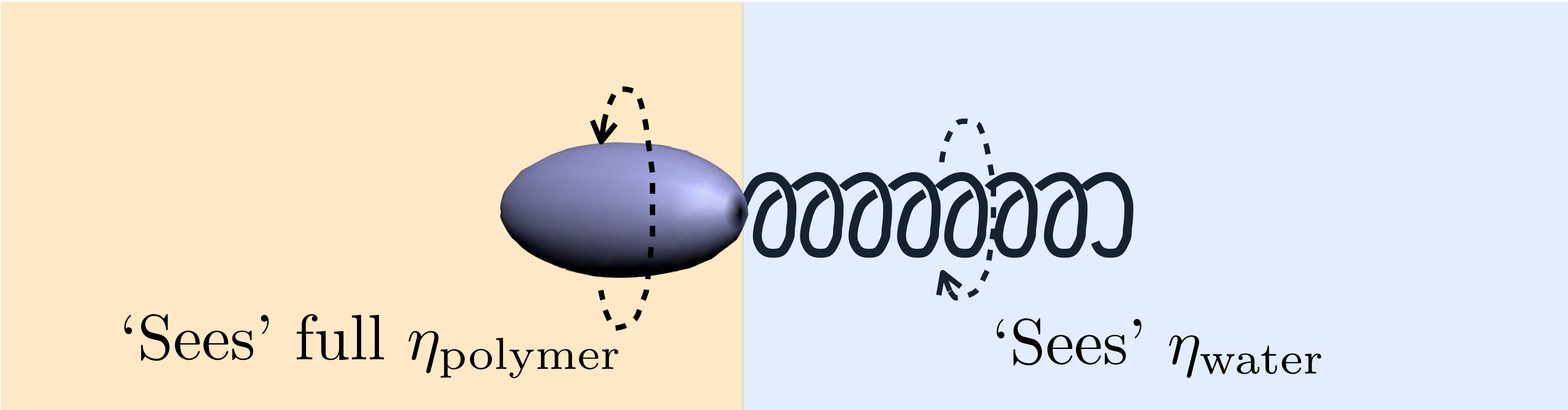


High polymers shear thin at such shear rates!

Shear rate $\sim \omega R/r \gg \omega$

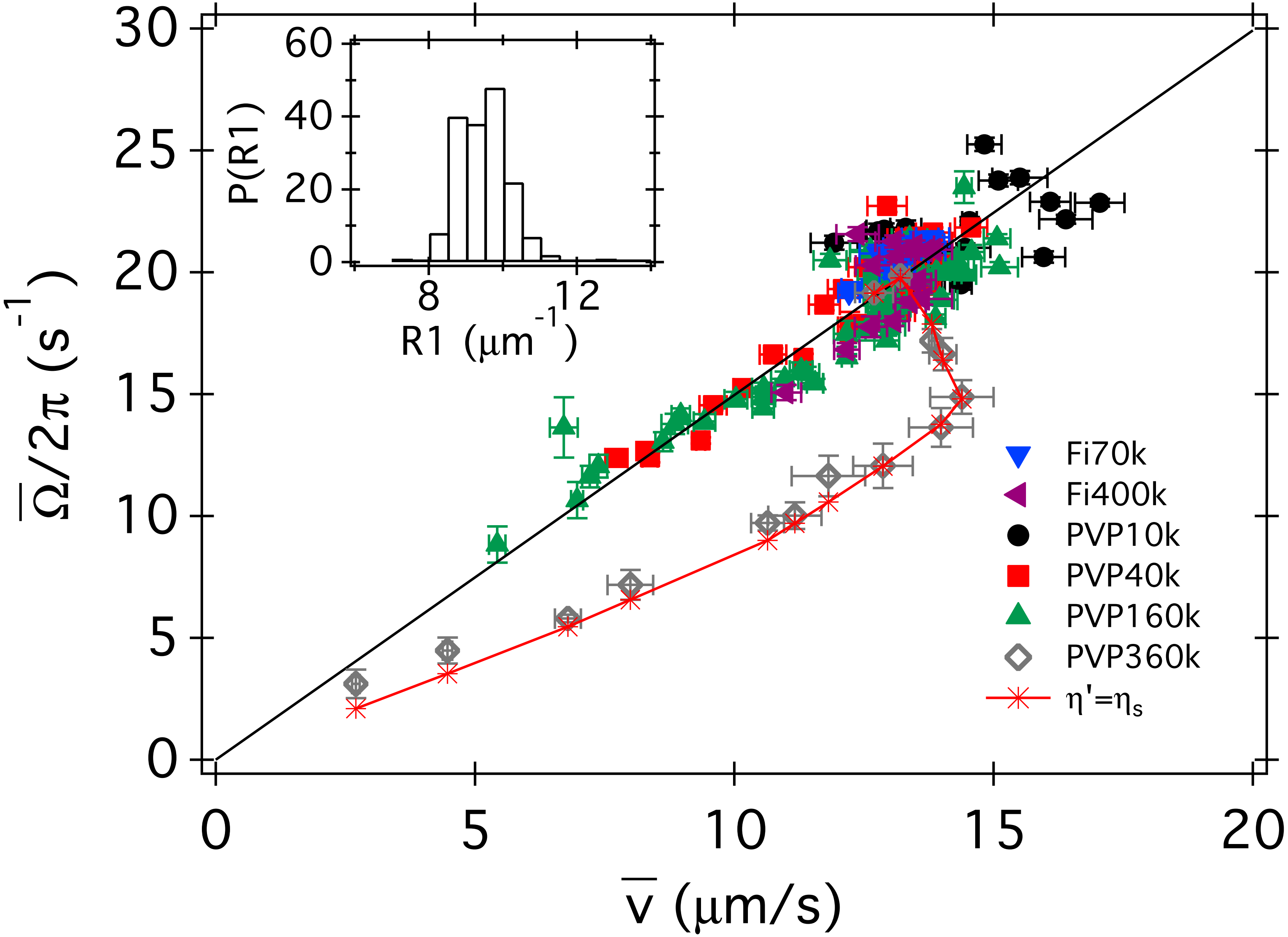
$\sim 200\pi \text{ s}^{-1} \times 10 \lesssim 10^4 \text{ s}^{-1}$

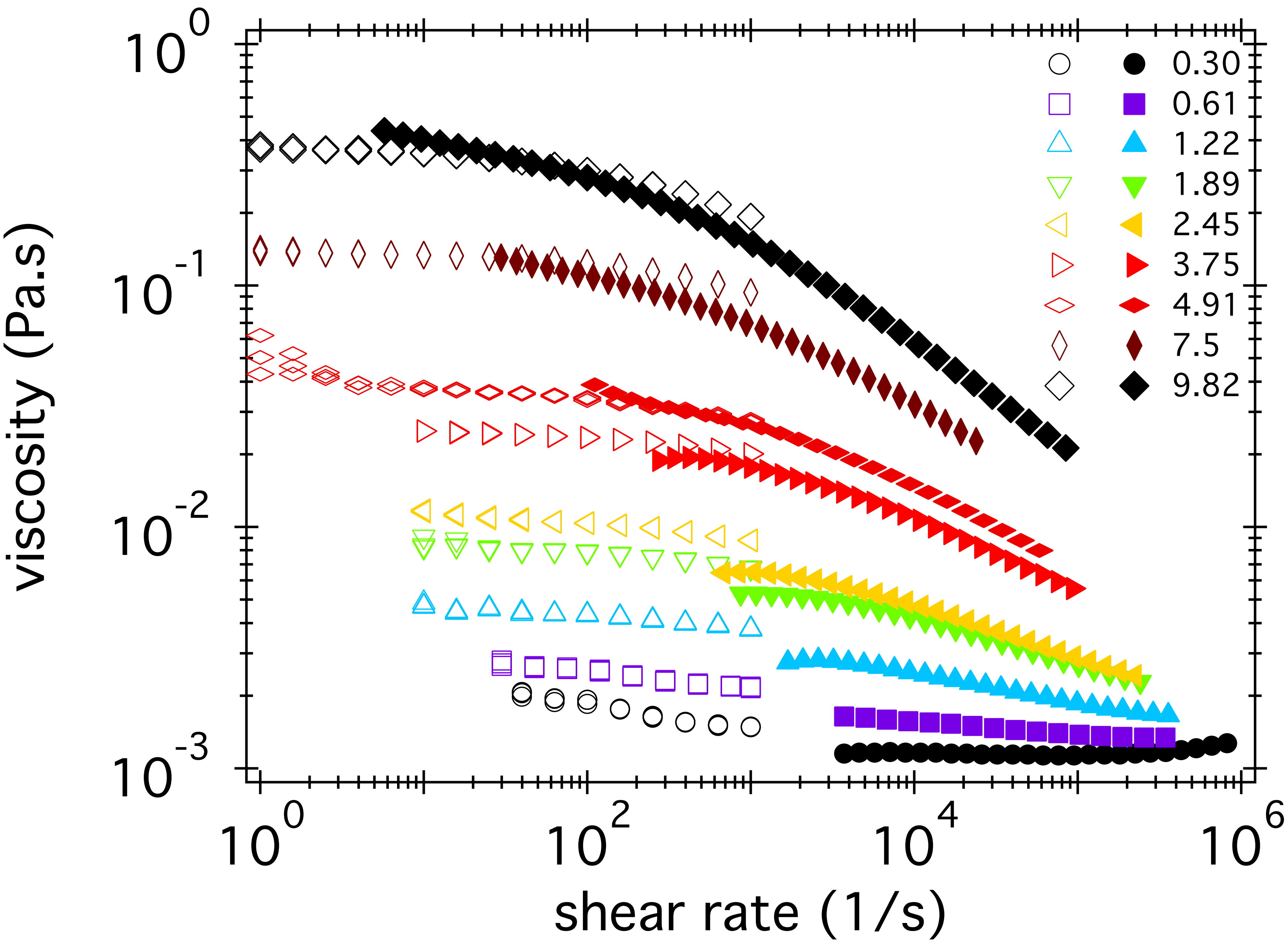
Assume most extreme shear thinning around flagella ...



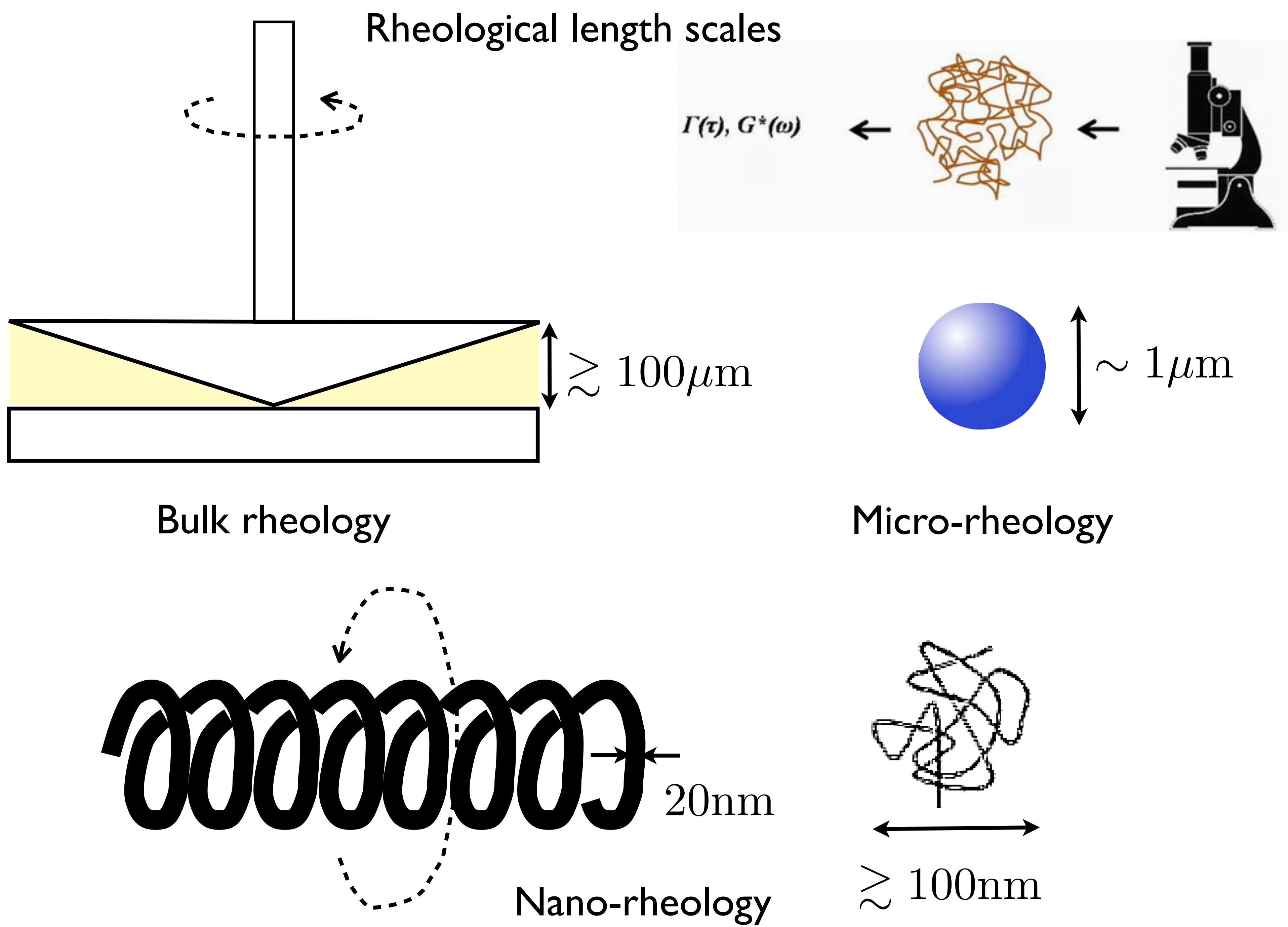
Predict $\Omega(v)$ using Purcell's (non-self-consistent) effective-flagellum *E. coli*

Honest, no fudge!

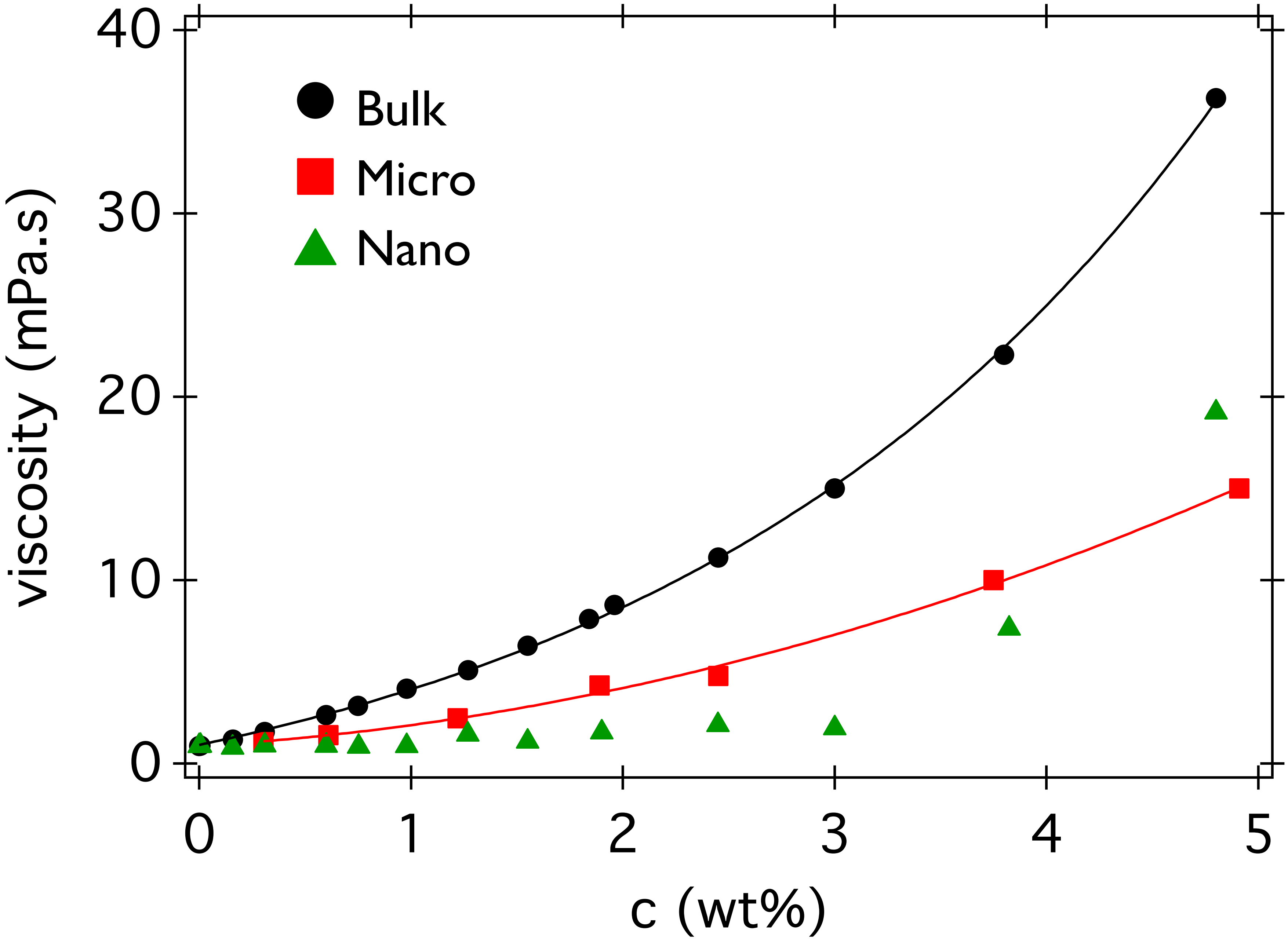


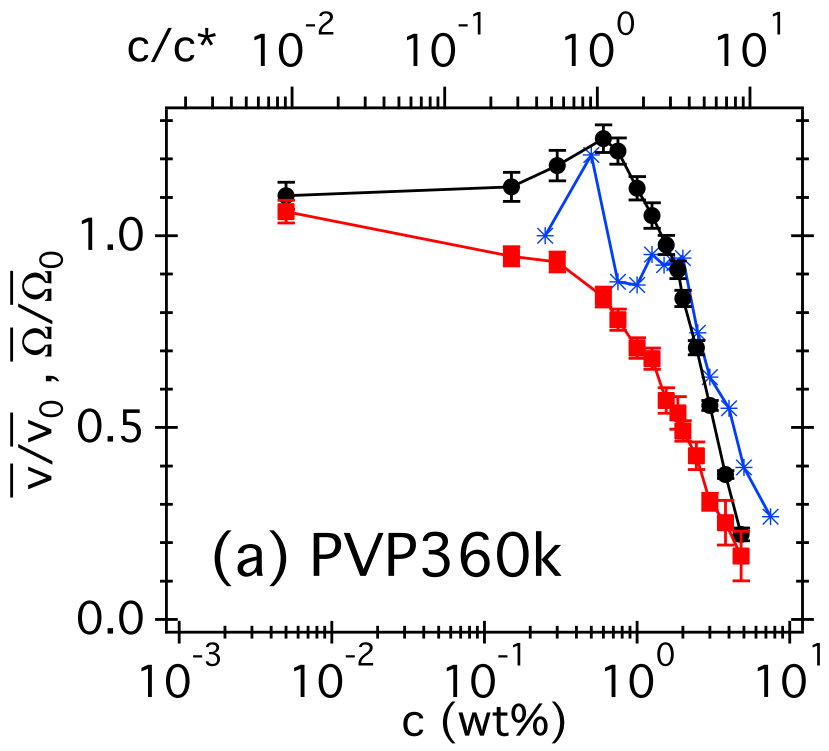


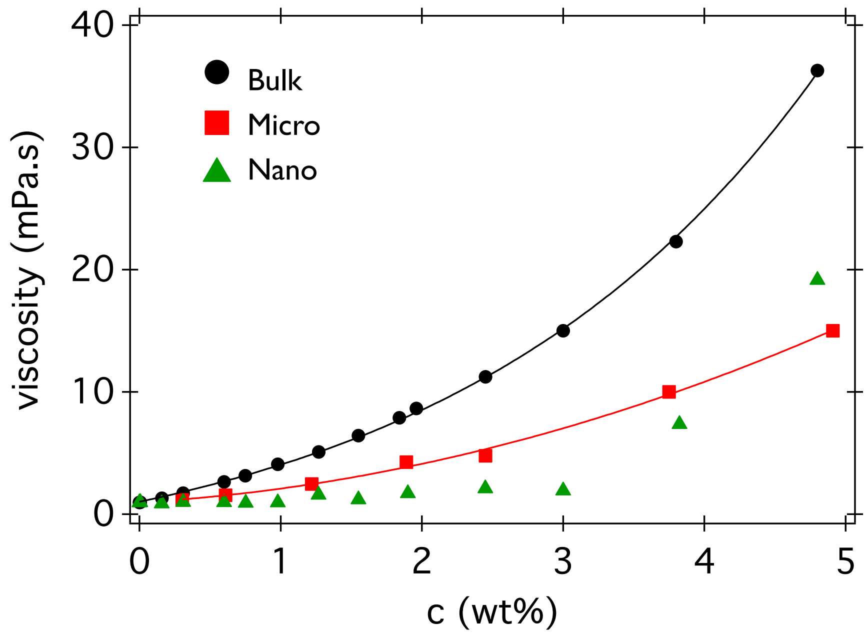
viscosity (Pa.s)
shear rate (1/s)
10^0
10^{-1}
10^{-2}
10^{-3}
10^0
10^2
10^4
10^6
0.30
0.61
1.22
1.89
2.45
3.75
4.91
7.5
9.82

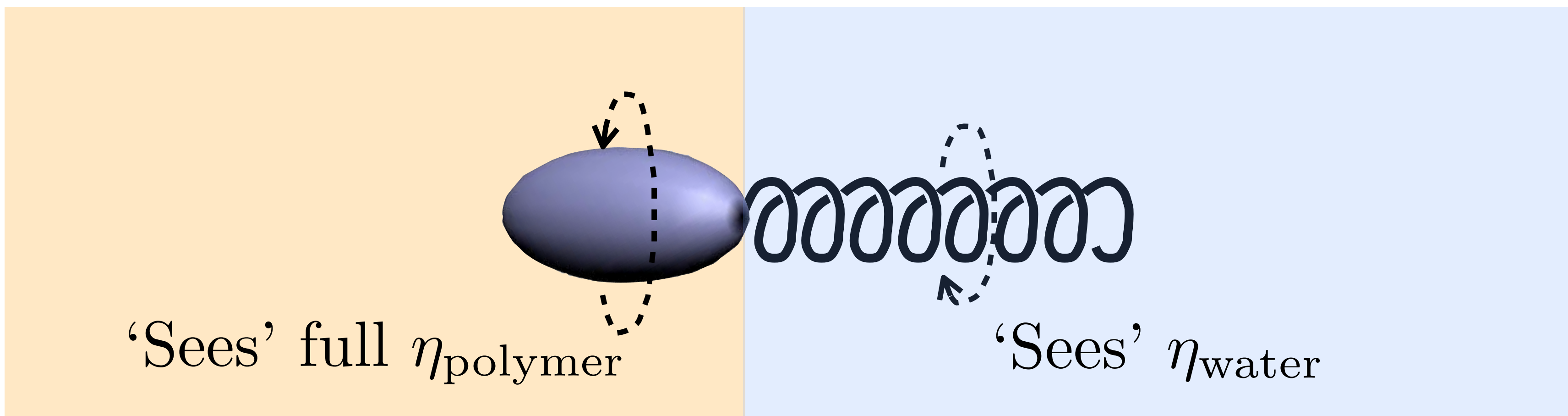


Rheological length scales
Γ(τ), G*(ω)
≳ 100μm
~ 1μm
Bulk rheology
Micro-rheology
20nm
Nano-rheology
≳ 100nm


Bulk
Micro
Nano
viscosity (mPa.s)
c (wt%)
0
10
20
30
40
0
1
2
3
4
5

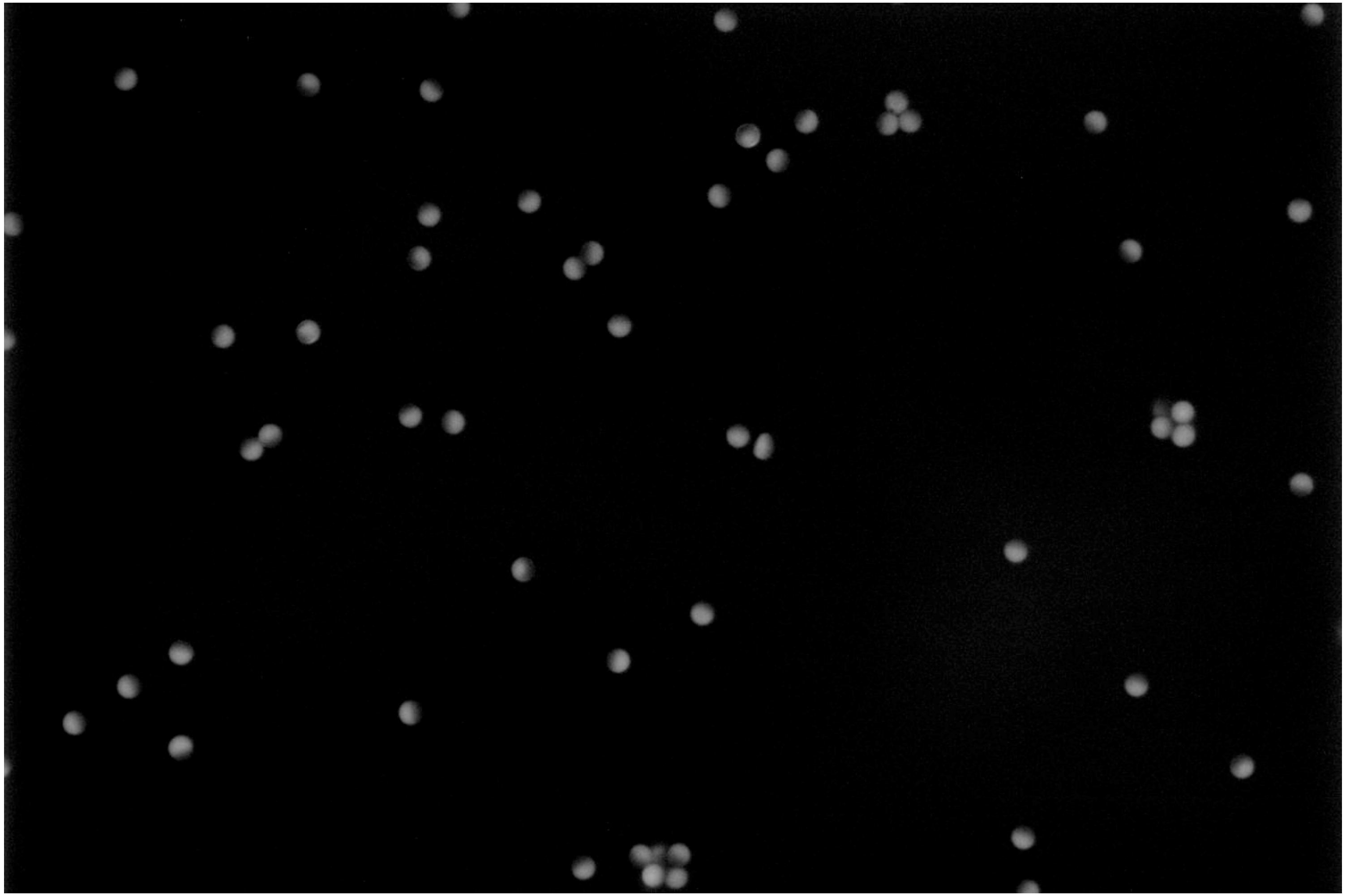




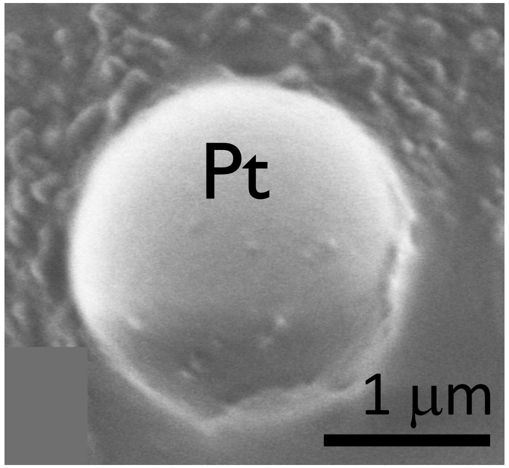


Bacterial flagella as nano-rheometer!

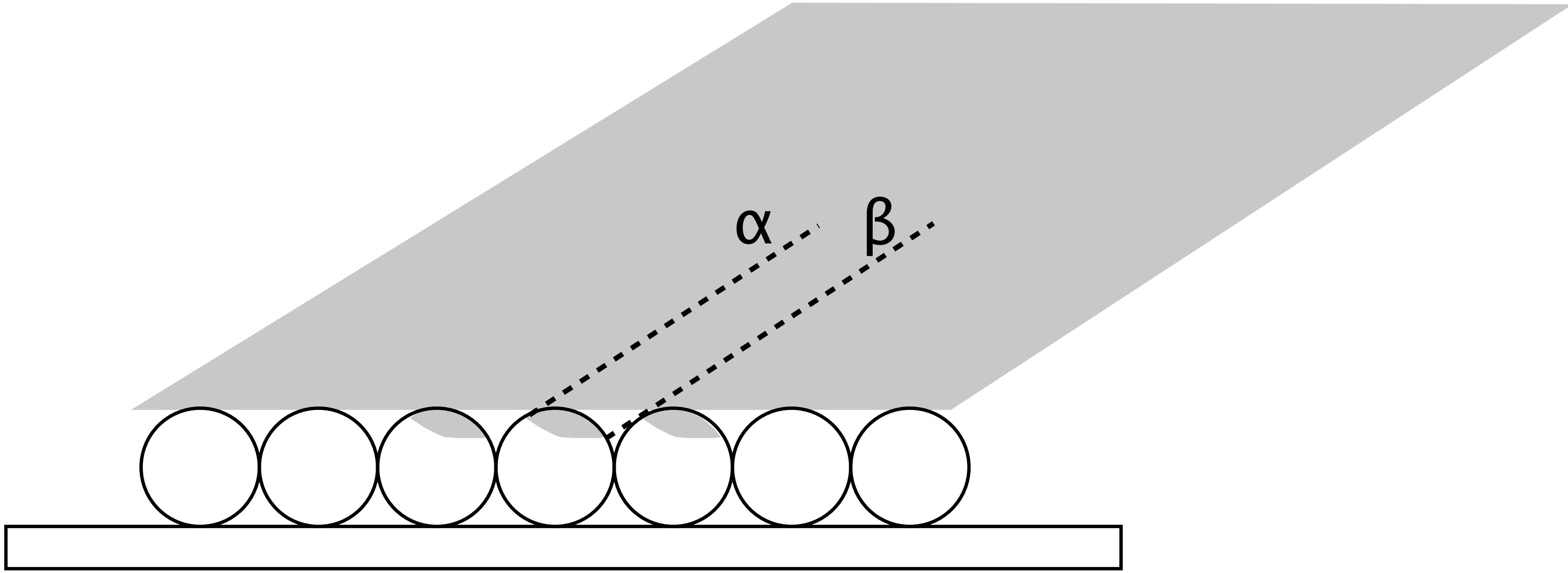
Now for something completely different ...



Aidan Brown



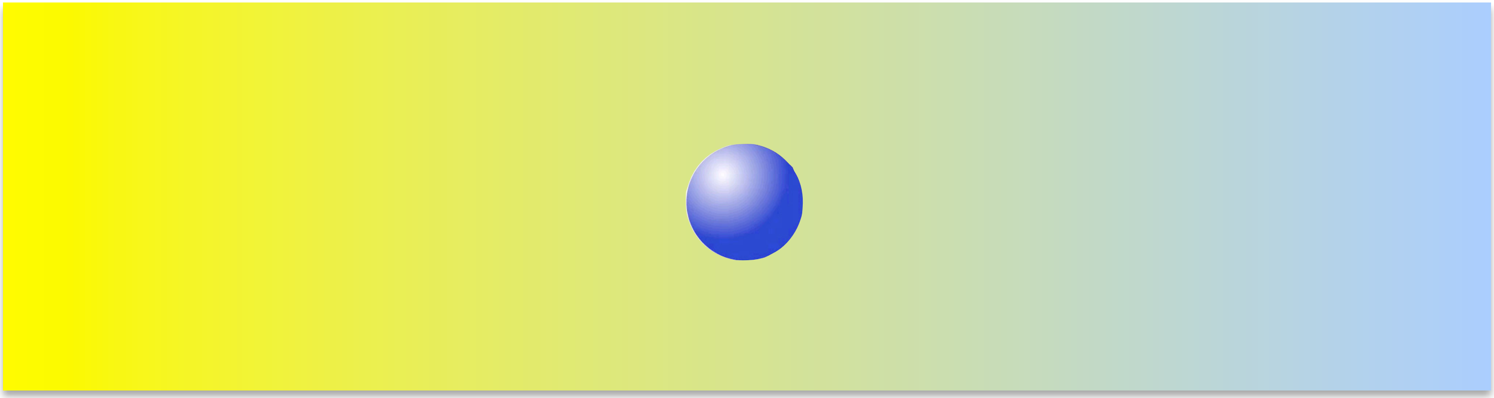
Made layer by layer …
… painfully low yield!



First demonstrated: Howse et al., *PRL* **99** (2007) 048102

Phoresis

Particle migration in gradients (T, c, $\boldsymbol{E}$, etc.)

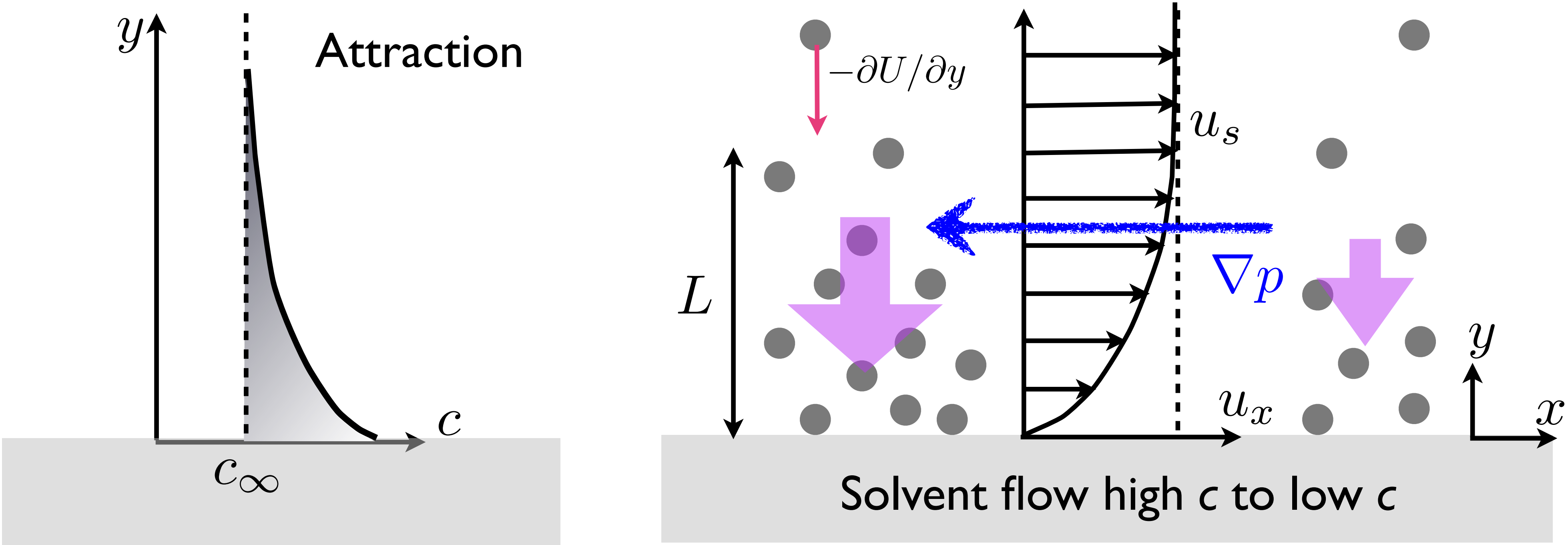


Put colloid in gradient of anything …

… it moves!

Janus particle creates its own gradients ...

... auto- or self-phoresis



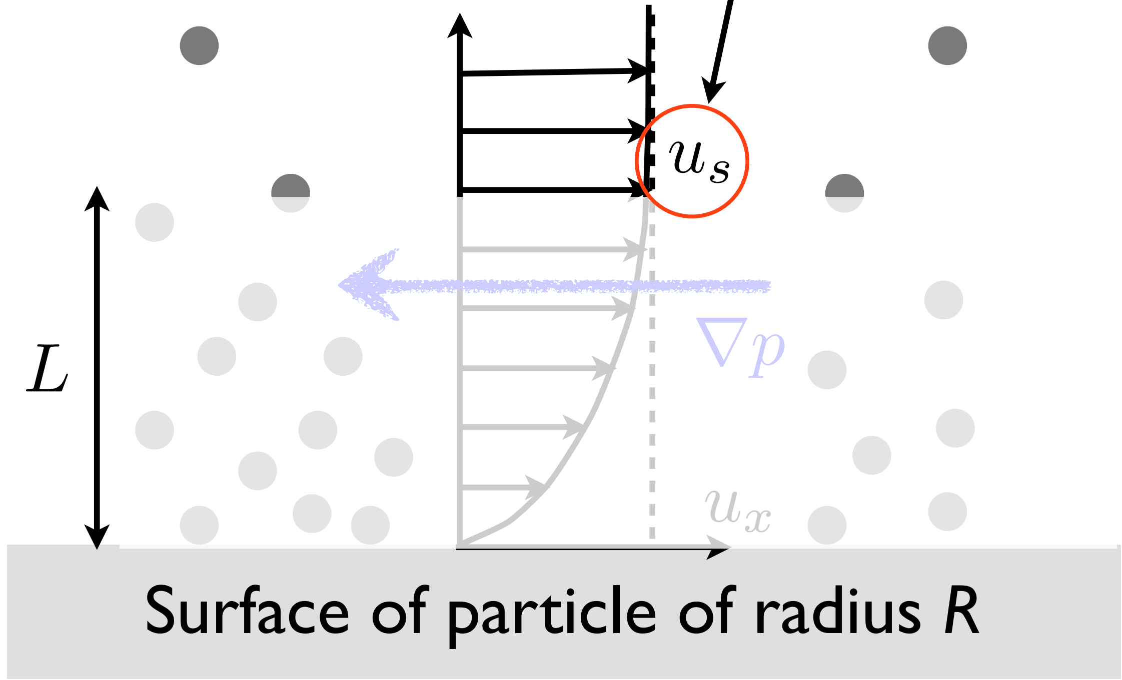
$$\text{Ideal solute: } P = ck_BT$$

$$\frac{dP}{dx} = k_BT\frac{dc}{dx} = \eta\frac{d^2u_x}{dy^2} \sim \eta\frac{u_s}{L^2}$$

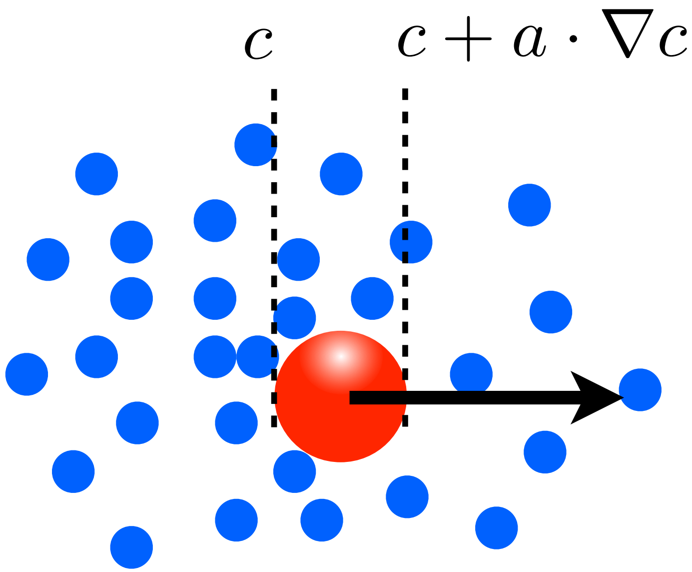
$$u_s \sim -\frac{k_BT}{\eta}L^2\frac{dc}{dx} \qquad u_{\mathrm{ph}} = -u_s$$

Up gradient if attractive
Down gradient if repulsive

Looks like slip boundary condition when *L* << *R*



A wrong argument



Ideal solute: $P = c k_B T$

Net pressure force $F \sim -(a \nabla c k_B T) a^2$

Particle drift velocity $\sim F/\eta a$

$$v \sim -\frac{k_B T}{\eta} a^2 \nabla c$$

$$u_s \sim -\frac{k_B T}{\eta} L^2 \nabla c$$

L: interaction length

Surface interaction with solute → force on fluid → flow

Propulsion of a Molecular Machine by Asymmetric Distribution of Reaction Products

Ramin Golestanian,[1,2,3] Tanniemola B. Liverpool,[1,3] and Armand Ajdari[4]
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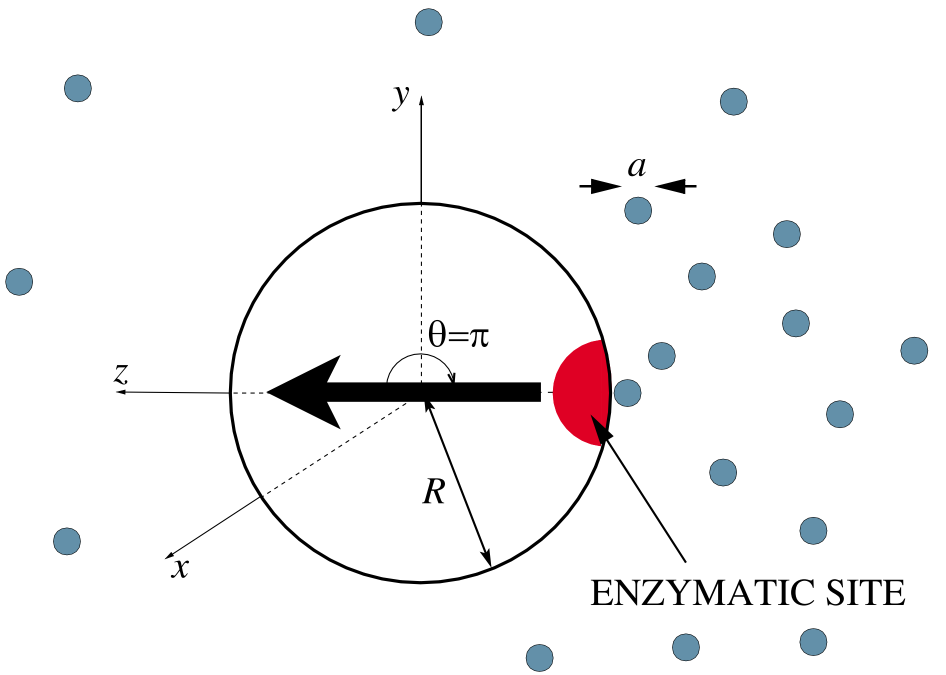
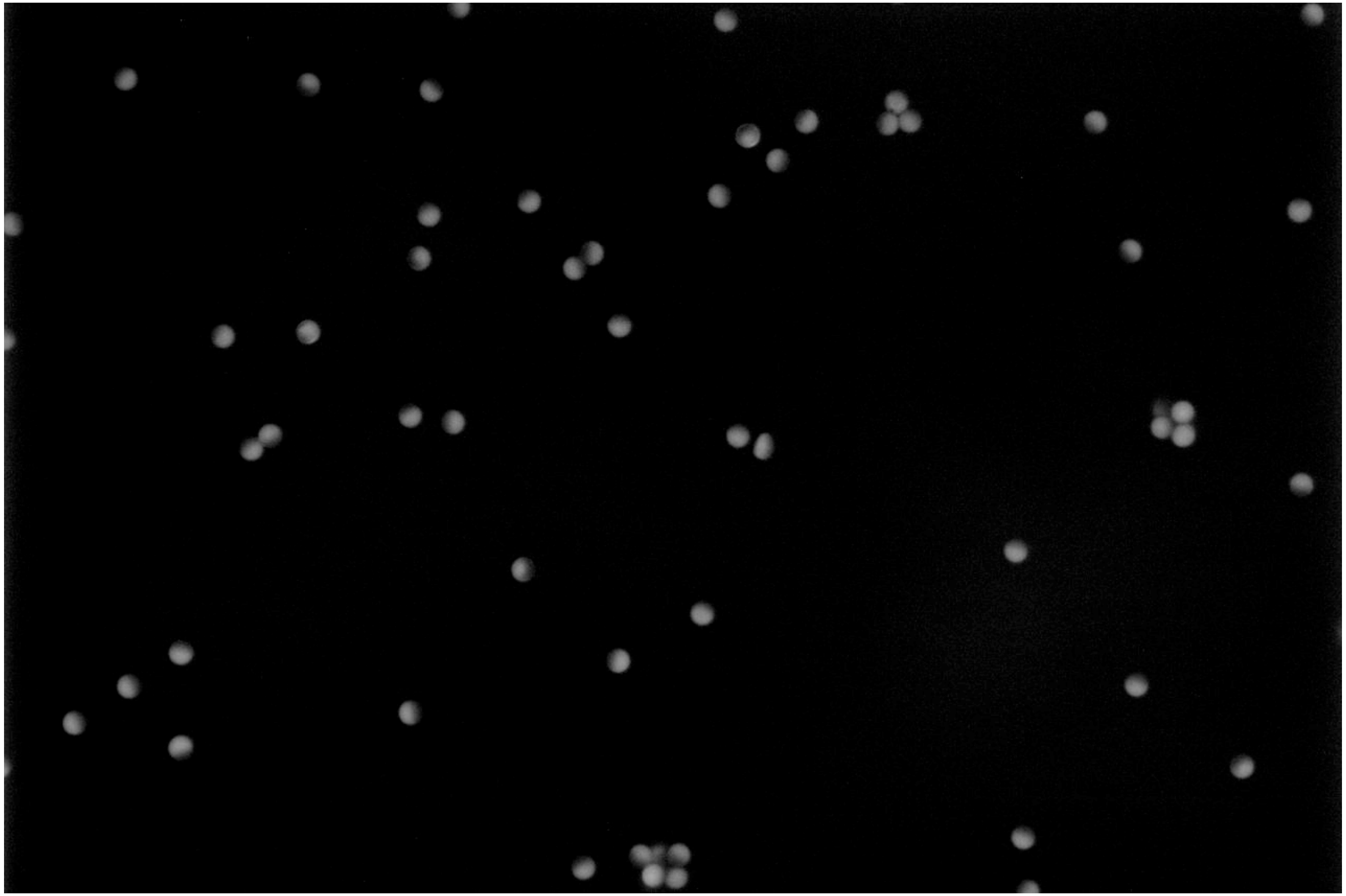
[2]Institute for Advanced Studies in Basic Sciences, Zanjan 45195-159, Iran
[3]Department of Applied Mathematics, University of Leeds, Leeds LS2 9JT, United Kingdom
[4]Laboratoire de Physico-Chimie Théorique, UMR CNRS 7083, ESPCI, 10 rue Vauquelin, F-75231 Paris Cedex 05, France
(Received 3 October 2004; published 10 June 2005)



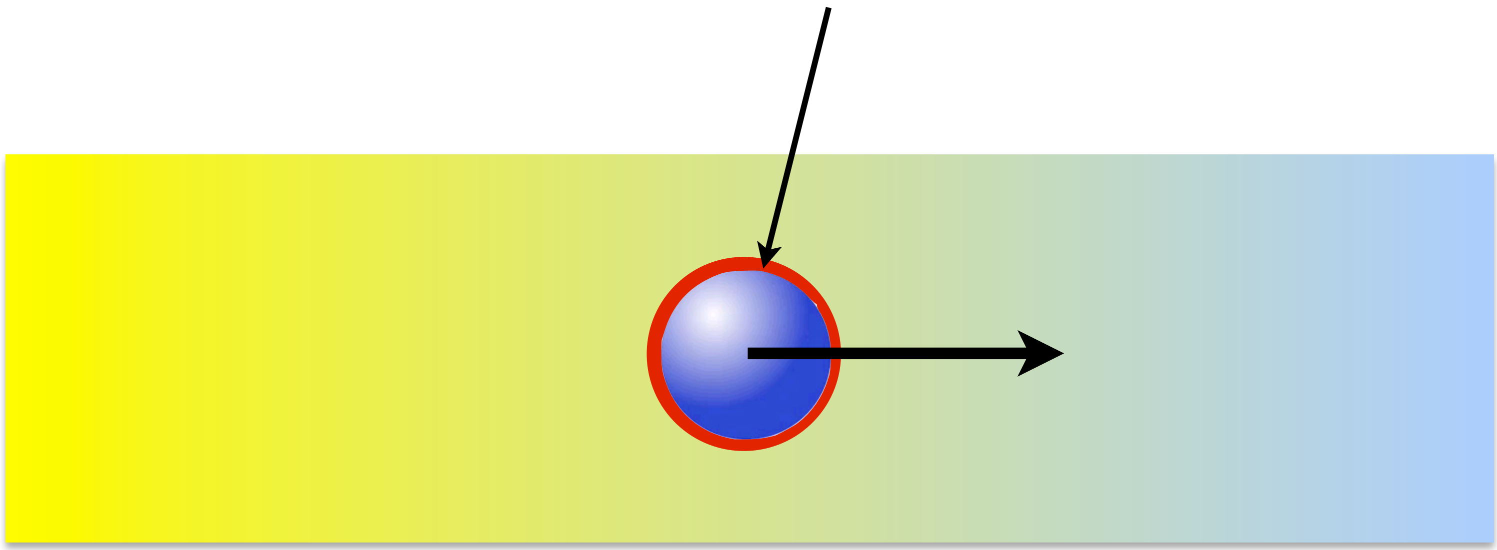
$2H_2O_2 \rightarrow 2H_2O + O_2$ Product = O_2

(Self) diffusiophoresis in gradient of catalytic decomposition product



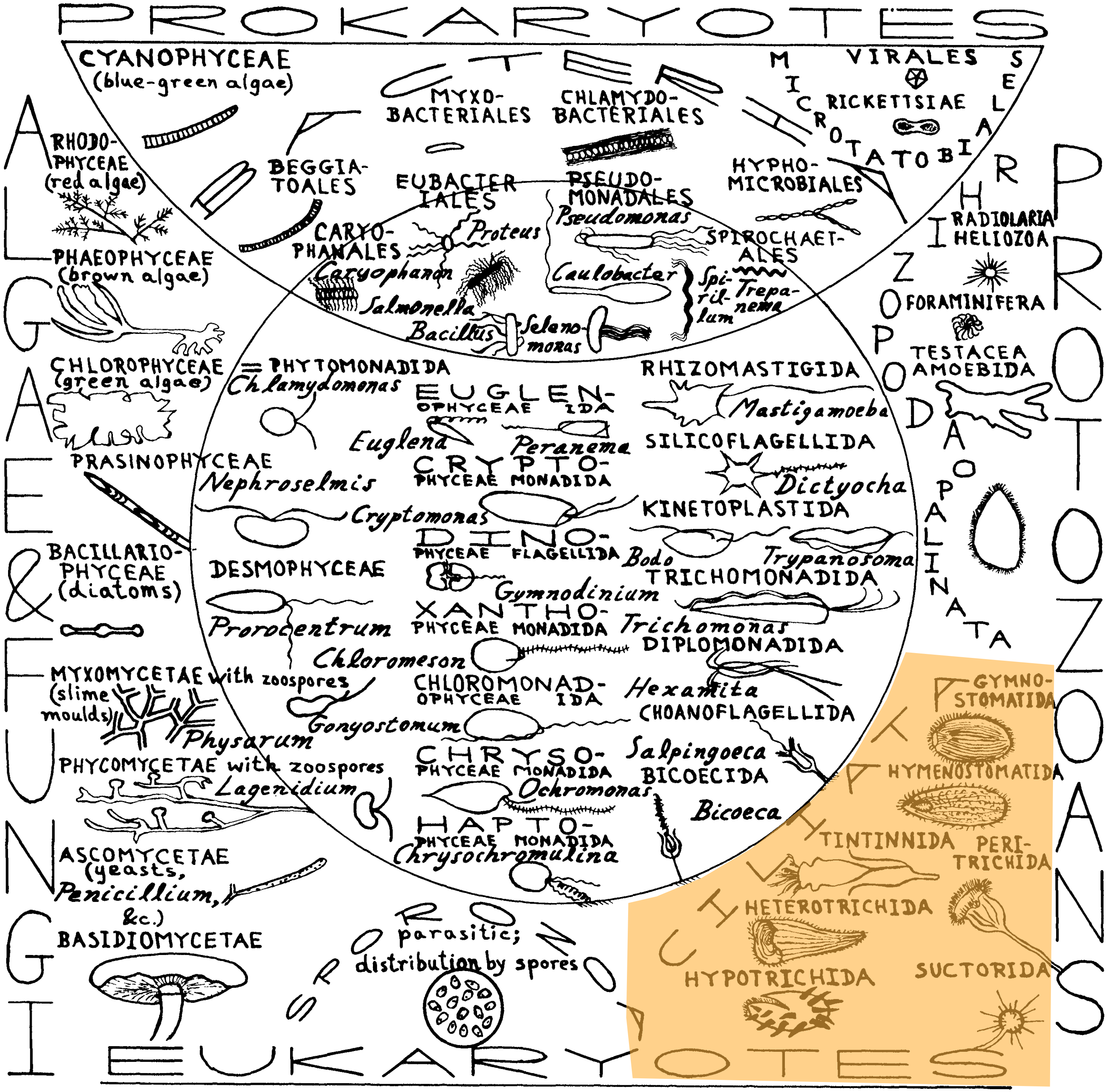
First demonstrated: Howse et al., *PRL* **99** (2007) 048102

Surface slip velocity $= f(\nabla c)$

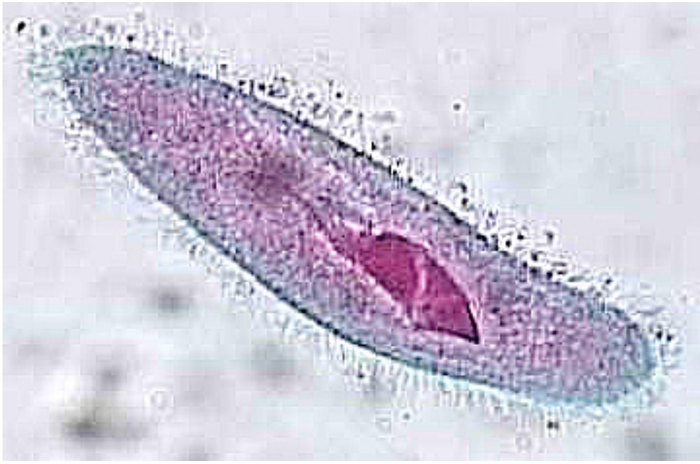


Swimmer with specified velocity field on surface …
'Squirmer'

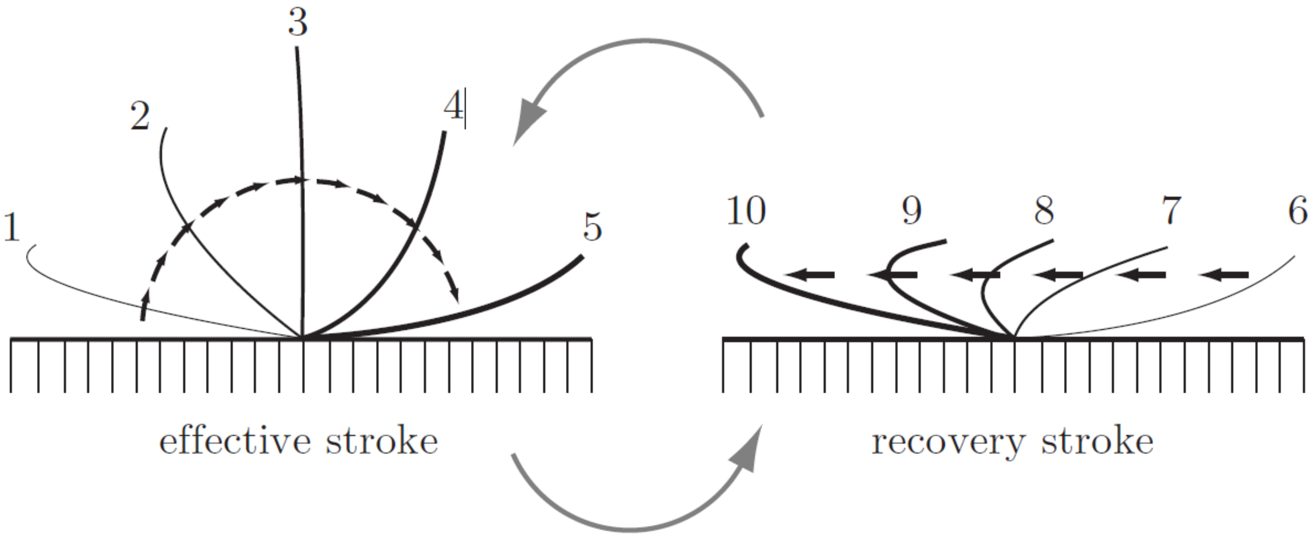
SOME MICROORGANISMS WITH FLAGELLA (CENTRAL CIRCLE) AND RELATED ORGANISMS

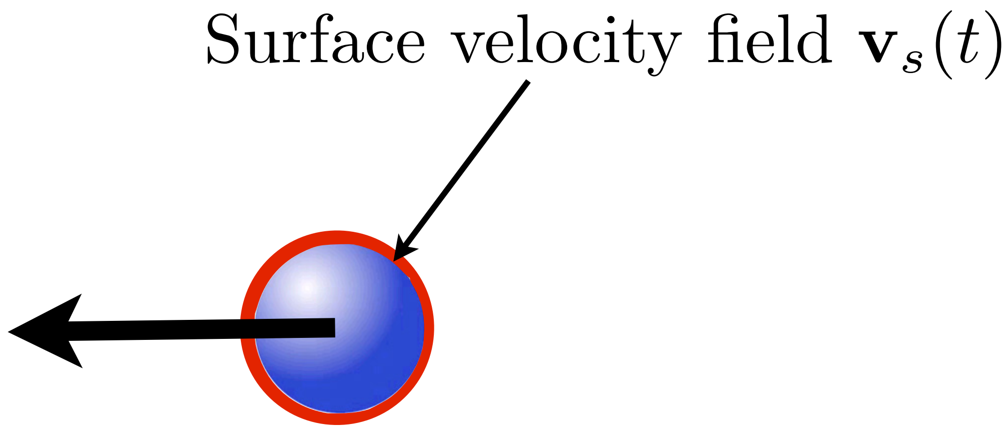


Paramecium: layer of beating cilia



Coordinated cilia beating (metachronal wave) → surface **v** field

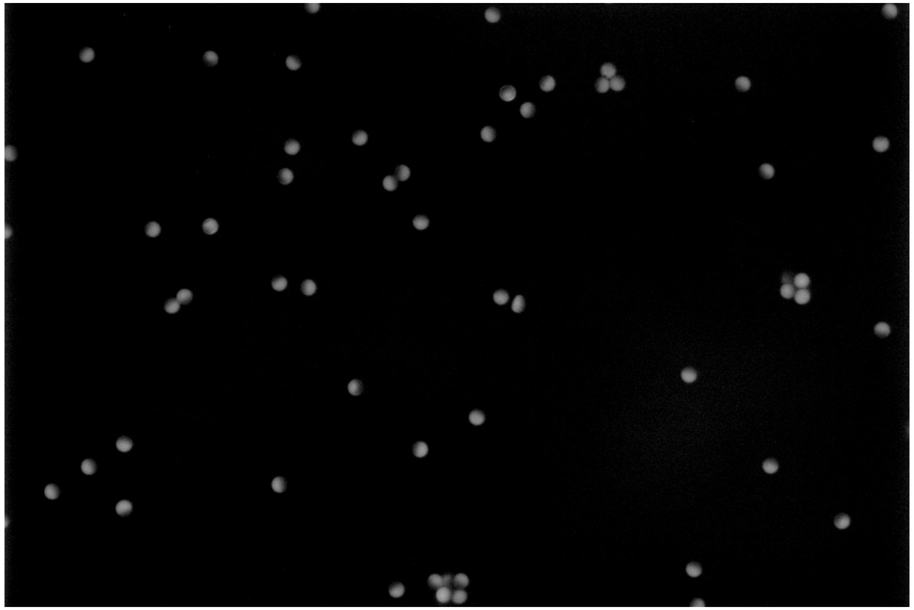


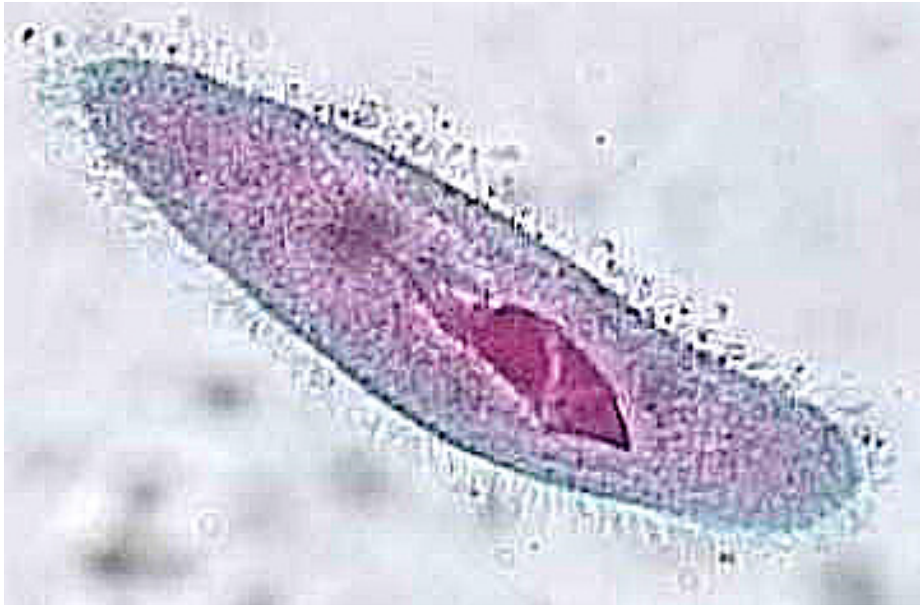


$$\mathbf{U}(t) = -\frac{1}{4\pi a^2}\iint_S \mathbf{v}_s(t)\, dS = -\langle \mathbf{v}_s \rangle$$

Proof from 'Lorentz reciprocal theorem'
e.g. Stone & Samuel *PRL* **77** (1996) 4102
(but already in Anderson & Prieve 1984)

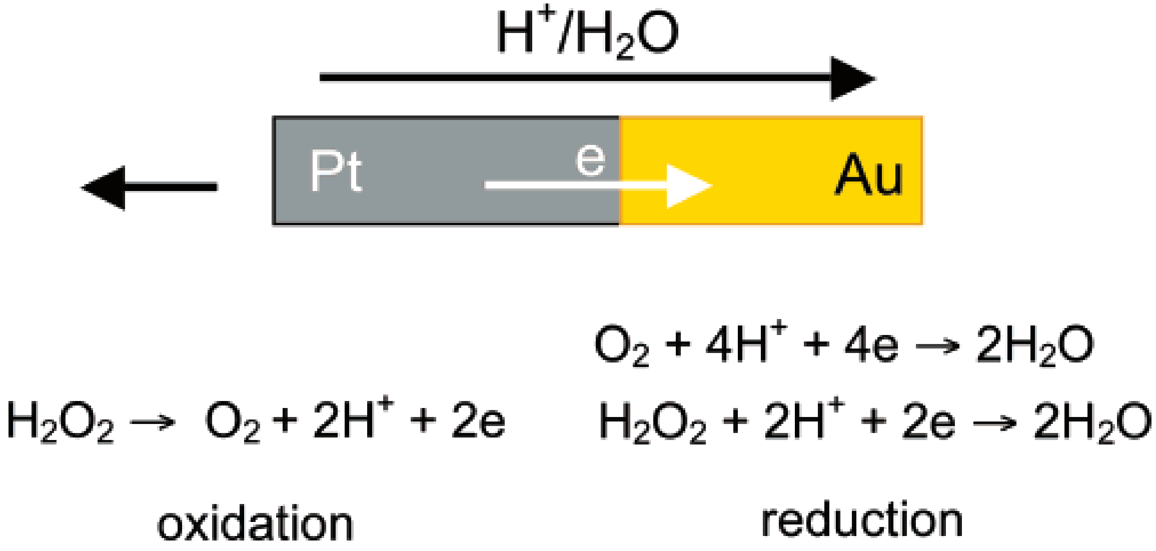
Conceptually similar ...





… artificial & natural squirmers

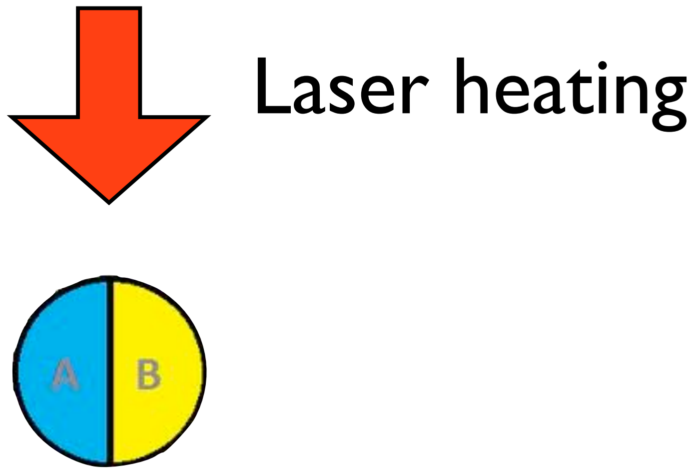
Scheme 1. Bipolar Electrochemical Decomposition of H_2O_2 at a Pt−Au Nanorod[a]



Self electrophoresis mechanism

Wang et al., *Langmuir* (2006)

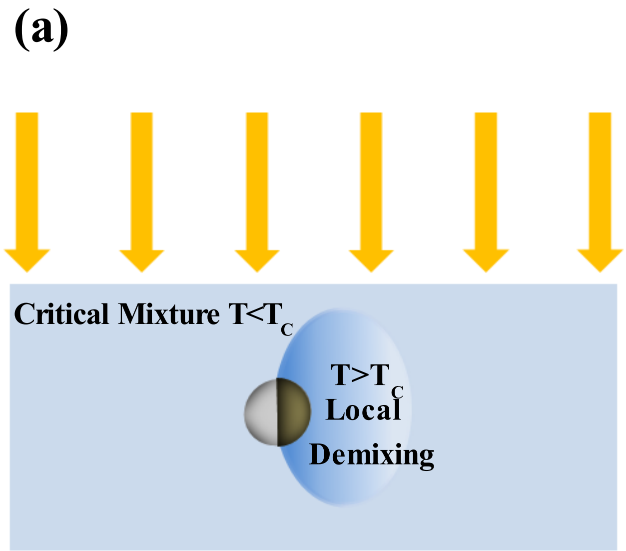
Thermophoresis: migration in temperature gradient

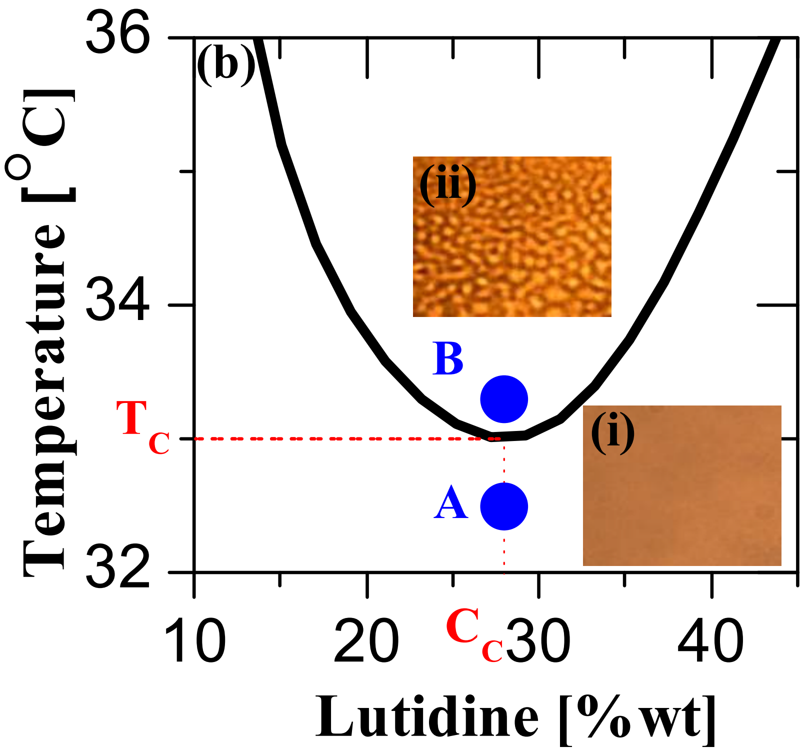


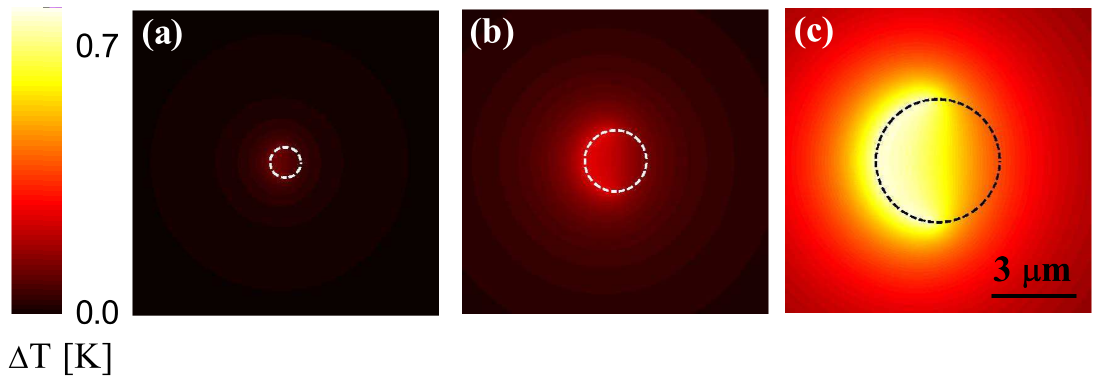
Uneven heating = temperature gradient

(Jiang et al., *PRL* (2010))

Concentration & temperature together

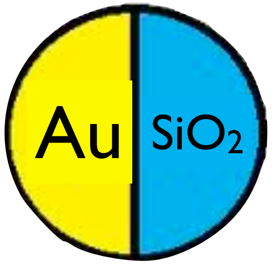






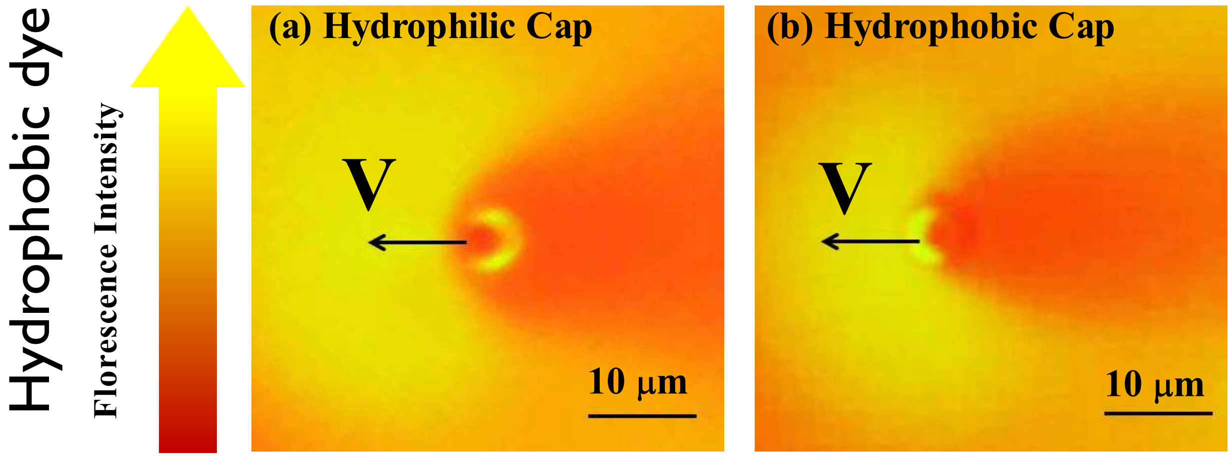
Bechinger *Soft Matter* (2011); arXiv:1110.2202v3

Hotter → demixing



Functionalised with SAM displaying hydrophobic *or* hydrophilic end groups

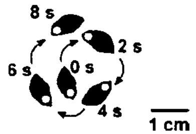
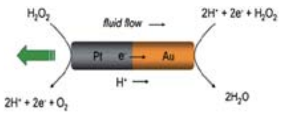
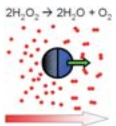
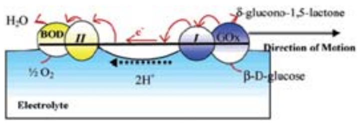
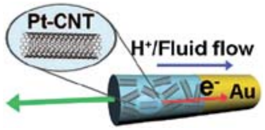
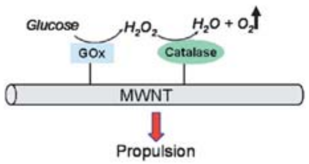
Changes direction of lutidine gradient



Hydrophilic cap   Hydrophobic cap

Table 1 Significant micro scale swimming devices classified according to type, and in chronological order

A: Experimentally realised autonomous chemically powered swimmers

Swimmer	*Schematic/Micrograph*	*Dimensions*	*Catalyst*	*Fuel*	*Mechanisms*	*Swim in:*	*Max. Velocity*
(A1) Whitesides and co-workers[8]	 White dot indicates Pt catalyst	1 cm length	Pt	H_2O_2	Bubble propulsion	Aqueous meniscus	2 cm s^{-1}
(A2) Sen and co-workers[9]		Diameter: 370 nm Length: 2 µm	Pt (+cathodic reactions at Au)	H_2O_2	Self electrophoresis/ Interfacial tension	Settled near boundary in aqueous solution	6.6 µm s^{-1}
(A3) Howse *et al.*[14]		Diameter: 1.62 µm	Pt	H_2O_2	Pure self diffusiophoresis	Free aqueous solution	3 µm s^{-1}[a]
(A4) Mano and Heller[35]		Diameter: 7 µm Length: 0.5–1 cm	Glucose oxidase and Biliruben oxidase	Glucose	Self electrophoresis	Aqueous meniscus	1 cm s^{-1}
(A5) Vicario *et al.*[37]		Diameter: 40–80 µm	Synthetic catalse	H_2O_2	Bubble/interfacial	Acetonitrile solution	35 µm s^{-1}
(A6) Wang *et al.*[23]		Diameter: 220 nm Length: 2 µm	Pt (CNT) (+cathodic reactions at Au)	H_2O_2/N_2H_4	Self electrophoresis	Settled near boundary in aqueous solution	>200 µm s^{-1}
(A7) Pantarotto *et al.*[36]		Diameter: 20–80 nm Length: 0.5–5 µm	Glucose oxidase and catalse	Glucose	Local oxygen bubble formation	Free aqueous buffer solution	0.2–0.8 cm s^{-1}

Propulsion of a Molecular Machine by Asymmetric Distribution of Reaction Products

Ramin Golestanian,[1,2,3] Tanniemola B. Liverpool,[1,3] and Armand Ajdari[4]
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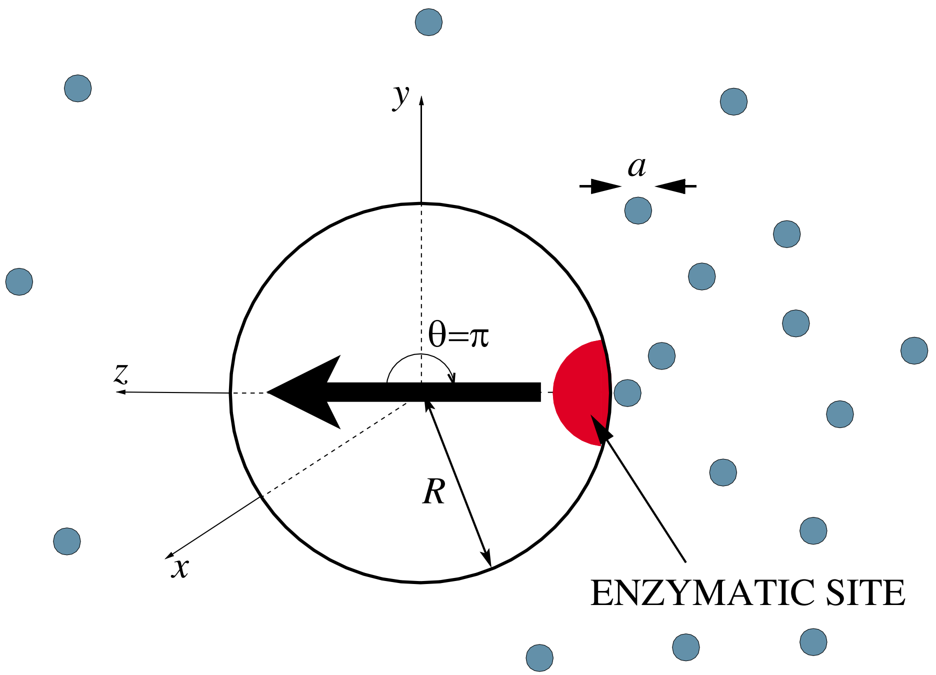
[2]*Institute for Advanced Studies in Basic Sciences, Zanjan 45195-159, Iran*
[3]*Department of Applied Mathematics, University of Leeds, Leeds LS2 9JT, United Kingdom*
[4]*Laboratoire de Physico-Chimie Théorique, UMR CNRS 7083, ESPCI, 10 rue Vauquelin, F-75231 Paris Cedex 05, France*
(Received 3 October 2004; published 10 June 2005)



Does it work?

Physical realisation

PRL **99,** 048102 (2007) PHYSICAL REVIEW LETTERS week ending 27 JULY 2007

Self-Motile Colloidal Particles: From Directed Propulsion to Random Walk

Jonathan R. Howse,[1] Richard A. L. Jones,[1,*] Anthony J. Ryan,[2] Tim Gough,[3] Reza Vafabakhsh,[4] and Ramin Golestanian[1,†]
[1]*Department of Physics and Astronomy, University of Sheffield, Sheffield S3 7RH, United Kingdom*
[2]*Department of Chemistry, University of Sheffield, Sheffield S3 7HF, United Kingdom*
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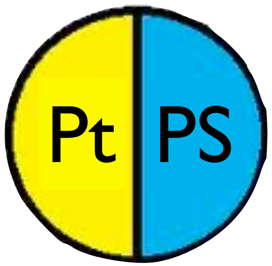
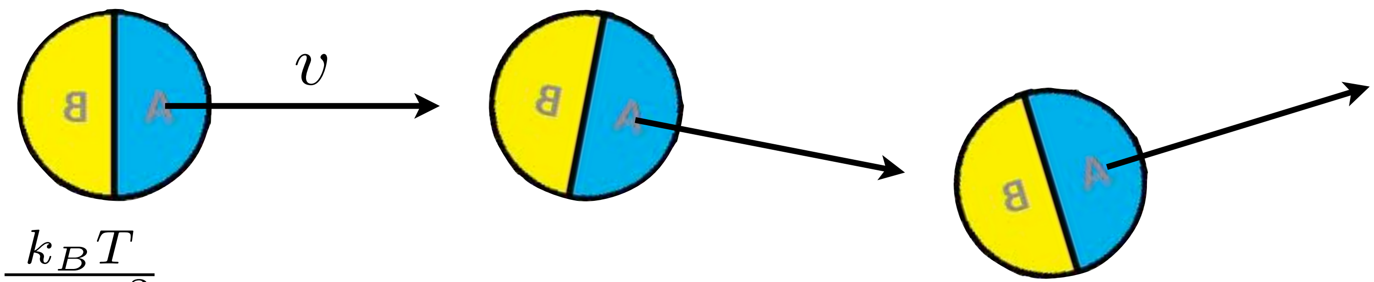
(Received 6 March 2007; published 27 July 2007)

$$2H_2O_2 \rightarrow 2H_2O + O_2$$



Polystyrene particles half-coated with Pt
Dispersed in H_2O_2

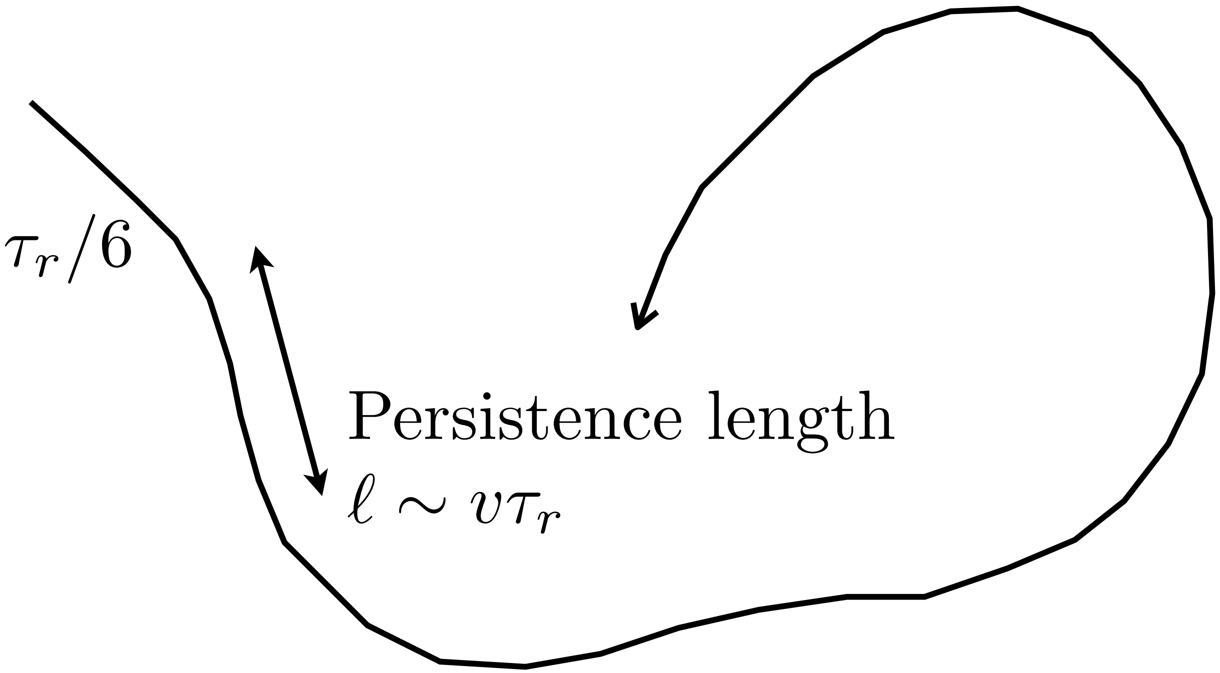
Linear propulsion + rotational diffusion

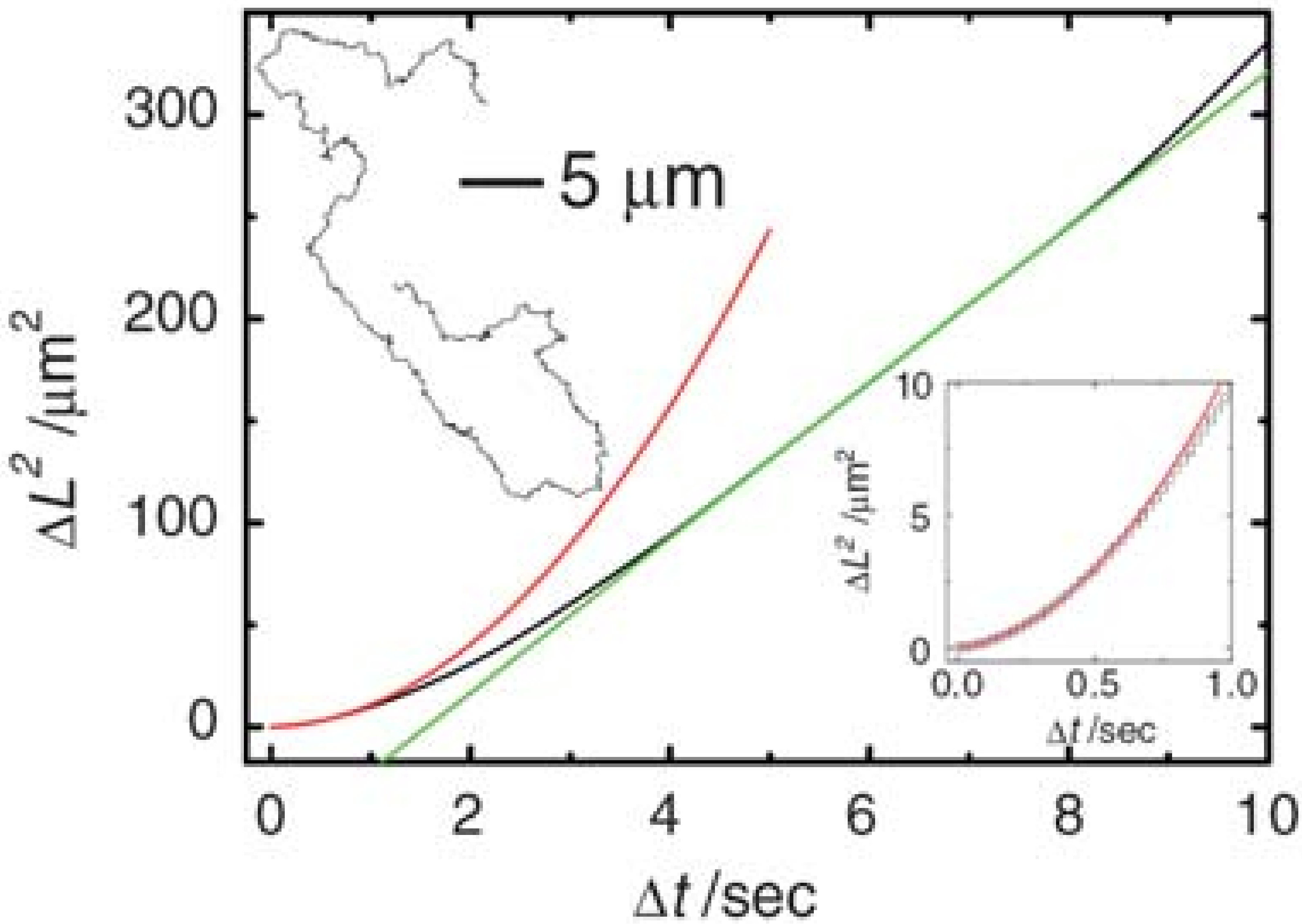


$$D_r = \frac{k_B T}{8\pi\eta a^3}$$

$$\langle\theta^2\rangle = D_r\tau_r = 1 \rightarrow \tau_r = D_r^{-1}$$

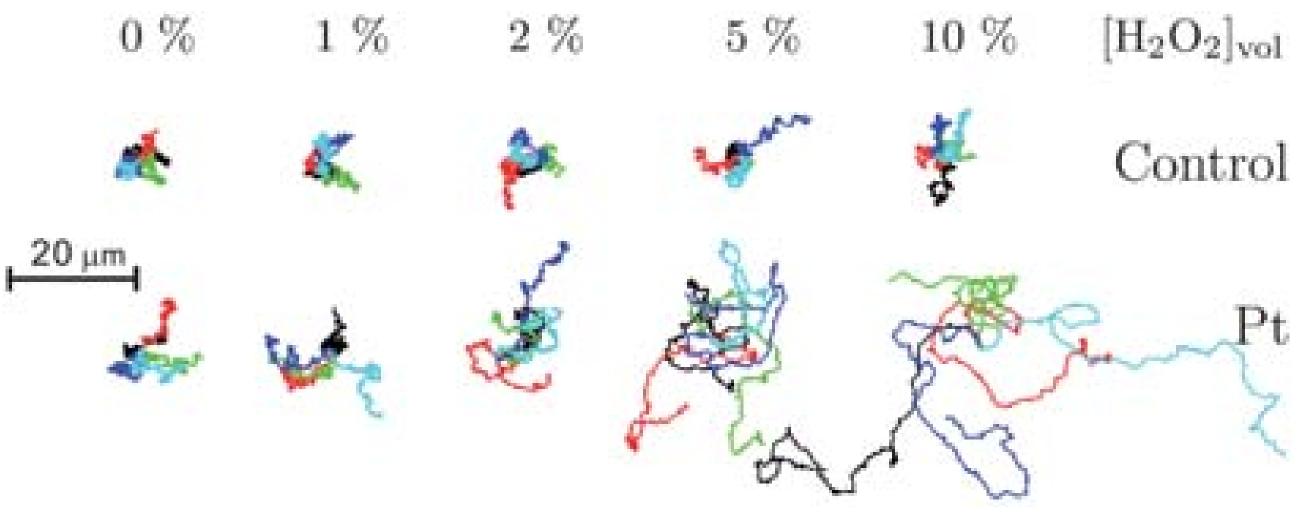
Ballistic at $t \ll \tau_r$
Diffusive at $t \gg \tau_r$
with $D_{\text{eff}} = D_0 + v^2\tau_r/6$





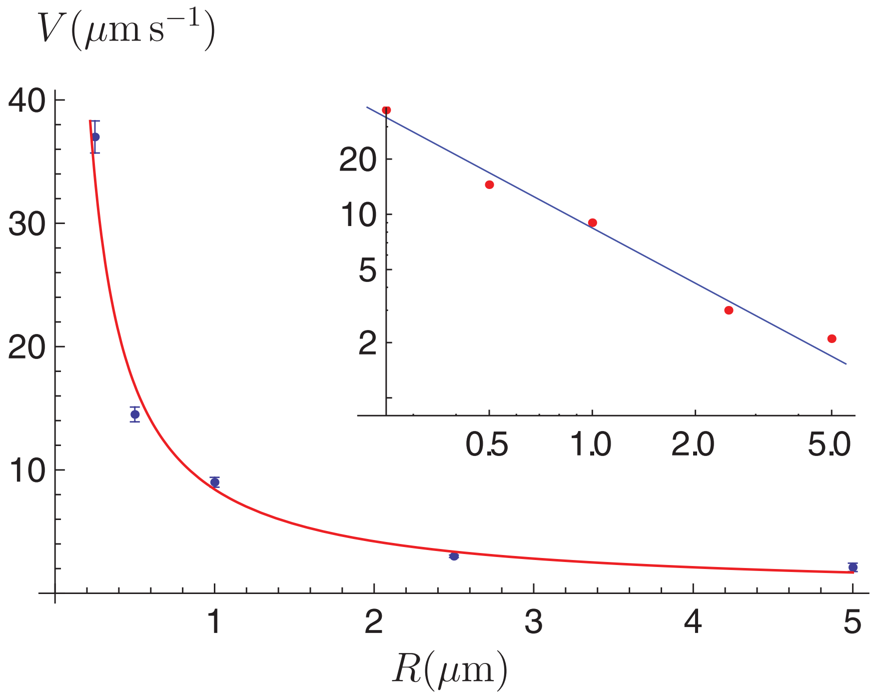
300
200
100
0
ΔL^2 /μm^2
5 μm
0
2
4
6
8
10
Δt /sec
10
5
0
0.0
0.5
1.0
ΔL^2 /μm^2
Δt /sec

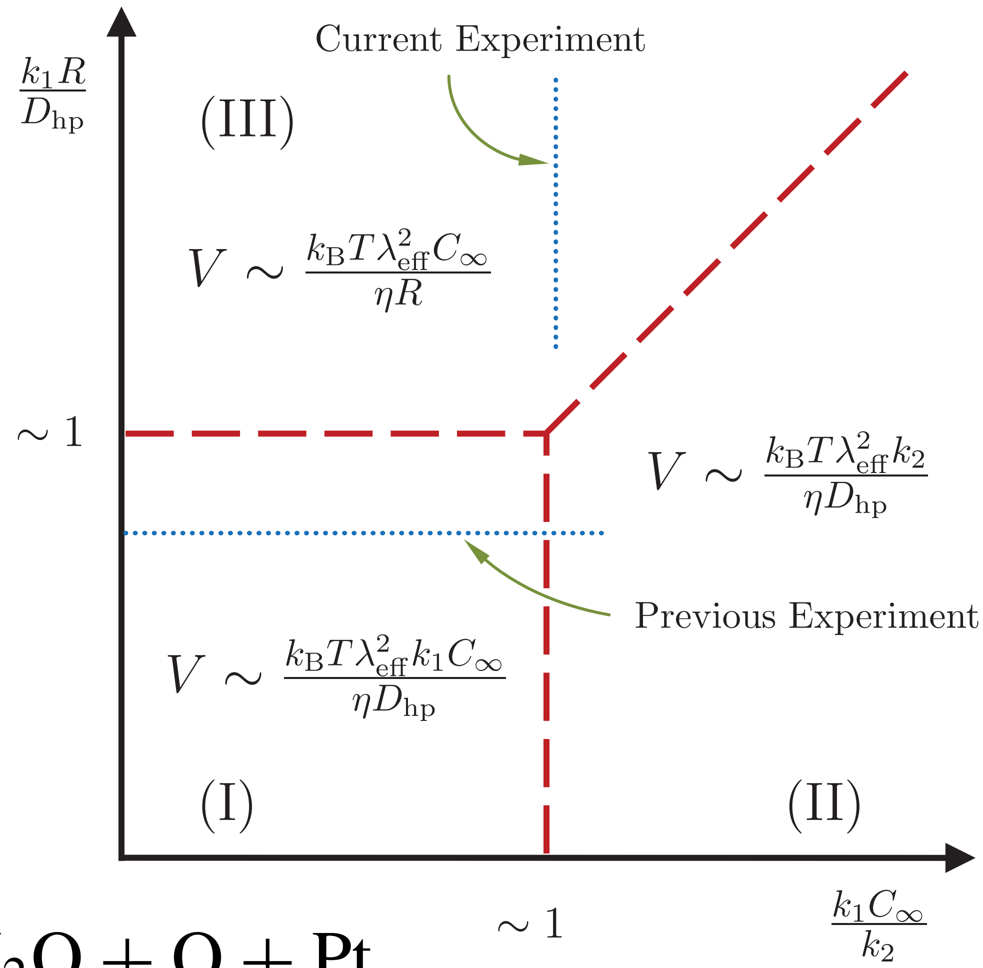
Tuning the propulsion



Ebbens et al., *PRE* **85** (2012) 020401

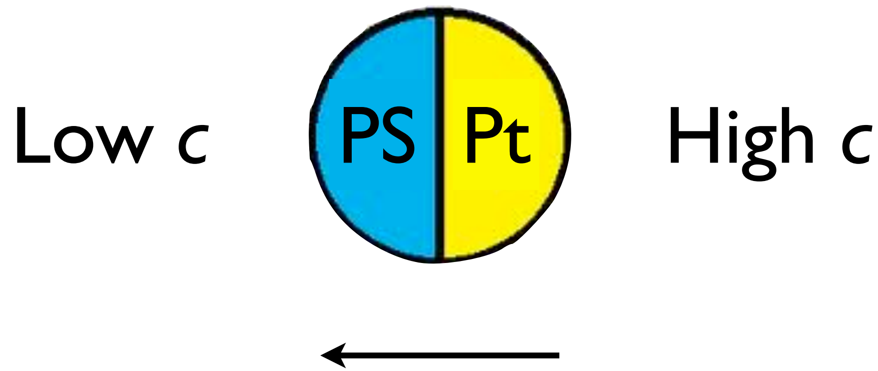
Solve reaction-diffusion equations



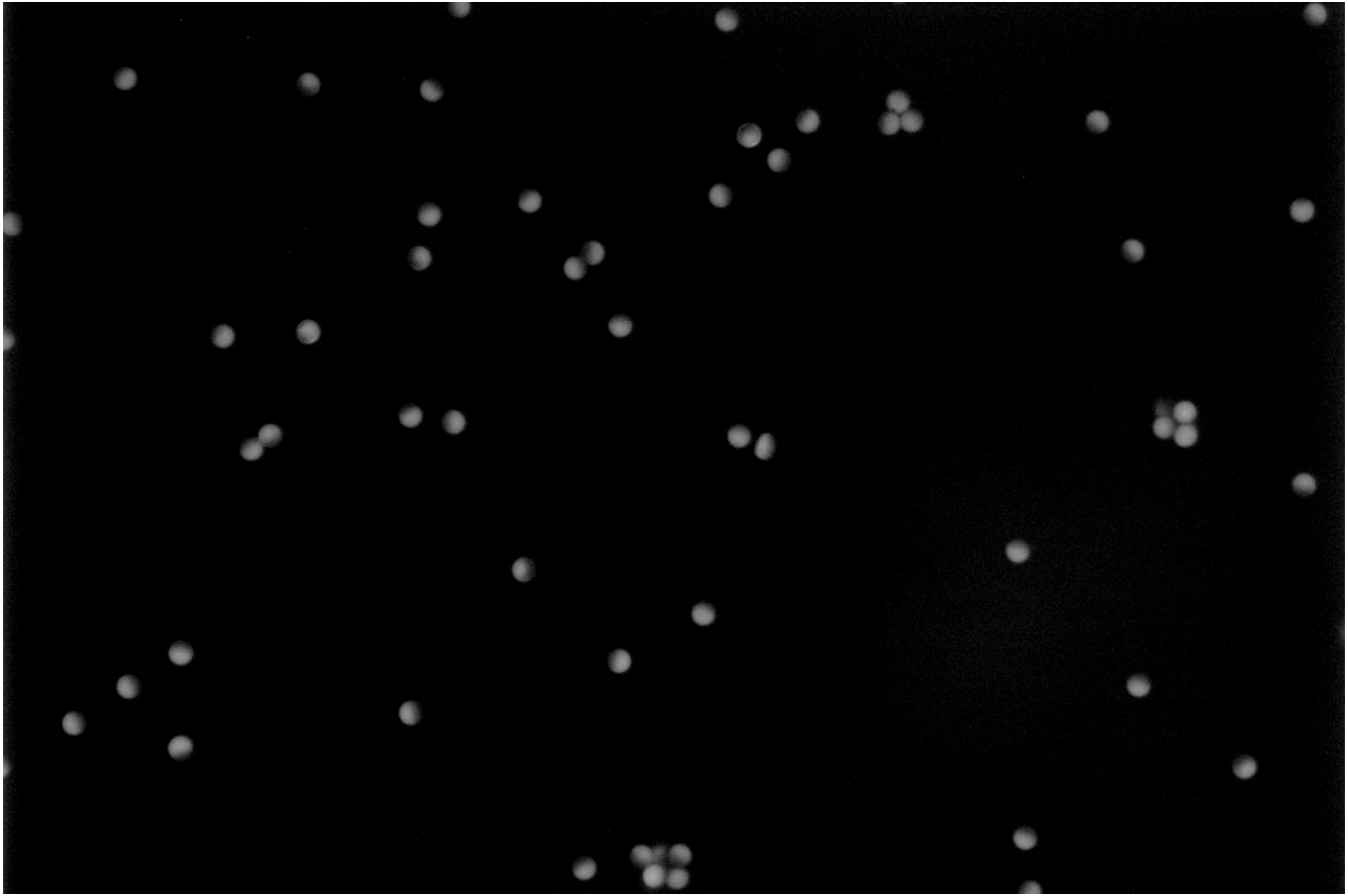


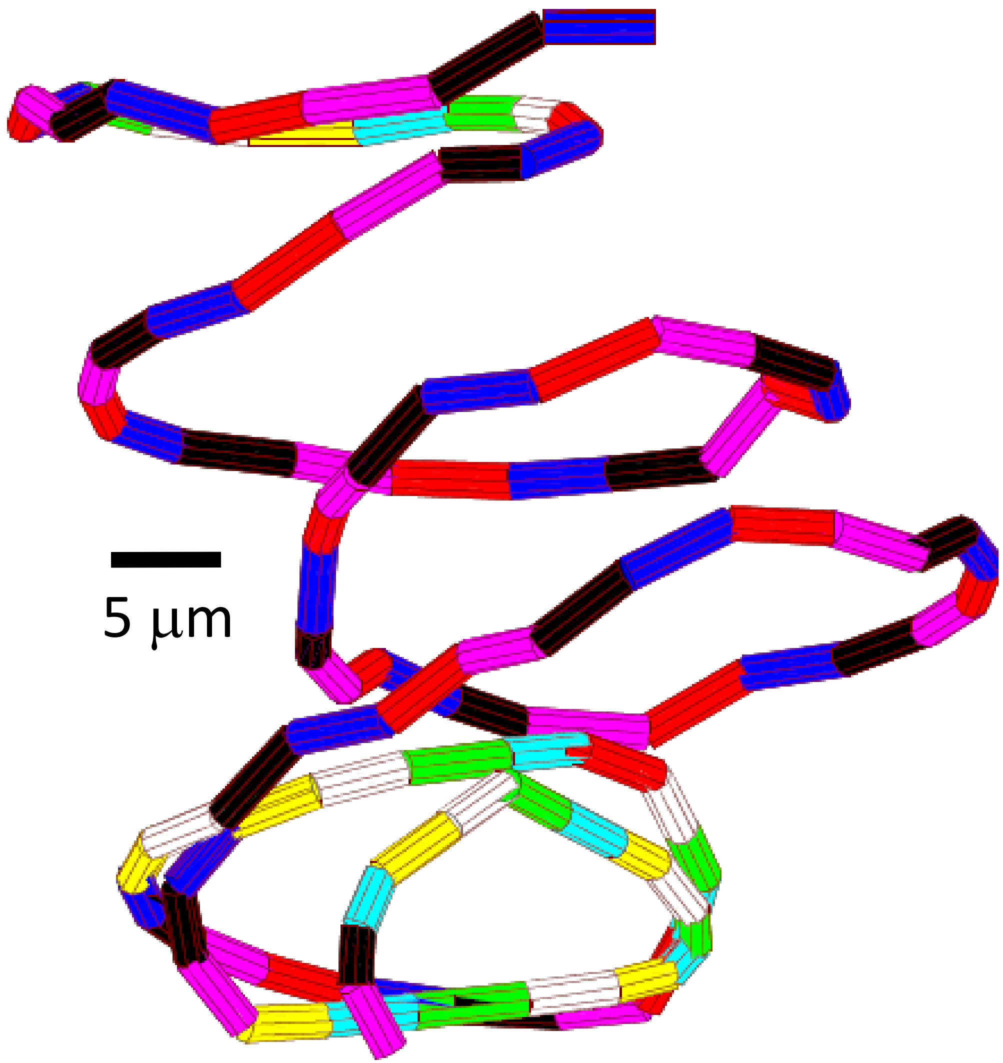
$$H_2O_2 + Pt \xrightarrow{k_1} Pt(H_2O_2) \xrightarrow{k_2} H_2O + O + Pt.$$

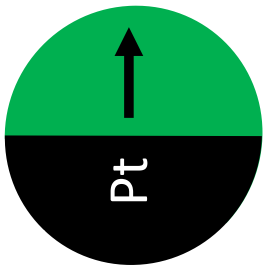
Which way does it move in?



That is what the Sheffield group observes.





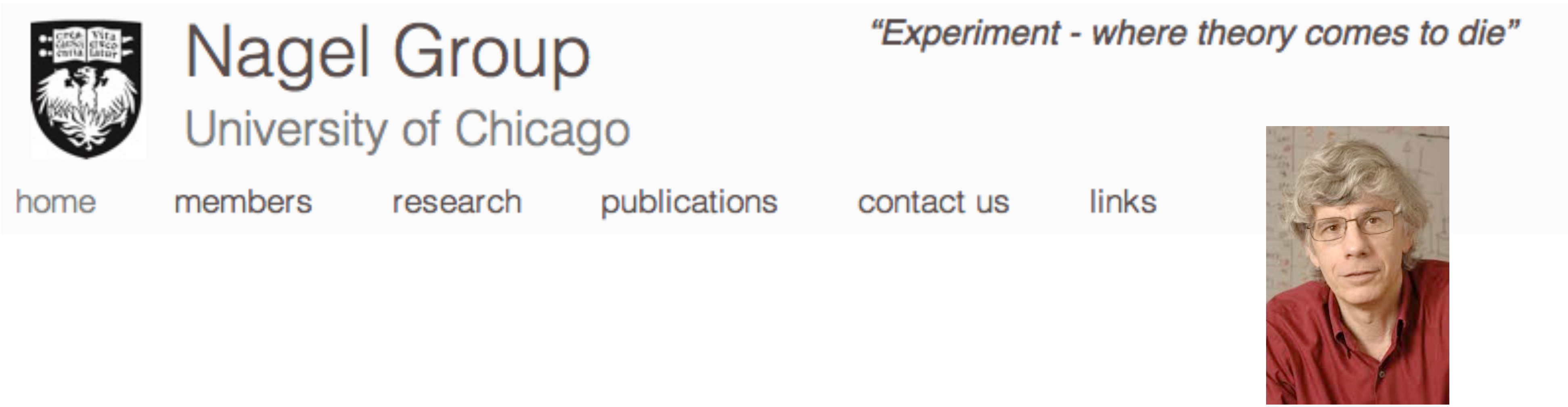


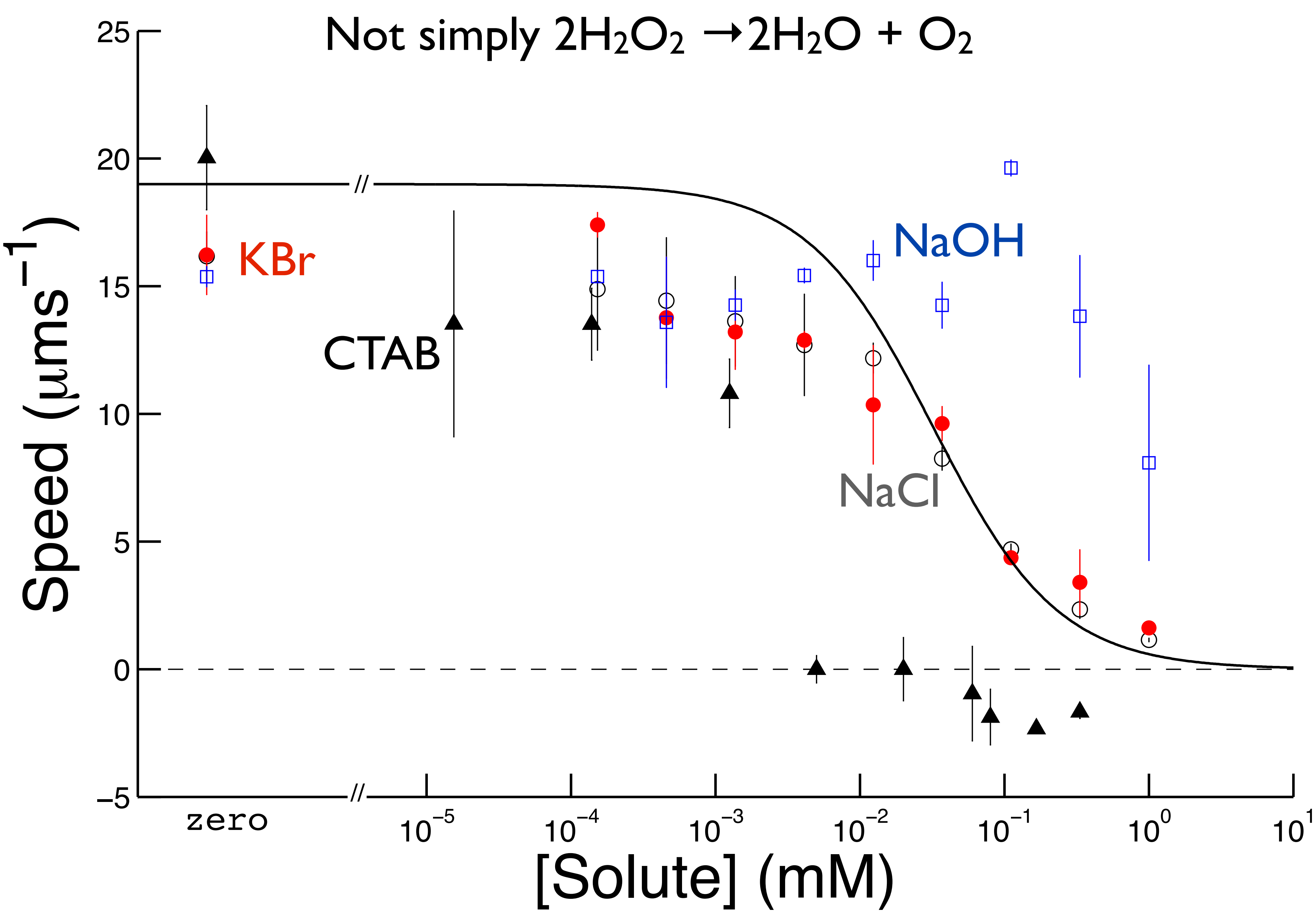
+ asymmetry

cf. *Chlamydomonas* gravitaxis

Theorem:

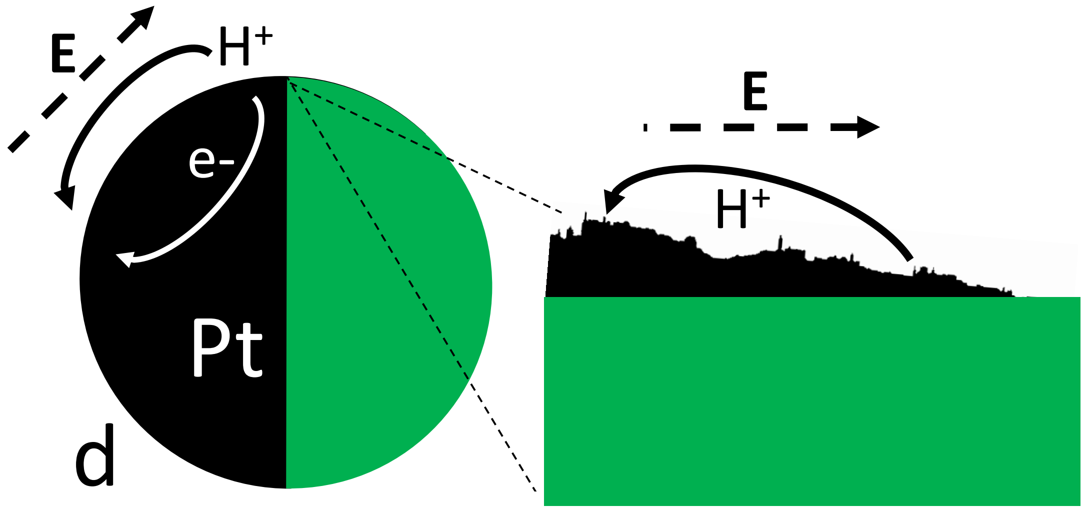
Don’t get too excited when theory agrees with experiment!




Not simply $2H_2O_2 \rightarrow 2H_2O + O_2$
Speed (μms^{-1})
25
20
15
10
5
0
−5
KBr
NaOH
CTAB
NaCl
zero
10^{-5}
10^{-4}
10^{-3}
10^{-2}
10^{-1}
10^{0}
10^{1}
[Solute] (mM)

$$H_2O_2 + 2\,e^- + 2\,H^+ \rightleftharpoons 2\,H_2O \quad \text{reduction}$$

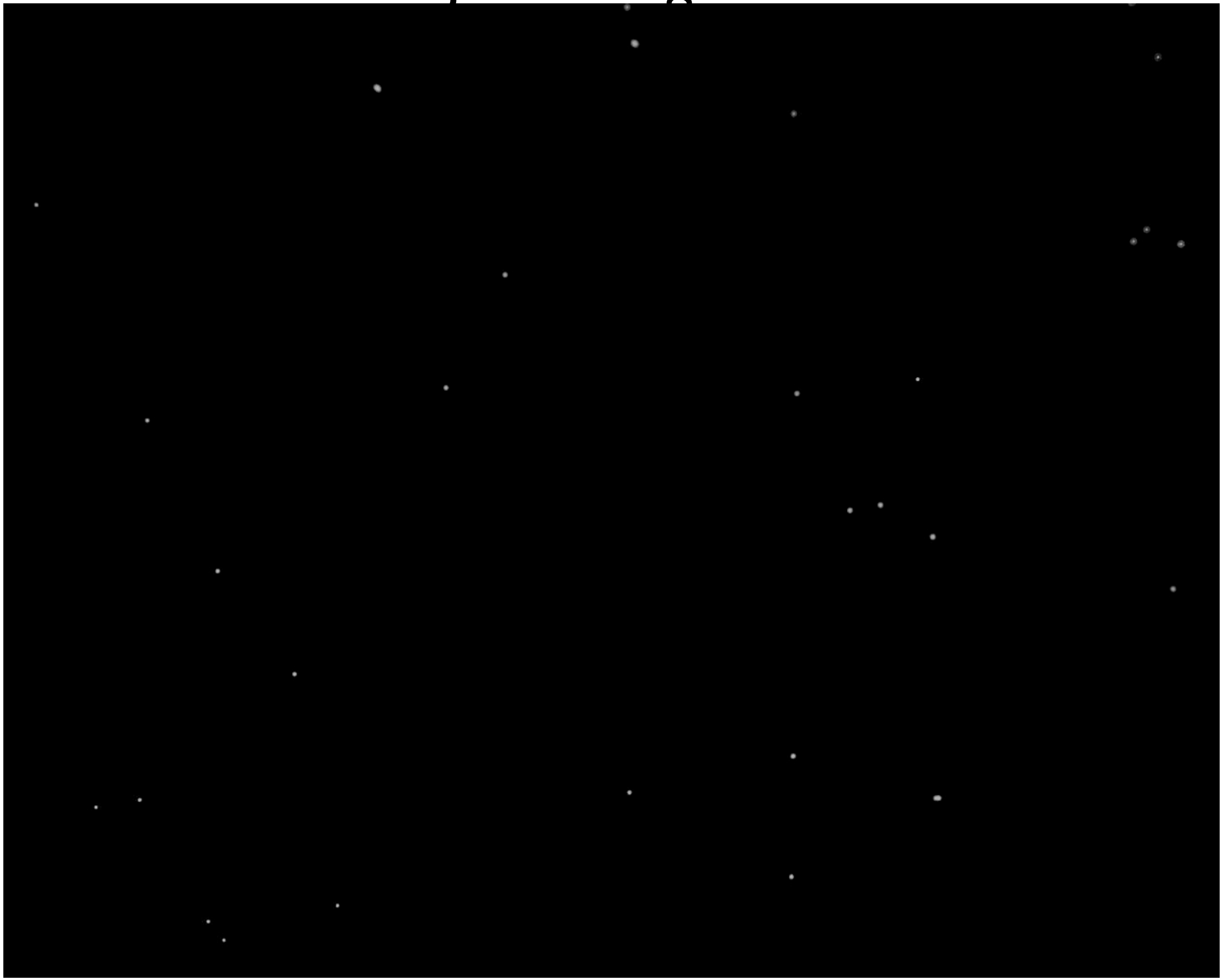
$$H_2O_2 \rightleftharpoons 2\,e^- + 2\,H^+ + O_2, \quad \text{oxidation}$$



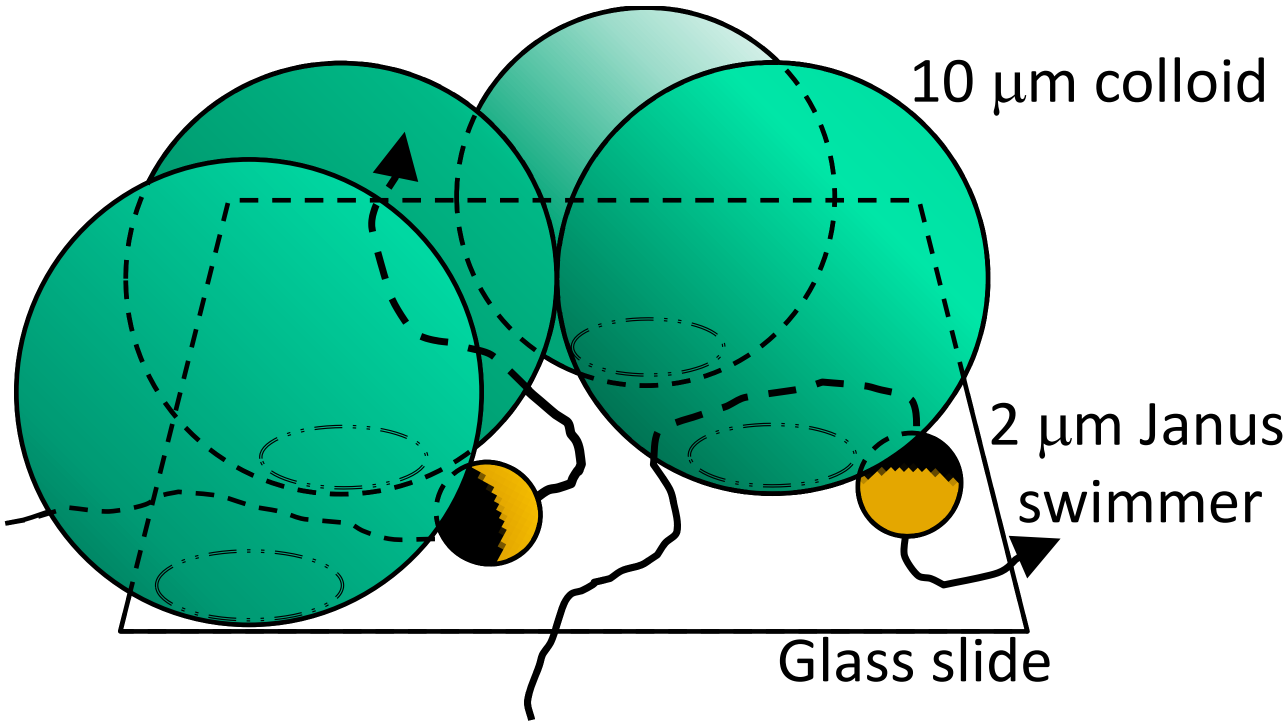
Moral: nothing is as simple as it looks!

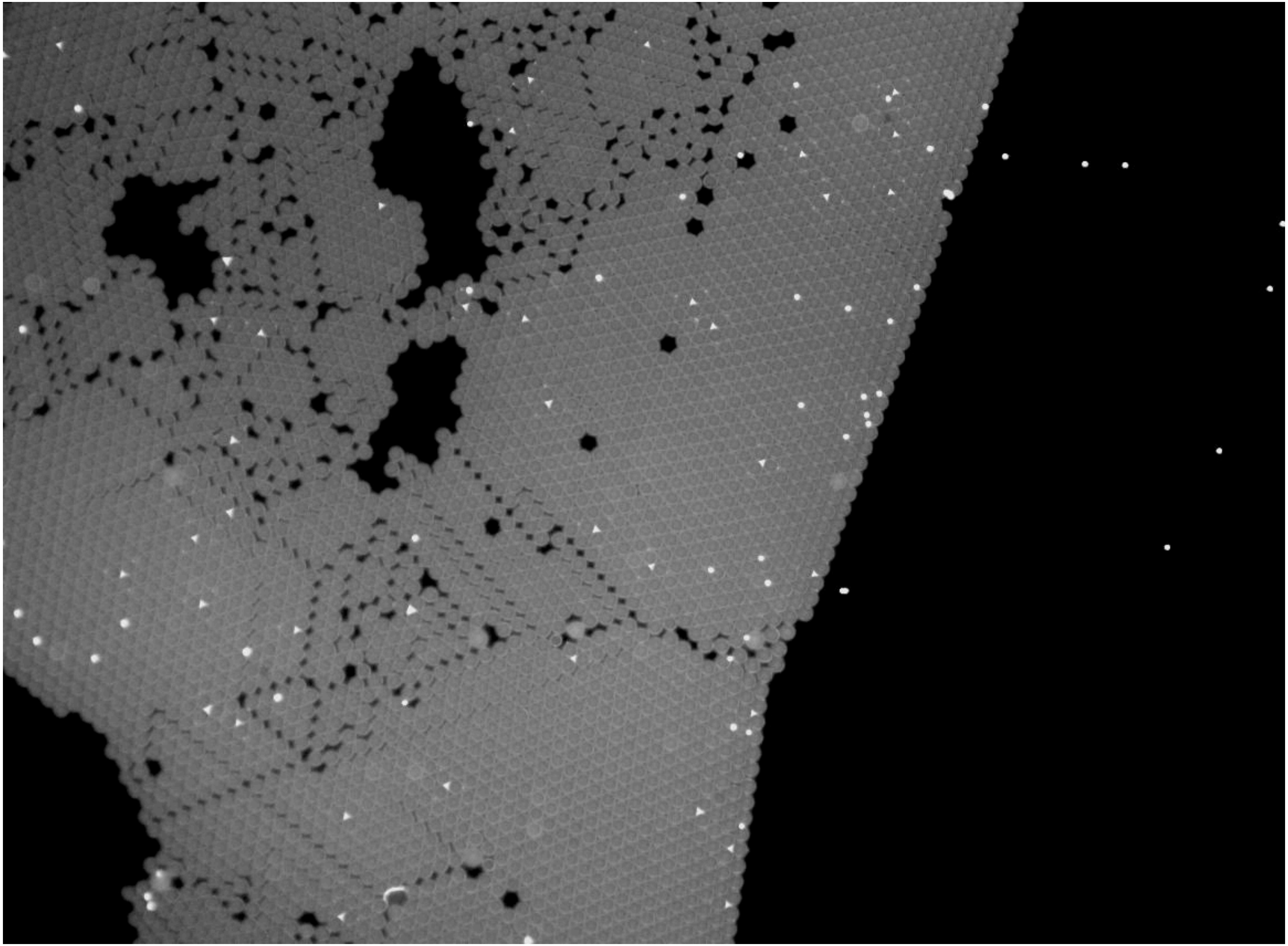
Swimmers are not all the same

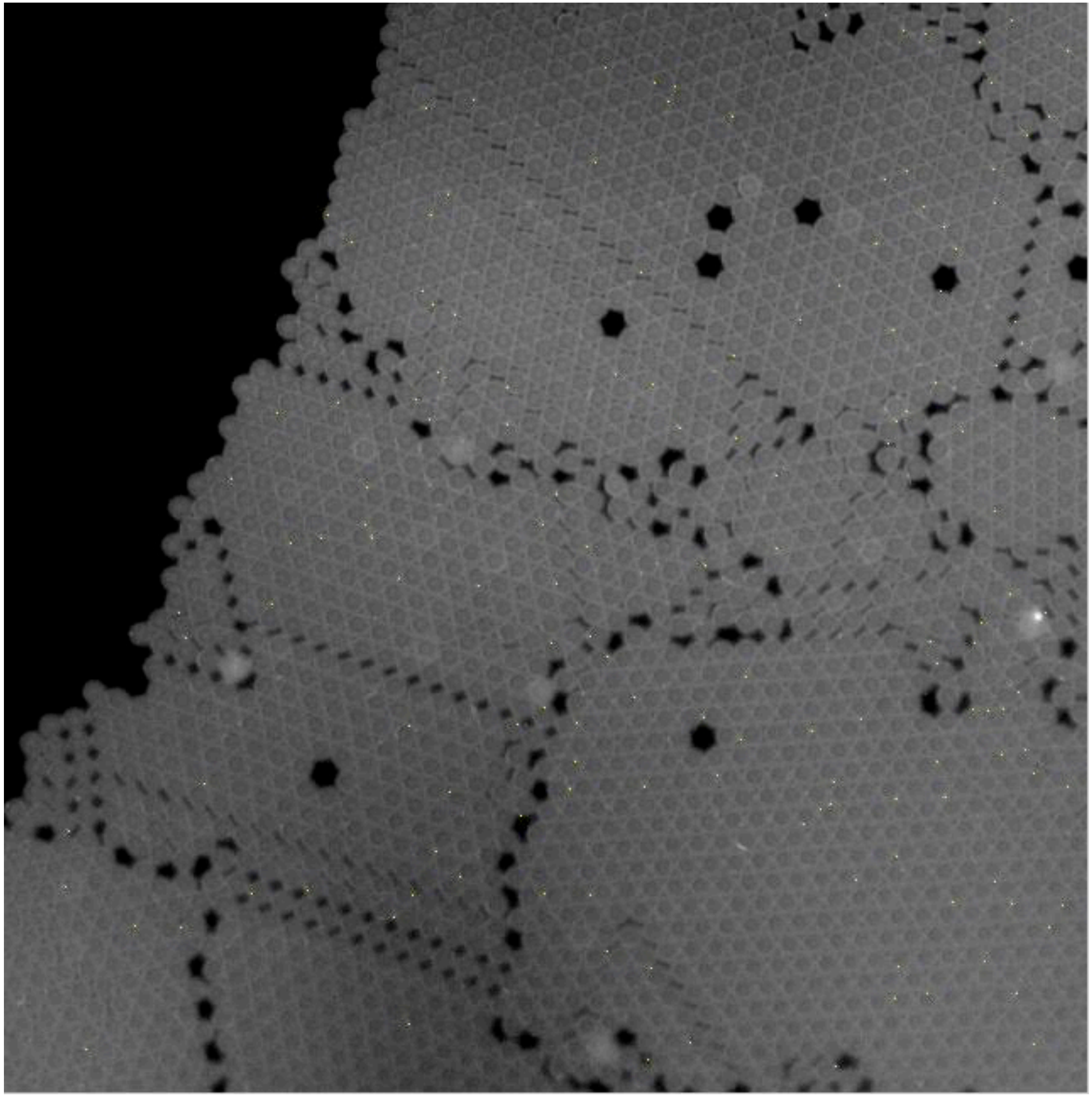
Janus on glass

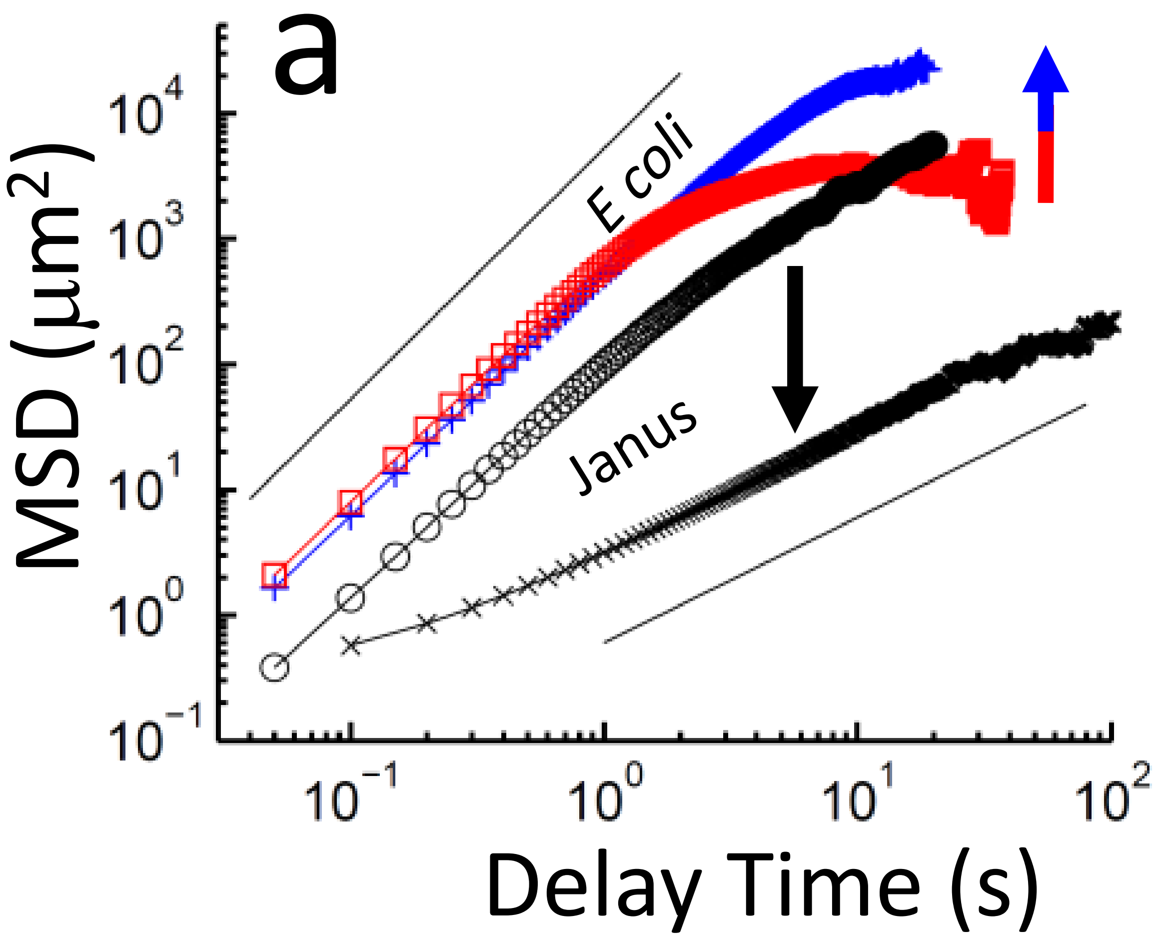


E. coli on glass


10 μm colloid
2 μm Janus swimmer
Glass slide



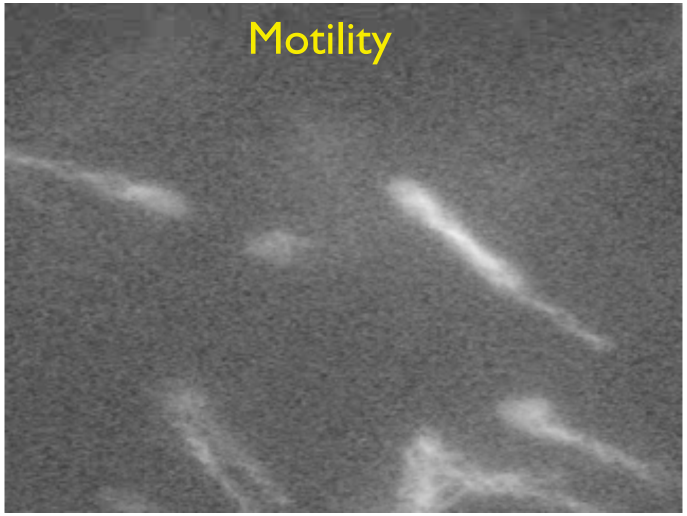




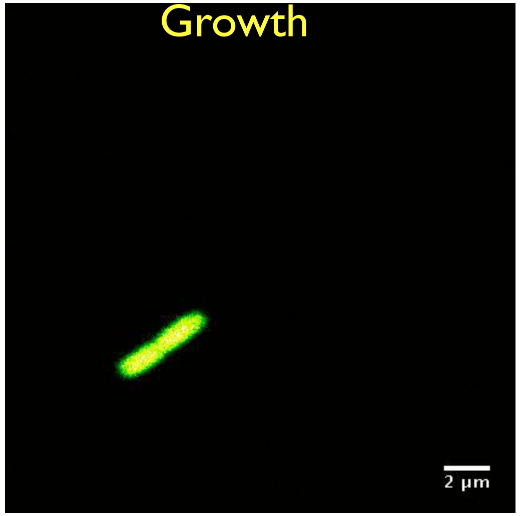
a
E coli
Janus
MSD (μm²)
Delay Time (s)
10^4
10^3
10^2
10^1
10^0
10^-1
10^-1
10^0
10^1
10^2

Now for something completely different again ...

Bacteria show two kinds of activity!

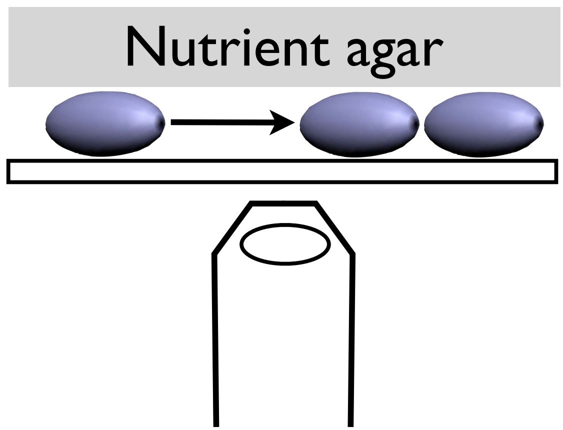


Now mimicked by synthetic colloids



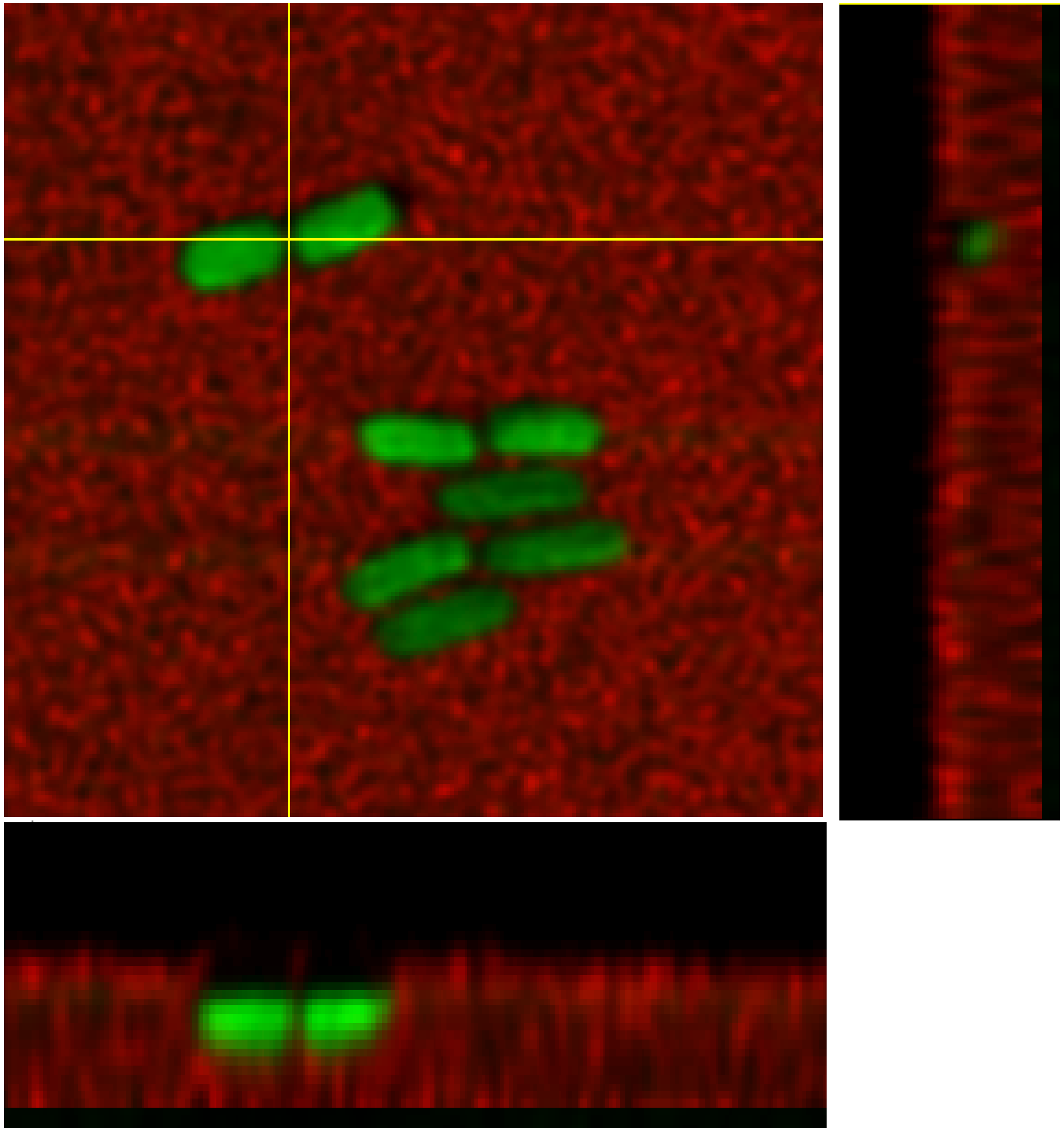
Fundamental characteristics of living things!

Bacteria growing into a colony 'on' agar ...



… is the 'hydrogen atom' of multicellular physics!

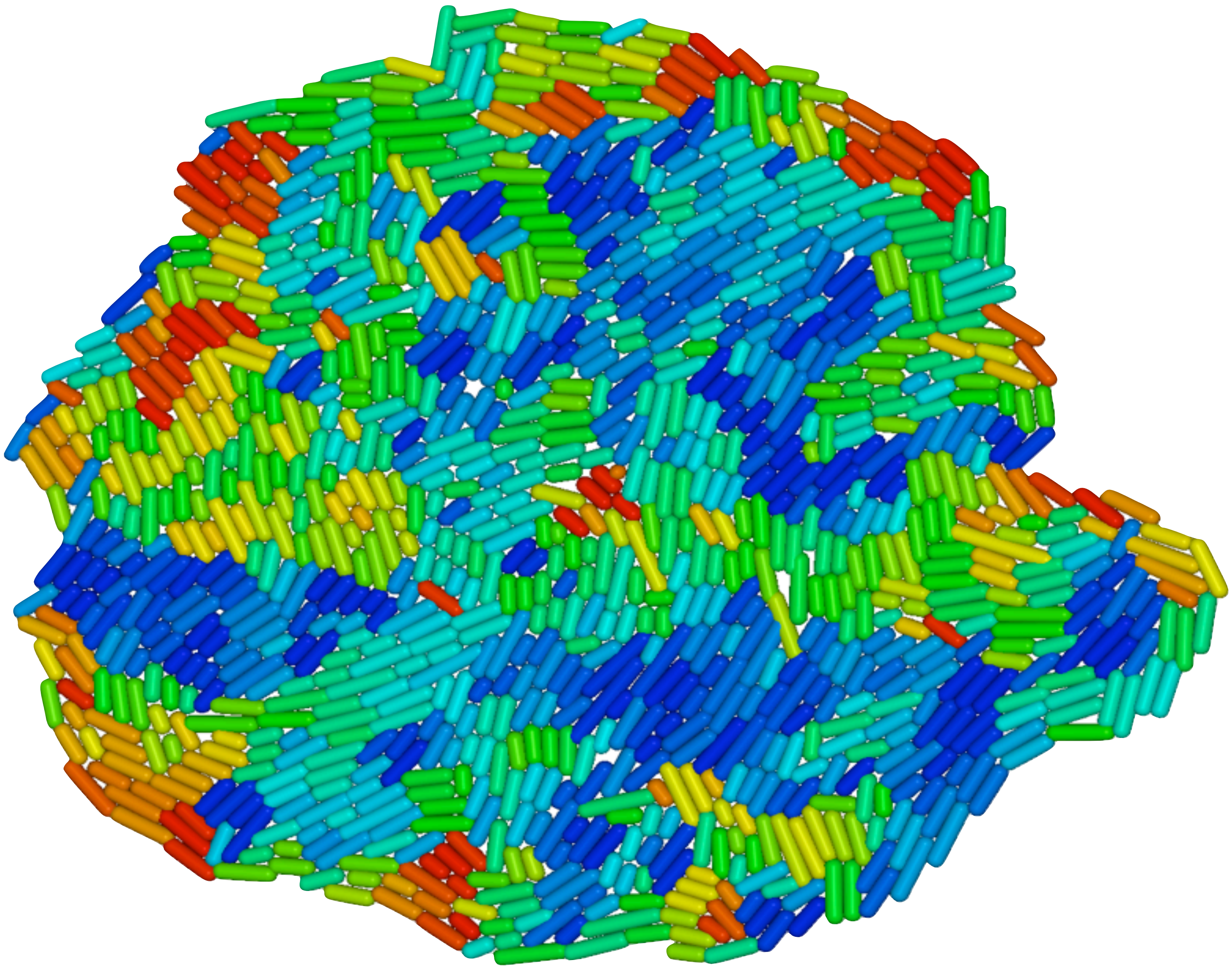
Bacteria grow inside top surface of agar



Loss of orientational order

Sudden *buckling* into the third dimension

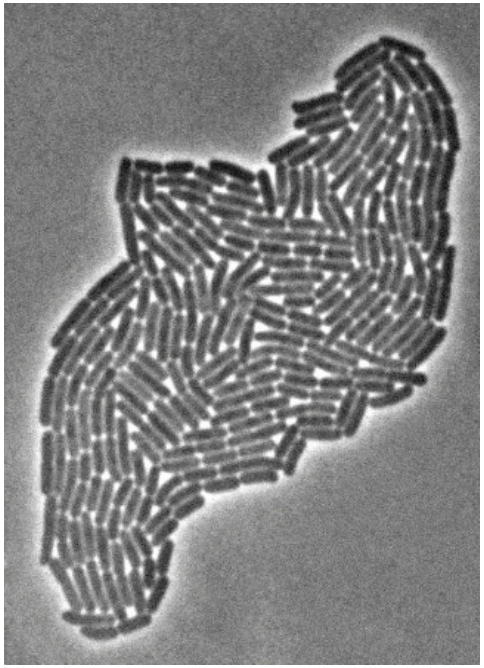
Spherocylinder fit to each cell in colony as function of time ...

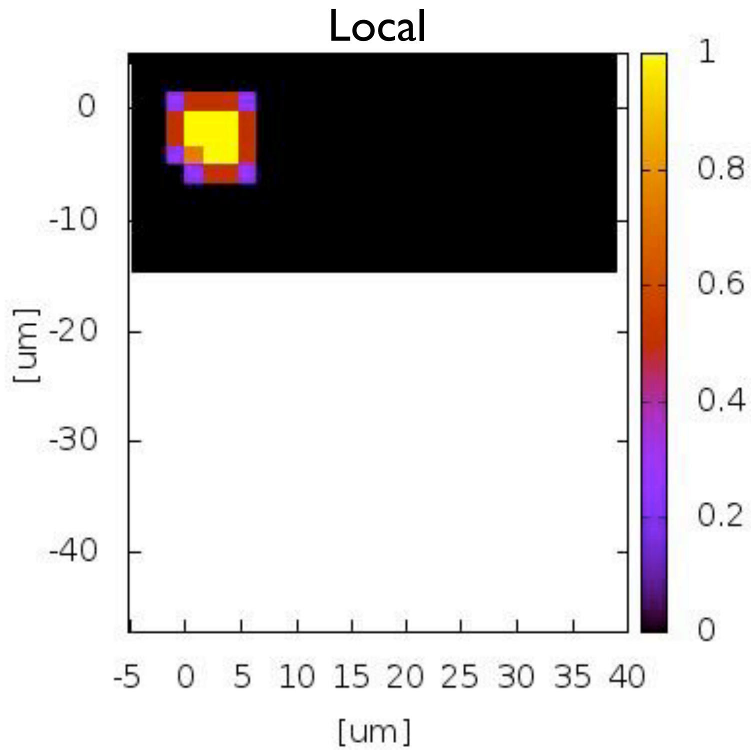


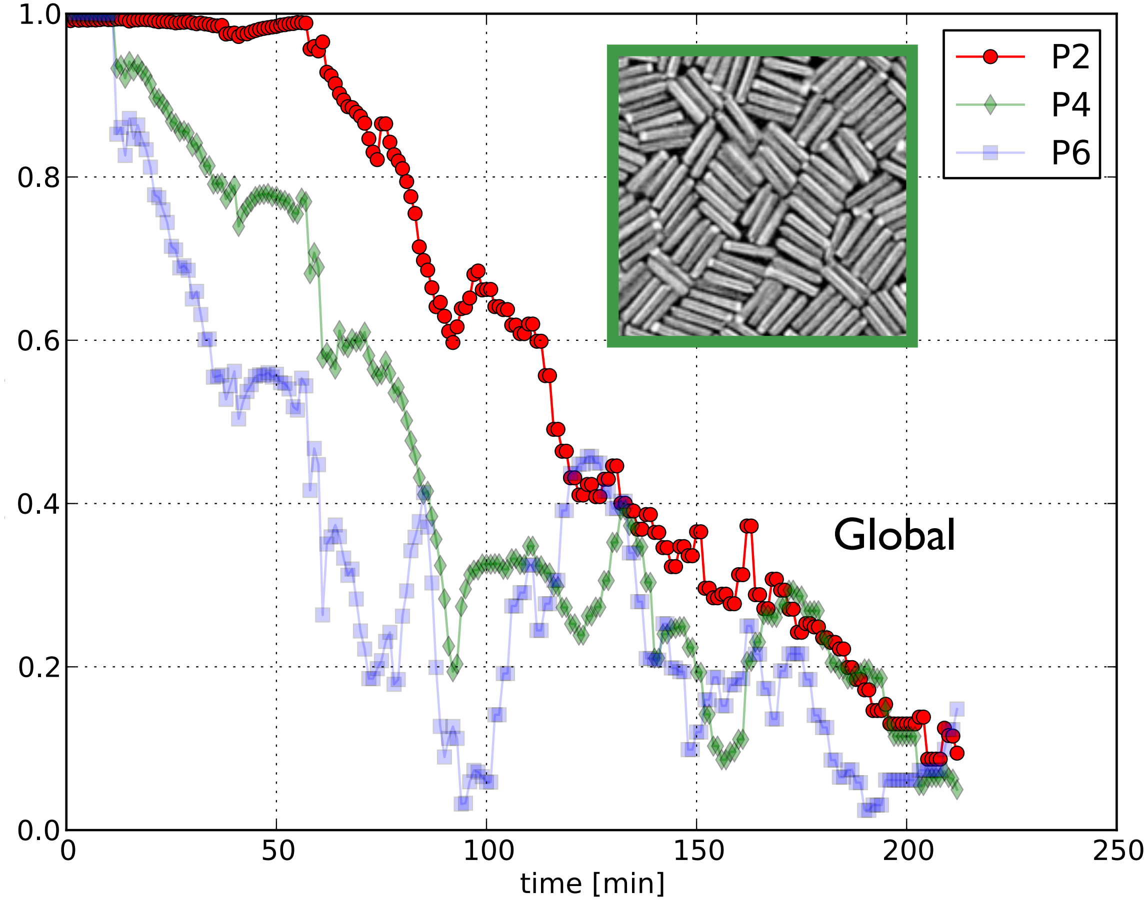
… until just before buckling into 3D (for now)

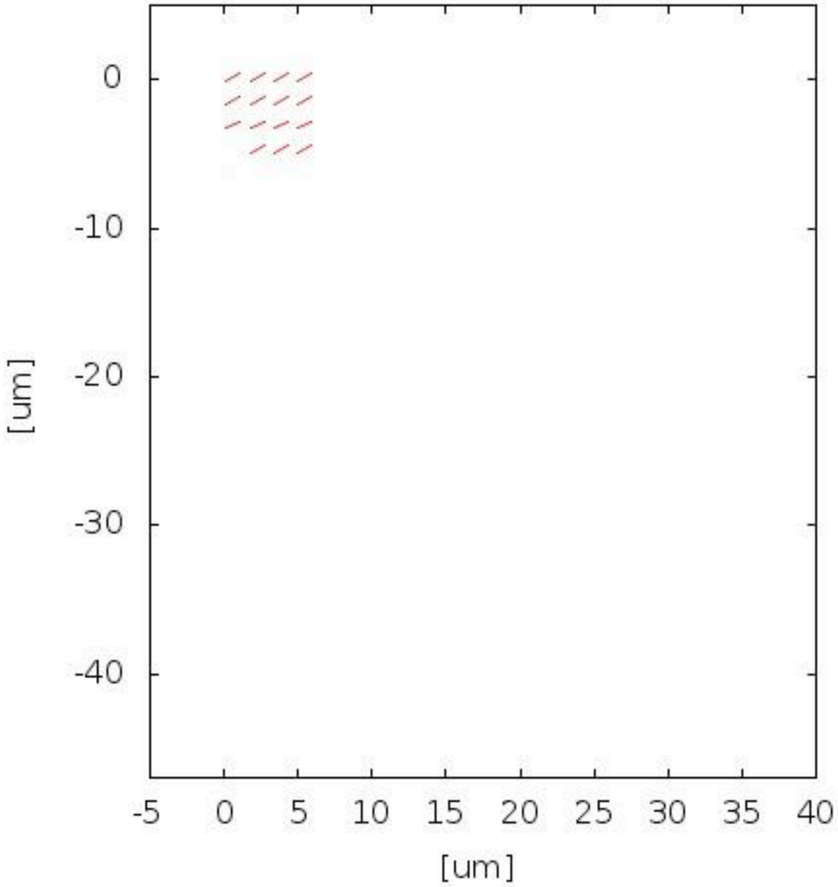
Scalar (nematic) order parameter

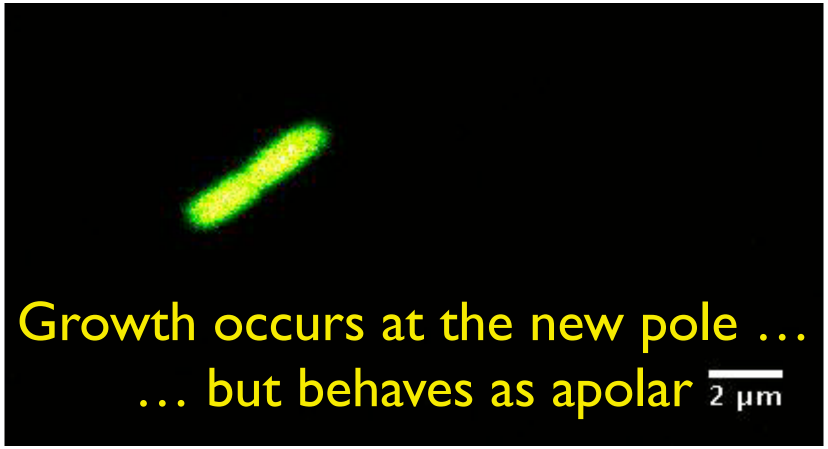
$$S = \langle 2\cos^2\theta - 1 \rangle$$

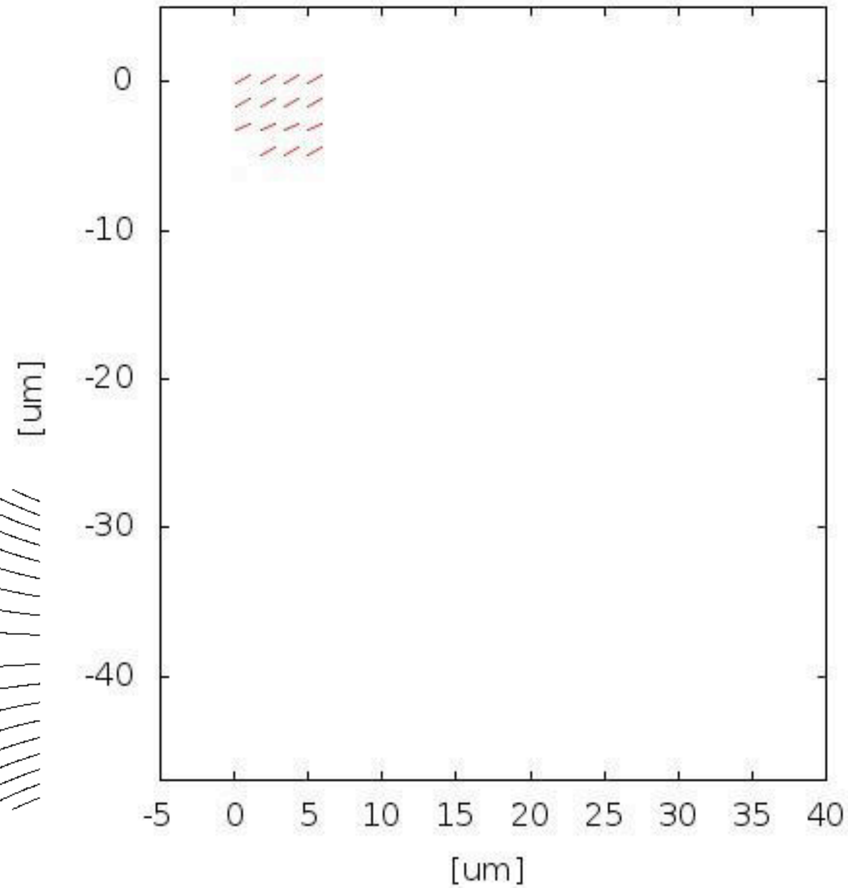










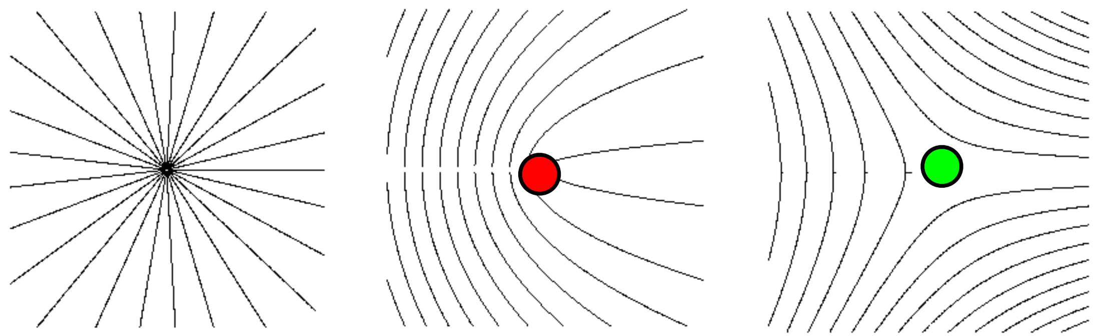


polar

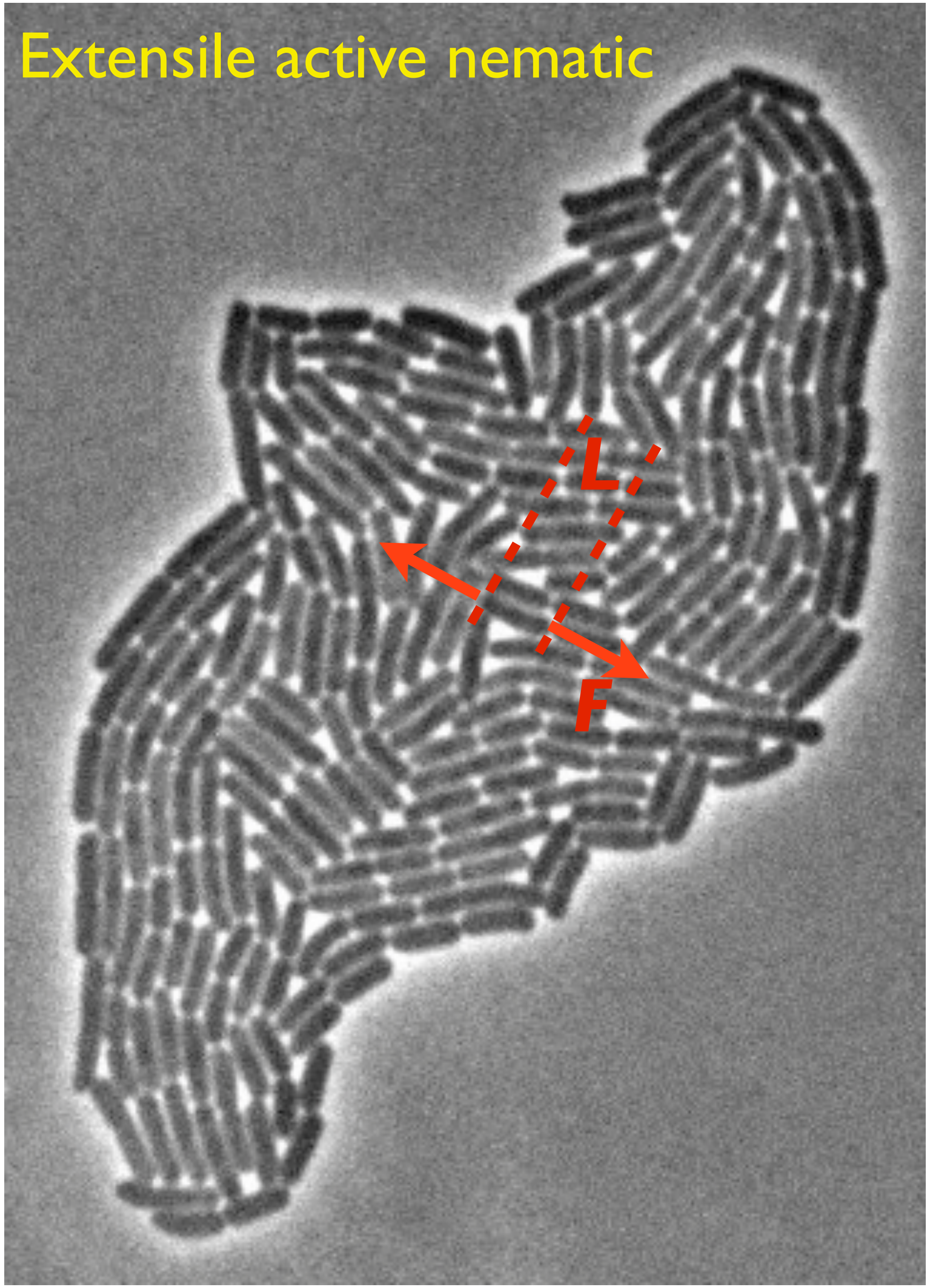
$\mathbf{n} \not\longleftrightarrow -\mathbf{n}$

apolar

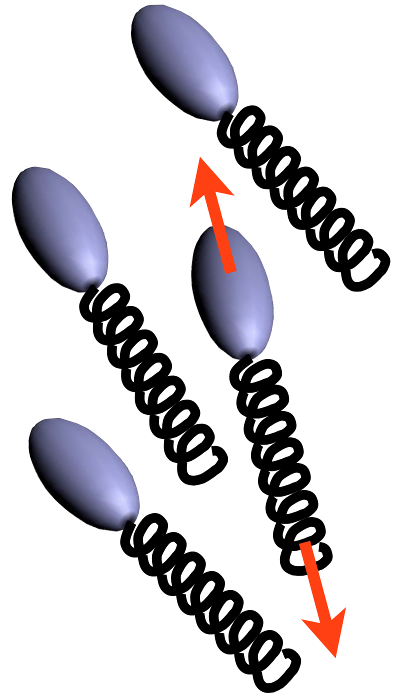
$\mathbf{n} \longleftrightarrow -\mathbf{n}$



m = 1 m = +1/2 m = -1/2



Cf.

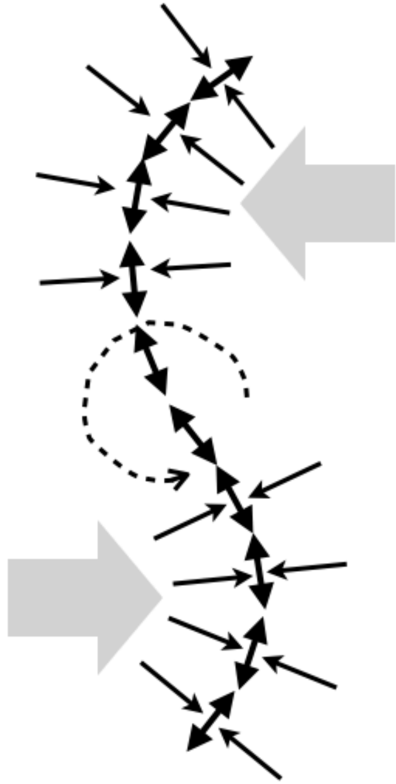


Hydrodynamic Fluctuations and Instabilities in Ordered Suspensions of Self-Propelled Particles

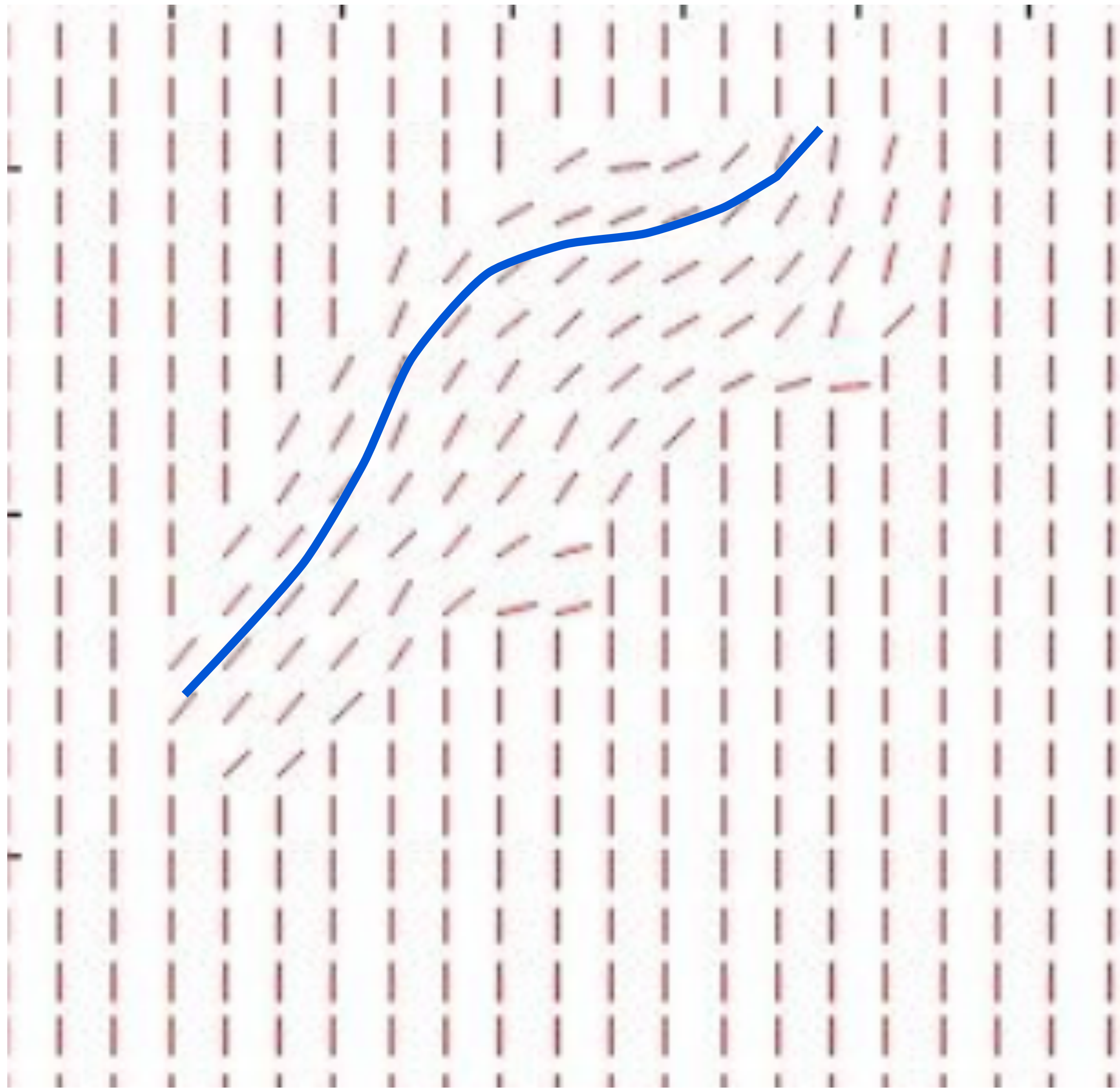
R. Aditi Simha* and Sriram Ramaswamy†

Centre for Condensed-Matter Theory, Department of Physics, Indian Institute of Science, Bangalore 560 012, India

(Received 18 August 2001; published 15 July 2002)



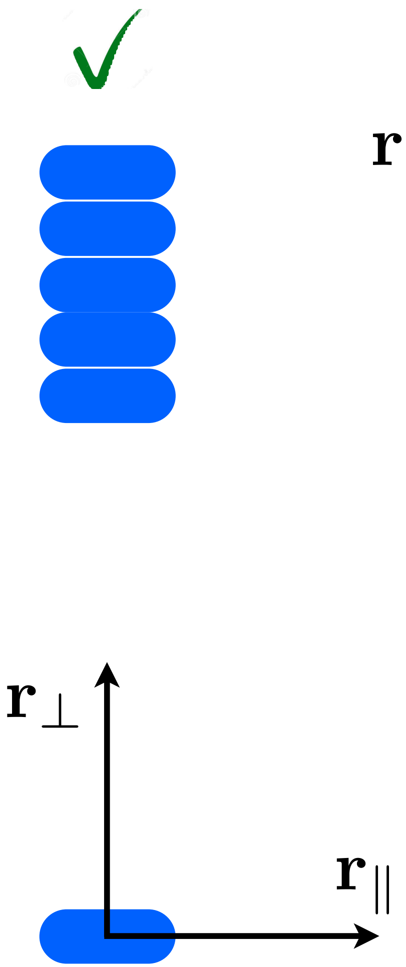
Extensile: unstable to bend

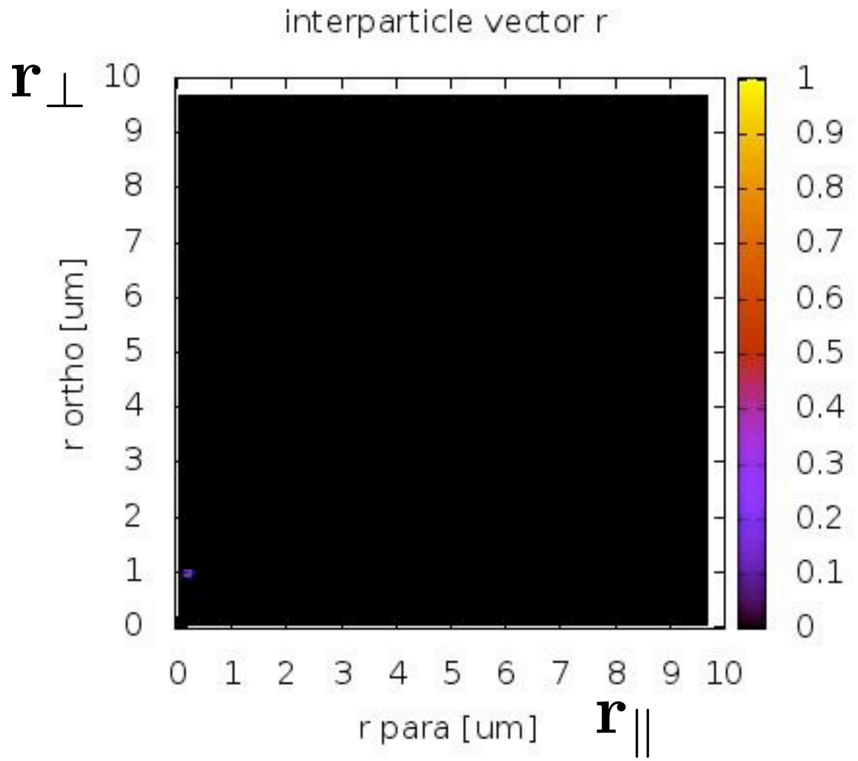


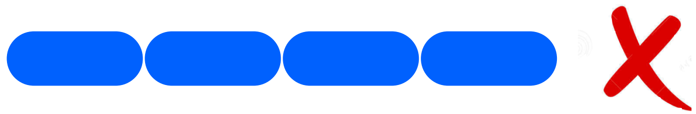
Anisotropic correlation function

$$\langle \cos[2\{\theta(\mathbf{0}) - \theta(\mathbf{r})\}] \rangle$$

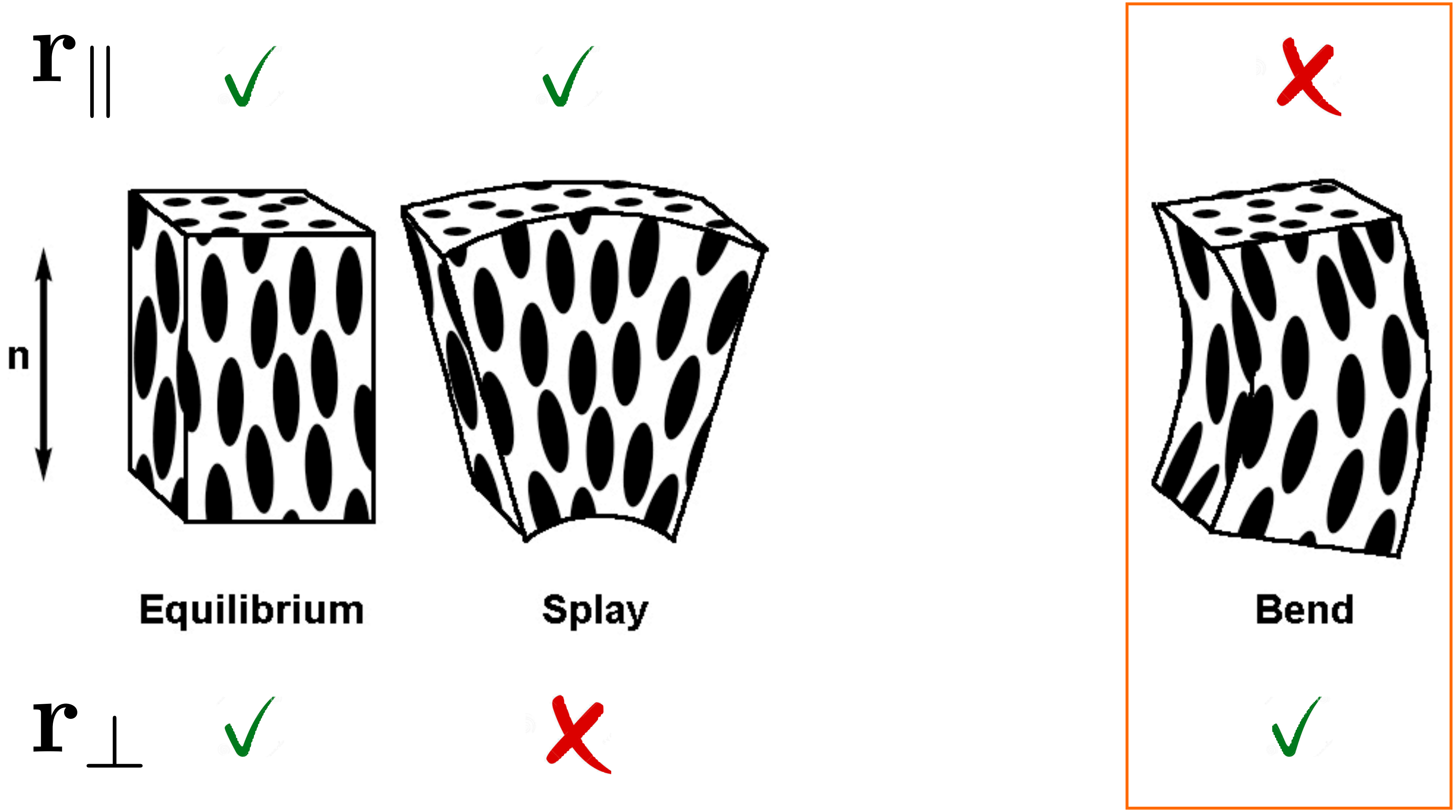
Bates & Frenkel, *JCP* (2000)







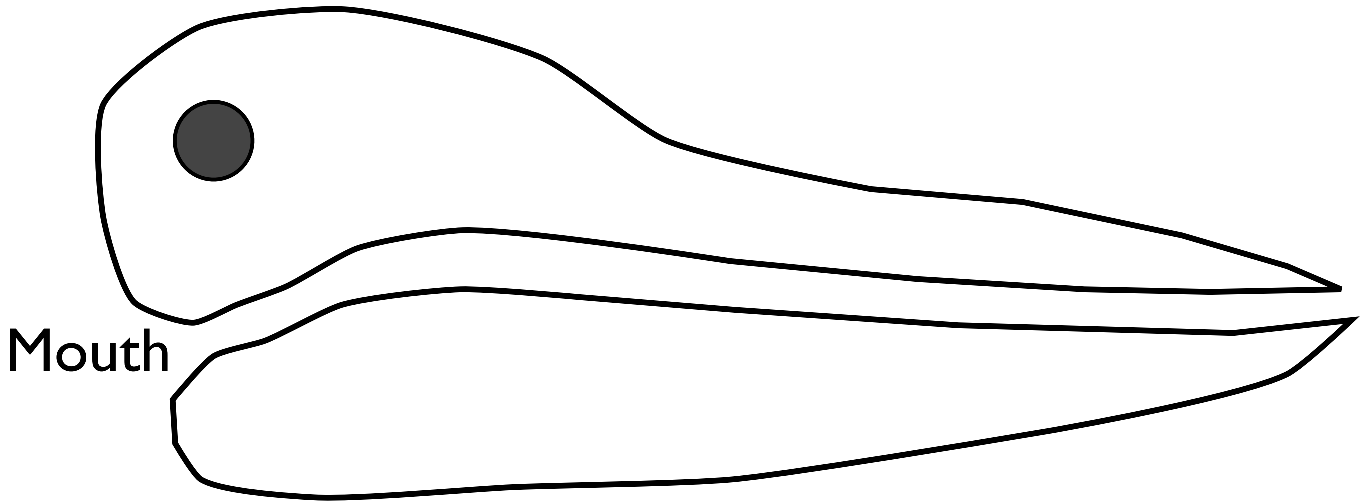
Distortions in nematic LCs

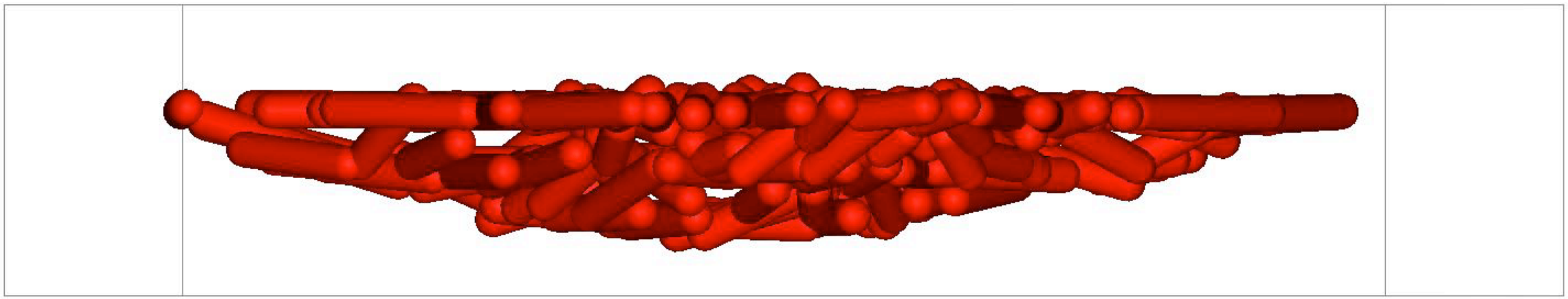


Sudden *buckling* into the third dimension ...

… the beginnings of you and me!

A 2D animal doesn't work ...





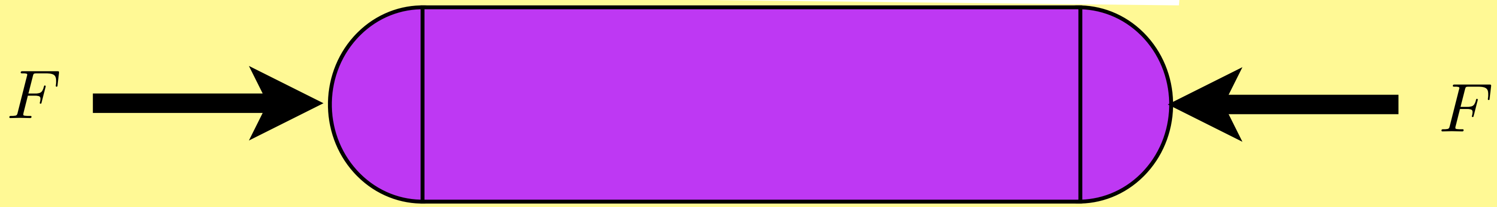

2 µm

Forces acting on a growing bacterium

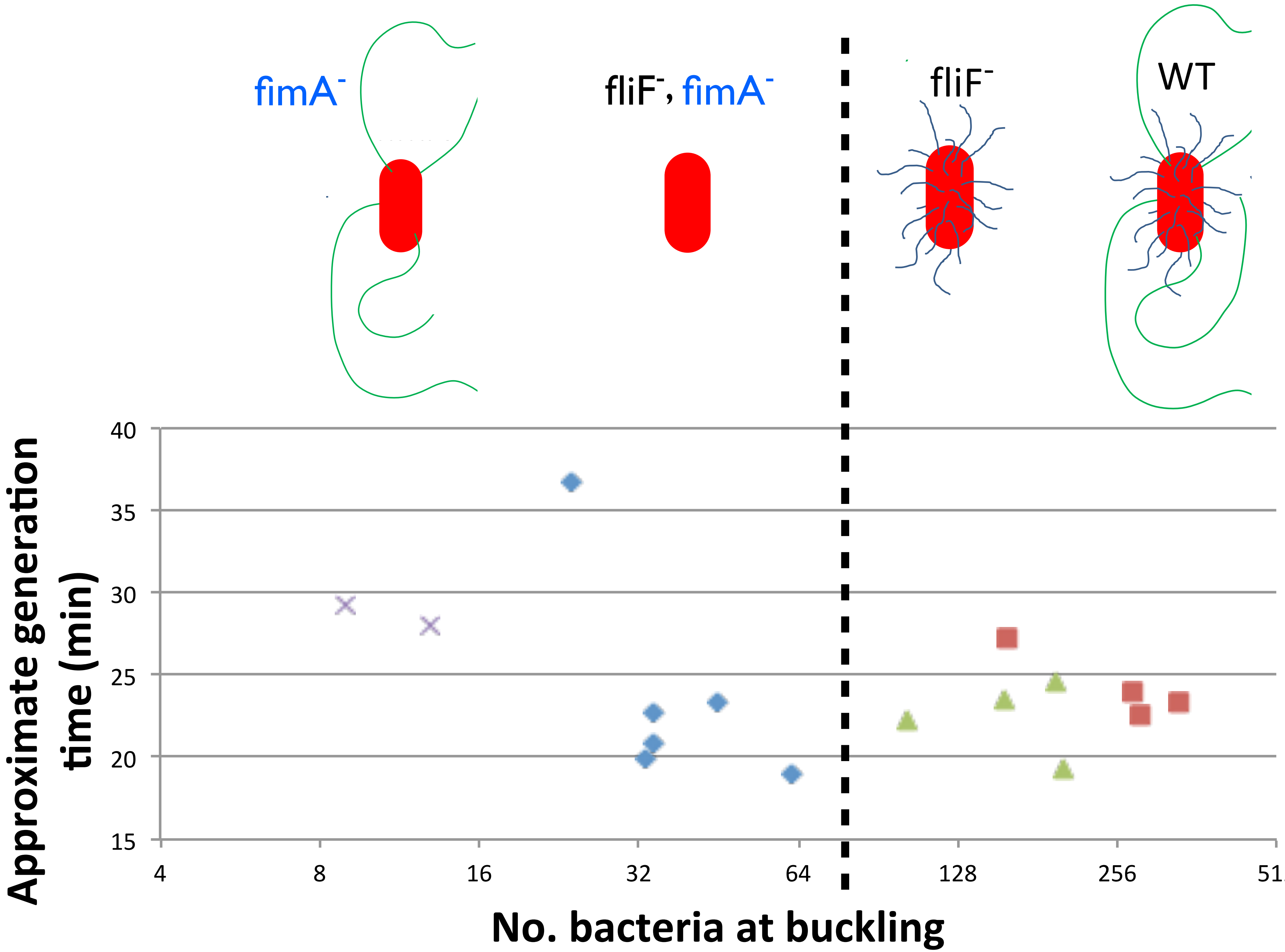
$$\text{Euler buckling force } = F_{\text{crit}} = \frac{\pi^2 EI}{L^2}$$

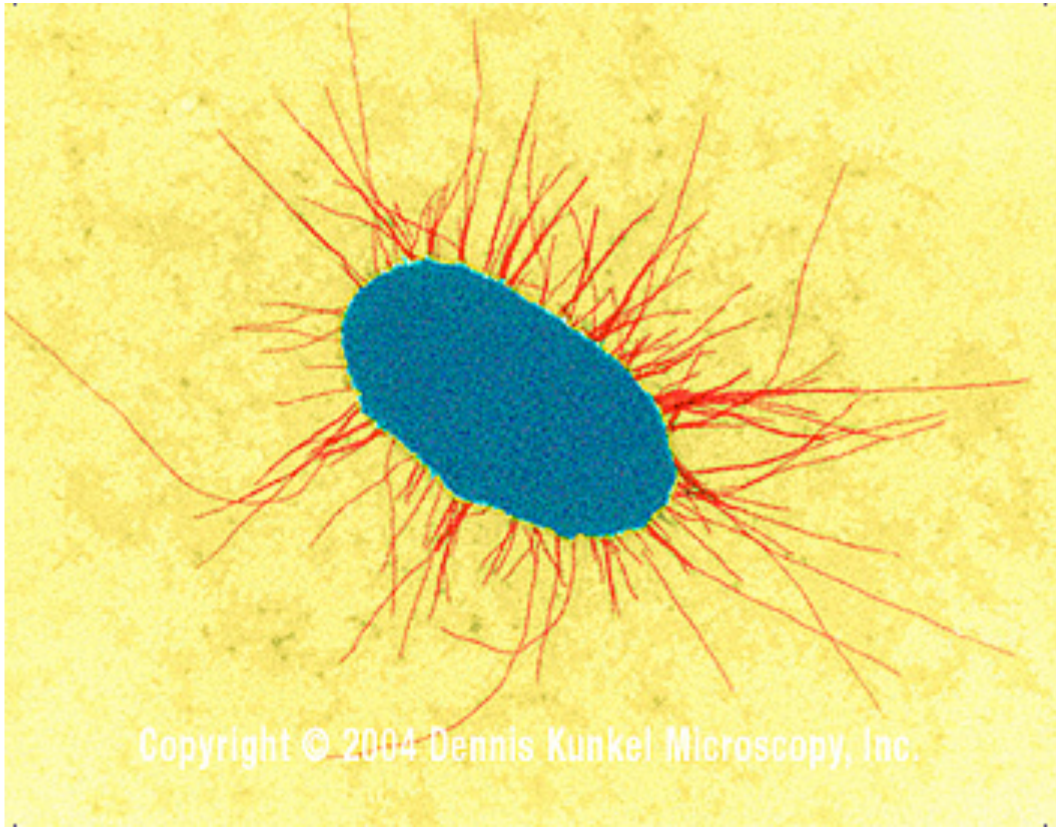
$$EI \approx 5 \times 10^{-20}\,\text{Nm}^2$$

$$F_{\text{crit}} \approx 3 \times 10^{-8}\,\text{N}$$



$$F \lesssim \sigma_{\text{break}} \times \pi a^2 \approx 30\,\text{kPa} \times 0.5\mu\text{m}^2 \approx 1.5 \times 10^{-8}\,\text{N}$$


fimA-
fliF-, fimA-
fliF-
WT
Approximate generation time (min)
40
35
30
25
20
15
4
8
16
32
64
128
256
512
No. bacteria at buckling



fimbriae - adhere to surfaces (and perhaps to each other)

Most of this process is not understood yet ...

… either as physics or biology!

Why is this interesting?

- Biological consequences:
  biofilms
  multicellularity in general
  the function of cell shape

- Medical consequences:
  as model for cancer tumour (Austin et al.)

- Towards a growth-driven self assembly

Summary

Bacteria are colloid^{++} because they swim and grow:

(1) They do things with colloidal analogues
sedimentation equilibrium, attractive phase transition

(2) They do things to colloids
enhanced diffusion

(3) They do things colloids don’t do
(filling emulsion drop, swimming in polymers)
growth in 2D and 3D colonies