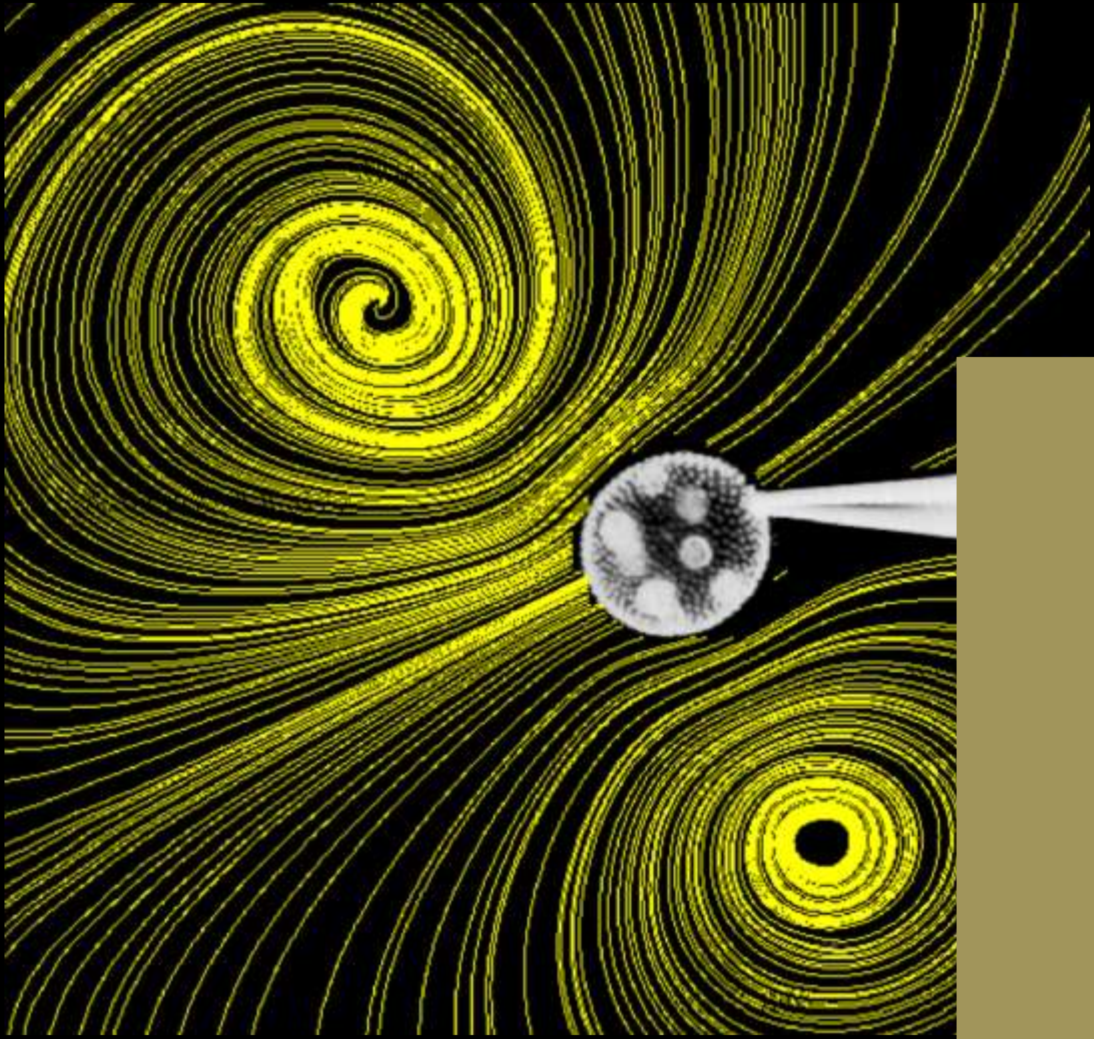
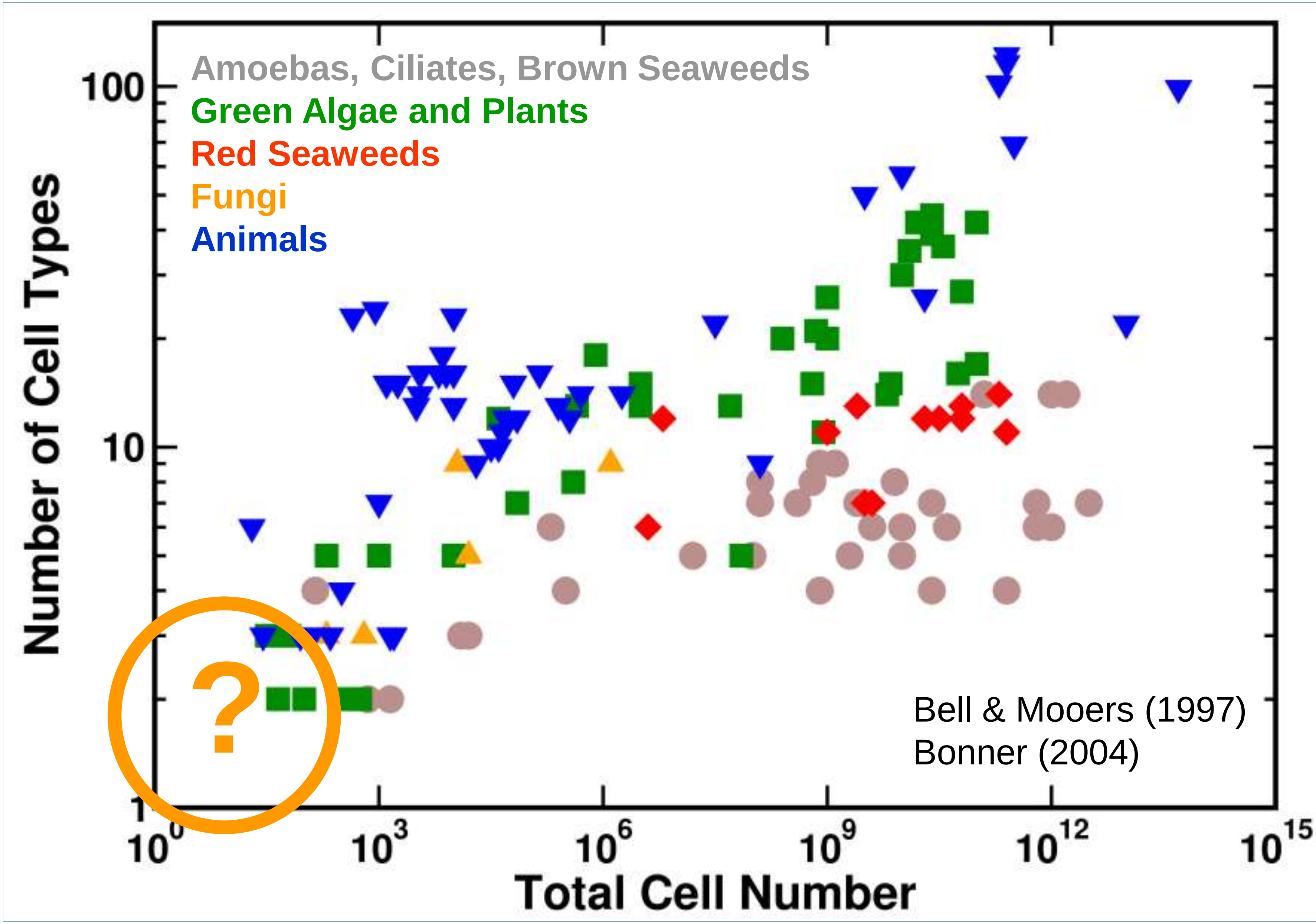
Stirring Tails of Evolution

R E Goldstein
DAMTP



www.damtp.cam.ac.uk/user/gold
www.youtube.com/Goldsteinlab

The Size-Complexity Relation



The Recent Literature

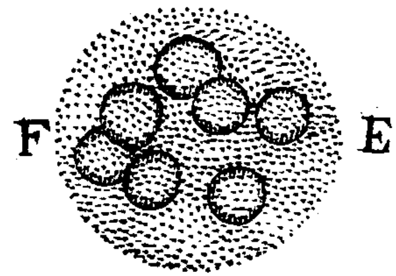
IV. *Part of a Letter from* Mr Antony Van Leeuwenhoek, *concerning the Worms in Sheeps Livers, Gnats, and Animalcula in the Excrements of Frogs.*

When I brought theſe particles before the Magnifying-glaſs, I did not only ſee that they were round, but that the outward skin of them was quite ſet over with many protuberant parts, which did ſeem to me to be triangular, and pointed towards the end; ſo that it ſeemed to me, that in the great circle of the roundneſs, ſtood ſuch particles, all orderly and equally from each other; ſo that on a ſmall body did ſtand about two thouſand of the before-mentioned convex or protuberant particles.

This was to me a very pleaſant ſight, becauſe the ſaid particles, as often as I did look on them, did never lye ſtill, and that their motion did proceed from their turning round; and that the more, becauſe I did fancy at firſt that they were ſmall animals, and the ſmaller theſe particles were, the greener was their colour; and on the contrary, in the greateſt, that were as big as a great corn of ſand, there was no green colour at all to be diſcerned on the outſide.

Theſe particles had each of them within included 5, 6, 7, nay, ſome to 12 ſmall round globules, of the ſame ſhape as the body was wherein they were included.

Fig: 5



Phil. Trans. **22**, 509-518 (1700)

CAROLI LINNÆI

EQUITIS DE STELLA POLARI,
ARCHIATRI REGII, MED. & BOTAN. PROFESS. UPSAL.;
ACAD. UPSAL. HOLMENS. PETROPOL. BEROL. IMPER.
LOND. MONSPEL. TOLOS. FLORENT. SOC.

SYSTEMA NATURÆ

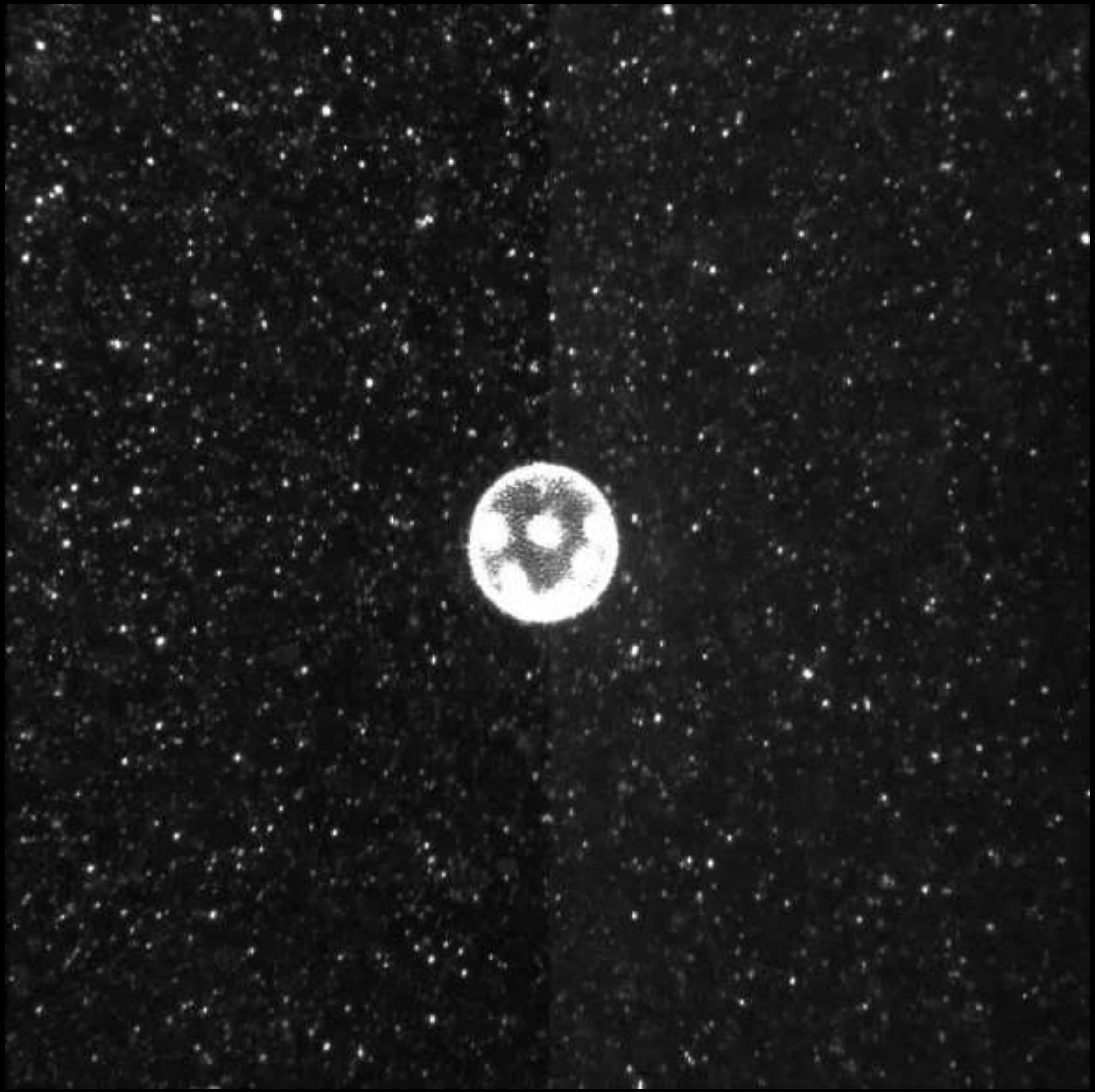
(1758)

312. VOLVOX. *Corpus* liberum, gelatinoſum, rotundatum, artubus deſtitutum.
Proles ſubrotundi, nidulantes, ſparſi.

Volvendo ſeque rotando celeriter movens abſque artubus! viviparus natis, nepotibus, pronepotibus, abnepotibus conſpicuis intra animalculum minutiſſimum.

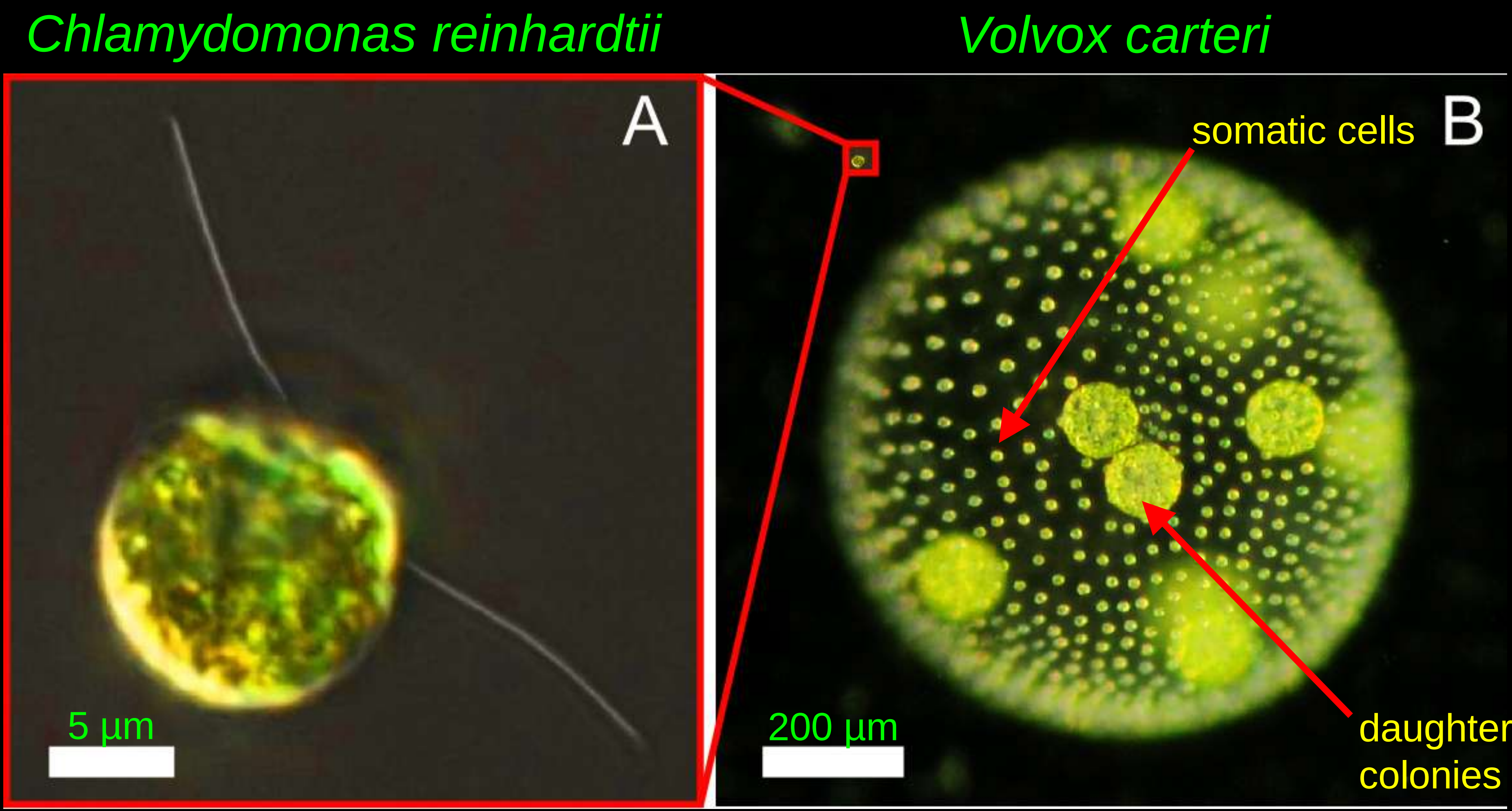
Volvox In Its Own Frame

Tracking microscope
 in vertical orientation
Laser sheet illumination
 of microscpheres

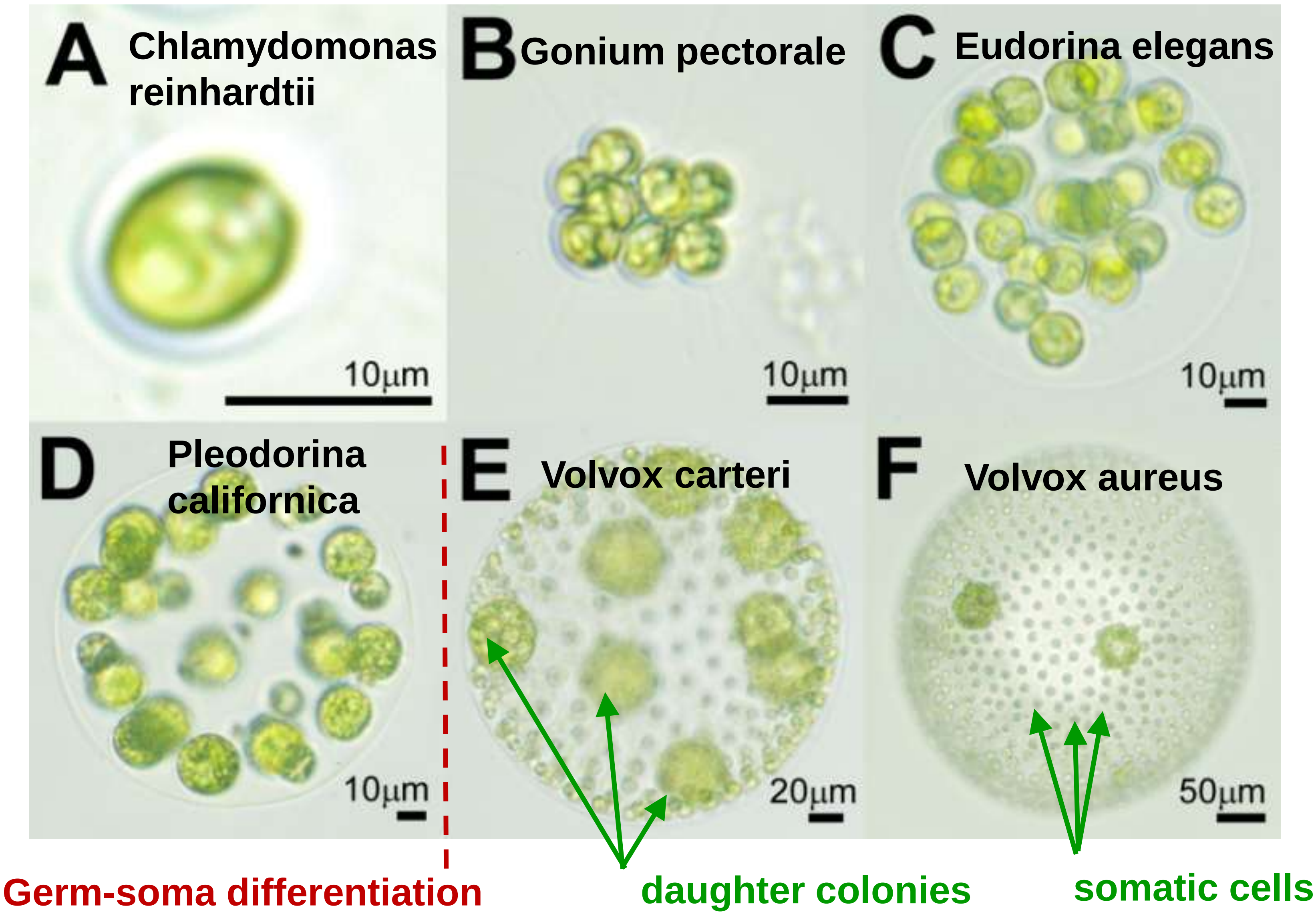


Drescher, Goldstein, Michel, Polin, and Tuval, *preprint* (2010)

Evolutionary Transition to Multicellularity

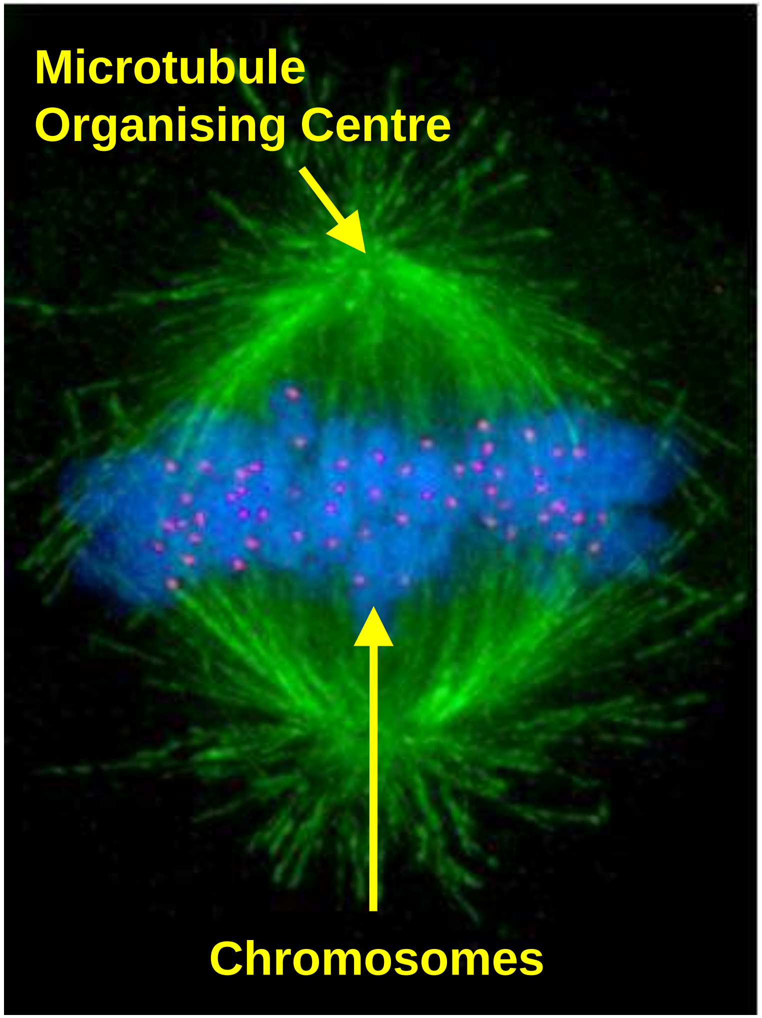


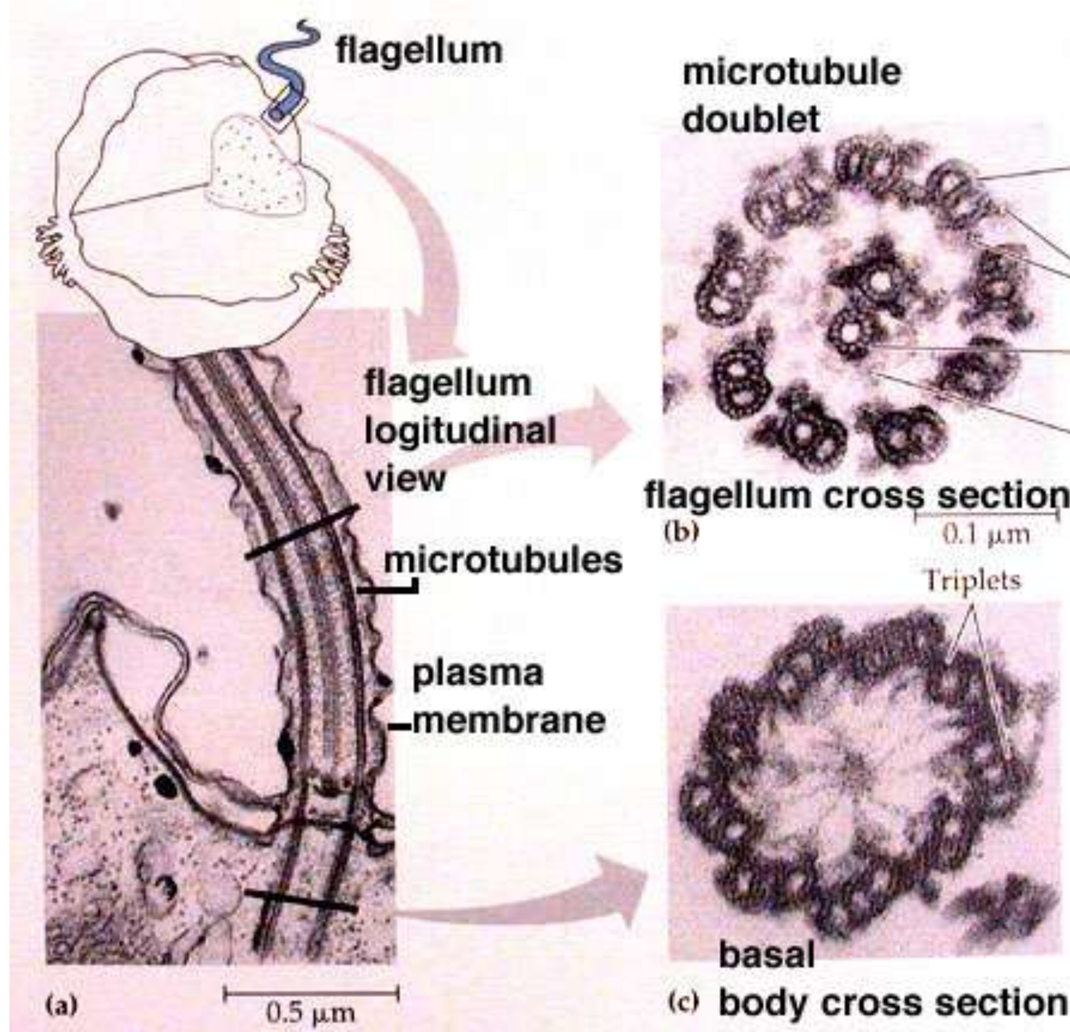
A Family Portrait



Altruism, apoptosis

Structure of Flagella & the Flagellation Constraint





Basal bodies are microtubule organizing centres
…flagella are resorbed during cell division (no multi-tasking)
(Bell & Koufopanou, ’85,’93)

Advection & Diffusion

If a fluid has a typical velocity **U**, varying on a length scale **L**, with a molecular species of diffusion constant **D**. Then there are two times:

$$t_{advection} = \frac{L}{U}$$

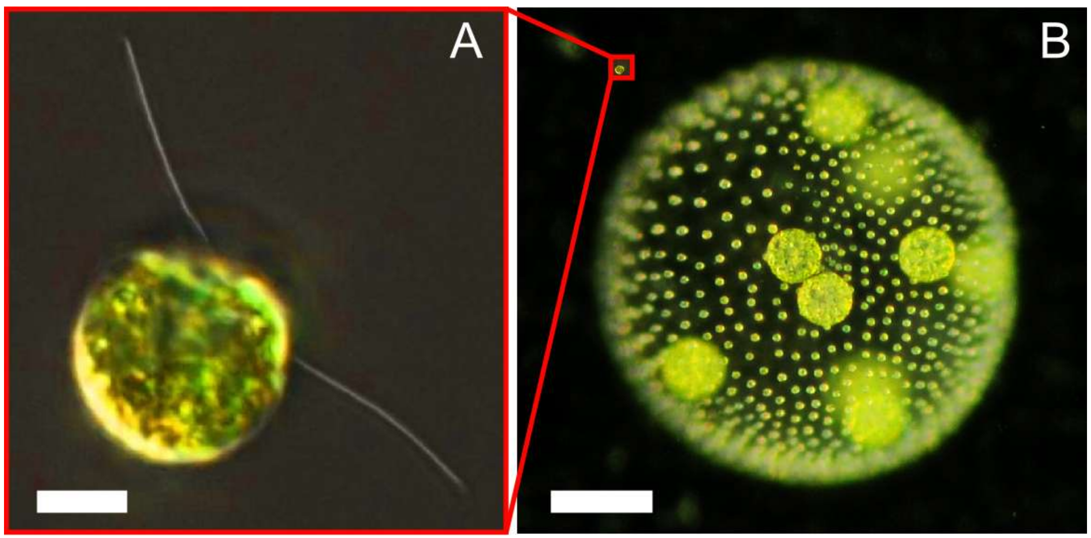
$$t_{diffusion} = \frac{L^2}{D}$$

We define the Péclet number as the ratio:

$$Pe = \frac{t_{diffusion}}{t_{advection}} = \frac{UL}{D}$$

This is like the Reynolds number comparing inertia to viscous dissipation:

$$Re = \frac{UL}{\nu}$$

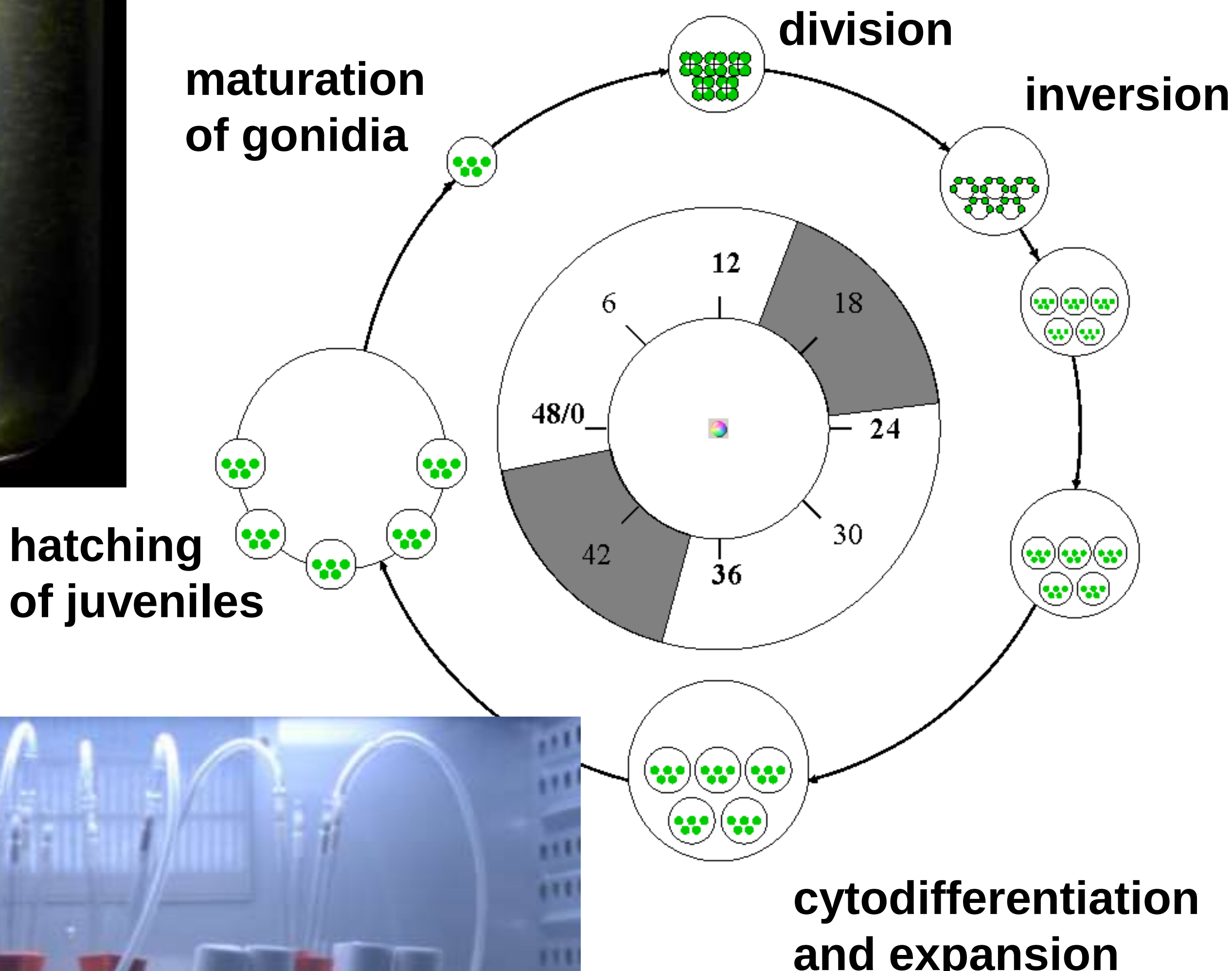


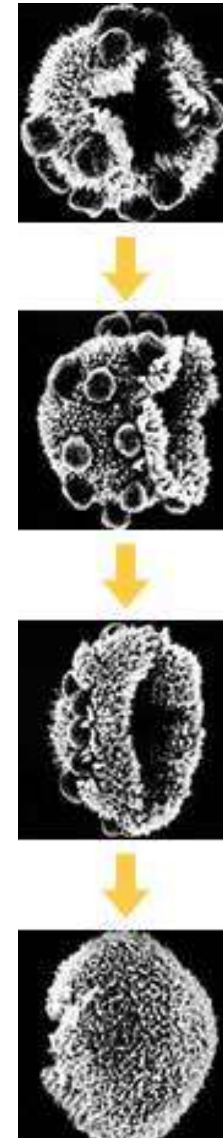
If U=10 μm/s, L=10 μm,
Re ~ 10^{-4}, Pe ~ 10^{-1}
At the scale of an individual cell, diffusion dominates advection.

The opposite holds for ***multicellularity****…*

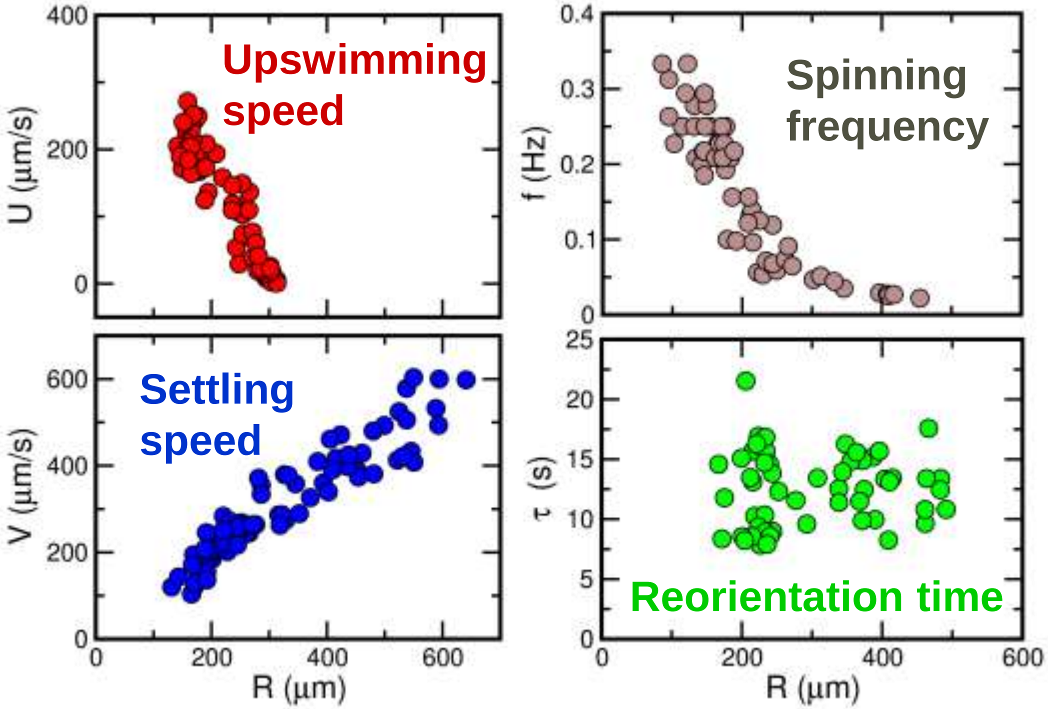
Solari, Ganguly, Michod, Kessler, Goldstein, *PNAS* (2006)
Short, Solari, Ganguly, Powers, Kessler & Goldstein, *PNAS* (2006)

Life Cycles of the Green and Famous



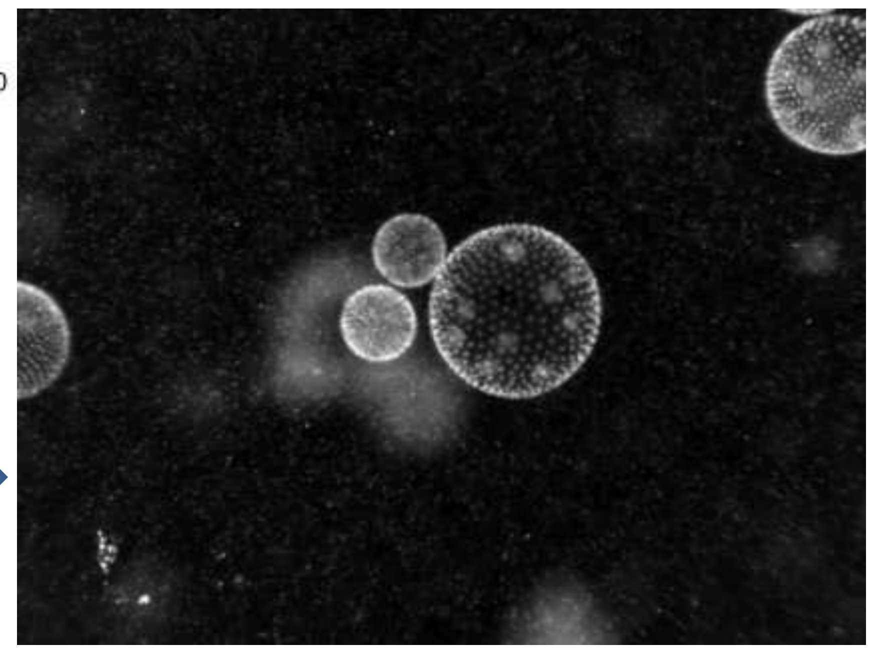


Volvox as a Model Organism for Biological Physics



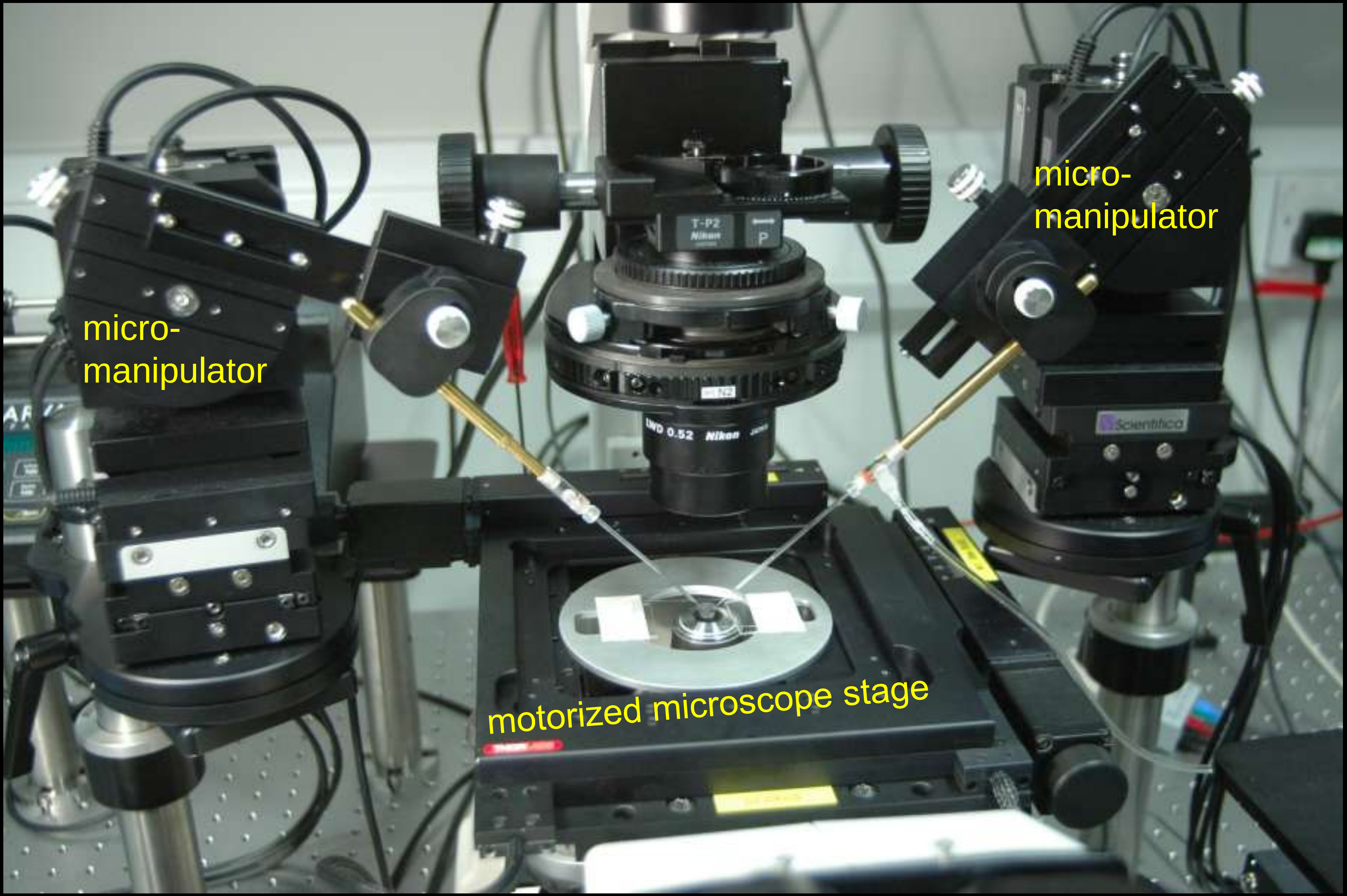
As the colonies grow they more systematically through the parameter space of swimming, sinking, spinning, and self-righting.

As an example, Volvox can exhibit "hydrodynamic bound states" which can be explained quantitatively using mutually advected force singularities.

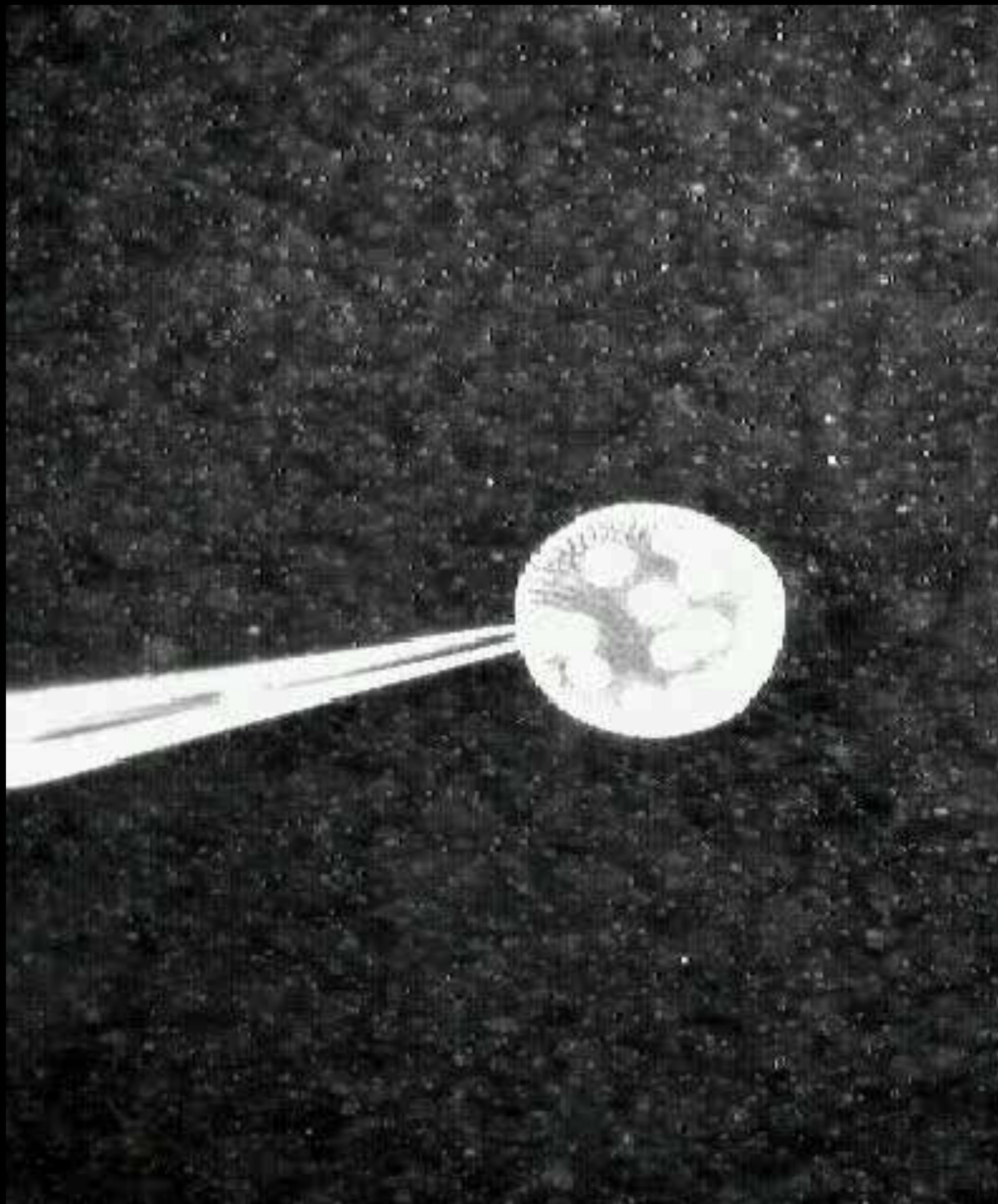


Drescher, Leptos, Tuval, Ishikawa, Pedley, Goldstein, *PRL* **102**, 168101 (2009)

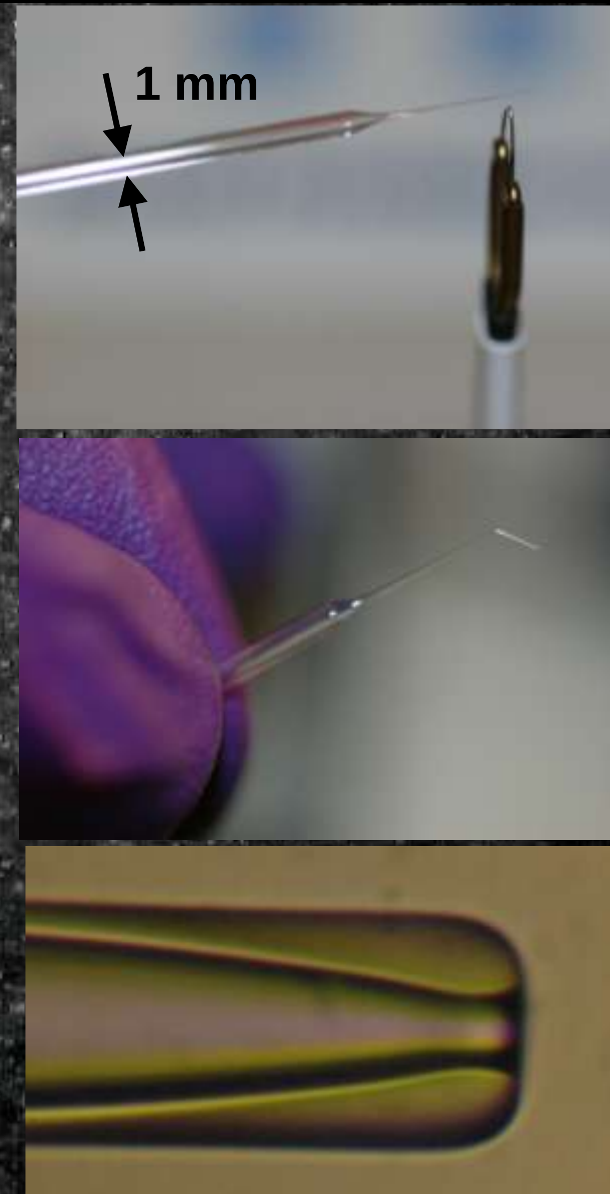
Microscopy & Micromanipulation



Stirring by *Volvox carteri*



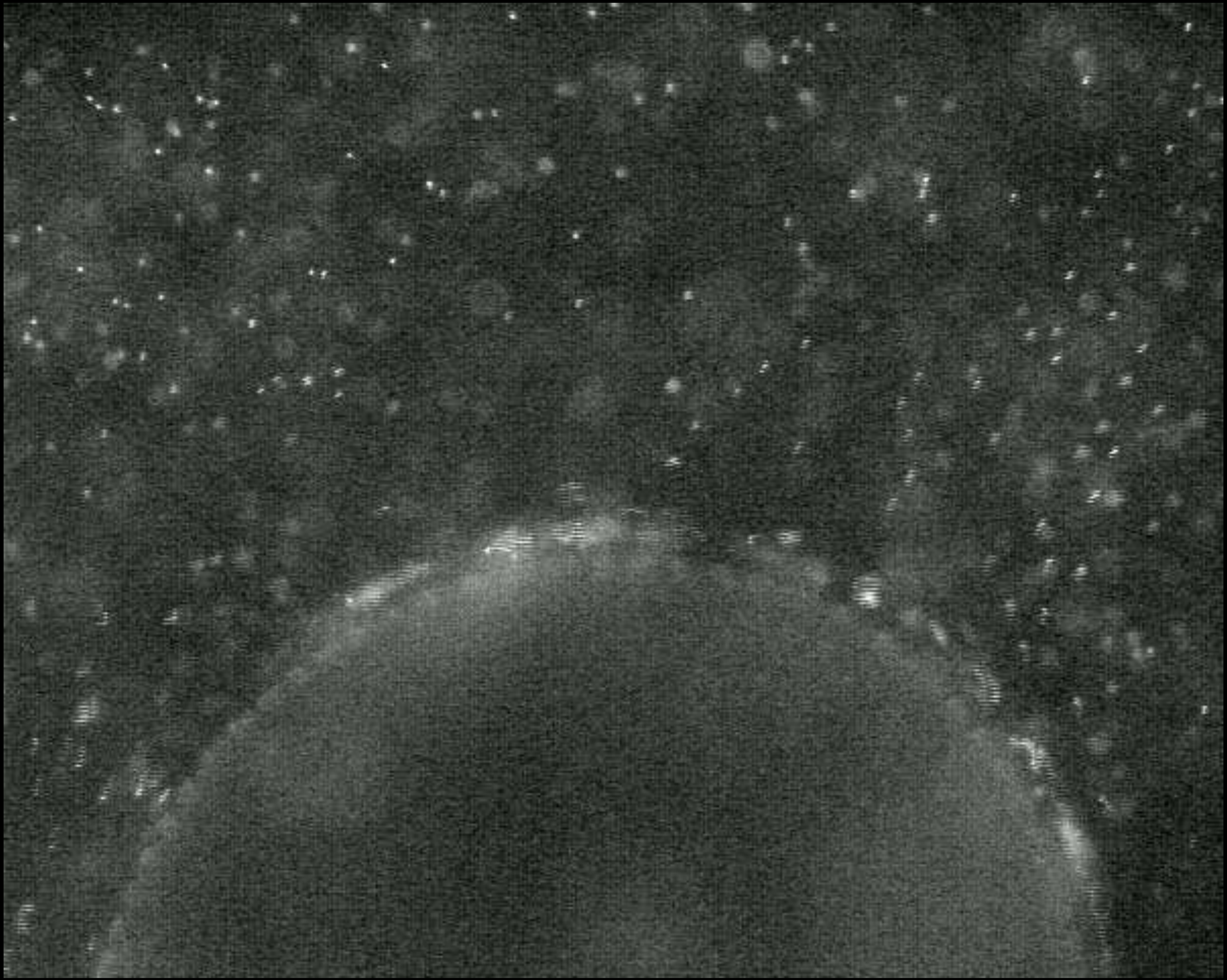
Pseudo-darkfield (4x objective, Ph4 ring)



Tools of the trade – micropipette preparation

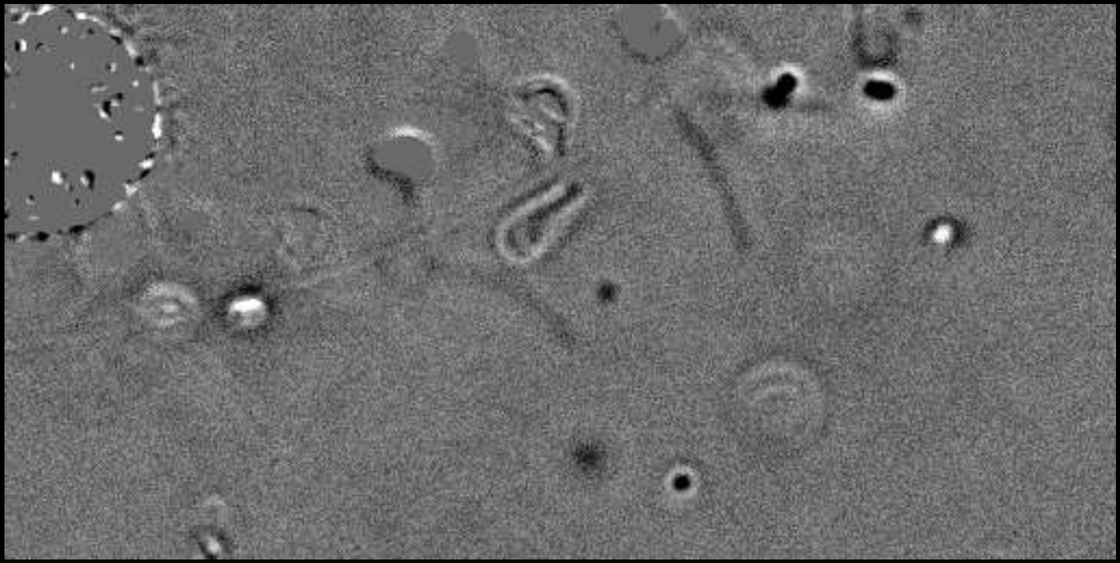
A Closer View

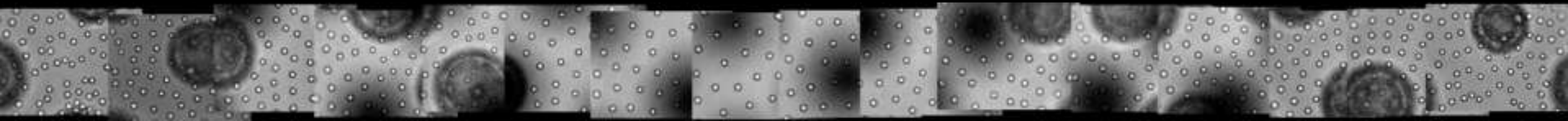
Fluorescence

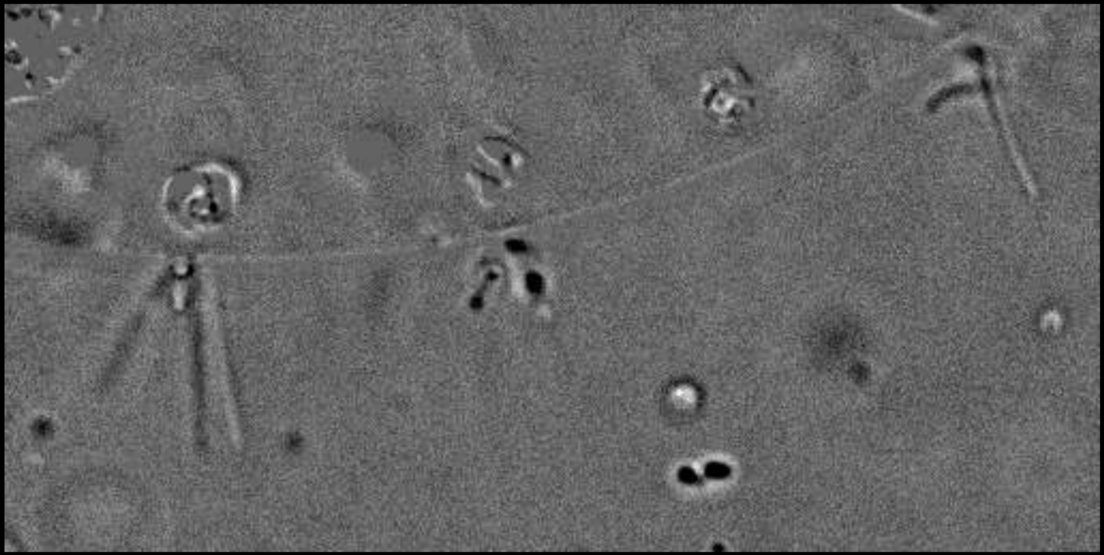


Flagella Beating/Symmetry

(2000 frames/s background subtraction)





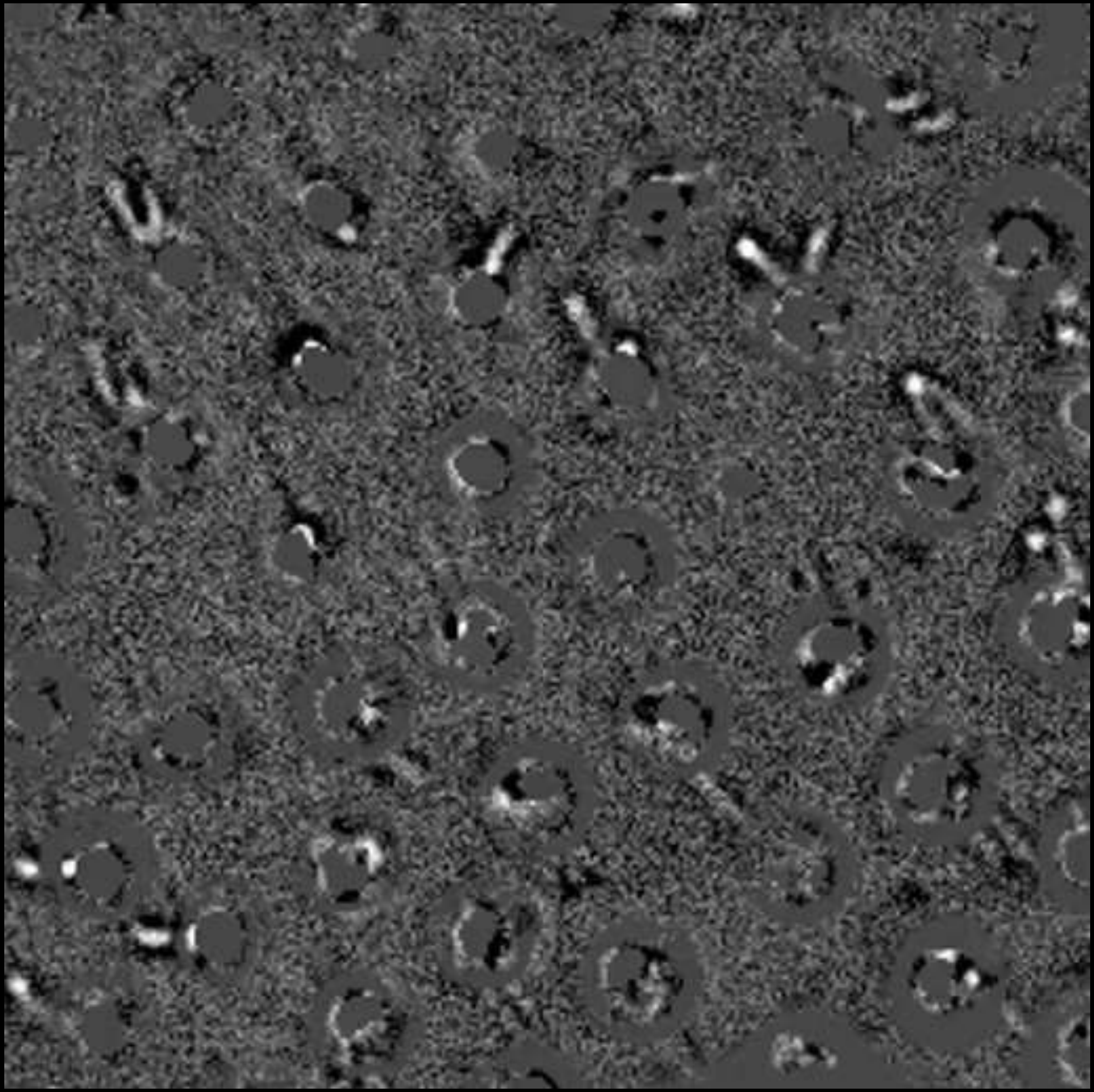


Polin, Tuval, Drescher & Goldstein (2009)

Metachronal Waves in *Volvox* (Side View)

Polin, Tuval, Pesci, Goldstein (2010)

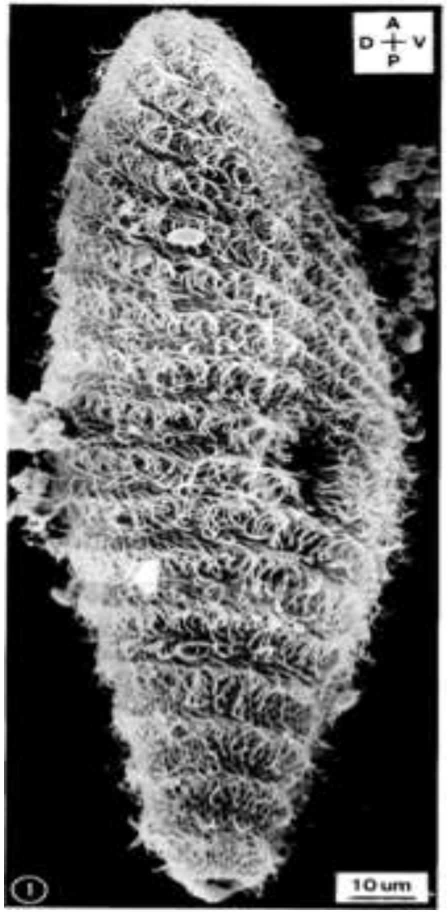
Metachronal Waves in *Volvox* (Top View)



Polin, Tuval, Pesci, Goldstein (2010)

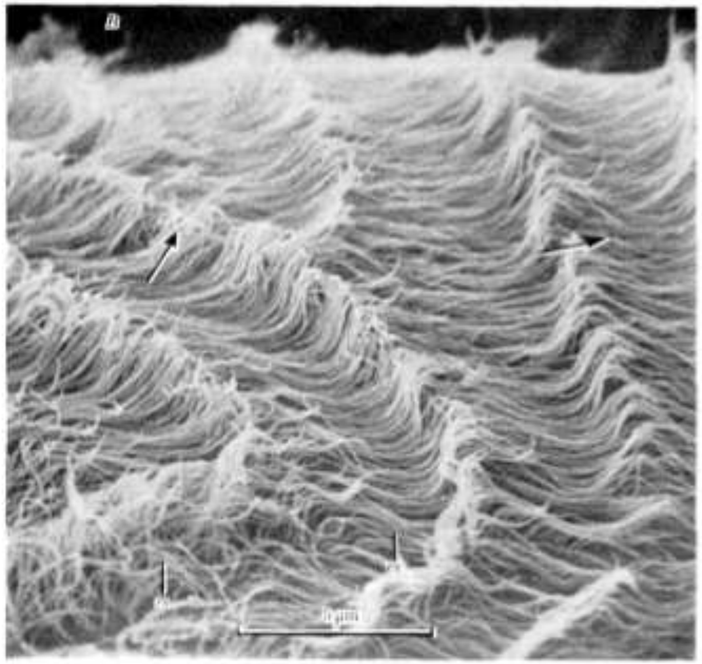
Flagellar Coordination in Eukaryotes

Paramecium **(protozoan)**



30 μm

Opalina **(protozoa)**



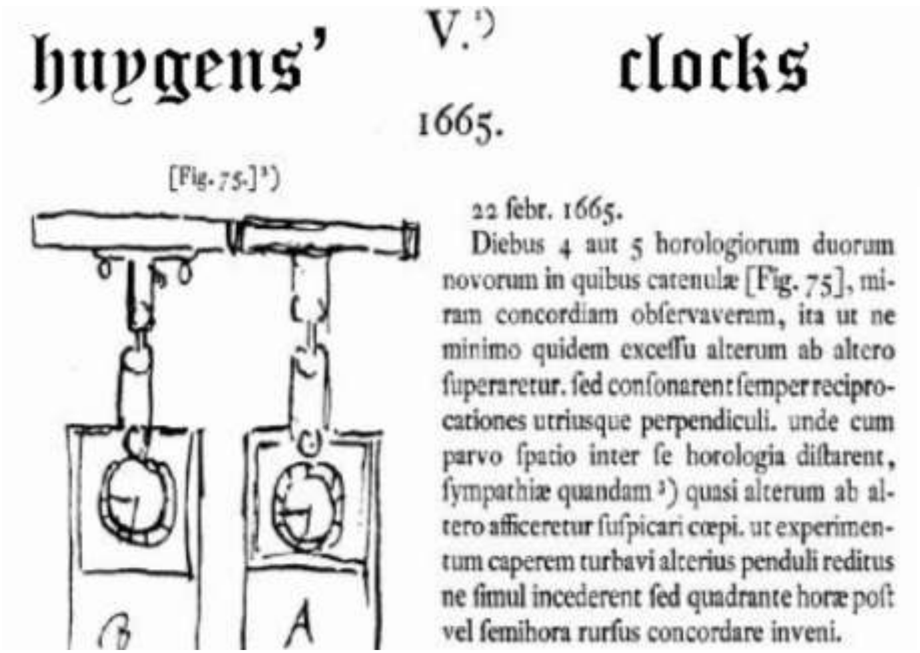
5 μm

Frog respiratory mucosa

10 μm

Brennen and Winet (1977)

Huygens’ Clock Synchronization (1665)


huygens’ V.[1] clocks

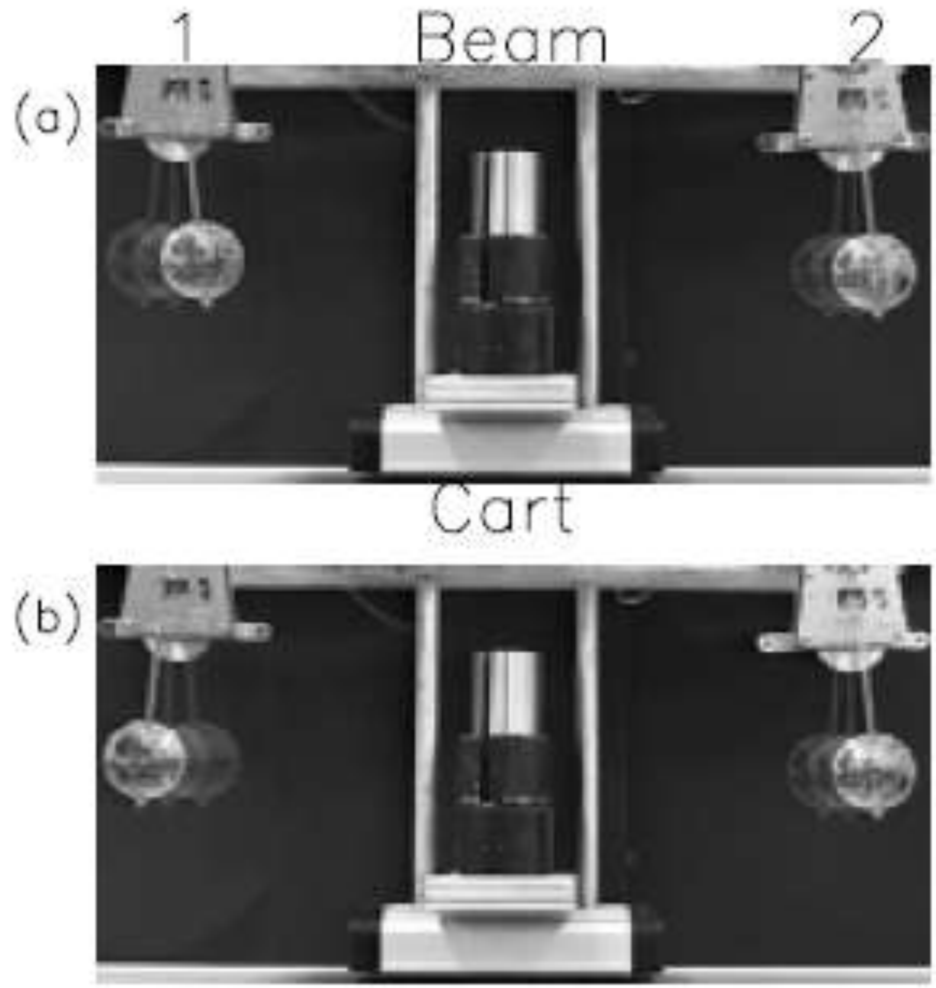
1665.

[Fig. 75.][1])

22 febr. 1665.

Diebus 4 aut 5 horologiorum duorum novorum in quibus catenulæ [Fig. 75], miram concordiam obſervaveram, ita ut ne minimo quidem exceſſu alterum ab altero ſuperaretur. ſed conſonarent ſemper reciprocationes utriusque perpendiculi. unde cum parvo ſpatio inter ſe horologia diſtarent, ſympathiæ quandam [2]) quasi alterum ab altero afficeretur ſuſpicari cœpi. ut experimentum caperem turbavi alterius penduli reditus ne ſimul incederent ſed quadrante horæ poſt vel ſemihora rurſus concordare inveni.

Pendulum clocks hung on a common wall synchronize out of phase!



Modern version of experiment confirms that vibrations in the wall cause the synchronization.

Schatz, *et al*. (Georgia Tech)

Coupled Metronomes (Lancaster University)

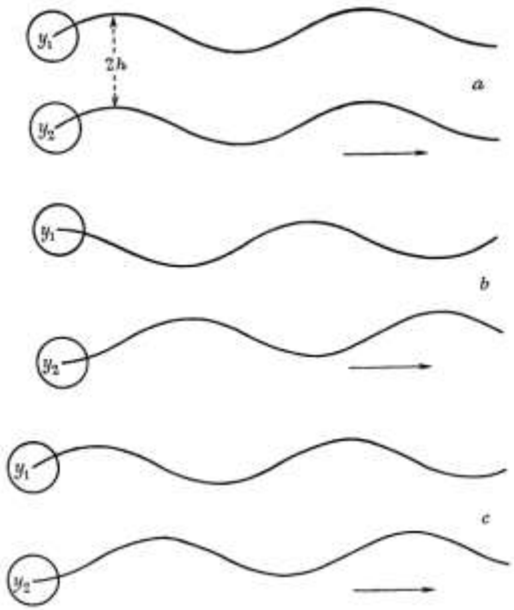
G. I. Taylor's Waving Sheets

Analysis of the swimming of microscopic organisms

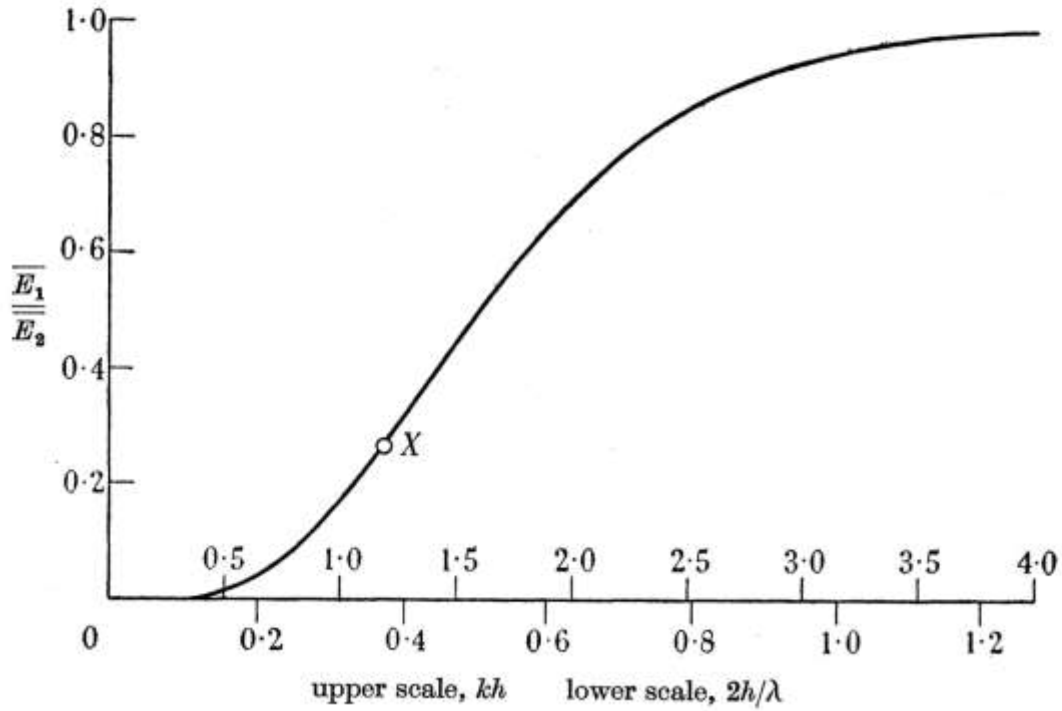
By Sir Geoffrey Taylor, F.R.S.

(*Received* 25 *June* 1951)

$$\frac{\text{energy dissipation rate in phase}}{\text{energy dissipation rate out of phase}}$$



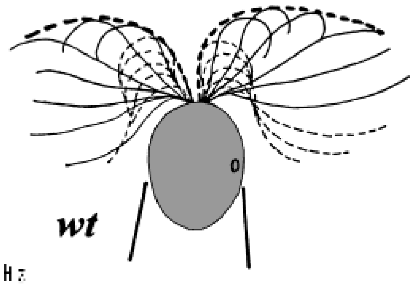
Sheets at various phase relative phase shifts



Scaled separation between sheets

Minimization of dissipation is not (in general) a principle from which to deduce dynamical behaviour...

Early Study of Flagella Synchronisation in *Chlamydomonas*



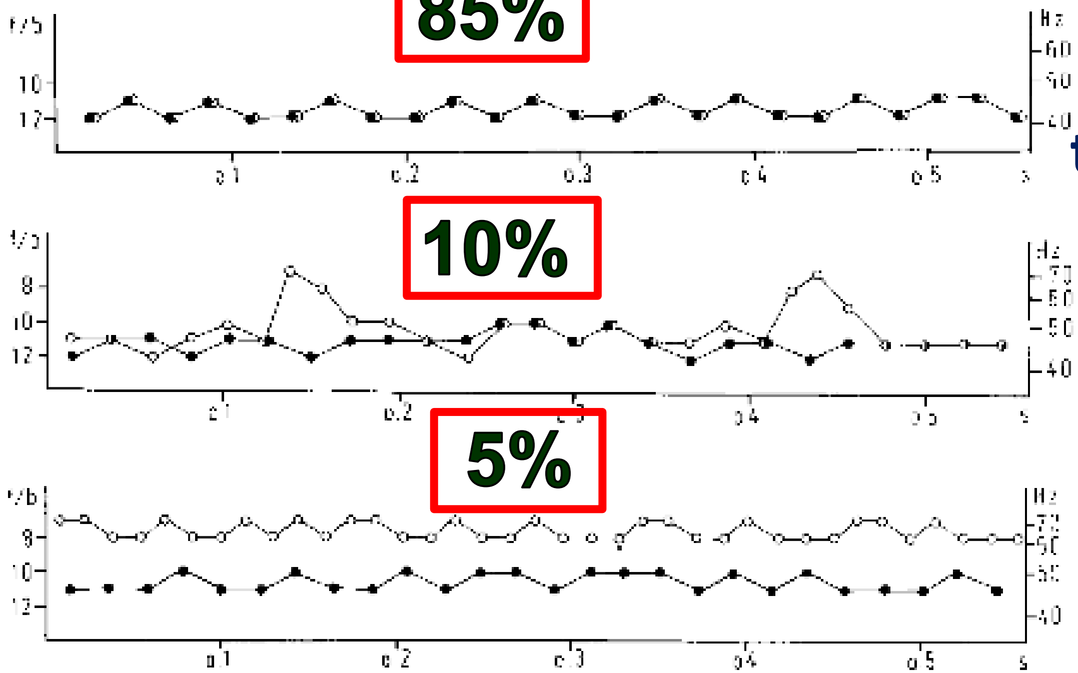
For <u>different</u> cells:

period

complete synchrony — **85%**

sporadic asynchronies — **10%**

different frequencies — **5%**



time

- *trans*
- *cis*

$\Delta\nu/\nu \sim 30\%$

Attributed to distinct sub-populations of cells

Rüffer and Nultsch, *Cell Motility and the Cytoskeleton* **7**, 87 (1987)

See also: Josef, Saranak, Foster**,** *Cell Motility and the Cytoskeleton* ***61***, 83 (2005)

Historical Background

- R. Kamiya and E. Hasegawa [*Exp. Cell. Res.* ('87)]
  (cell models – demembranated)
  intrinsically different frequencies of two flagella
- U. Rüffer and W. Nultsch [*Cell Motil*. ('87,'90,'91,'98)]
  short observations (50-100 beats at a time, 1-2 sec.)
  truly heroic – hand drawing from videos
  synchronization, small phase shift, occasional "slips"

Key issue: control of phototaxis

"Phase oscillator" model used in e.g. circadian rhythms, etc.

strokes of flagella

$$S_1(t) = A_1 \cos[\theta_1(t)]$$
$$S_2(t) = A_2 \cos[\theta_2(t)]$$

amplitudes

"phases" or angles

$$\frac{d\theta_1}{dt} = \omega_1 + \cdots$$
$$\frac{d\theta_2}{dt} = \omega_2 + \cdots$$

natural frequencies

Without coupling, the phase difference simply grows in time

$$\Delta \equiv \frac{\theta_1 - \theta_2}{2\pi} = (\nu_1 - \nu_2)t + \cdots$$

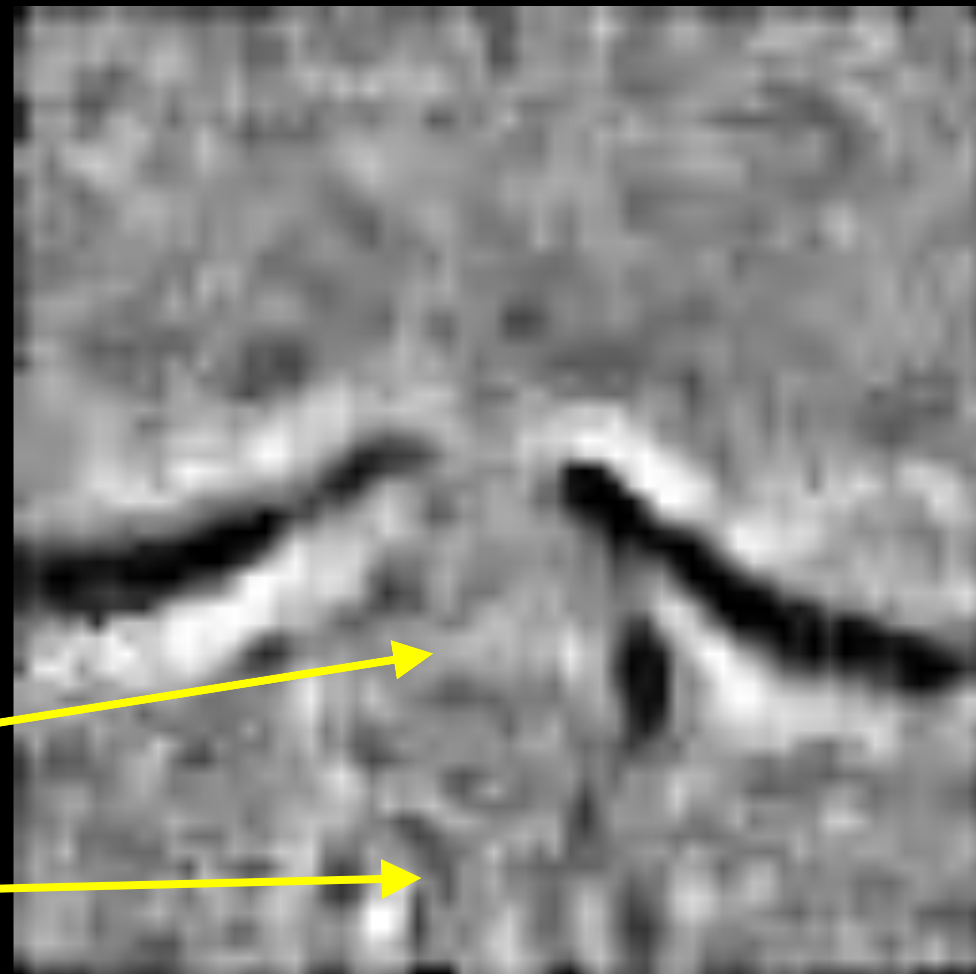
So, is this seen?

Noisy Synchronization

Experimental methods:

- **Micropipette manipulation with a rotating stage for precise alignment**
- **Up to 2000 frames/sec**
- **Long time series (50,000 beats or more)**
- **Can impose external fluid flow**

Frame-subtraction

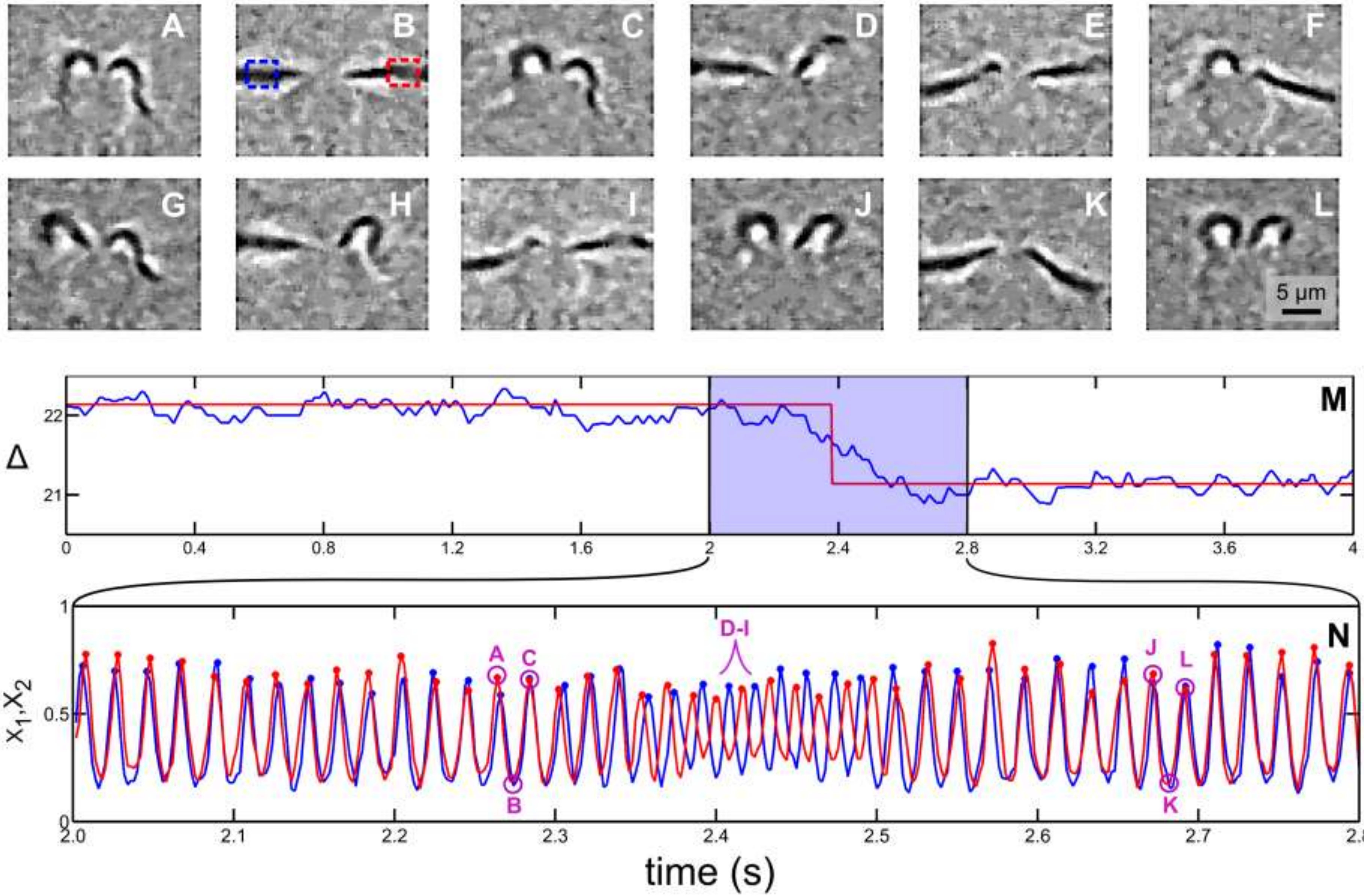


Cell body

Micropipette

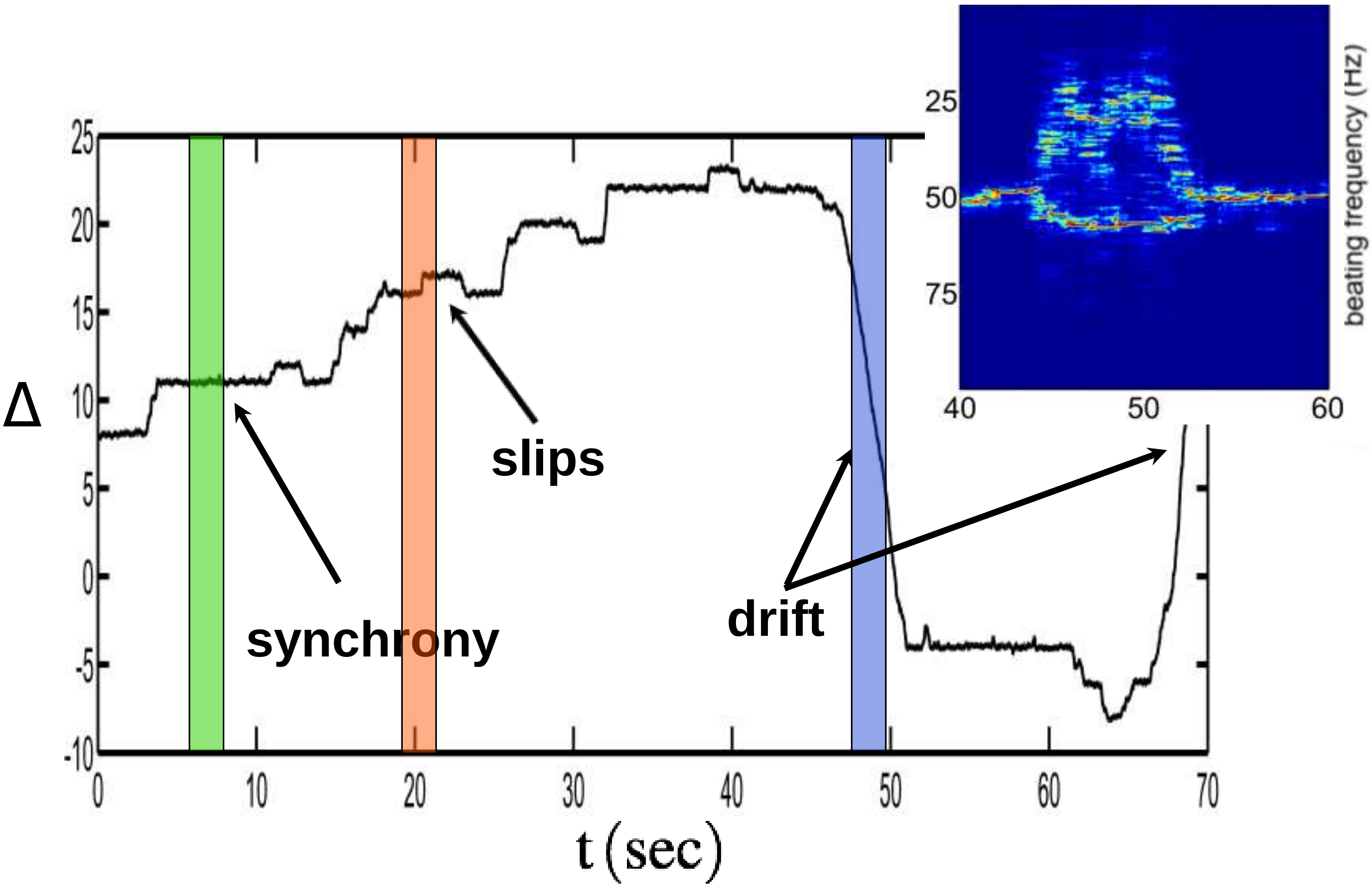
Polin, Tuval, Drescher, Gollub, Goldstein, *Science* **325**, *487* (2009)

A Phase Slip



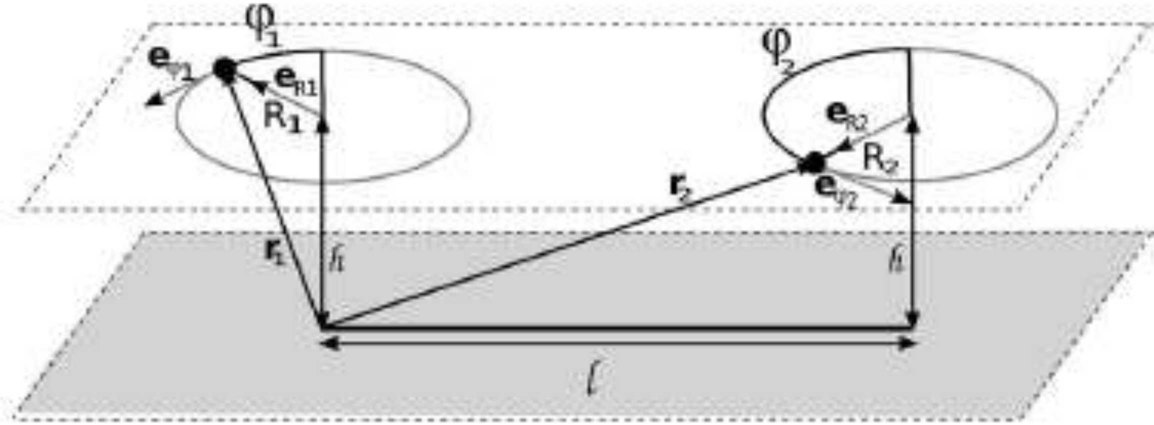
Goldstein, Polin, Tuval, *Phys. Rev. Lett.* ***103***, 168103 (2009)

A Single Cell Displays All Three Regimes (!)



Polin, Tuval, Drescher, Gollub, Goldstein, *Science* ***325***, 487 (2009)

Model for Phase Evolution



Spheres forced in circular orbits by an azimuthal force, with elasticity to maintain orbit radius, and sphere-sphere hydrodynamic interactions *(deterministic)*

Niedermayer, Eckhardt, and Lenz, *Chaos* (2008)
See also: Guirao and Joanny, *Biophys. J.* (2007)
Vilfan and Julicher, *PRL* (2006)

We see clear evidence of stochasticity …
which suggests the stochastic **Adler** equation:

$$\dot{\Delta} = \delta\nu - 2\pi\varepsilon \sin(2\pi\Delta) + \xi(t)$$

Intrinsic frequency mismatch

coupling Strength (hydrodynamics?)

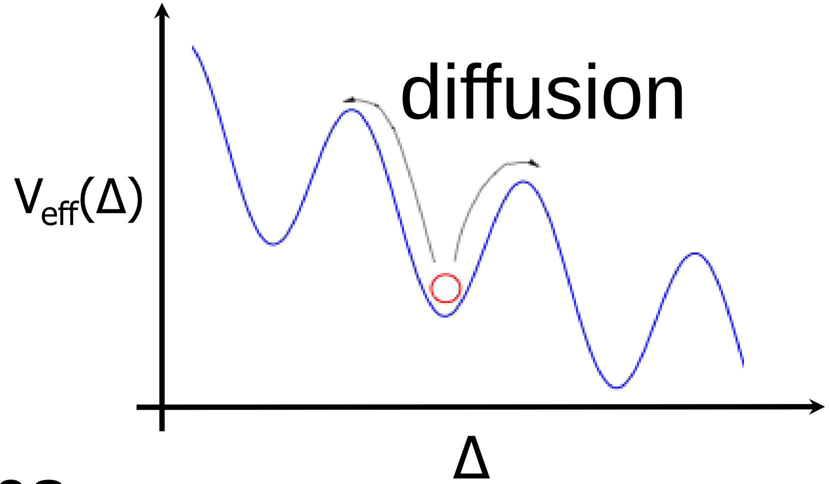
Quasi-universal form for phase oscillators (Kuramoto)

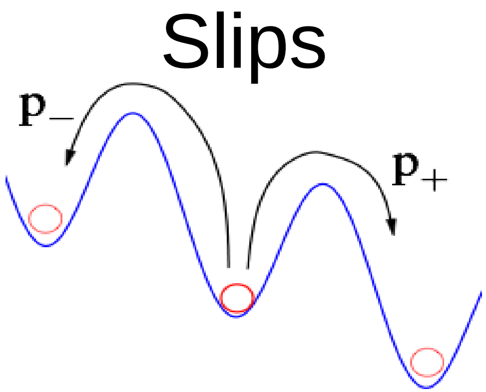
biochemical noise

$$\langle \xi(t) \rangle = 0$$

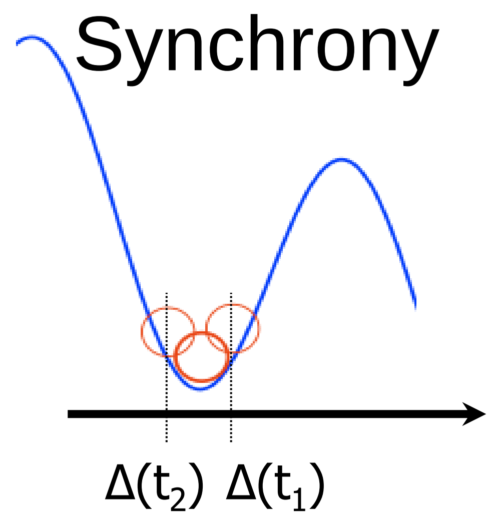
$$\langle \xi(t)\xi(s) \rangle = 2T_{eff}\,\delta(t-s)$$

Model for Phase Evolution



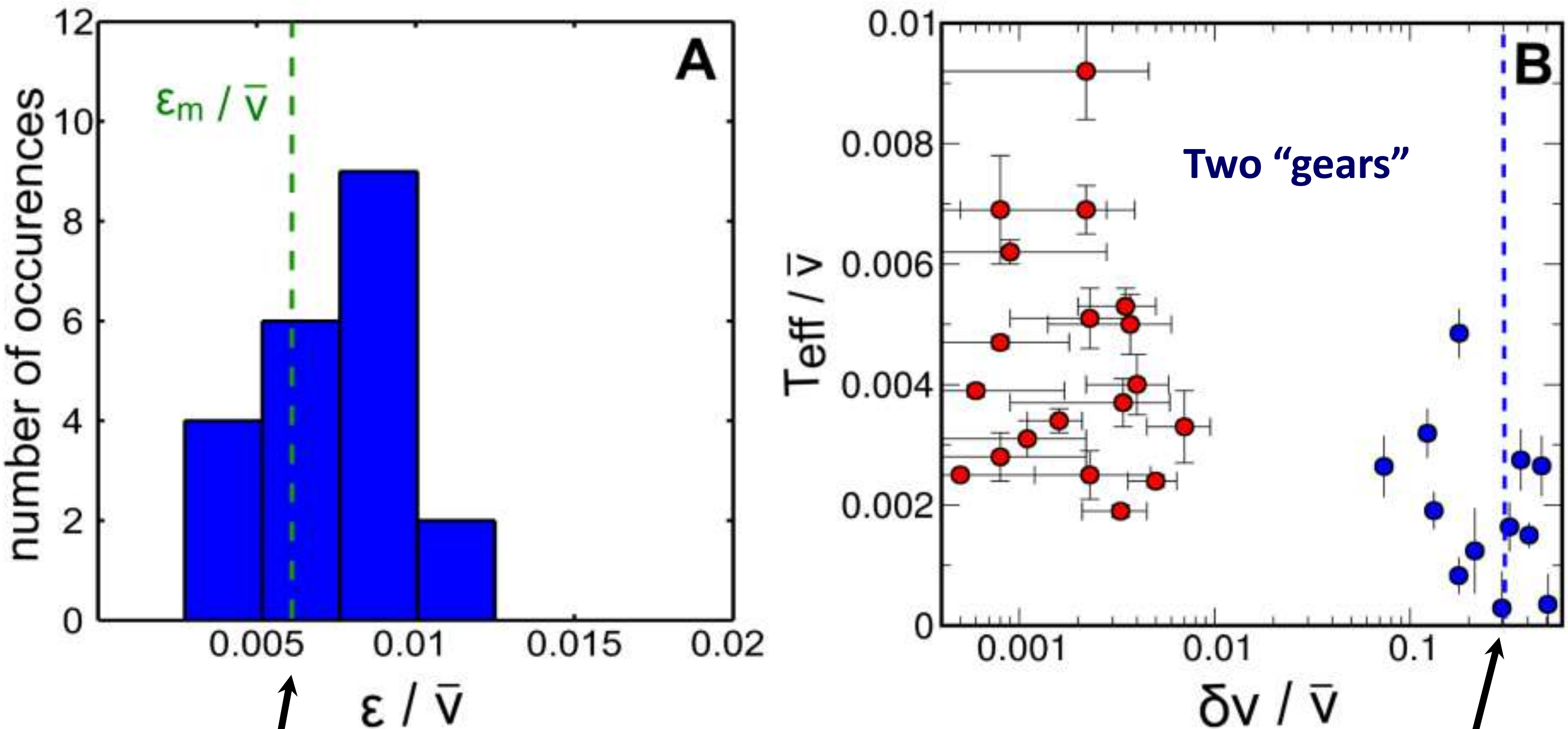


Relative probability of +/- slips
Yields the frequency difference $\delta\nu$



Amplitude and autocorrelation function of fluctuations in the synchronised state yields T_{eff} and ε

Model Parameters



estimate of hydrodynamic coupling

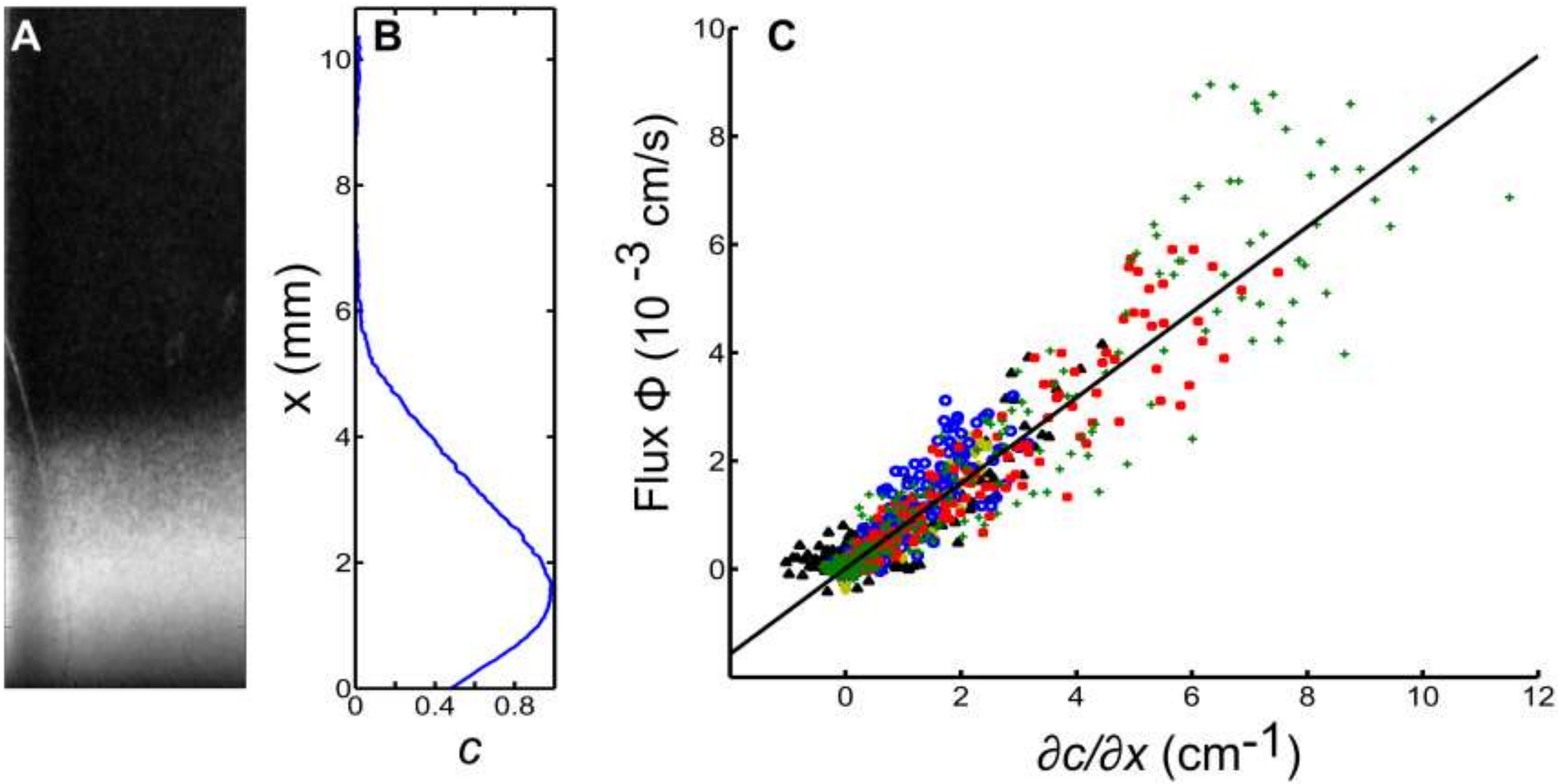
$$\varepsilon \approx \tau_r \nu_L \nu_R$$

$$\tau_r = \frac{3\pi\eta a l^3}{\kappa}$$

expected value for intrinsic frequency difference

Polin, *et al.*, *Science* ***325***, 487 (2009)

Direct Demonstration of *Chlamydomonas* Diffusion

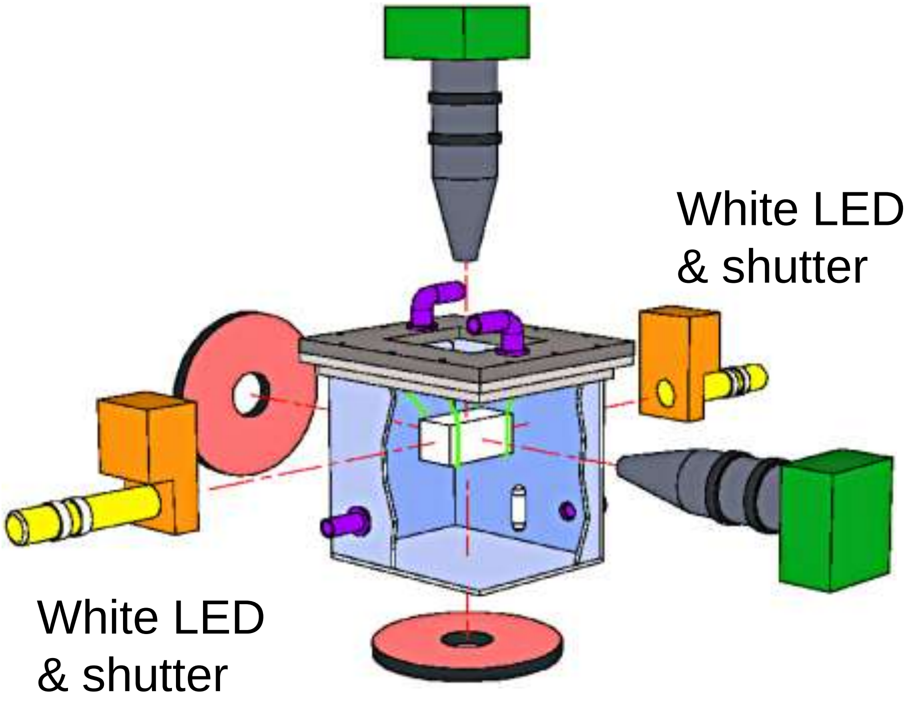


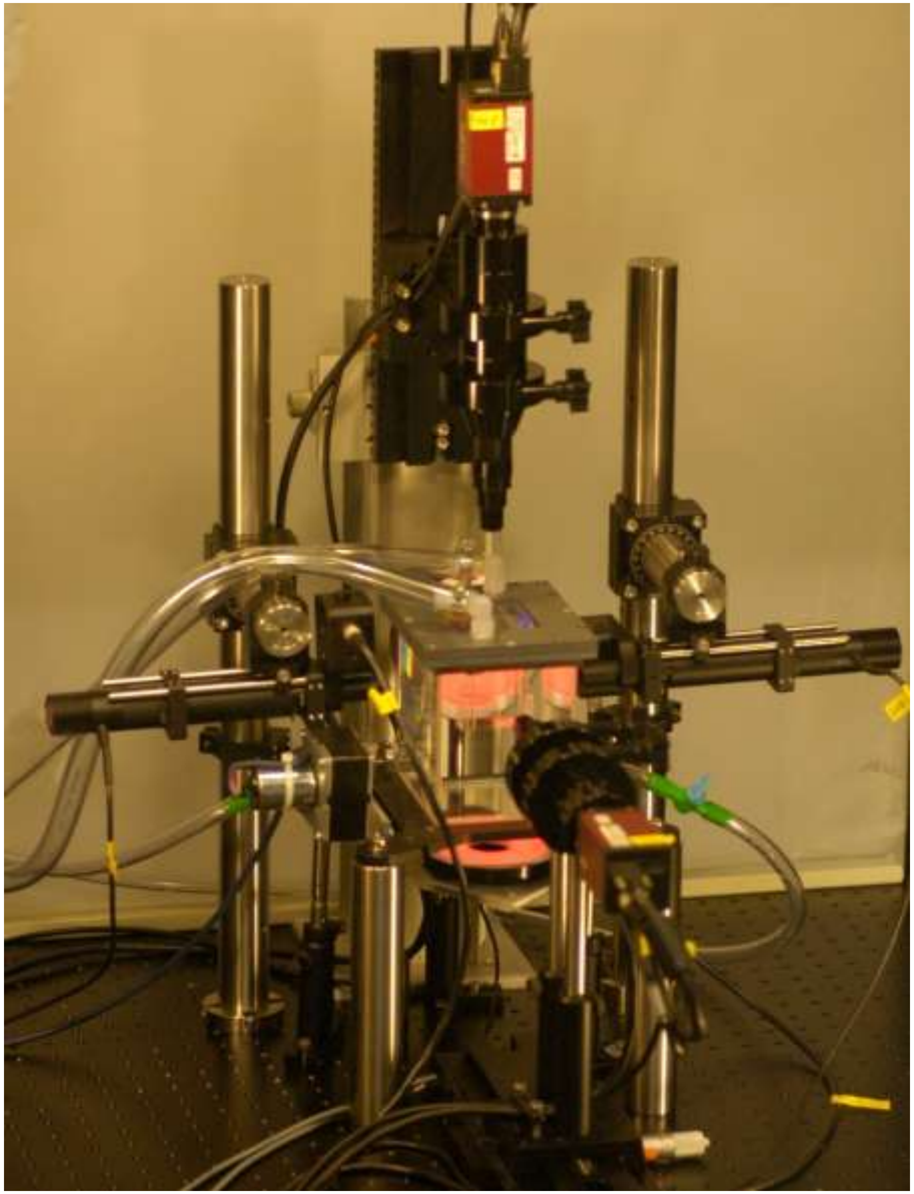
$D_{exp} \sim (0.68 \pm 0.11) \times 10^{-3}\ cm^2/s$

Since $D \sim u^2 \tau$ and u~100 μm/s, there must be a time τ~10 s

Polin, Tuval, Drescher, Gollub, Goldstein, *Science* **325**, 487 (2009)

Dual-View Apparatus Free of Thermal Convection

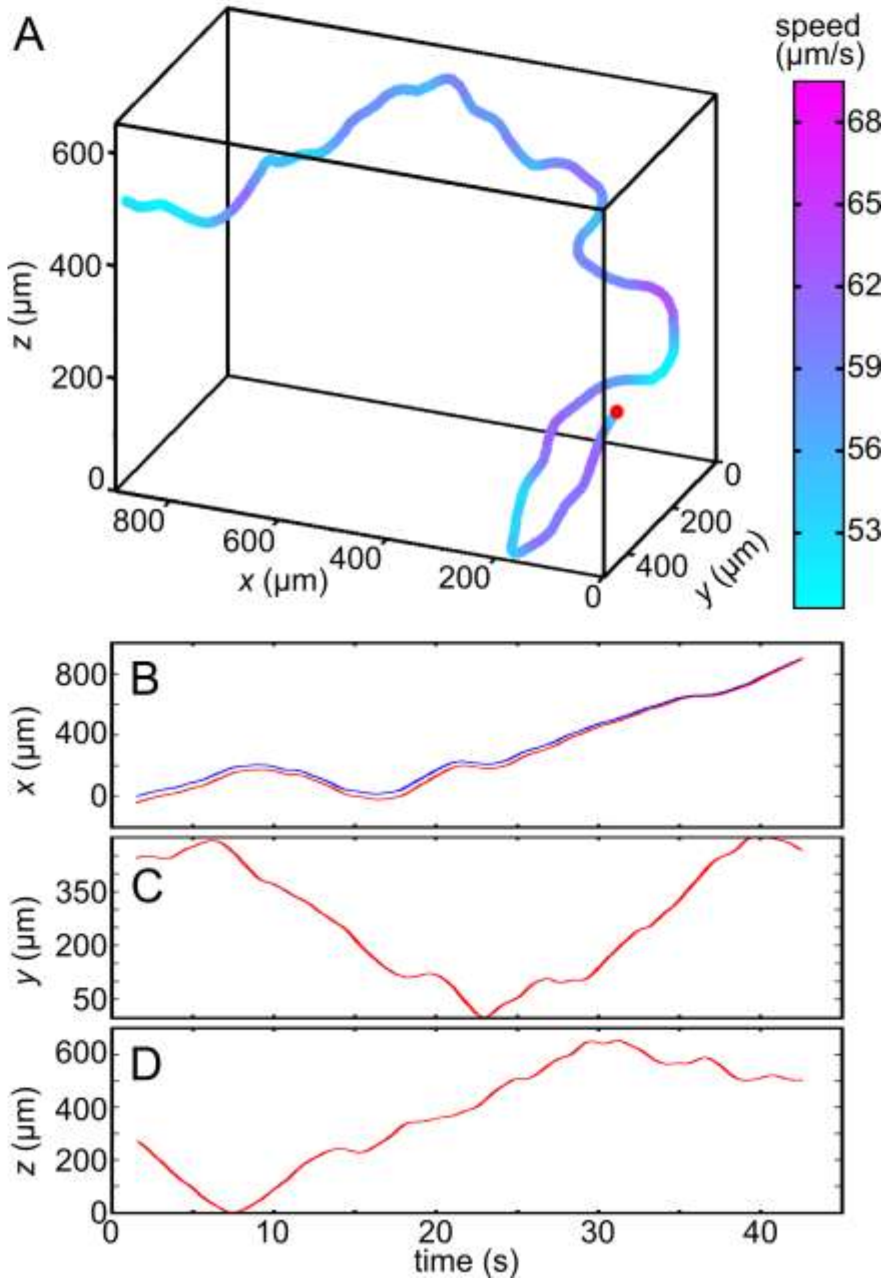




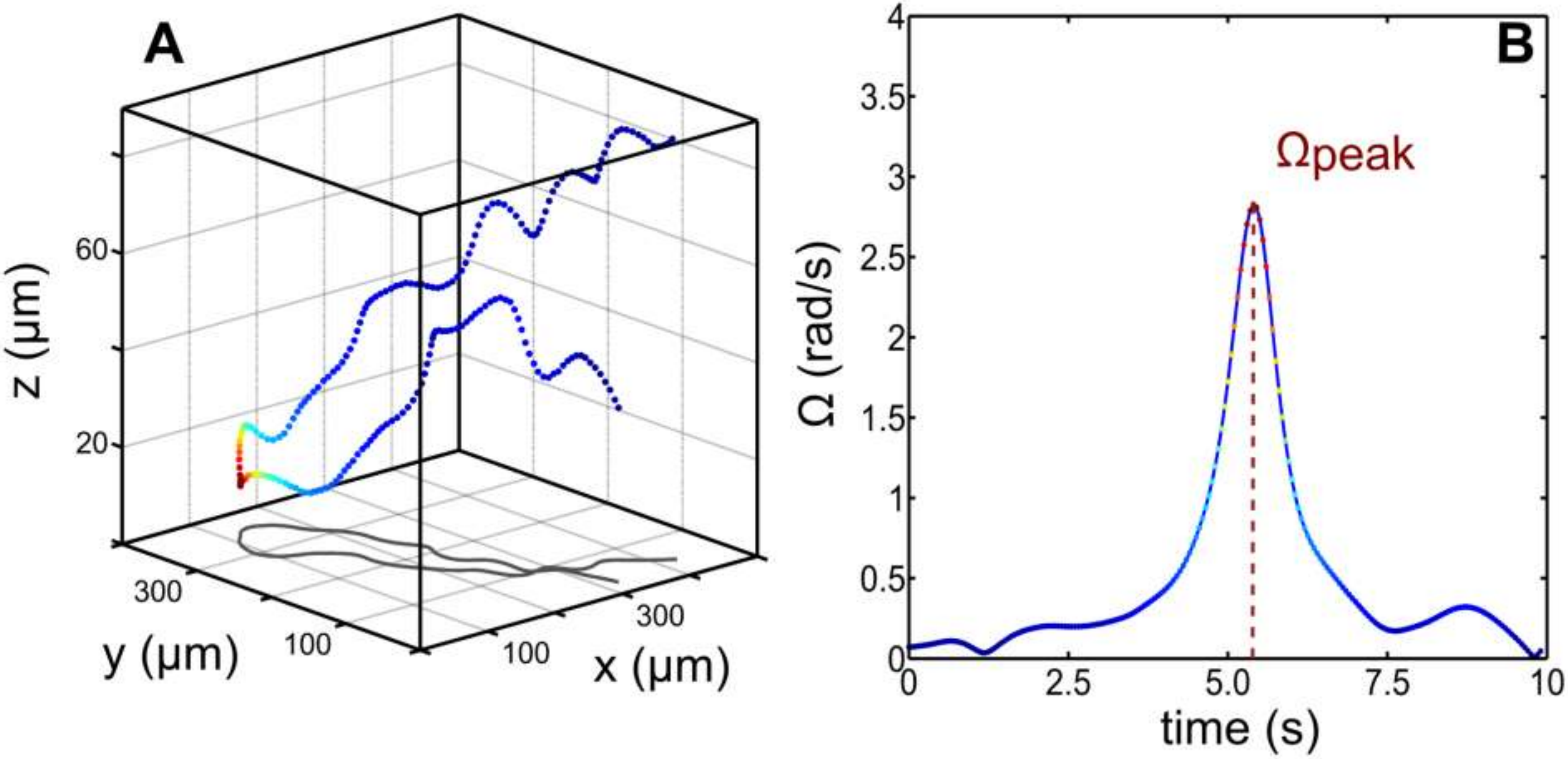
Capable of imaging protists from 10 μm to 1 mm, with tracking precision of ~1 micron, @ 20 fps.

Drescher, Leptos, Goldstein,
Review of Scientific Instruments **80**, 014301 (2009)

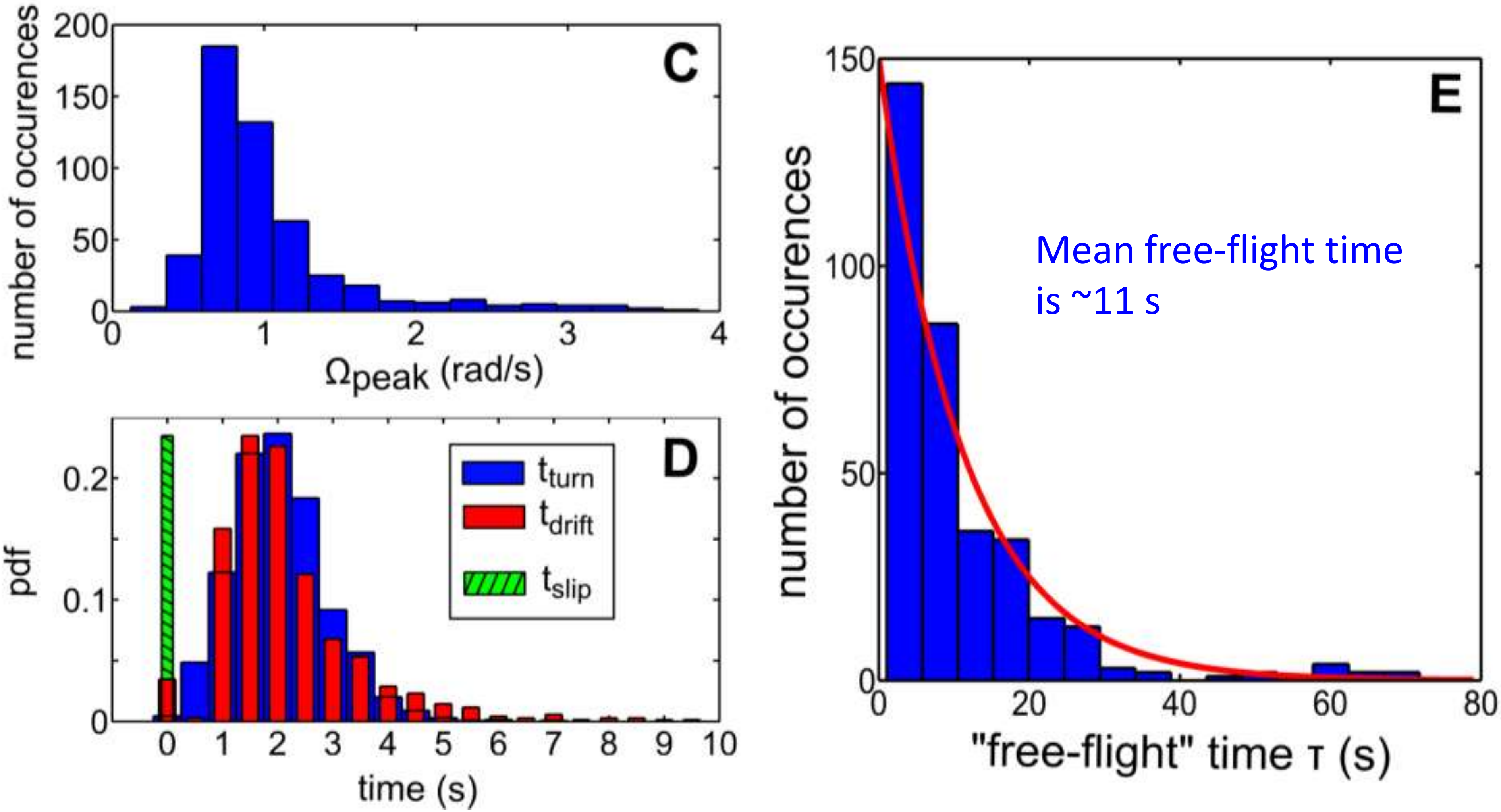
Reconstructing a Trajectory



Chlamydomonas Tracking in Detail – A Sharp Turn



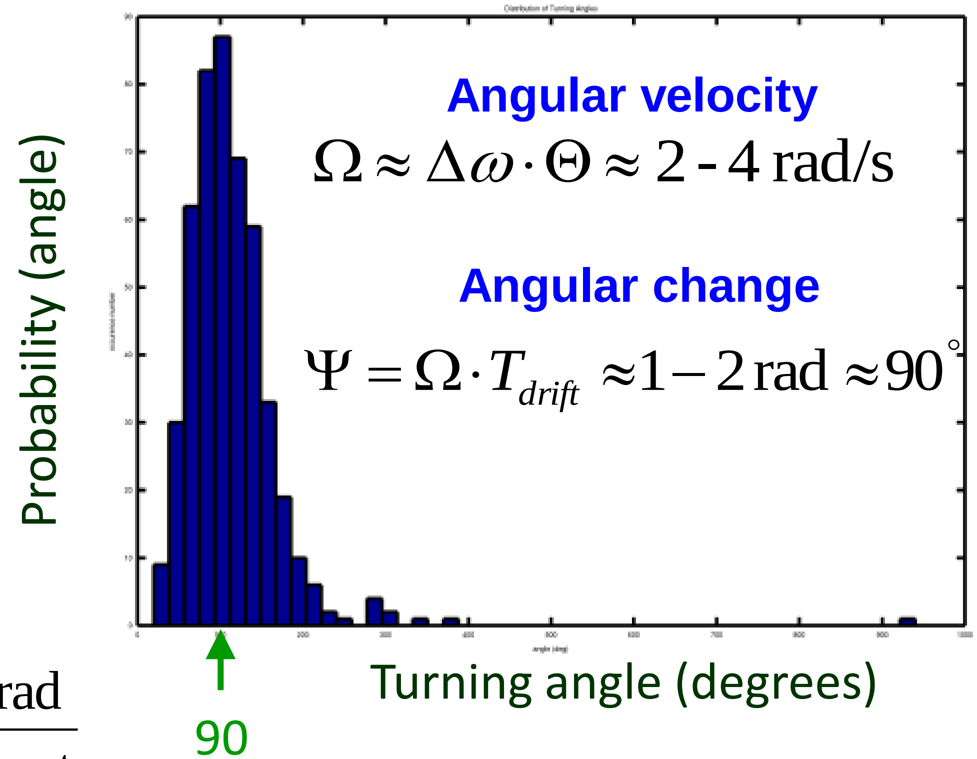
Statistics of Sharp Turns: Origin of Diffusion



Turns and drifts have identical statistics,
much longer than slips.

Geometry of Turning

***Chlamy* w/single flagellum, rotating near a surface**



Angular velocity

$$\Omega \approx \Delta\omega \cdot \Theta \approx 2\text{-}4 \text{ rad/s}$$

Angular change

$$\Psi = \Omega \cdot T_{drift} \approx 1 - 2 \text{ rad} \approx 90^{\circ}$$

Angle per beat - $\Theta = \frac{2\pi}{\sim 16 \text{ beats}} \approx 0.4 \frac{\text{rad}}{\text{beat}}$

Frequency difference - $\Delta\omega \approx 5\text{-}10 \frac{\text{beats}}{\text{s}}$

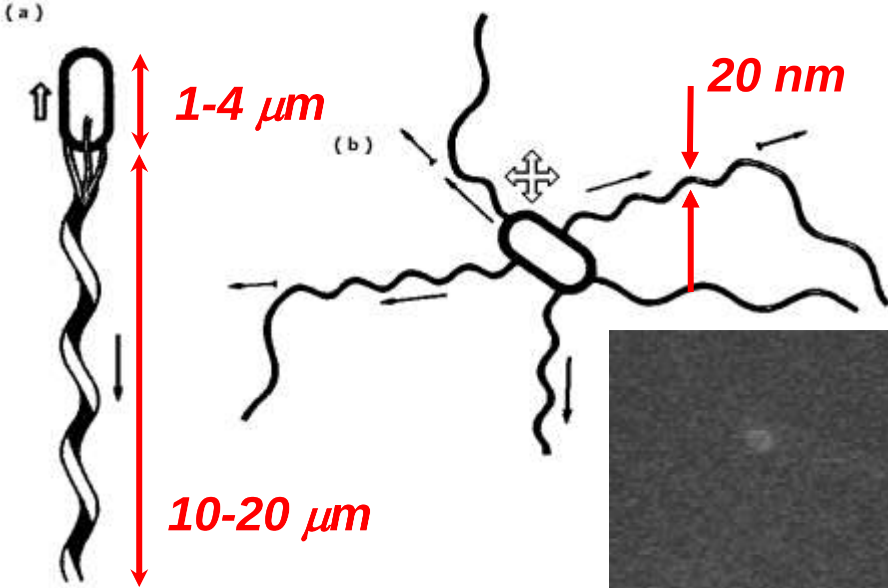
"Drift" duration- $T_{drift} \approx 25 - 50 \text{ beats}$

$$\approx 0.5\text{-}1\text{s}$$

$$D = \frac{u^2 \tau}{3(1 - \cos\theta)}$$

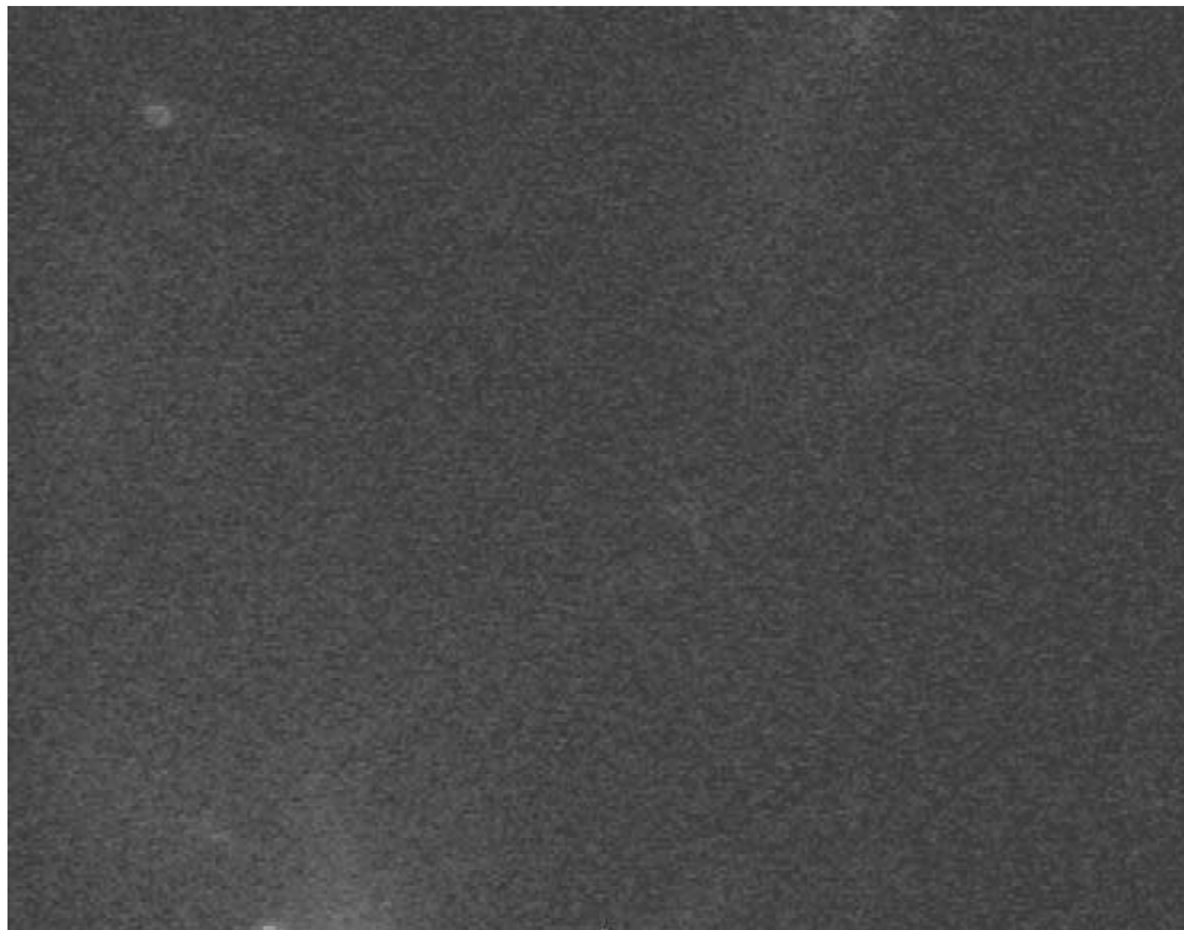
$D_{est} \sim (0.47 \pm 0.05) \times 10^{-3}$ cm^2/s

Run-and-Tumble Locomotion of Bacteria

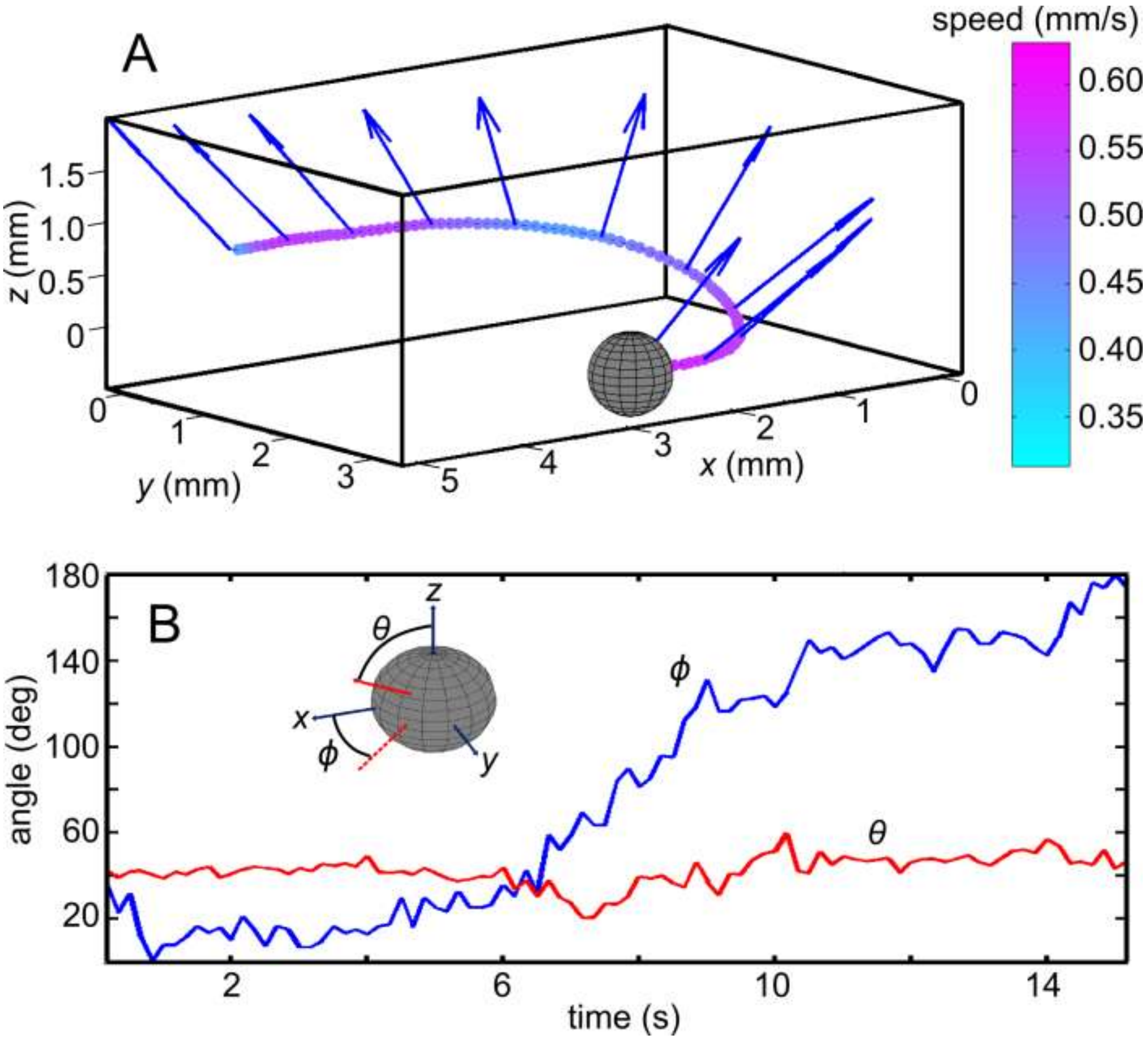


Macnab and Ornstein (1977)

Turner, Ryu, and Berg (2000)



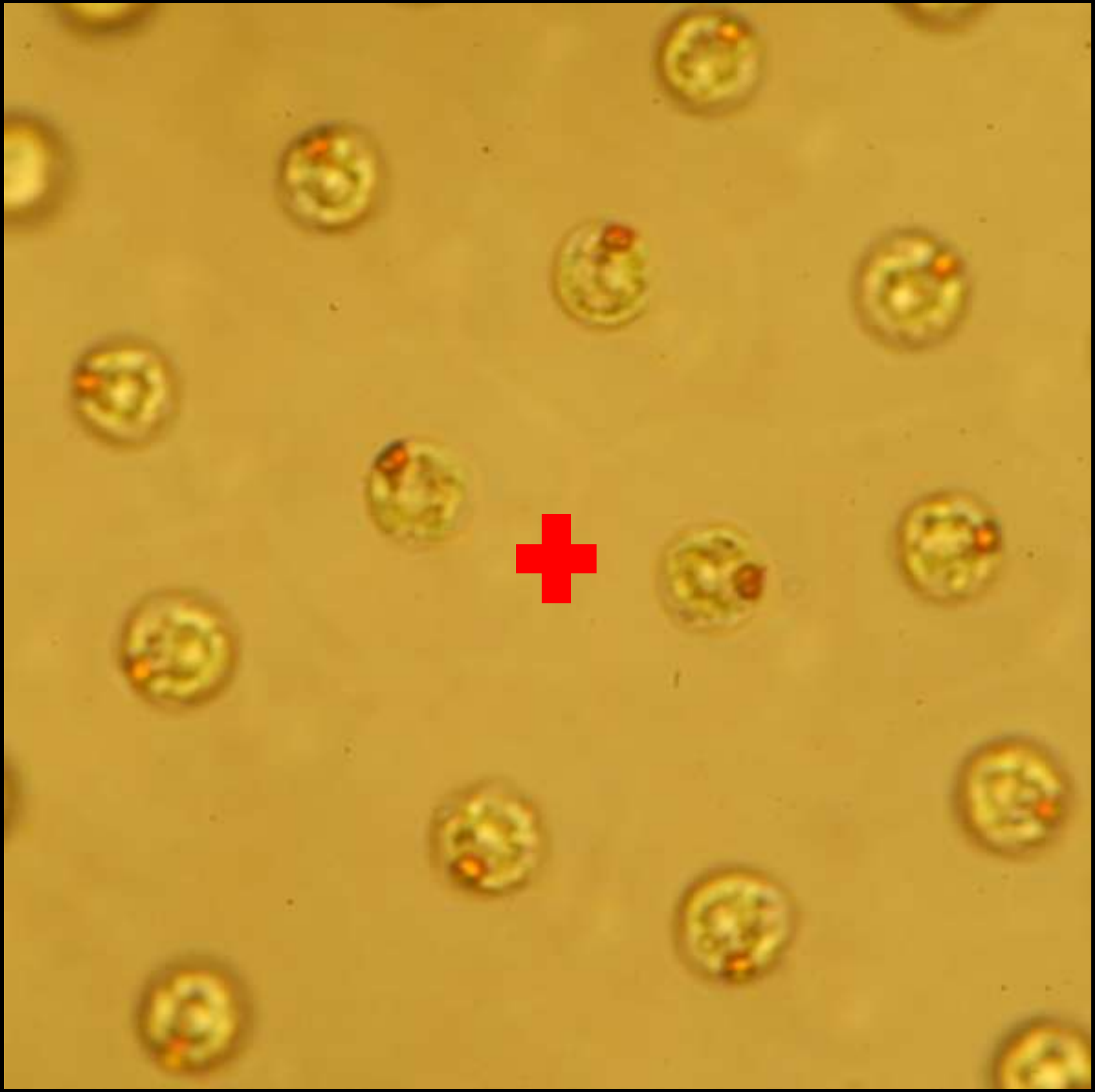
A Phototurn (*V. barberi*) With Bottom-Heaviness



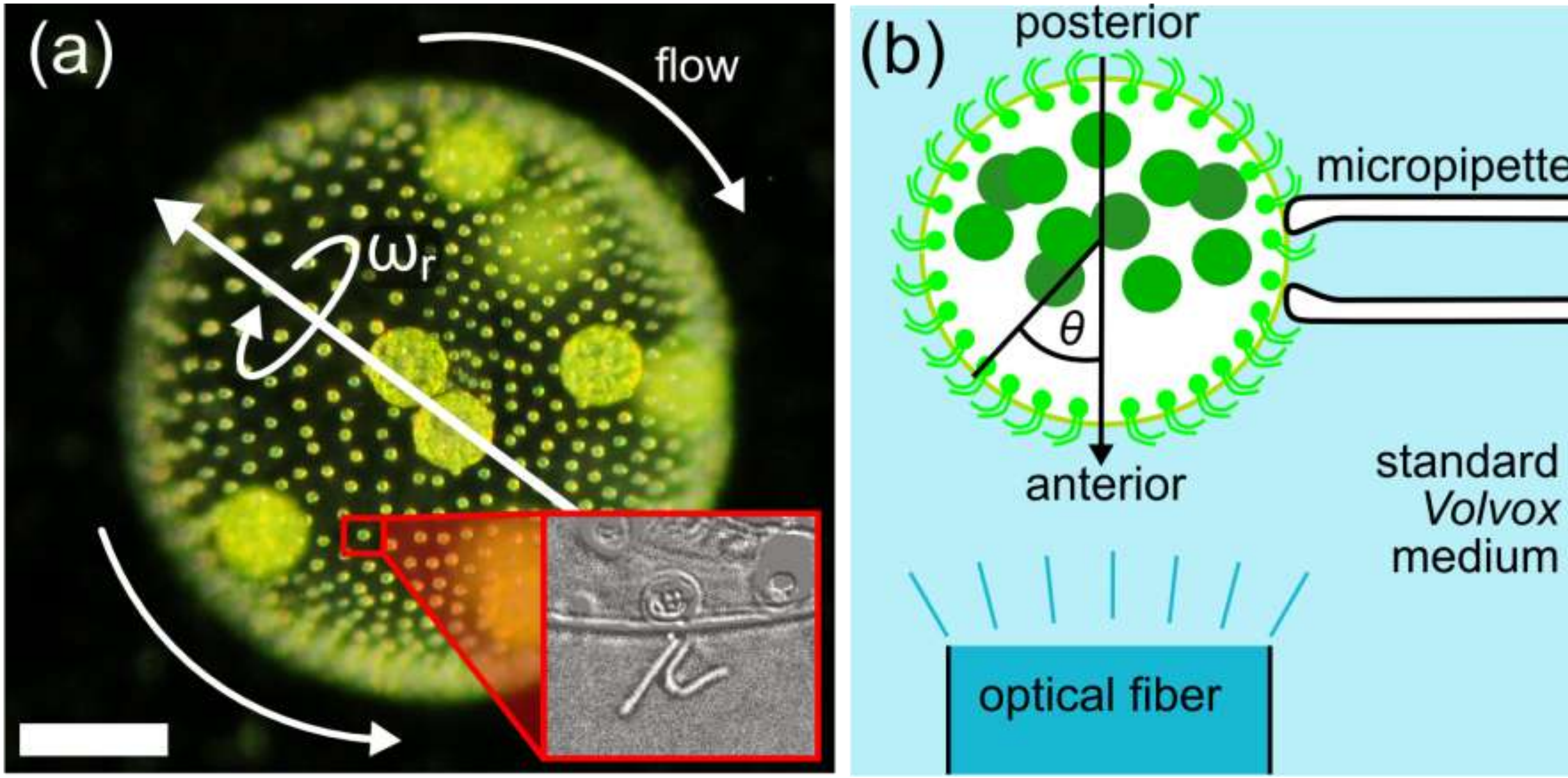
Drescher, Leptos, Goldstein, *Rev. Sci. Instrum.* (2009)

Volvox Eyespots

Top view at anterior pole

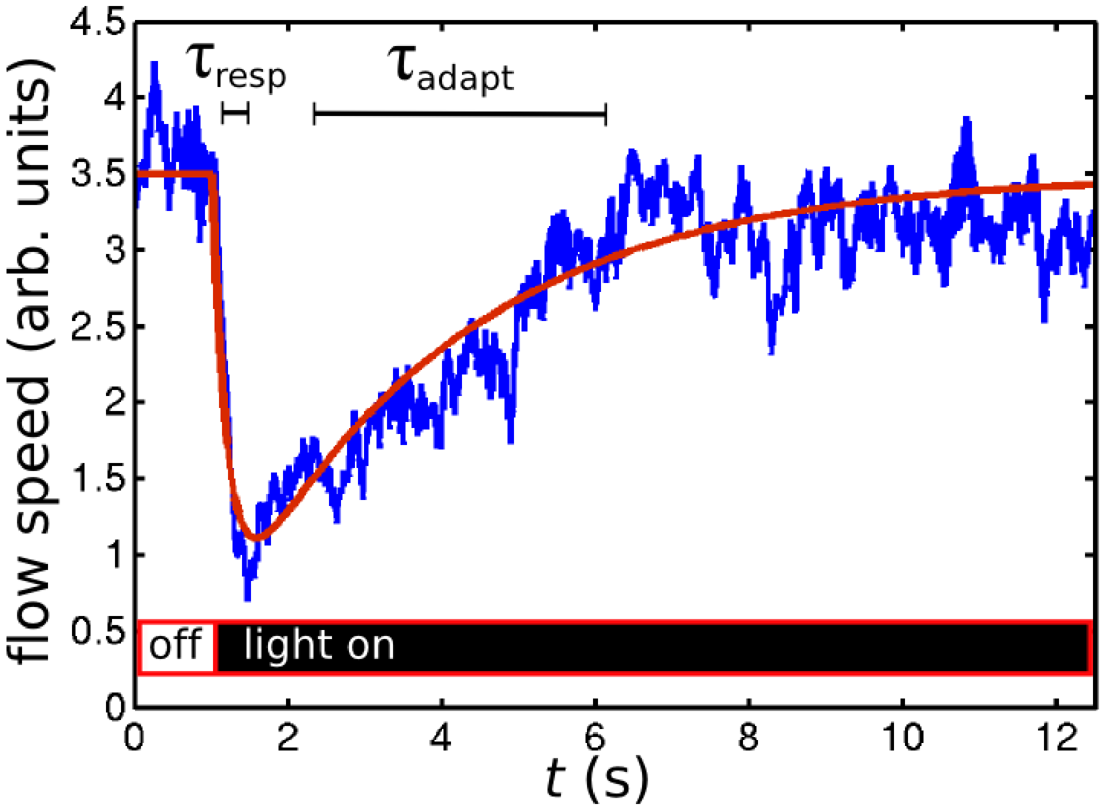


Adaptive Flagellar Dynamics and the Fidelity of Multicellular Phototaxis



Drescher, Goldstein, Tuval, *preprint* (2010)

Dynamic PIV Measurements – Step Response



Adaptive, two-variable model

$$\dot{p} = \frac{(s-h)-p}{\tau_r}$$

$$\dot{h} = \frac{s-h}{\tau_a}$$

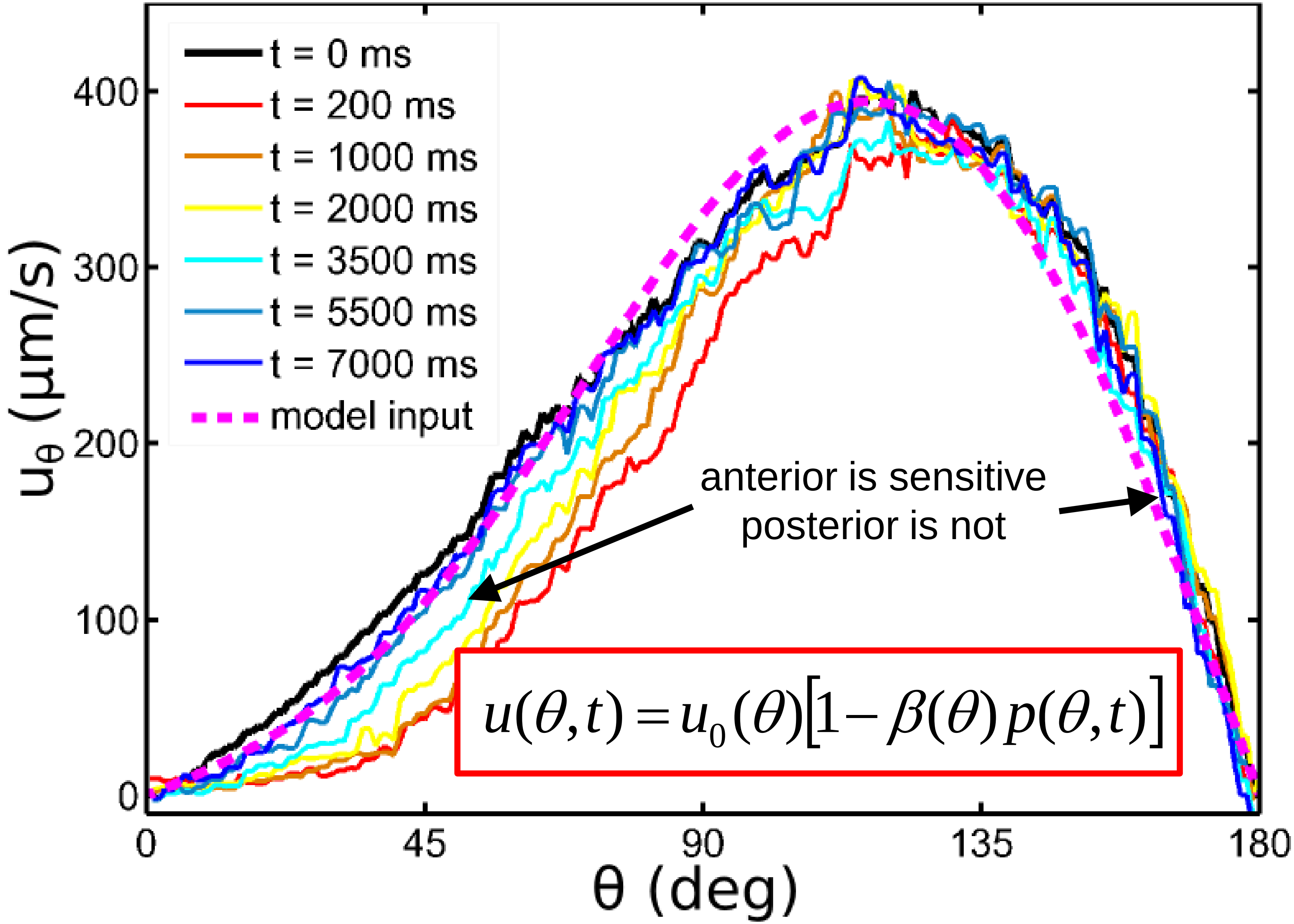
p="photoresponse" amplitude
h="hidden" biochemistry

$$u = u_0(1-\beta p)$$

Simple modulation of flow

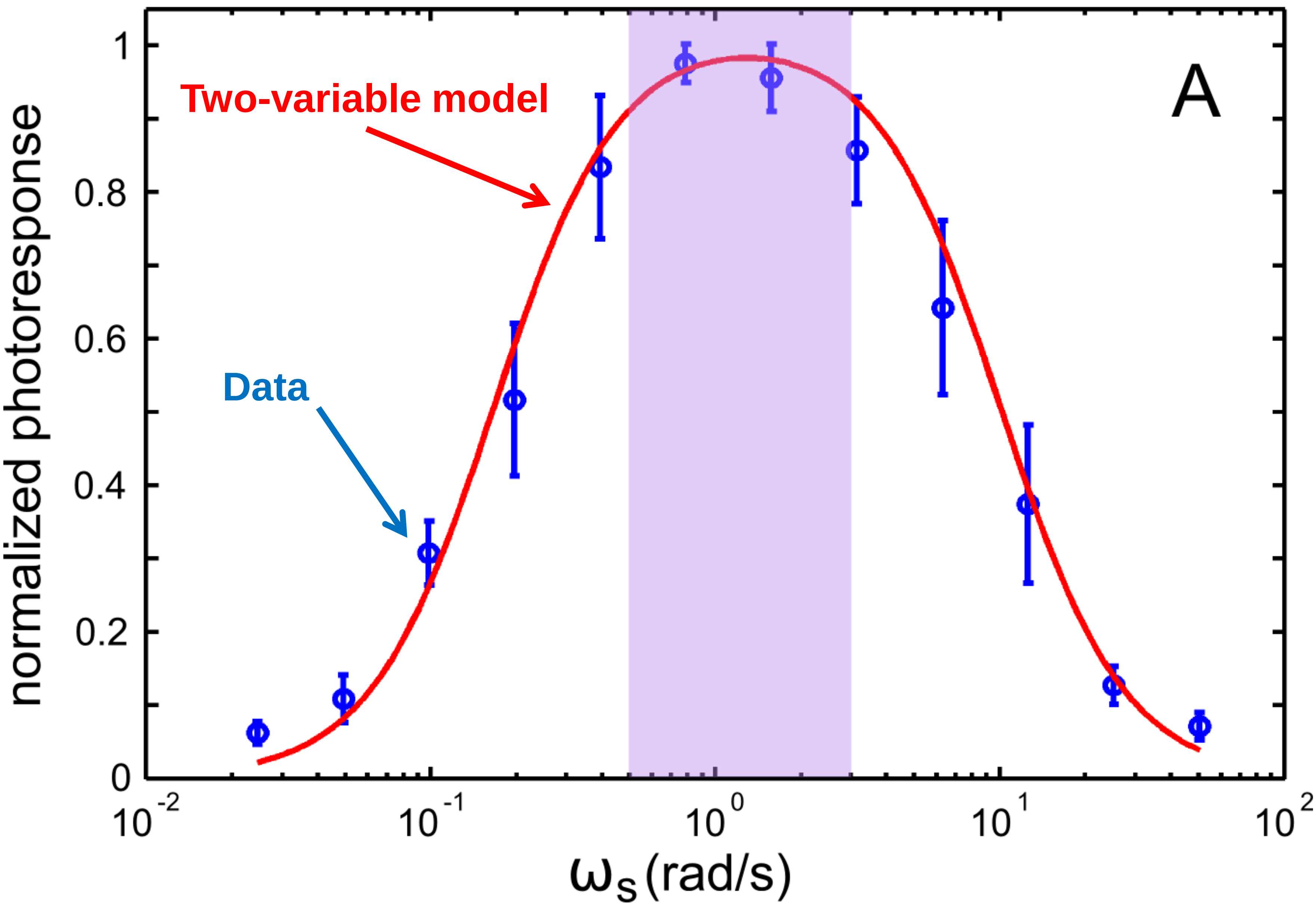
Adaptive dynamics also play a role in sperm chemotaxis: Friedrich and Jülicher (2007,09)

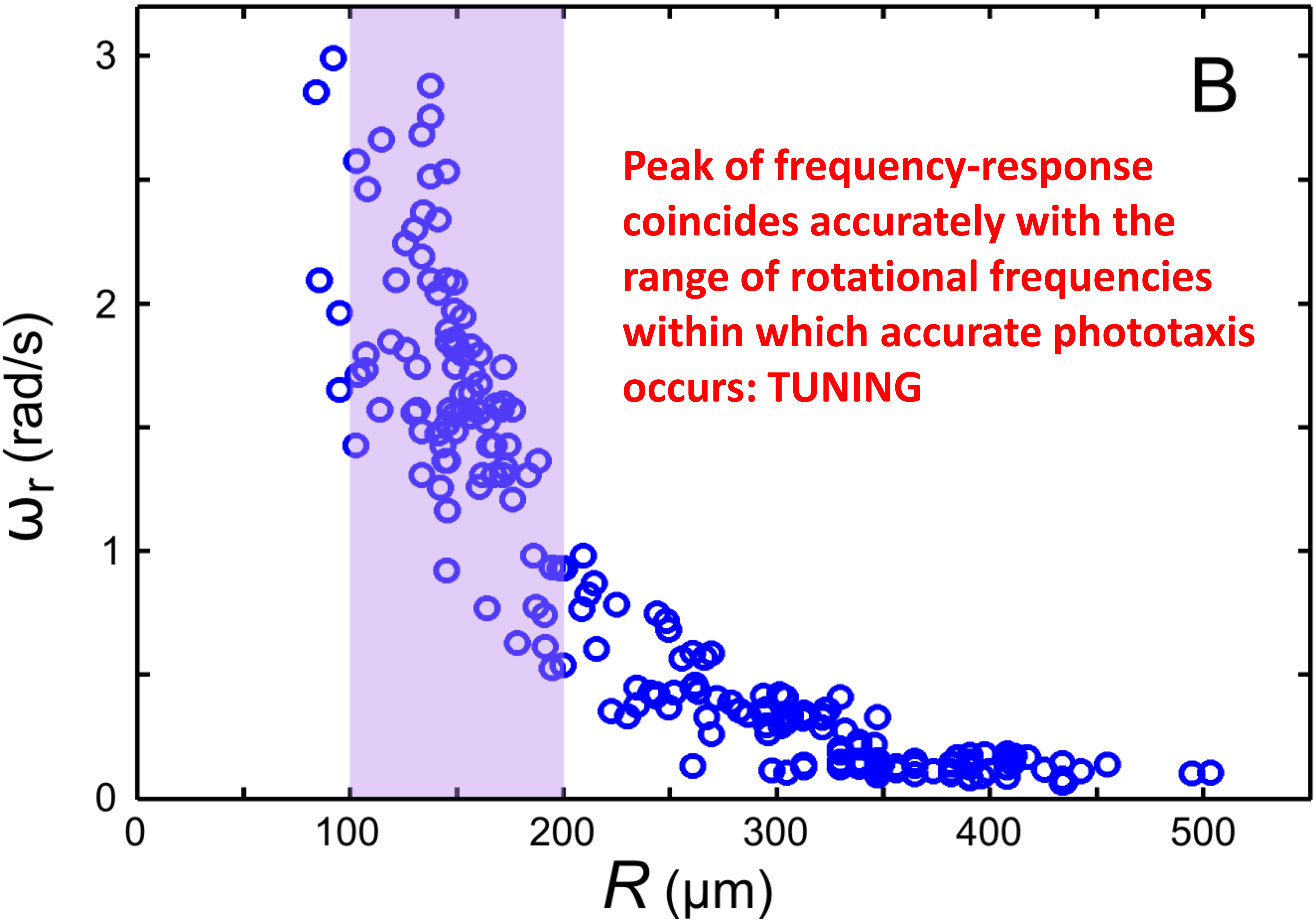
Angular Dependence of the Transient Response



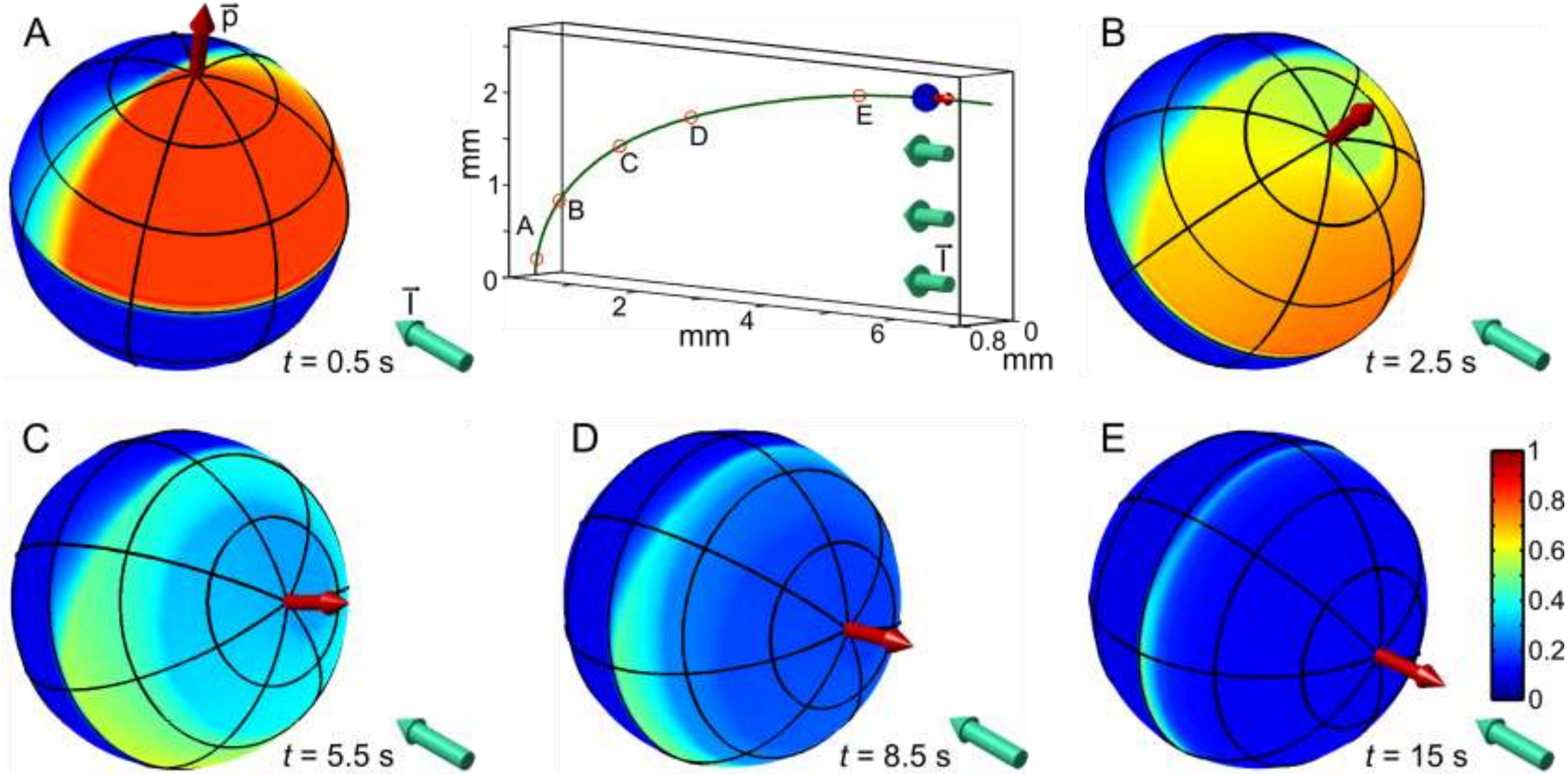
$$u(\theta,t) = u_0(\theta)\left[1 - \beta(\theta)\, p(\theta,t)\right]$$

Frequency-Dependent Response




B
Peak of frequency-response coincides accurately with the range of rotational frequencies within which accurate phototaxis occurs: TUNING
ω_r (rad/s)
0
1
2
3
0
100
200
300
400
500
R (μm)

Multicellular Phototaxis as Dynamic Phototropism



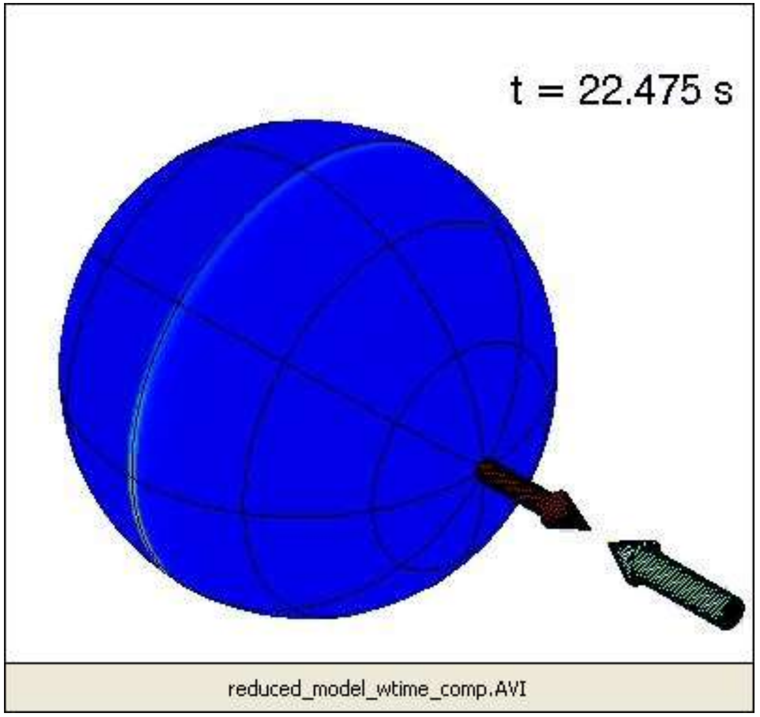
Initial: illuminated anterior region has strongly diminished flagellar beating, colony rotates toward the light

Midway: modulation amplitude decreases as colony axis tilts toward light

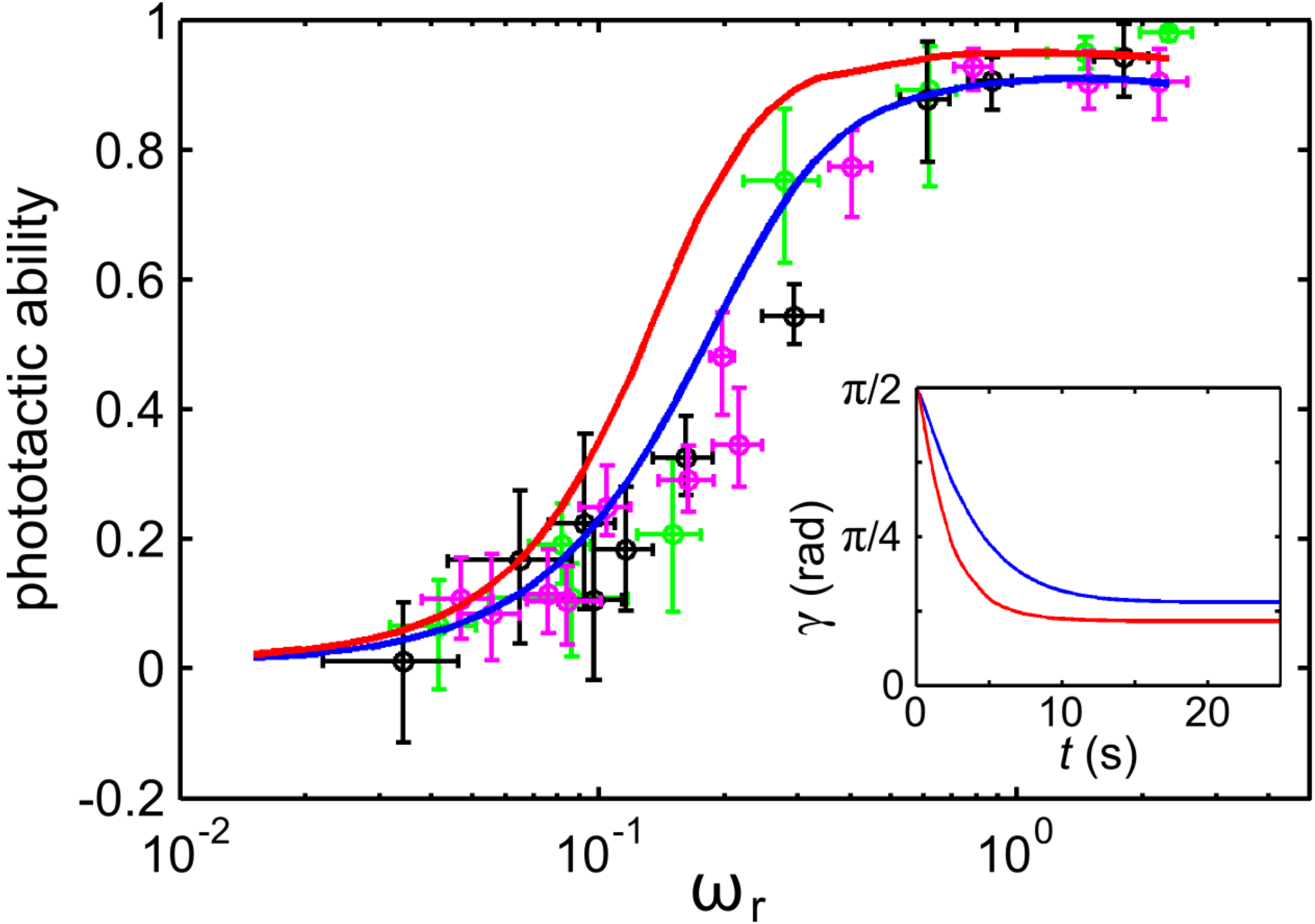
Done: no more modulation of flagellar beating, axis aligned

K. Drescher, R.E. Goldstein & I. Tuval, *preprint* (2010)

Phototaxis: The Movie



A Test of the Theory



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