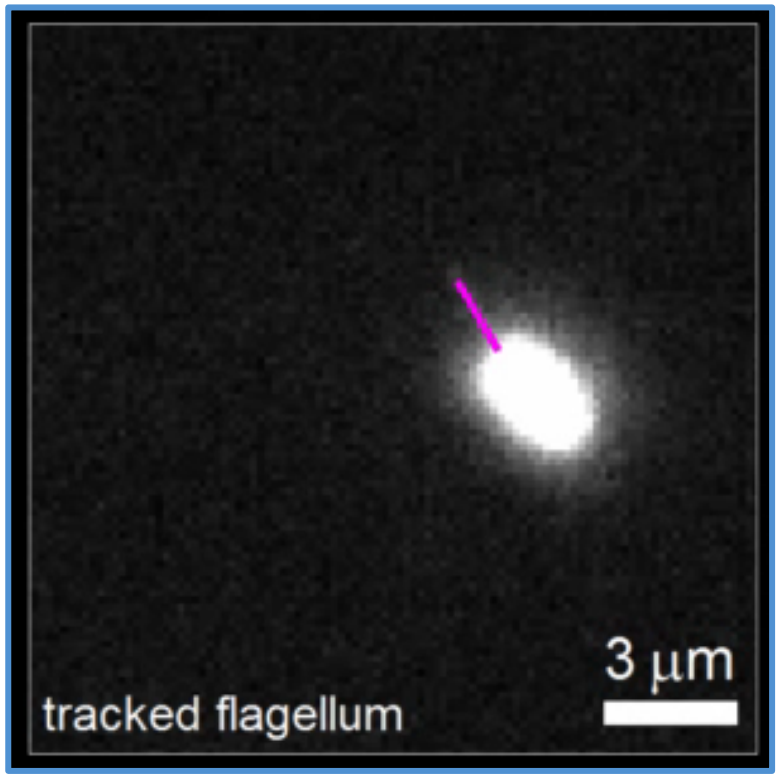
From failure to function:

Flagellar buckling reorients marine bacteria



Son, Guasto, & Stocker, *Nat Phys* 2013

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Roman Stocker, MIT


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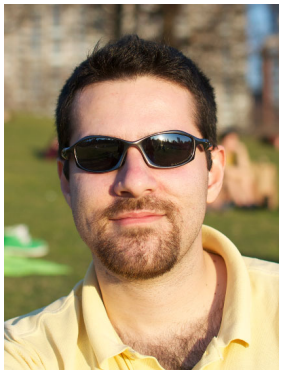
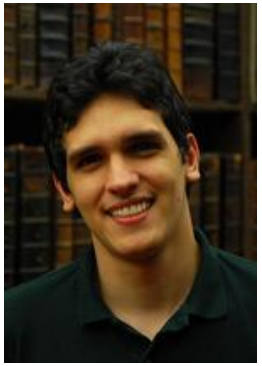

F.Menolascina, MIT


Peko Hosoi, MIT


Lisa Burton, MIT


Jerry Gollub, HC


Karl Johnson, HC


H. Gadelha, Oxford


Orr Shapiro, Weizmann

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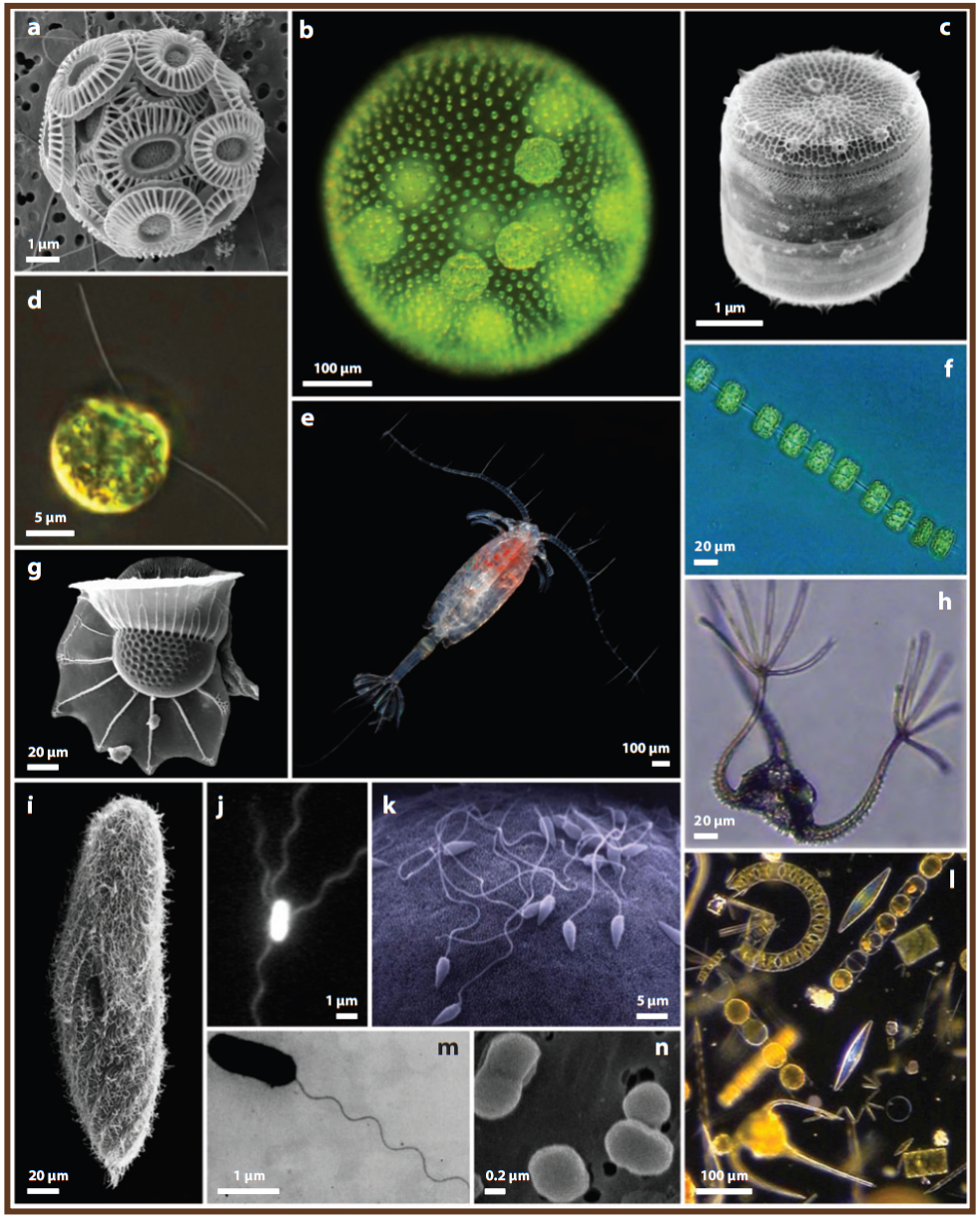
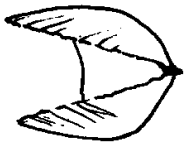
The prevalence of flagellar motility



Guasto, Rusconi, & Stocker, *ARFM* 2012

The Scallop Theorem

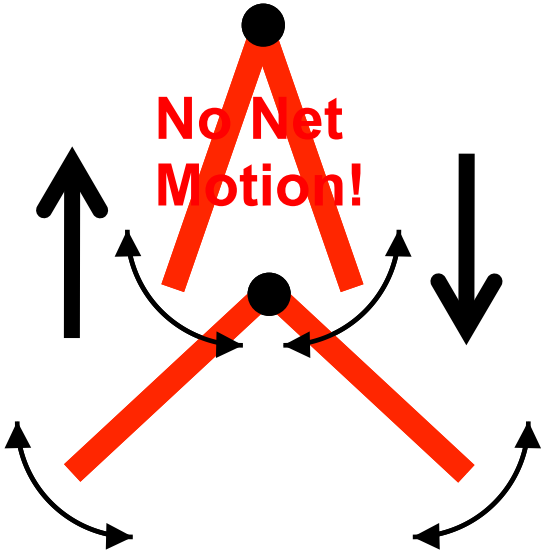
Purcell, *Am J Phys* 1977



Navier - Stokes:

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

If $Re \ll 1$:



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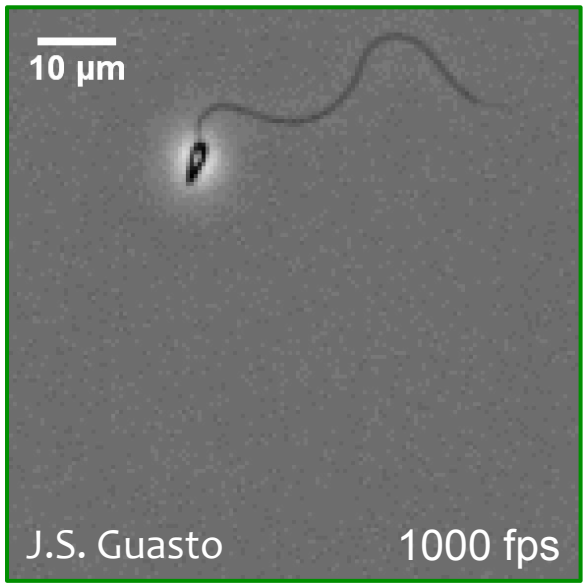
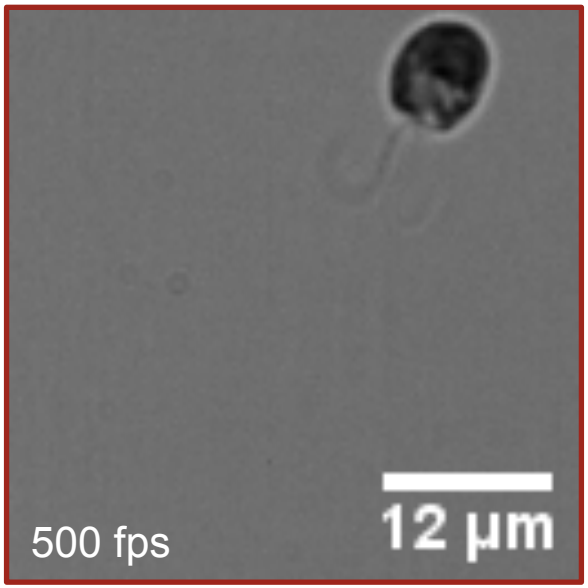
Nature's solutions for motility

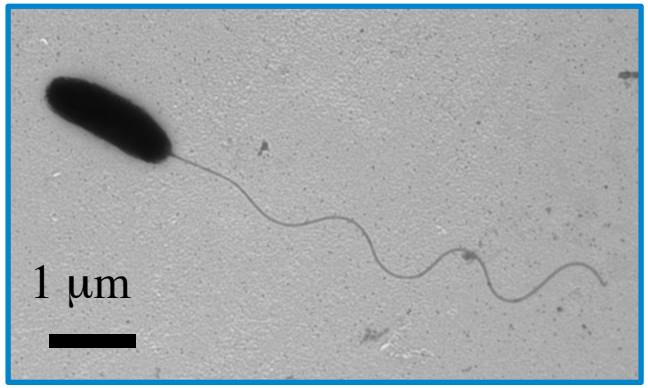
- Flexible flagella (eukaryotes)



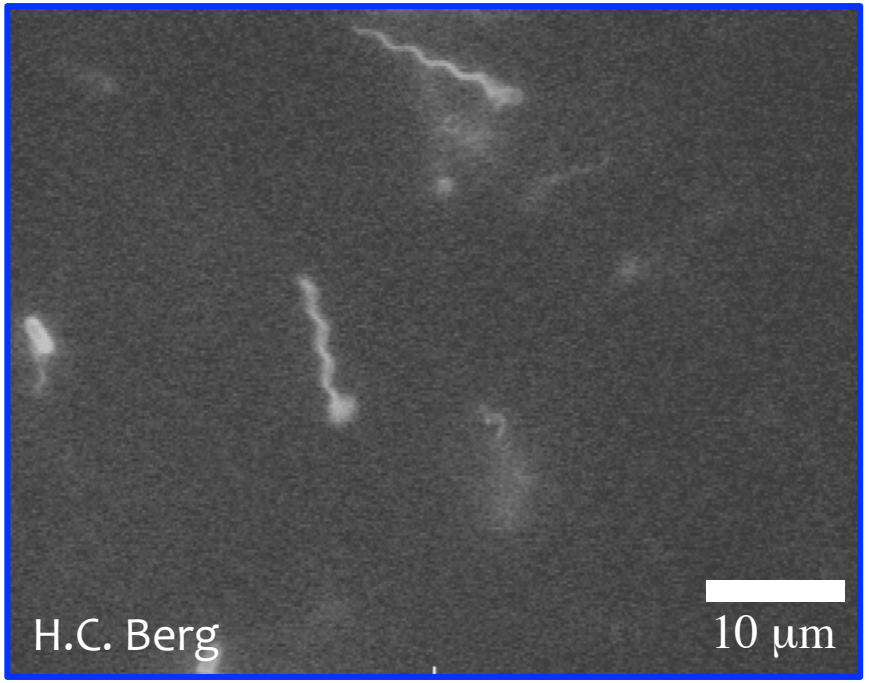


Guasto et al, *PRL* 2010

- Rigid flagella (prokaryotes)



Son et al, *Nat Phys* 2013



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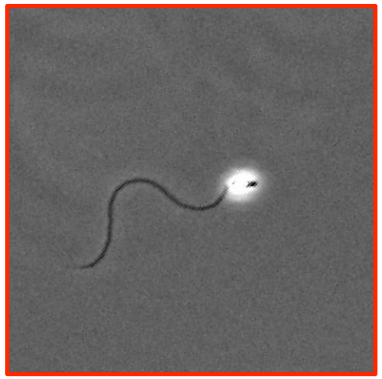
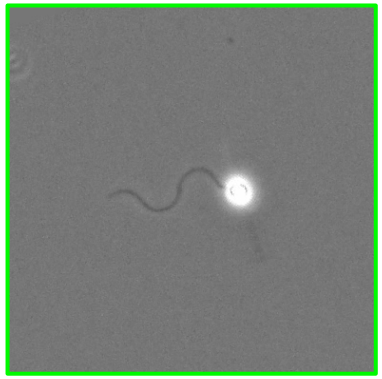
Mechanics of flagellar propulsion

Flagellar Kinematics

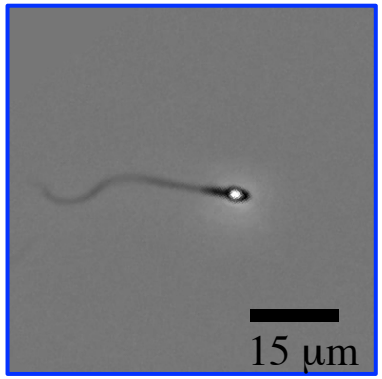
urchin



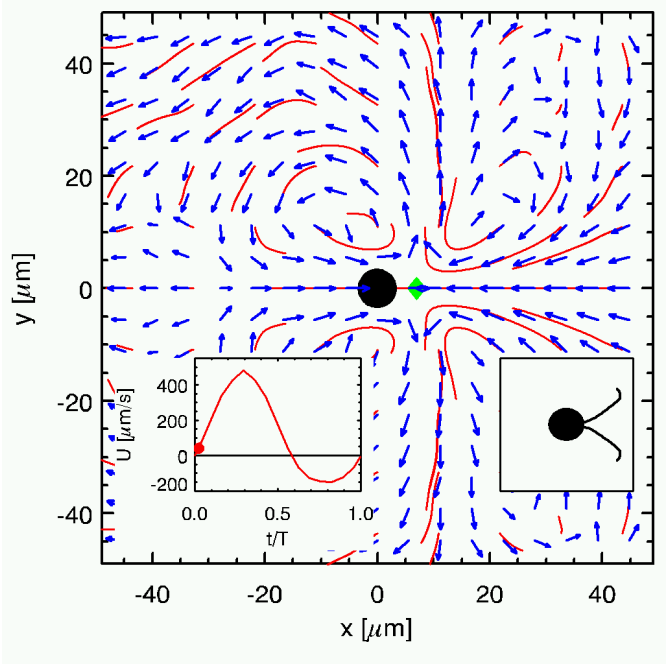
zebrafish

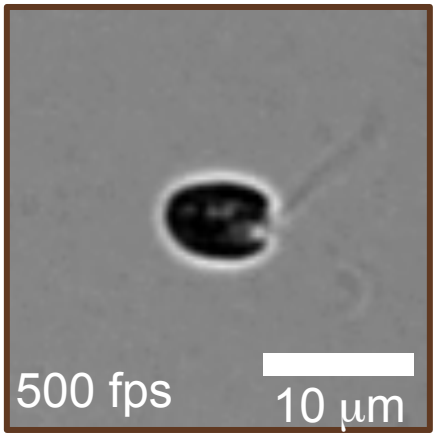


human

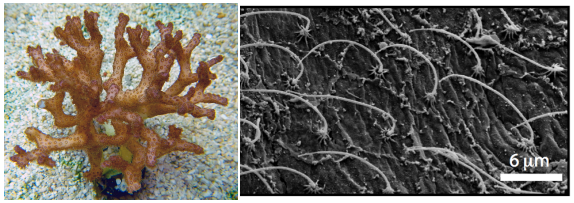


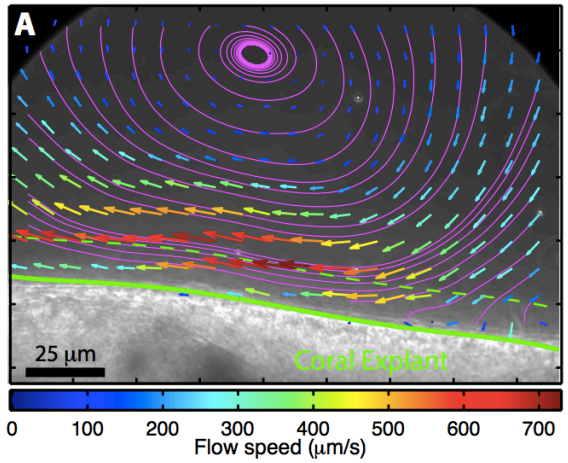
Single Cell Propulsion

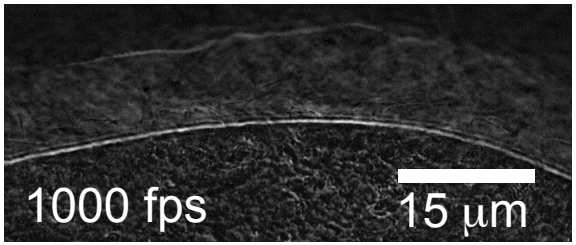




Coral Ciliary Flows







Son, Guasto, & Stocker, *Nat Phys 2013*
Guasto, Johnson, & Gollub, *PRL 2010*
Shapiro et al, *in review* 2014

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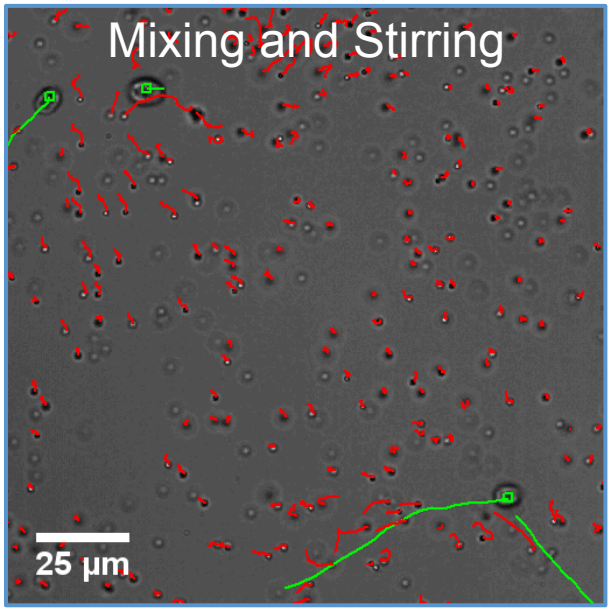
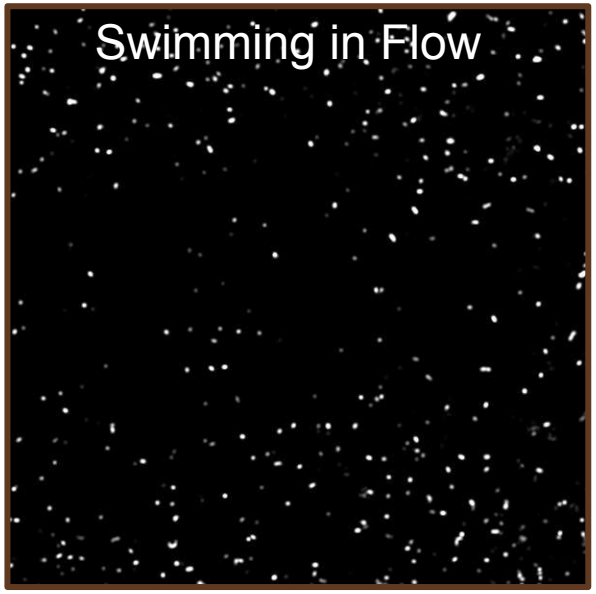
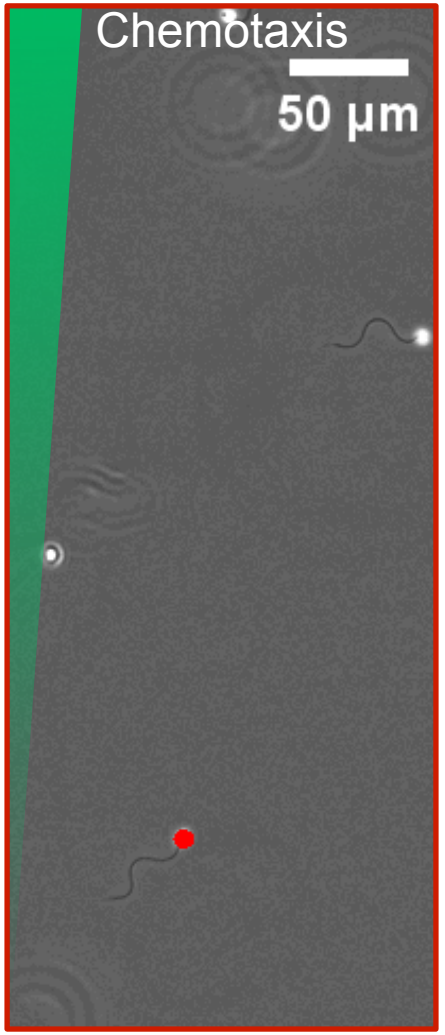
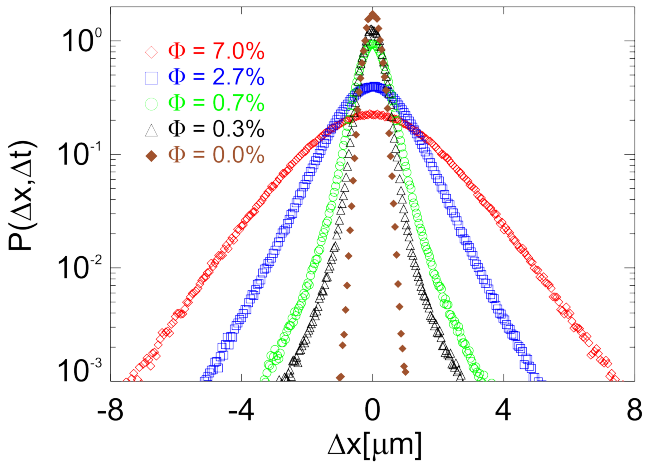
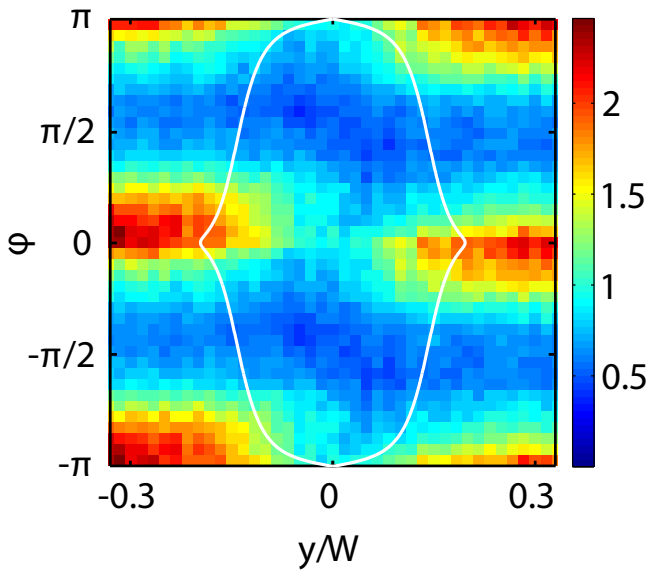
Transport processes in active suspensions







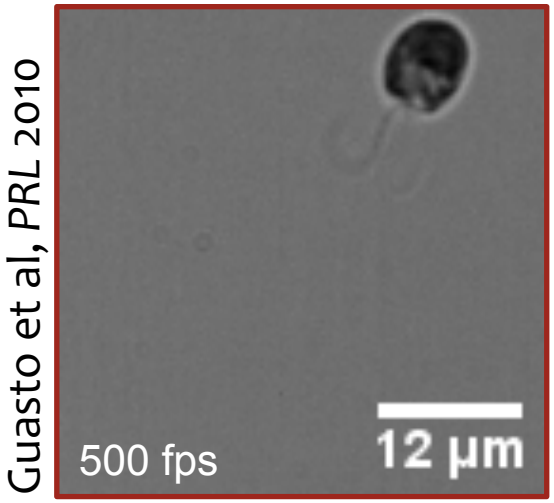


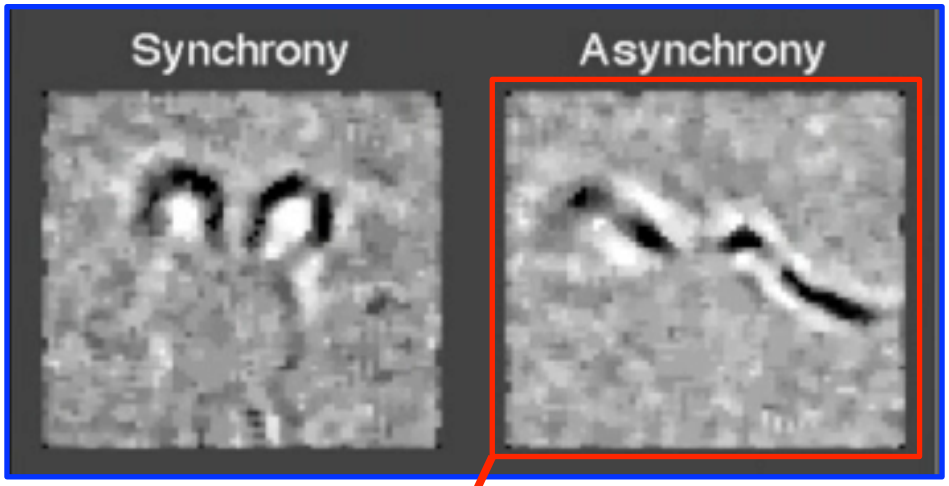


Kurtuldu et al, *PNAS* 2011
Leptos et al, *PRL* 2009

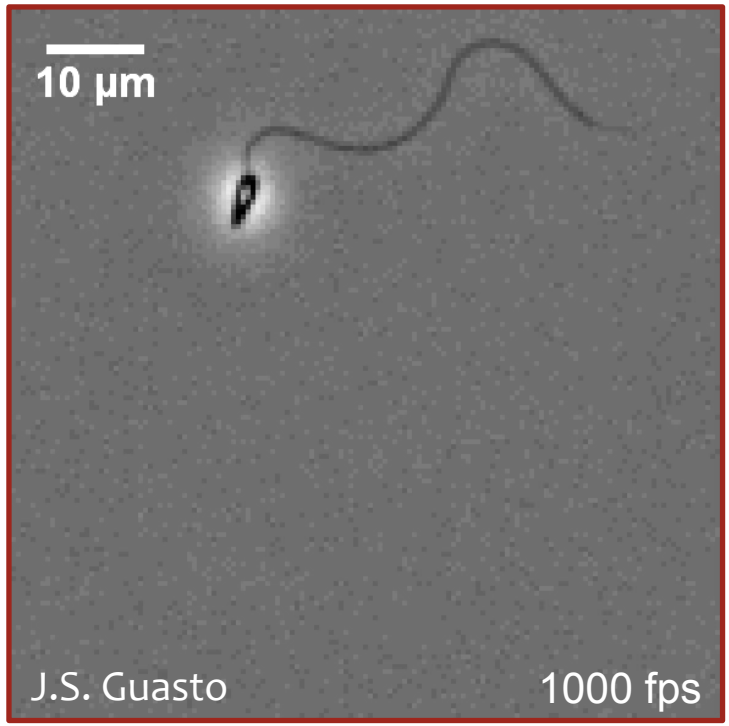
Rusconi, Guasto, & Stocker, *Nat Phys* 2014

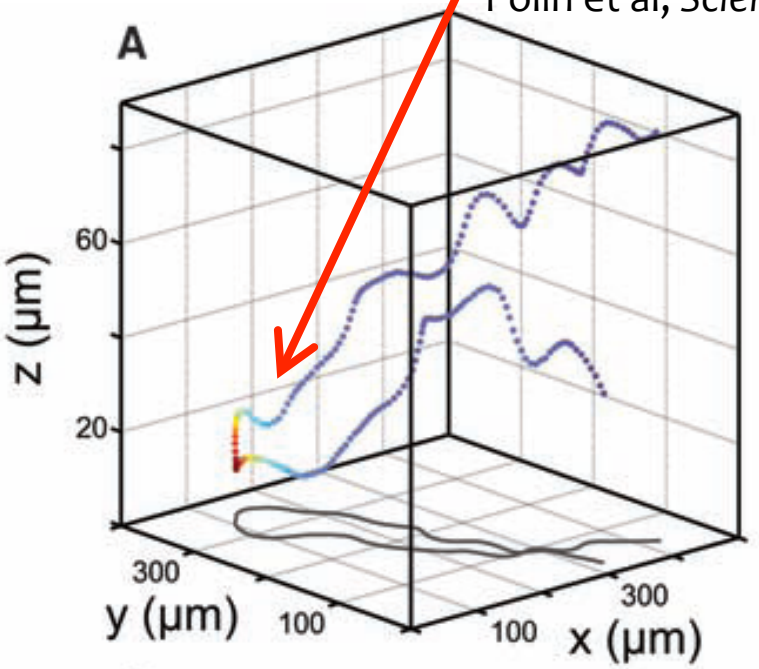
Propulsion is only half of the story …





Polin et al, *Science* 2009





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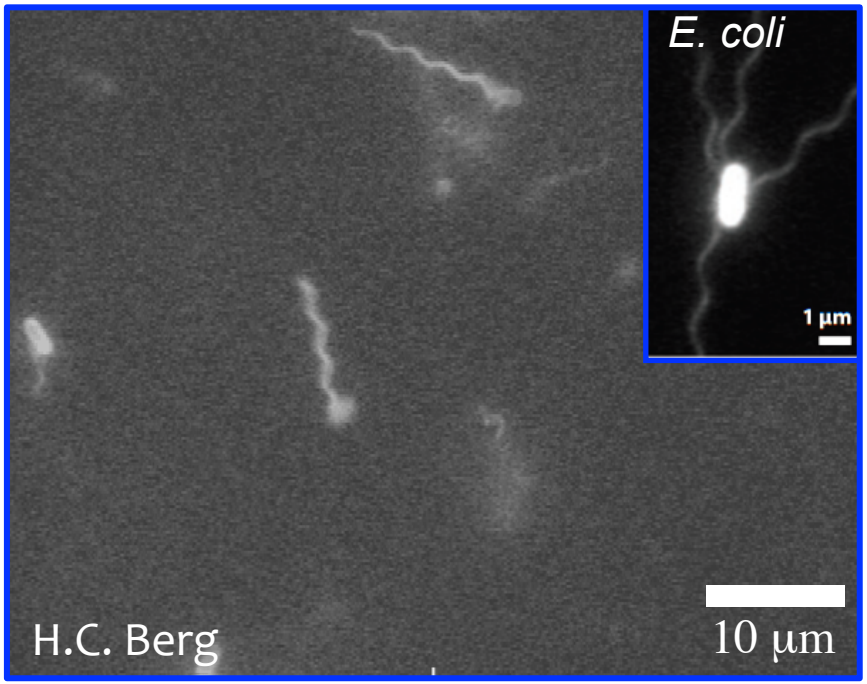
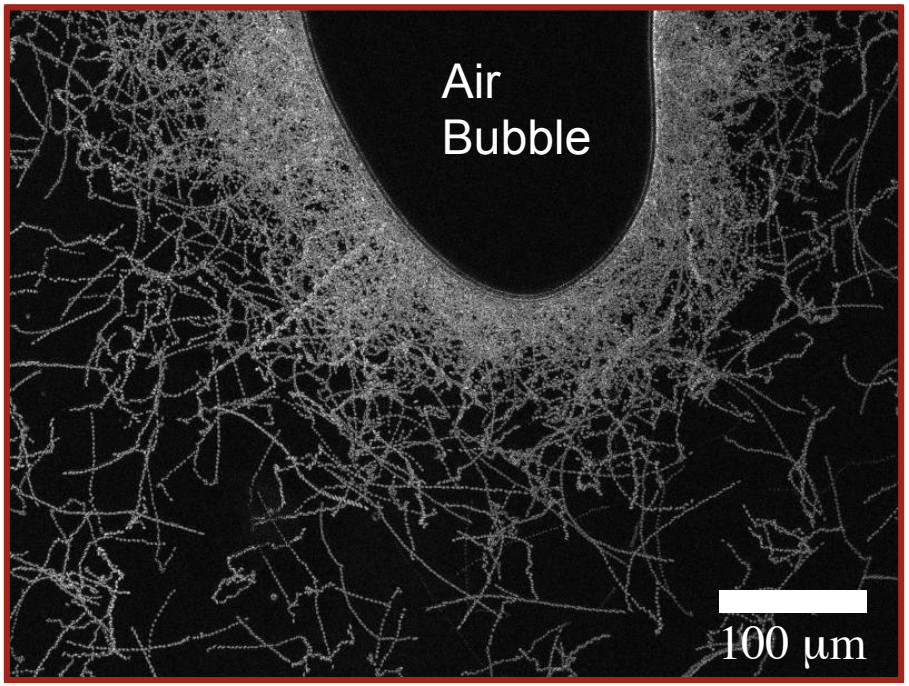
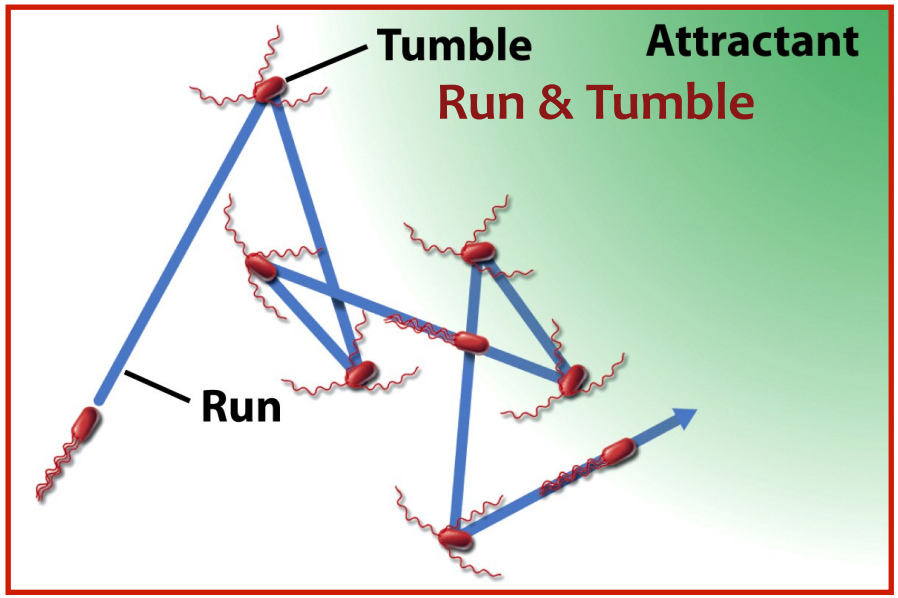
Turning is crucial for bacterial survival strategies







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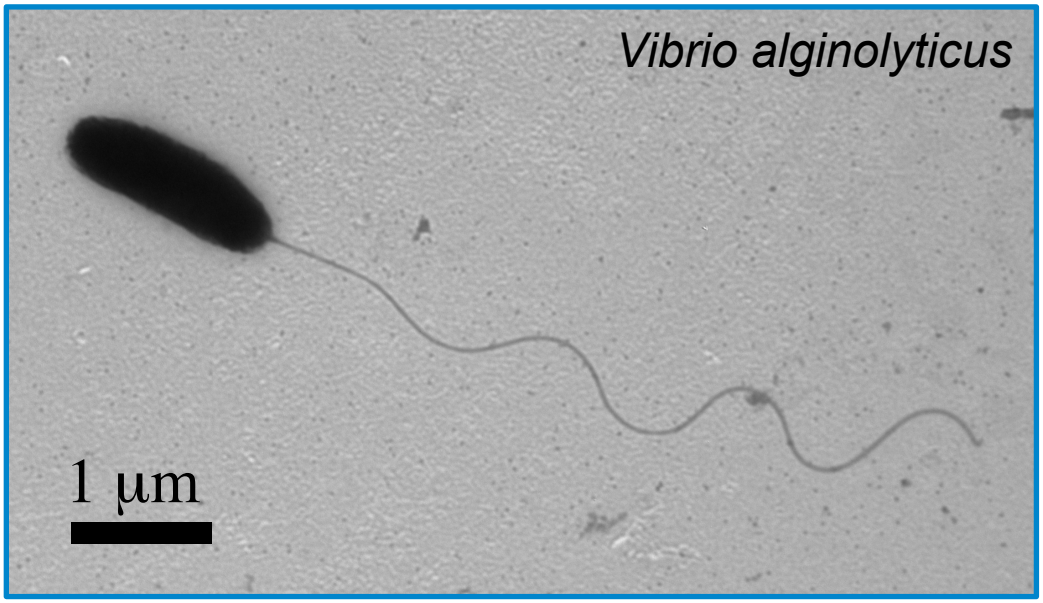
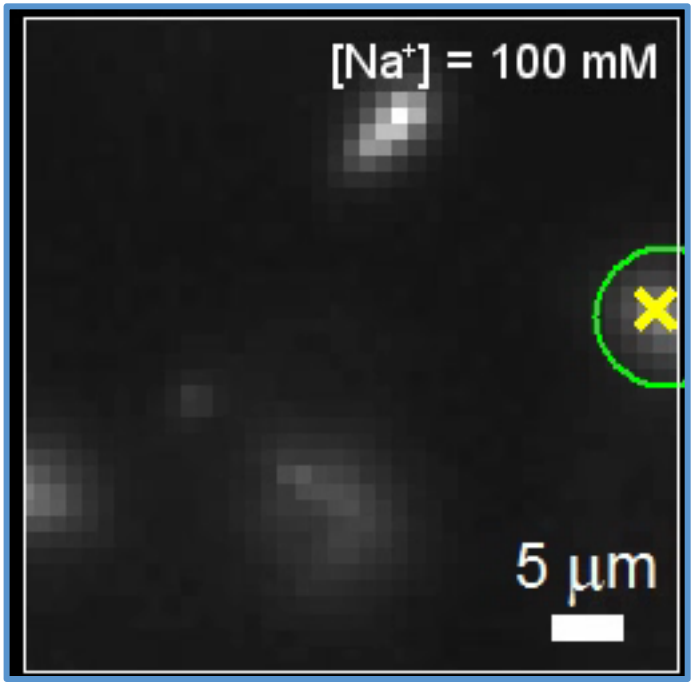
Many bacteria have only *one* flagellum





- **95%** of marine bacteria:
  - *Vibrio alginolyticus*
  - *Vibrio cholerae*
  - *Shewanella putrefaciens*
  - *Pseudoalteromonas haloplanktis*

- Previous view:
  - Cells **only** swim **forward and backward** ('run and reverse') via rotary motor control

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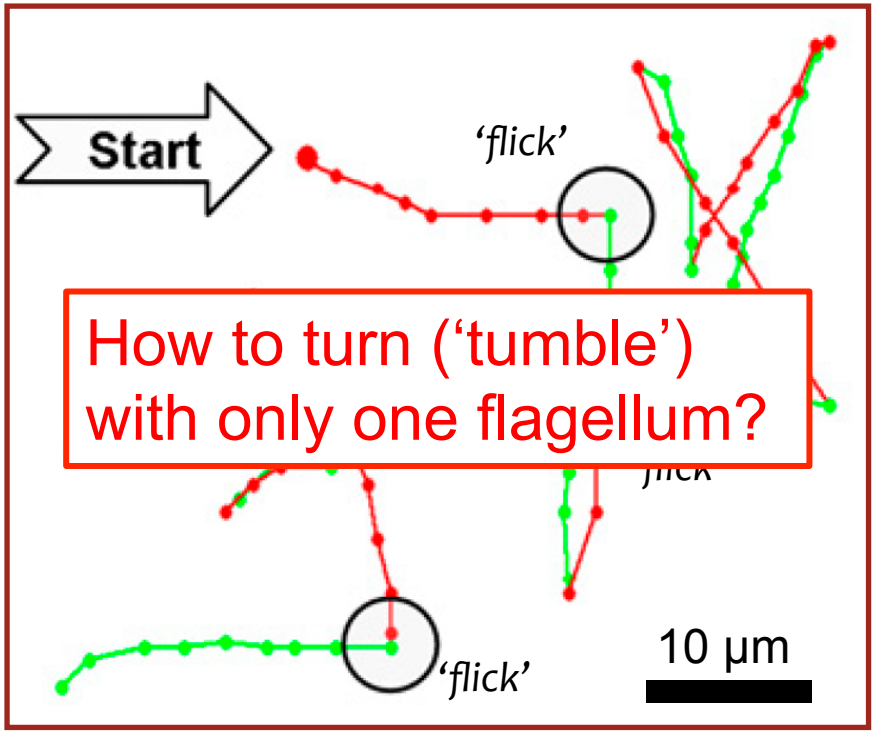
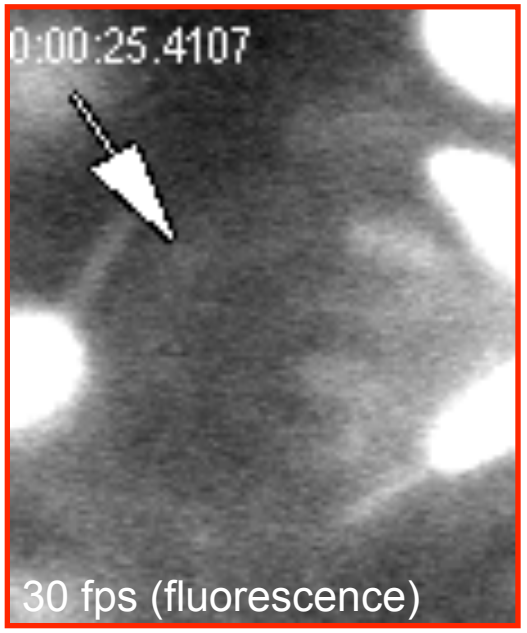
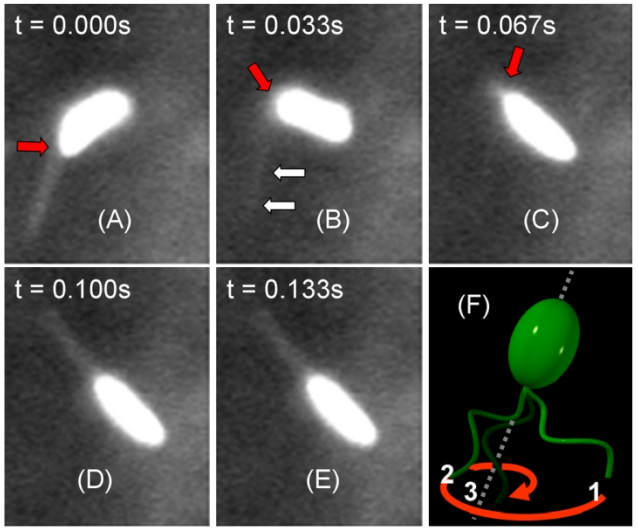
Run, reverse, & flick motility



Xie et al, *PNAS* 2011
Stocker, *PNAS* 2011





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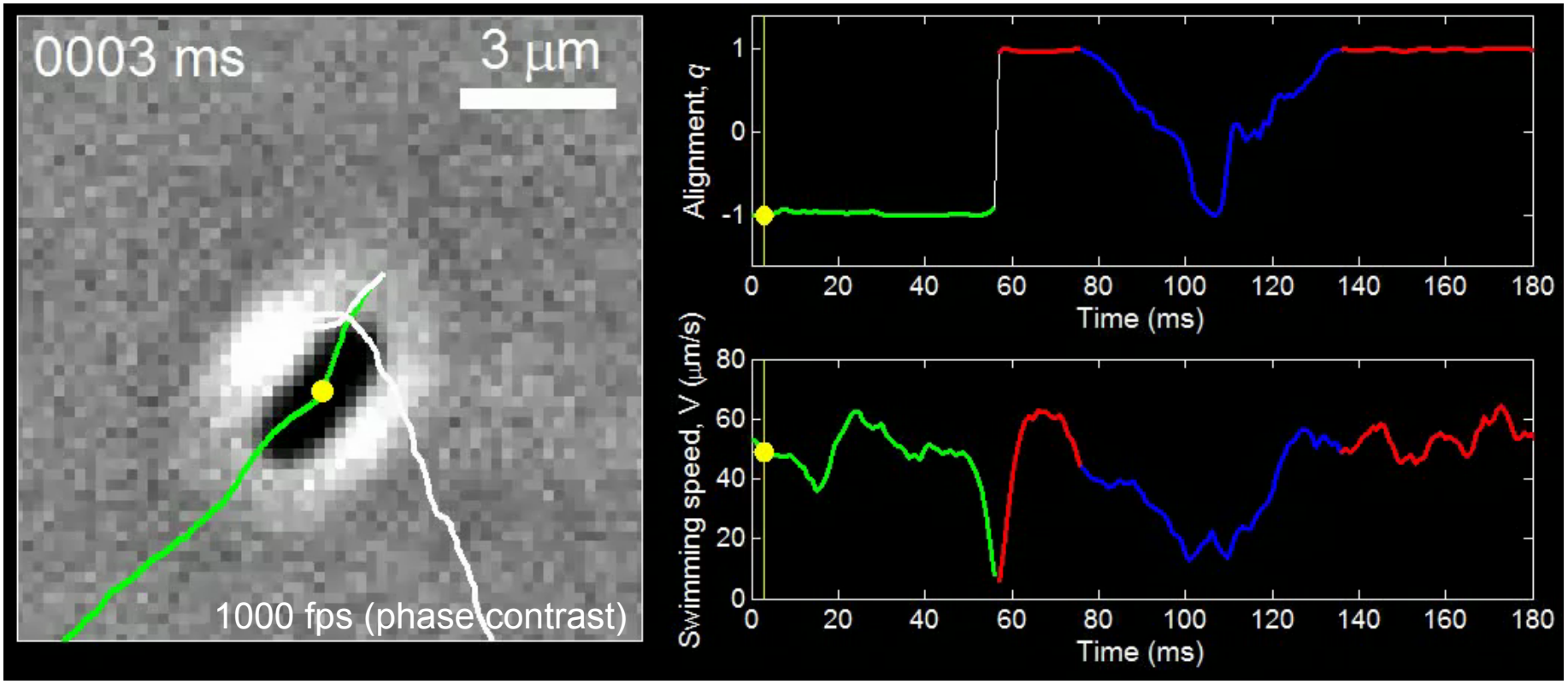
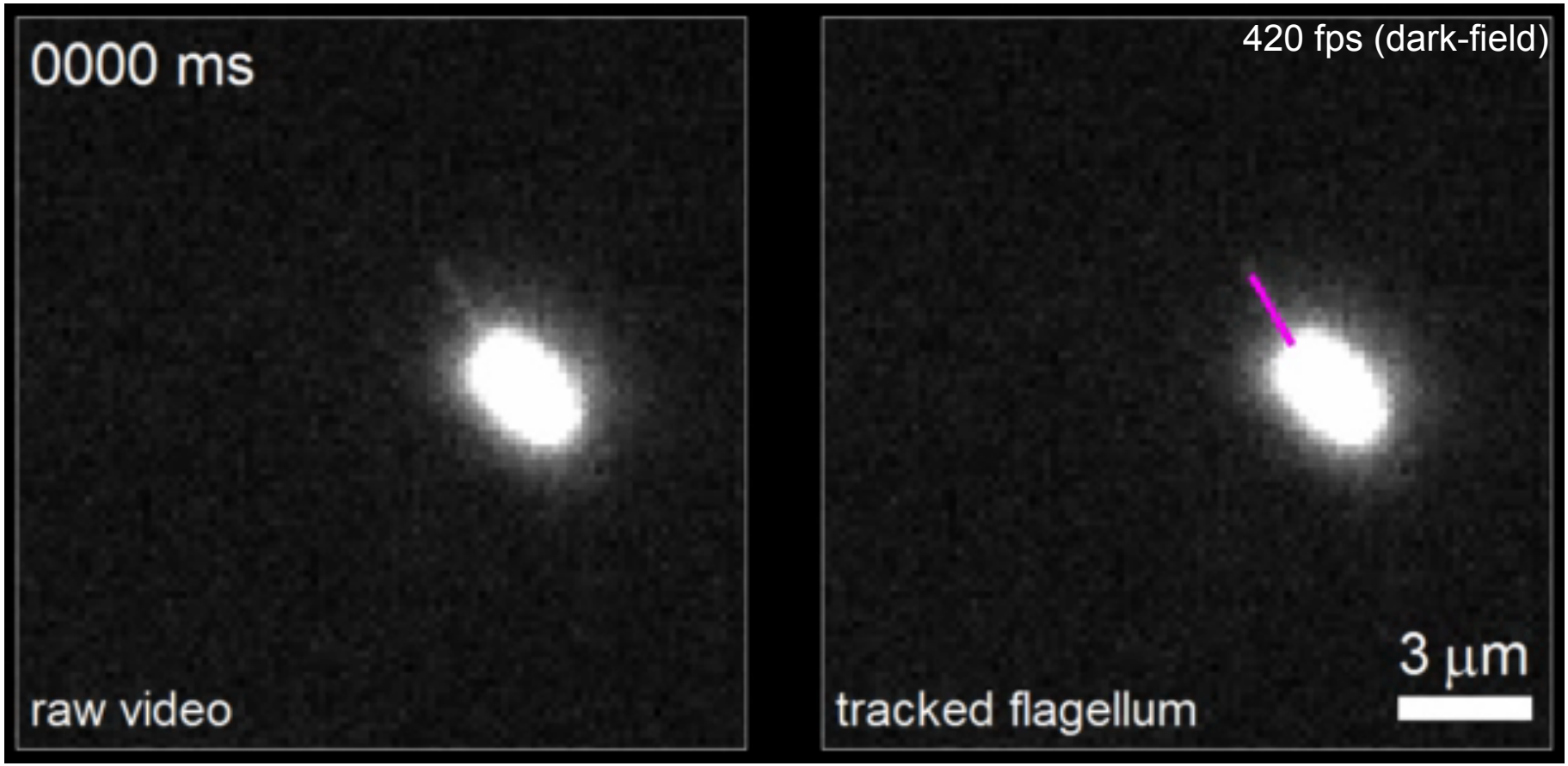
Cells swim forward prior to ‘flick’



Flagellar bending concentrated at base



- 20 nm diameter flagellum

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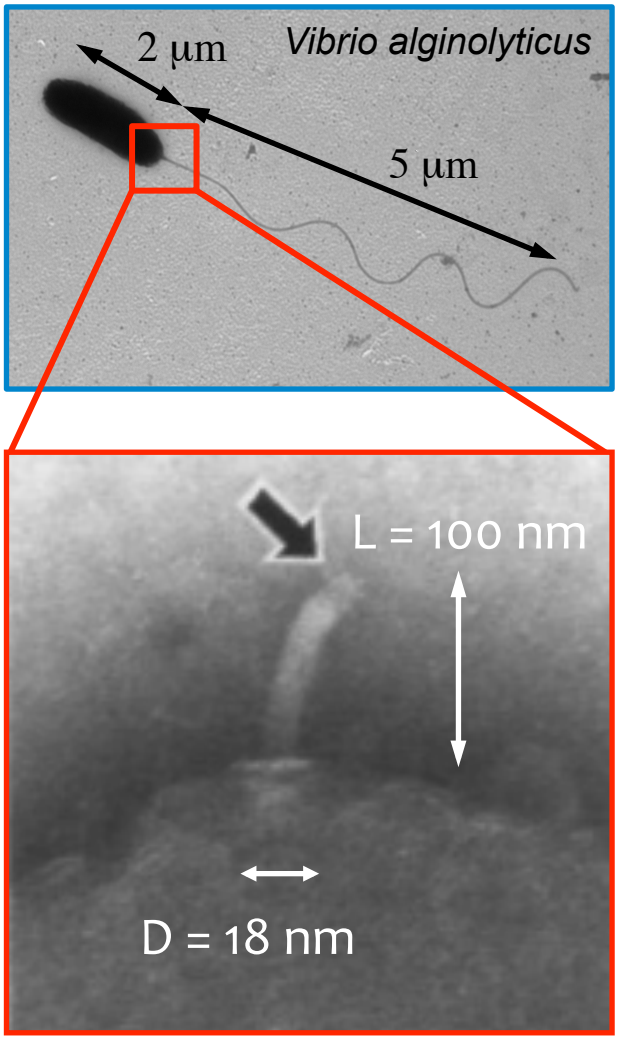
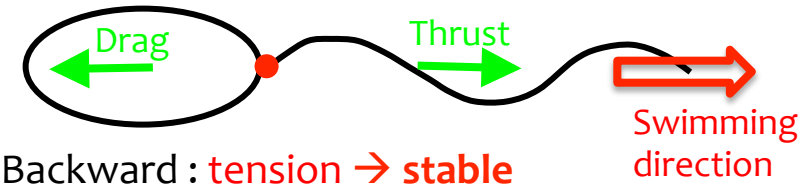
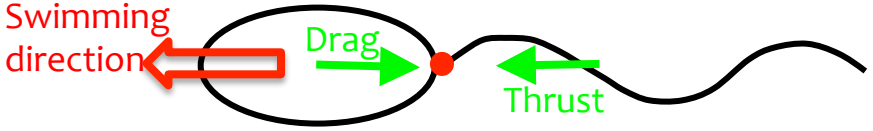
Forward swimming implies compression



Nishioka et al, 1998



Backward : tension → **stable**



Forward : compression → **unstable**

H.C. Berg

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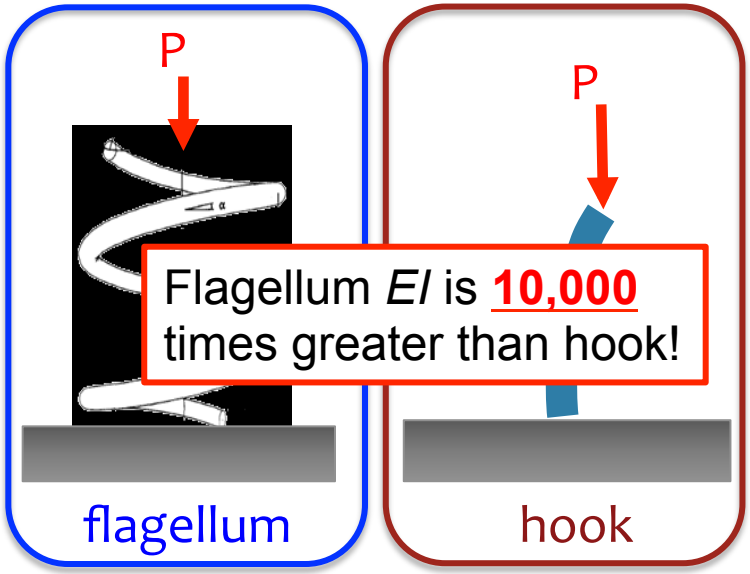
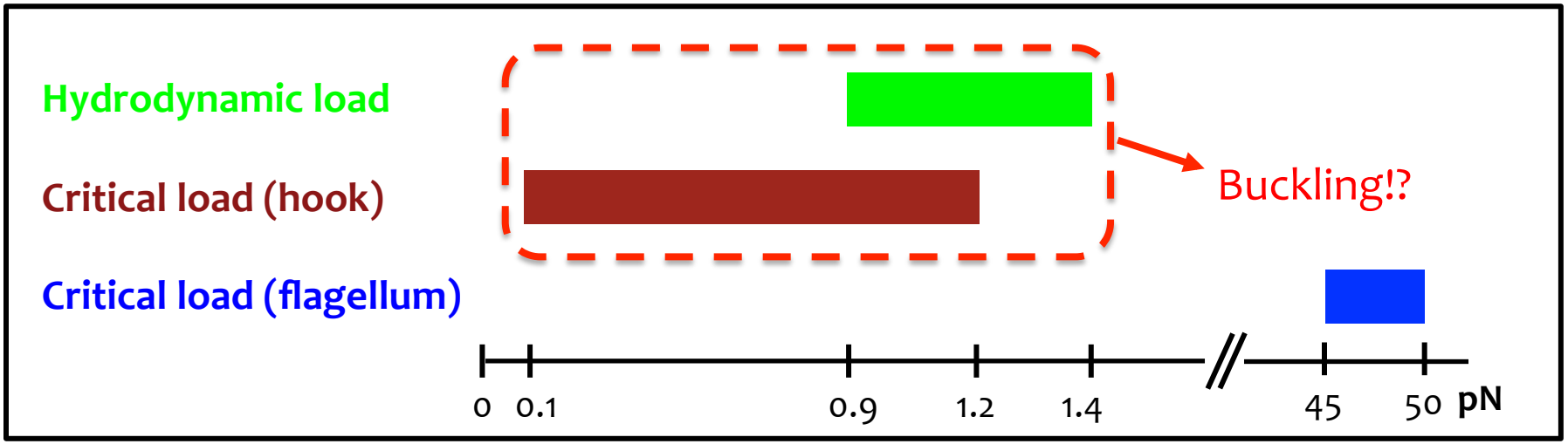
Turning by buckling

- **Hydrodynamic load:** $P_{visc} \sim \mu a V$
- **Critical buckling load:** $P_{cr} \sim \frac{EI}{L^2}$





Shum & Gaffney, *Phys Fluids* 2012
Vogel & Stark, *Euro Phys J* 2012

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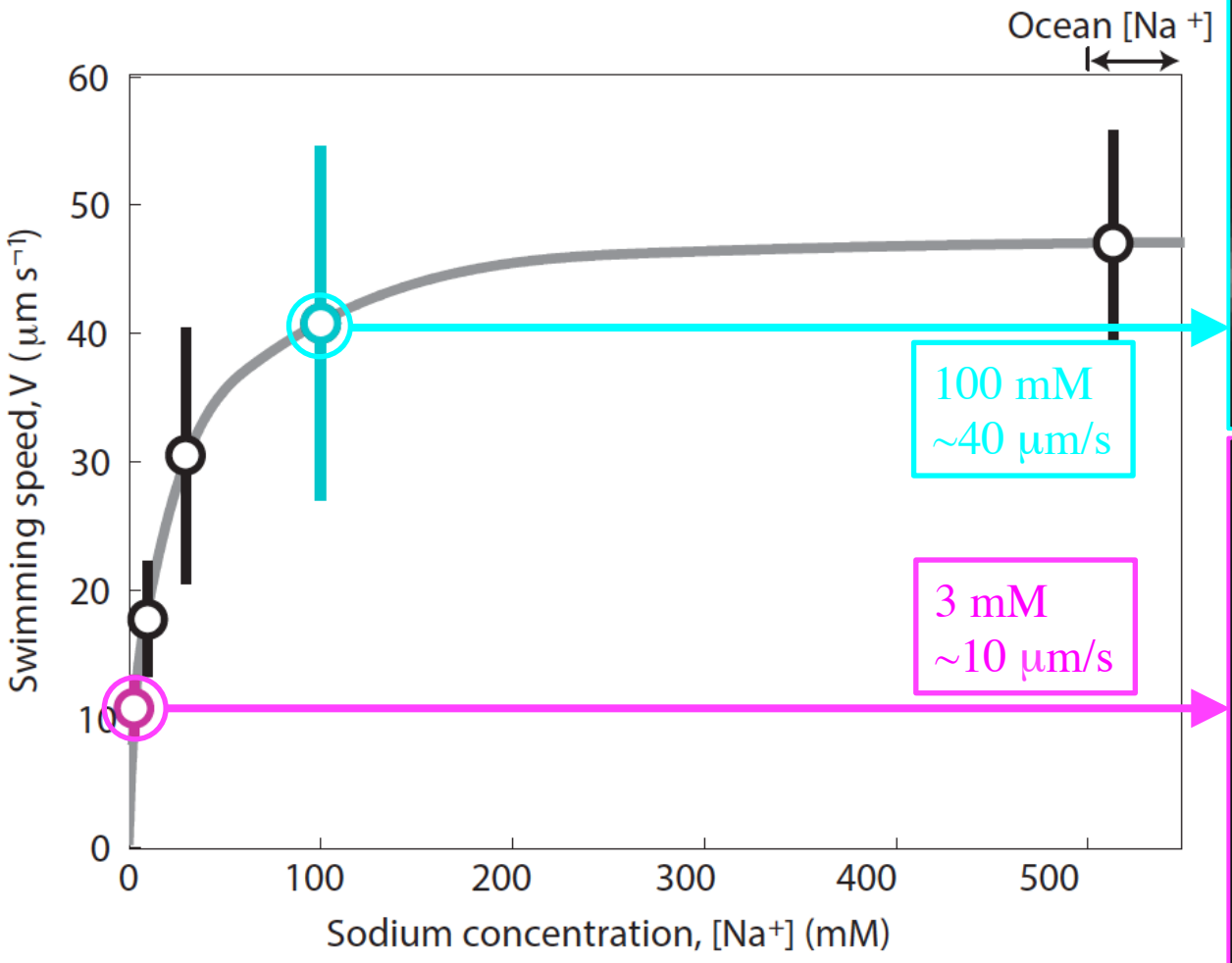
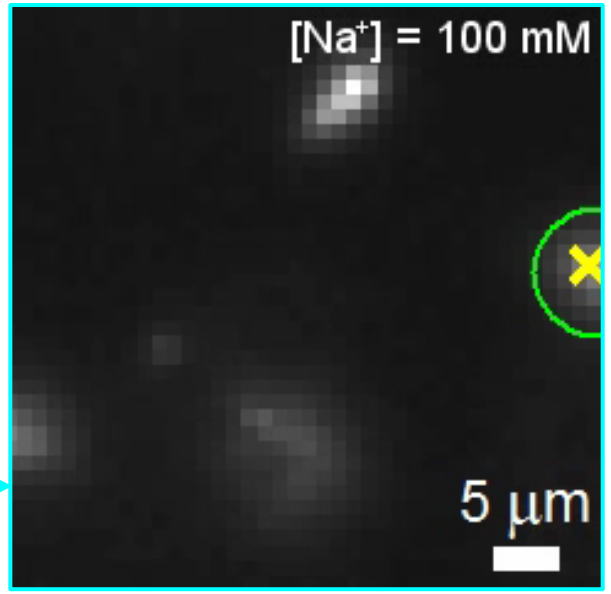
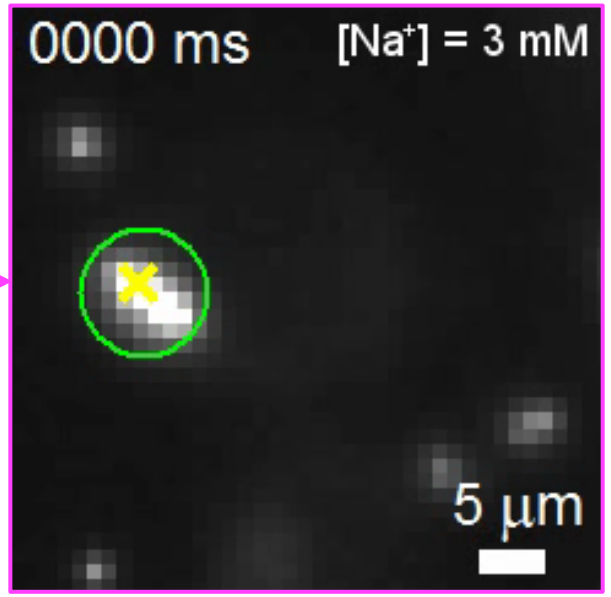
Slow down bacteria to test for buckling

Swimming speed ↓ → Hydrodynamic load ↓ → Flicks ↓







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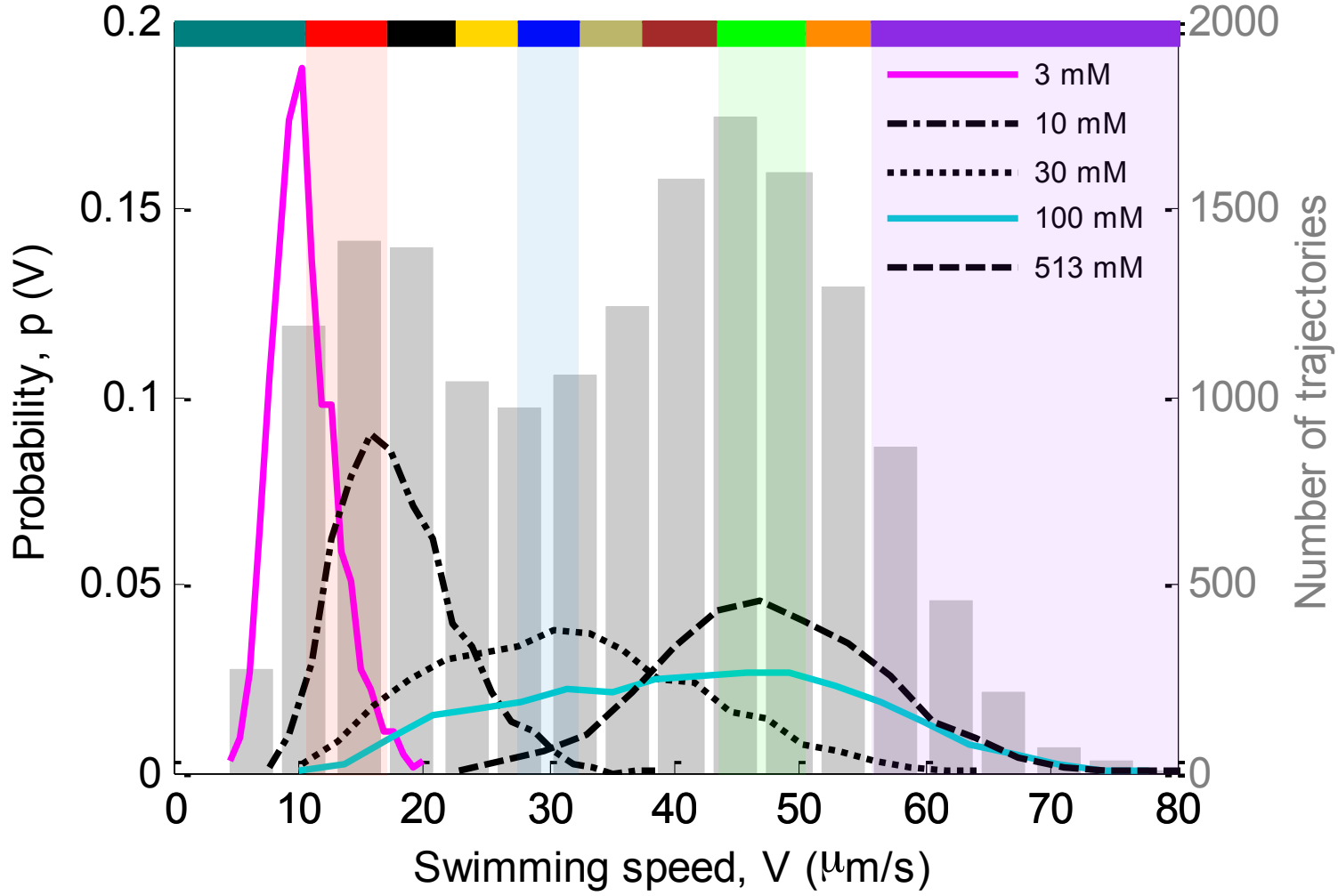
Swimming speed distribution



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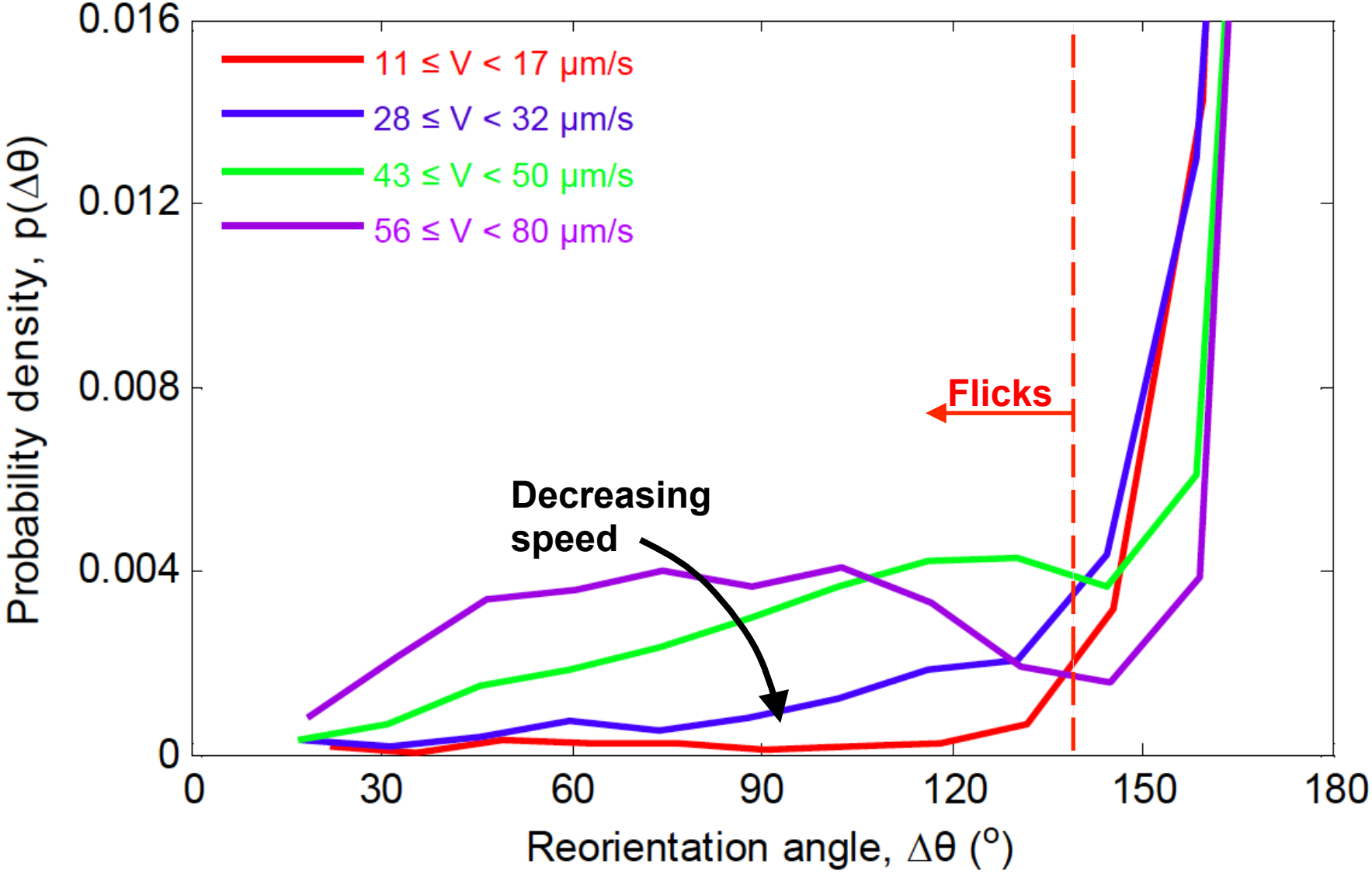
Slowing down suppresses turning



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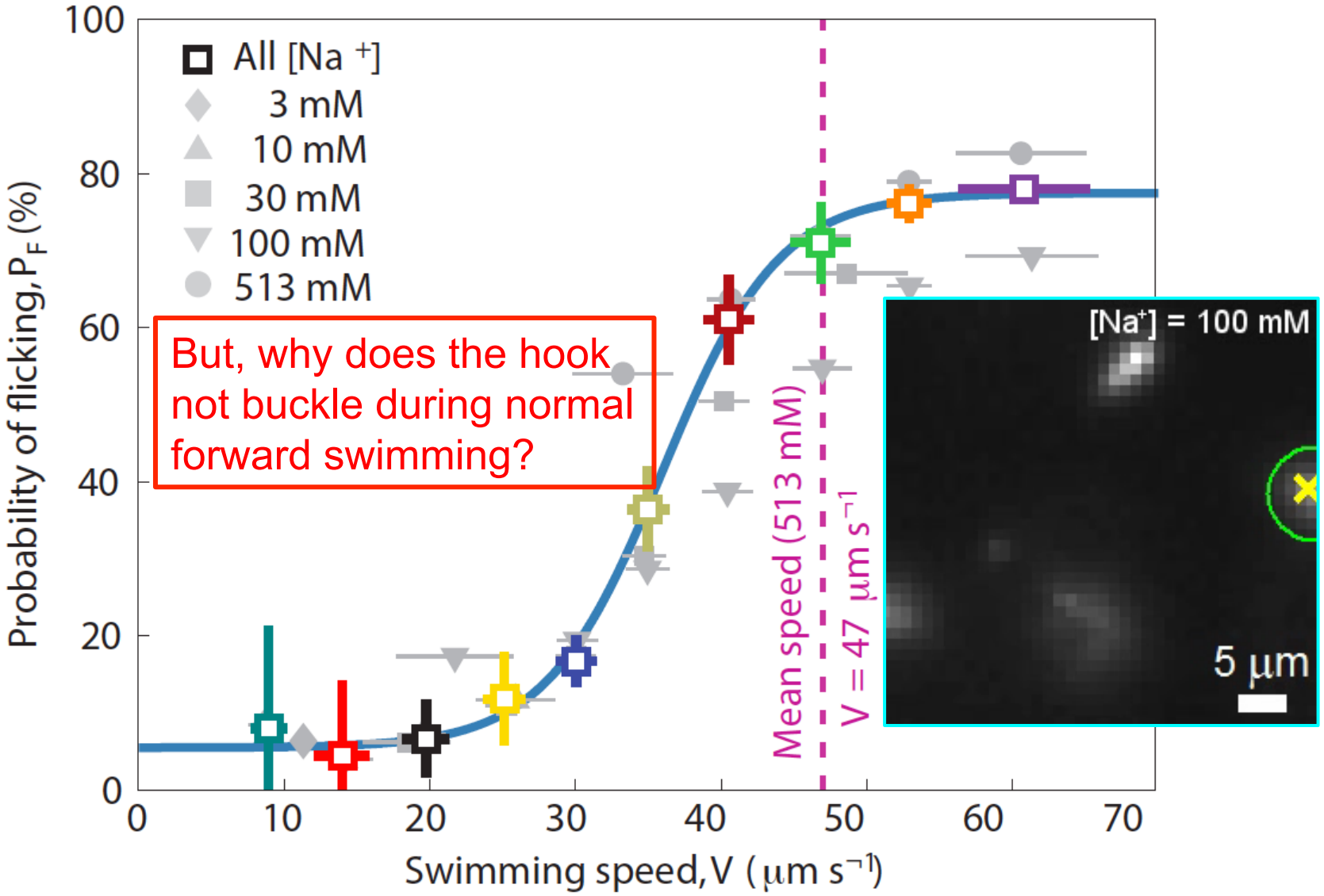
Transition between turning states



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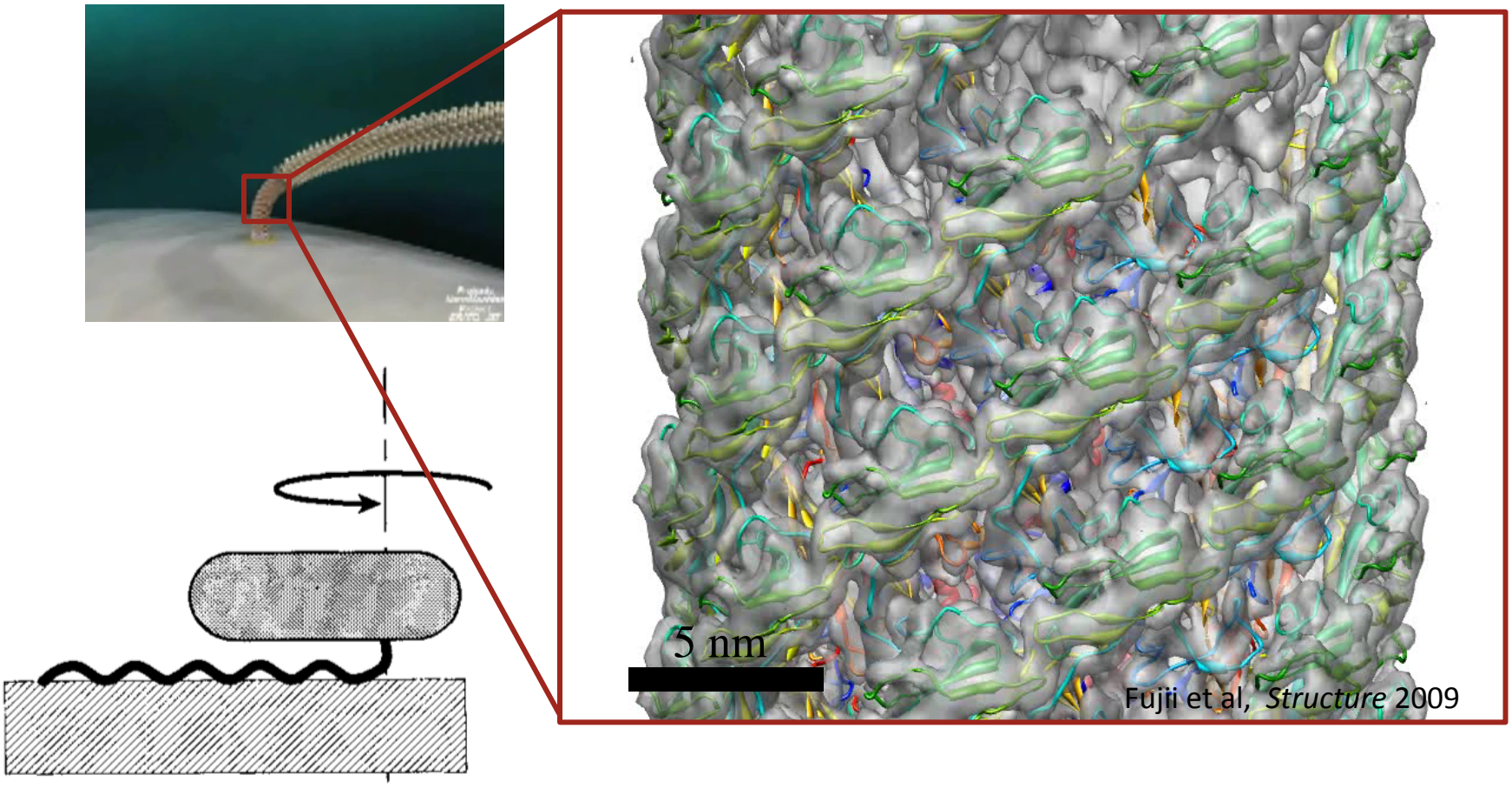
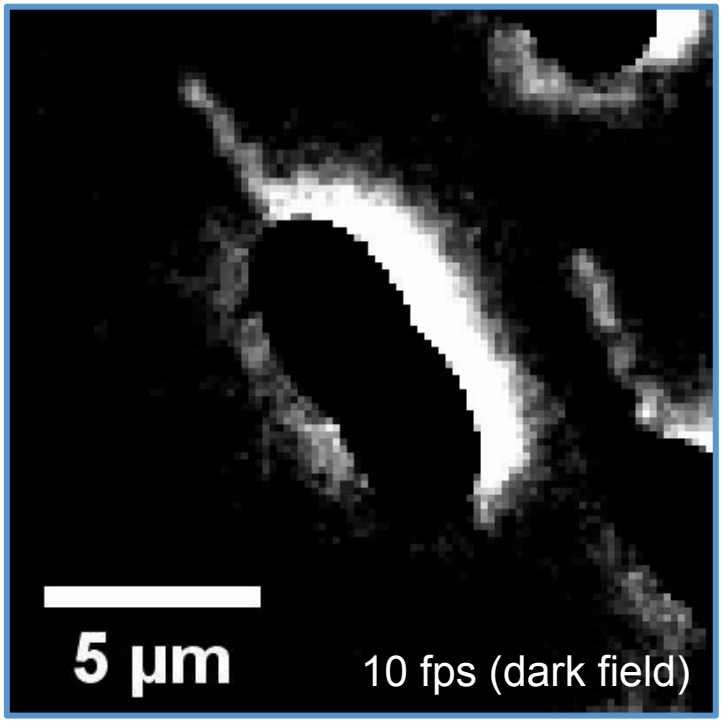
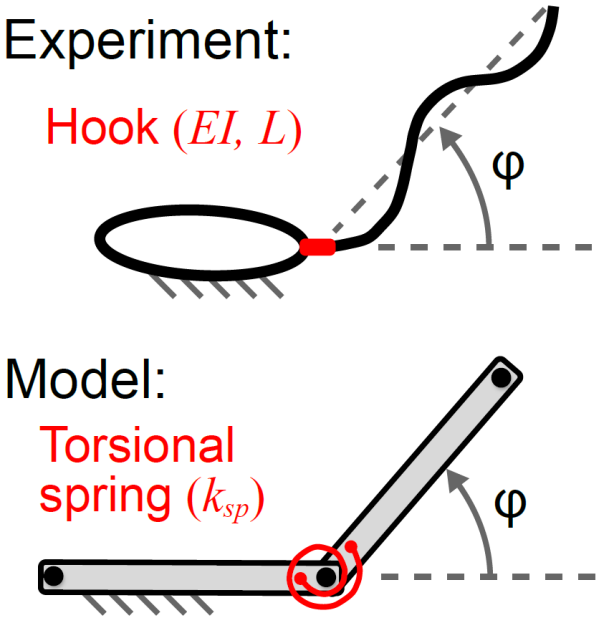
Twisting stiffens the hook

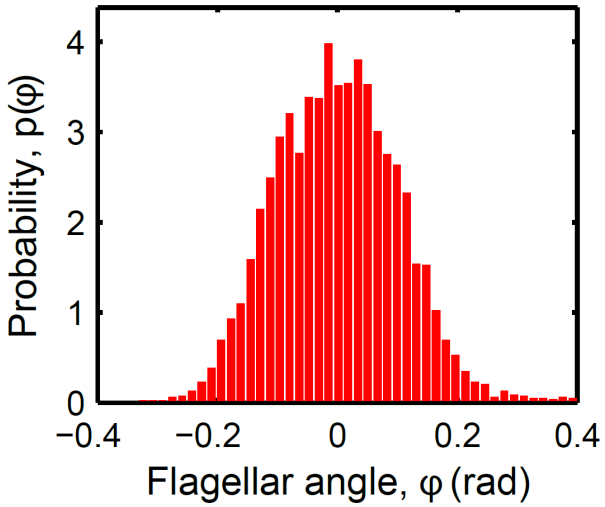


- During **normal swimming** the **hook is twisted**
  - it 'locks up' beyond a half turn (Block & Berg, *Nature* 1991)
- Spaces between protofilaments compress under torsional load
  → ***EI* likely increases** (Samatey et al, *Nature* 2004)

Estimating hook stiffness – relaxed hook







$$EI_{RELAX} = \frac{k_B T}{\langle \phi^2 \rangle} L \approx 3.6 \times 10^{-26} \text{ Nm}^2$$

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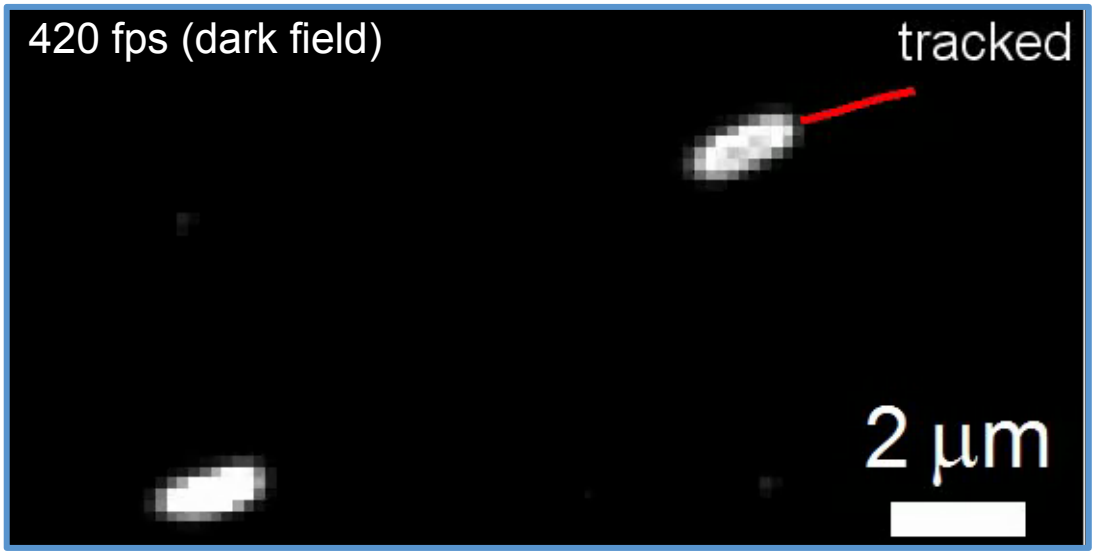
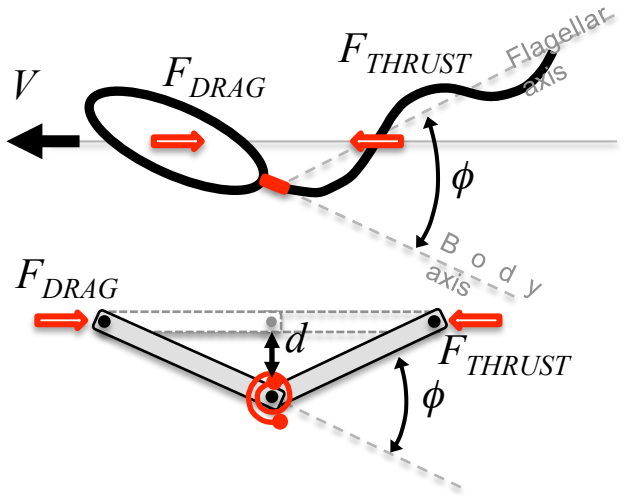
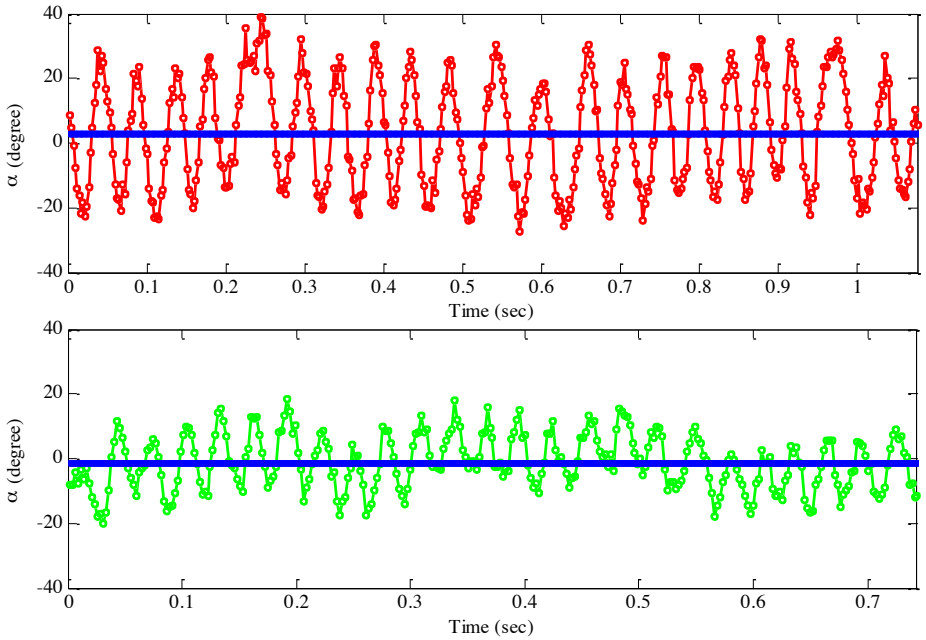
Estimating hook stiffness – stiffened hook





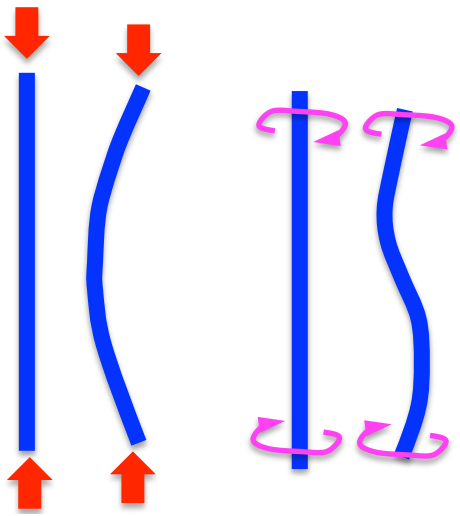


~10x Higher!!

$$EI_{LOADED} = \frac{F_{DRAG} d}{(\phi_F - \phi_B)} L \approx 2.2 \times 10^{-25}\ \mathrm{Nm}^2$$

Hook stability near a turn

compression torsion

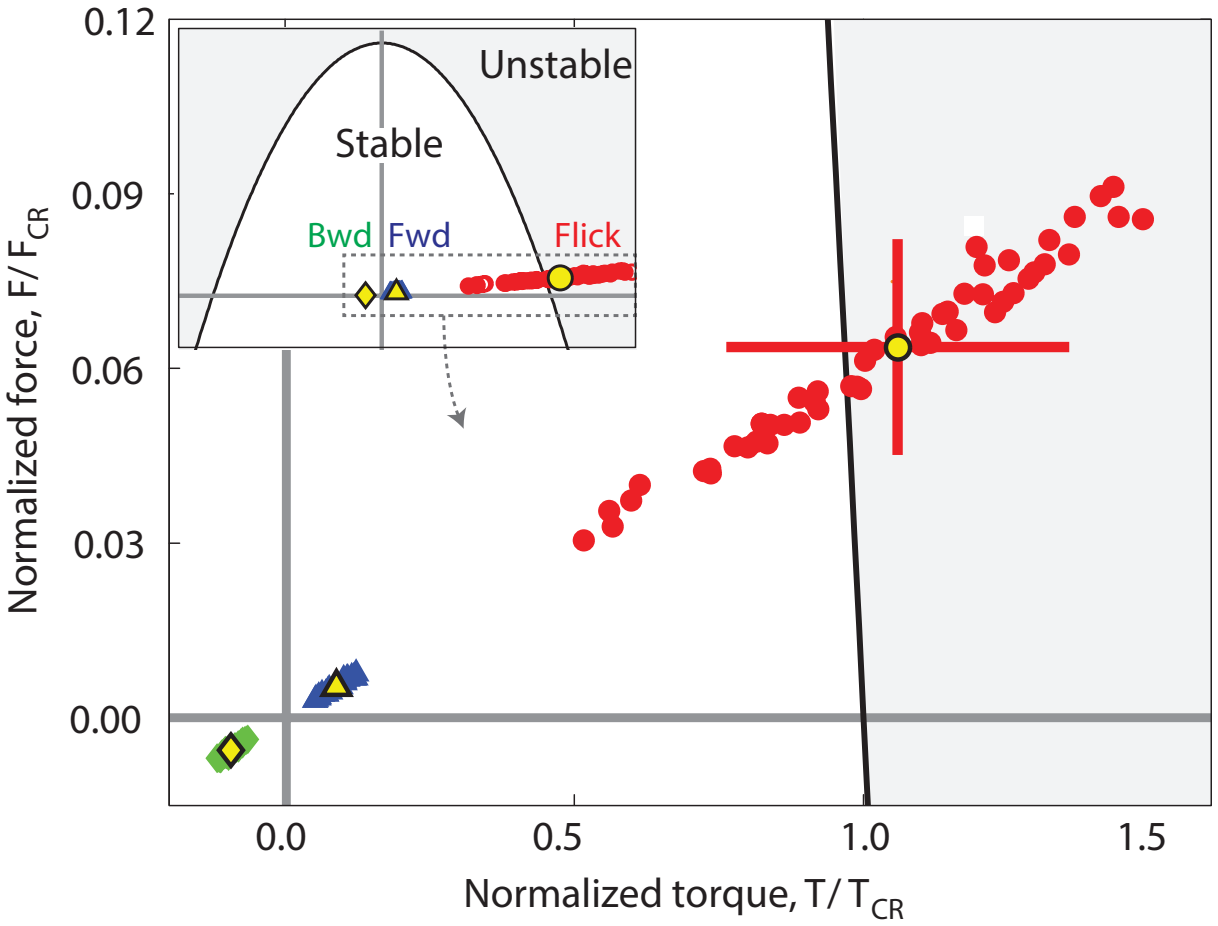


$$F_{CR} = \pi^2 \frac{EI}{L^2} \qquad T_{CR} = 2\pi \frac{EI}{L}$$

$$\frac{F}{F_{CR}} + \left(\frac{T}{T_{CR}}\right)^2 \leq 1$$

Timoshenko, 1961

Note: for Euler buckling, critical forces/torques depend only upon *EI*, not upon *GJ*.



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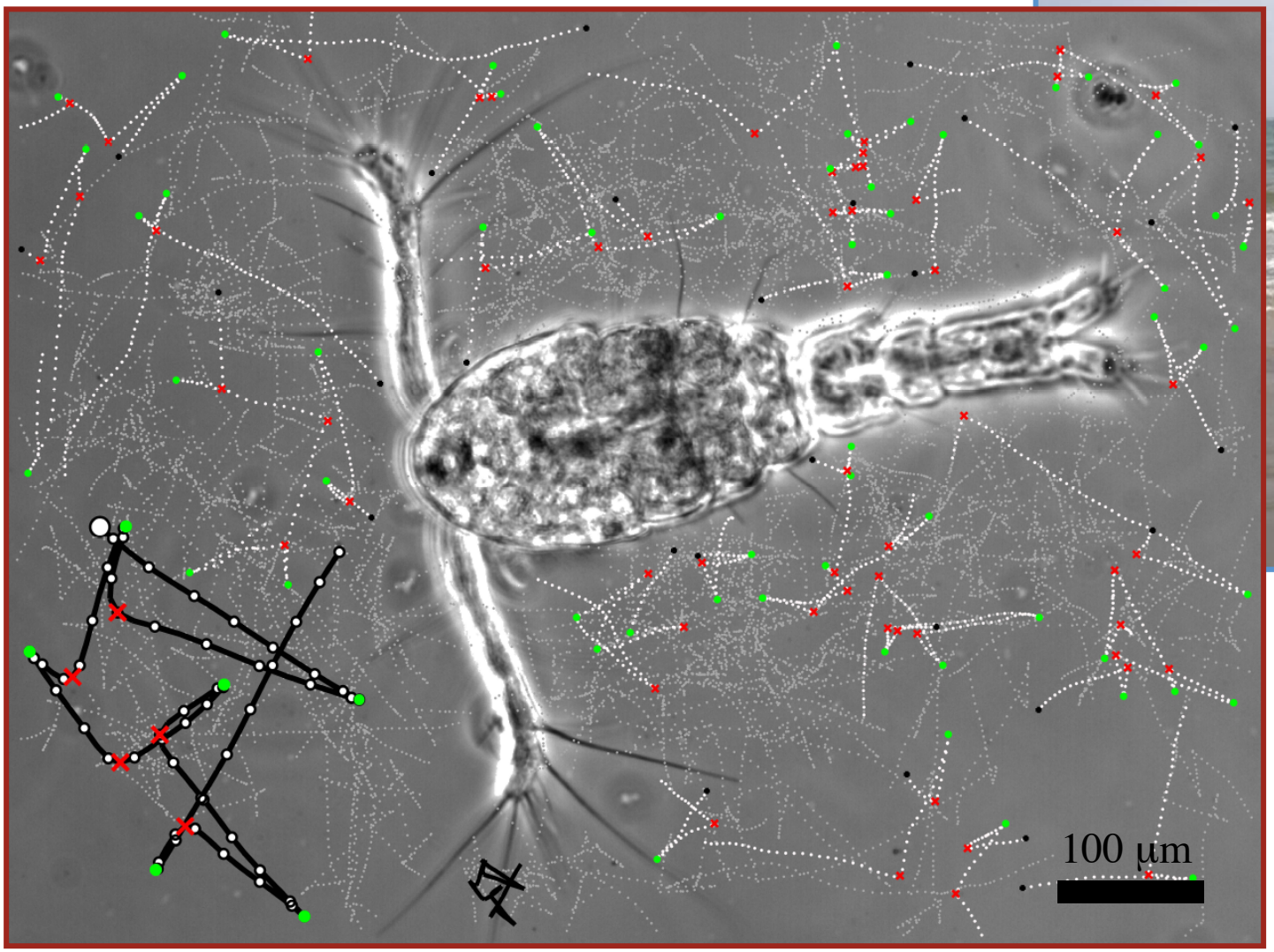
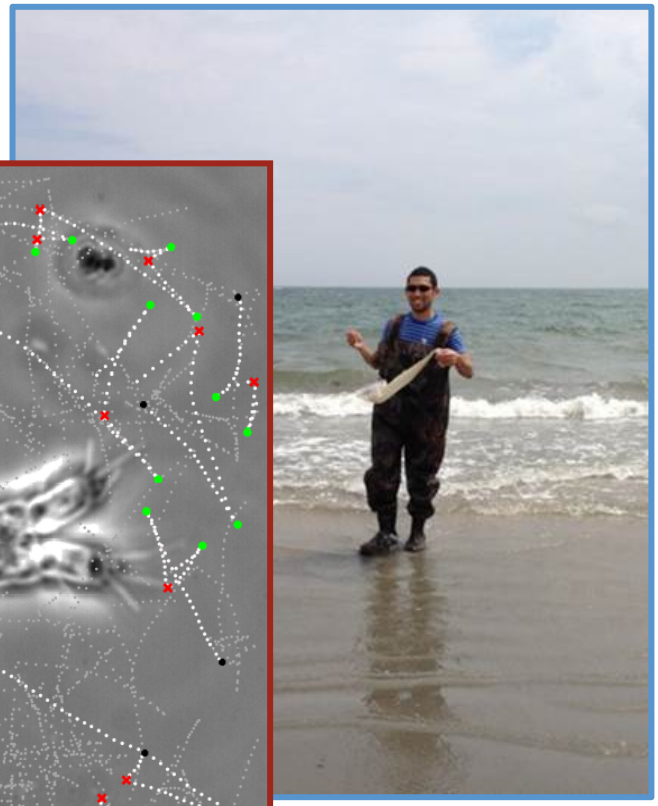
Turning by buckling may be ubiquitous

- Observed in 60-70% of cells





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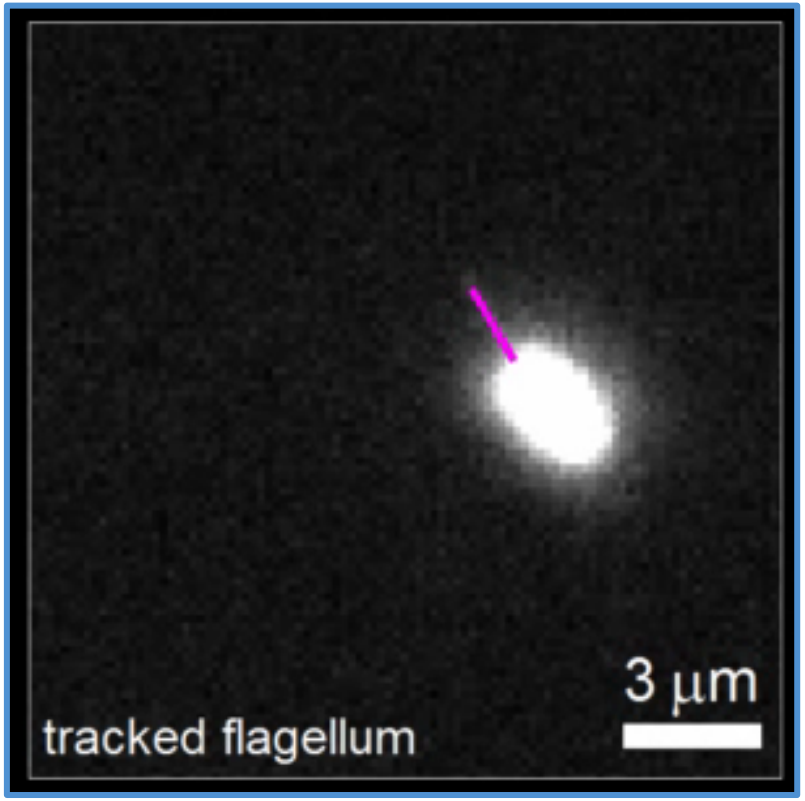
Turning by buckling

- **Ubiquitous** amongst monotrichous bacteria
- **Biologically cheap** mechanism in bacterial locomotion
- **Functional failure** in engineered microsystems and robotics
  → **under-actuated dynamics**



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Bacteria can exploit a flagellar buckling instability to change direction

Kwangmin Son[1], Jeffrey S. Guasto[2] and Roman Stocker[2]*

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