Swimming at low Reynolds numbers

Experiments ...
… but with enough theory to understand as much of it as possible!

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EPSRC
Engineering and Physical Sciences Research Council

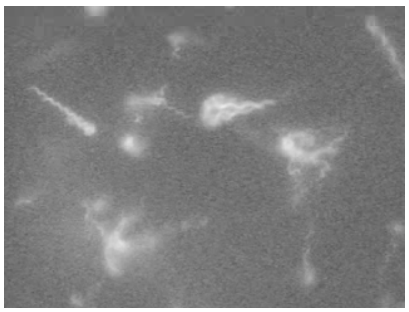
erc
European Research Council

한국에 초대해 주셔서 감사합니다

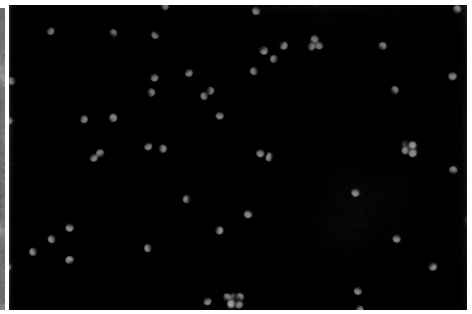
Focus on single-particle properties ...

Detailed understanding of this in water
→ swimming in polymer solutions

Maybe brief introduction

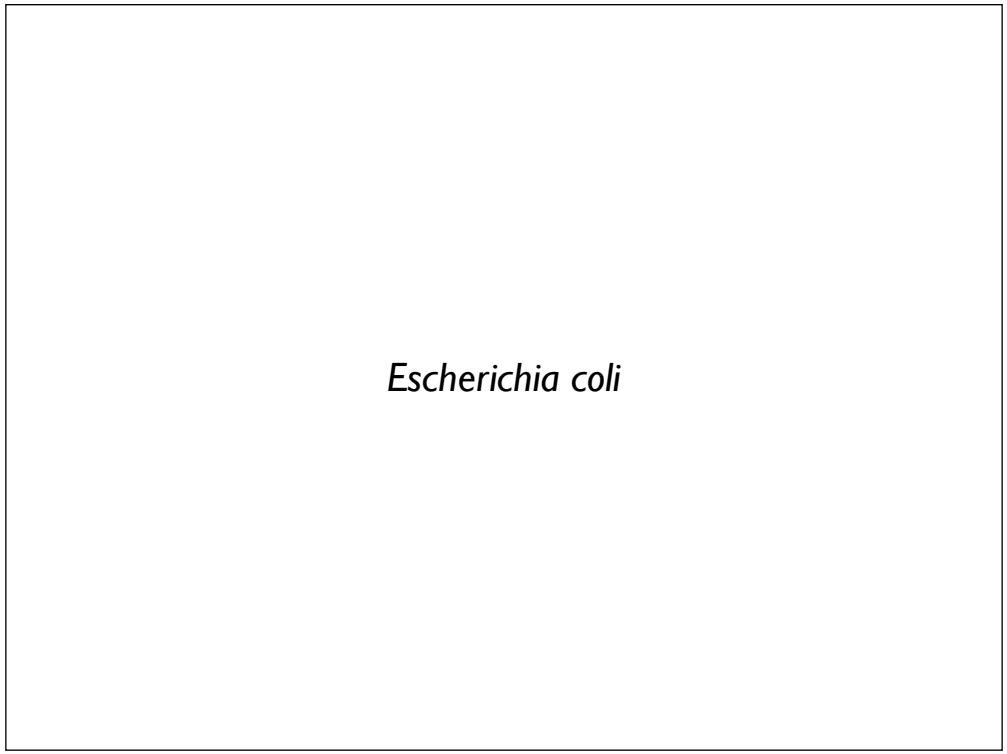


E. coli



Pt-PS Janus in H_2O_2

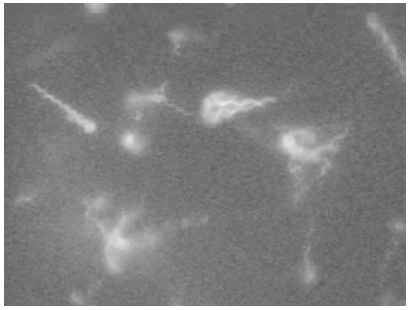
… because there are still many mysteries!

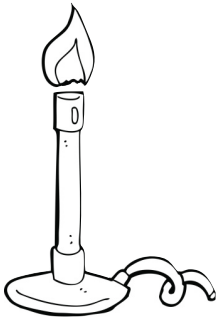

Escherichia coli

Section 0: Working with *E. coli* for physicists

Rule 1:

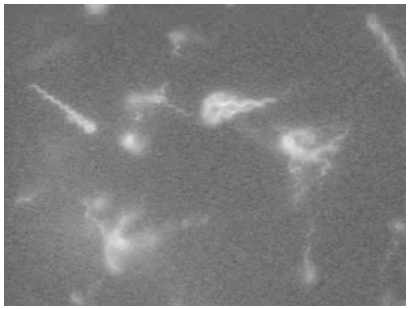
E. coli comes in many strains. Handling K-12 and its relatives ('Category 1') is less dangerous than going to the toilet ('Category 2')





is a far greater danger to the average physicist!

Rule 2:
Don’t believe the protocol of anyone who is not a motility expert

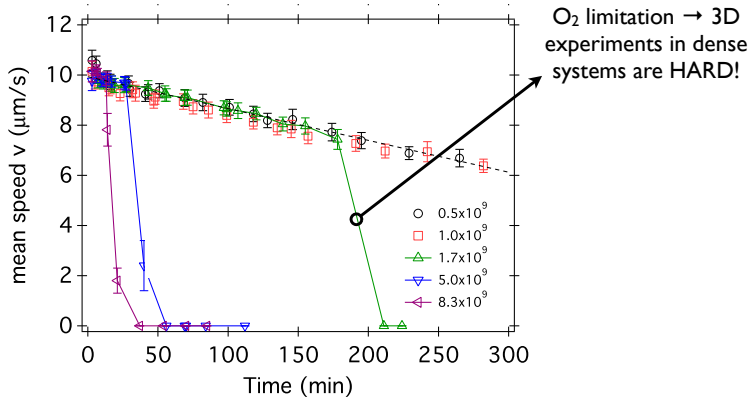


Growing in glucose gives few flagella
Everyday pipette tips/filtration will shear off flagella

Corollary: if in doubt (and even if not), look!

Rule 3:

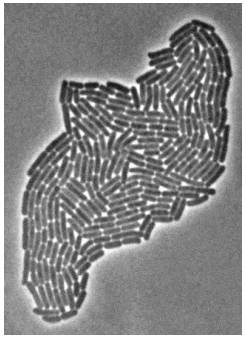
Assume everything is time dependent unless proven otherwise



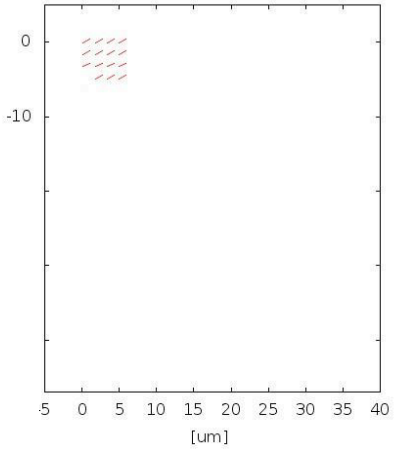
O_2 limitation → 3D experiments in dense systems are HARD!

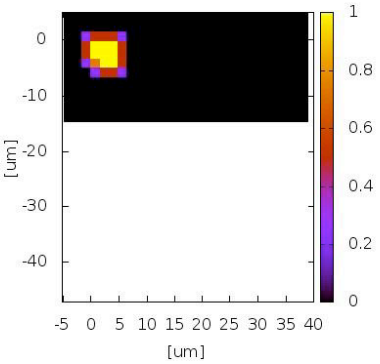
Swimming *E. coli* in sealed capillary in 'motility buffer'

Interlude: active matter on your T-shirt



↓ Defect creation/annihilation





← Local nematic order parameter <Q>

Back to swimmers

Section 1: Theoretical background

1. Revision (low Re theory)
2. Introduction to swimming micro-organisms
3. Real vs. model *E. coli*
4. Detailed theory of model *E. coli*

Section 1

1. Revision (low Re theory)
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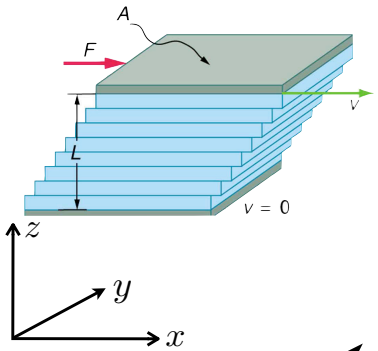
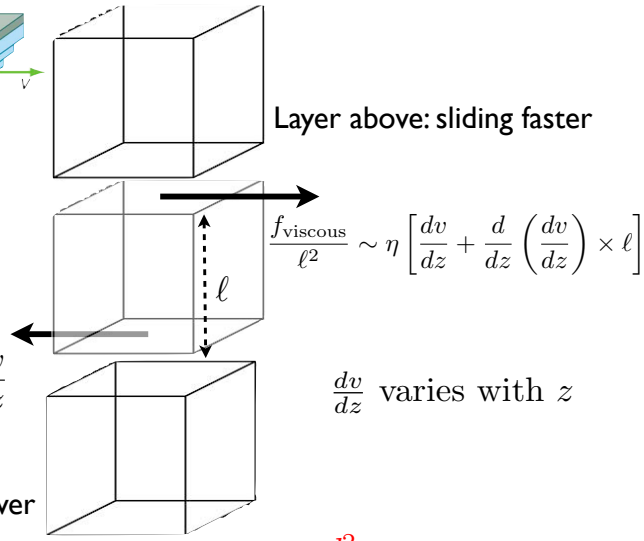
Theorem: Anything that's worth hearing is worth hearing twice (from a different perspective).

Viscosity: friction between fluid layers in a velocity gradient *dv/dz*





Layer above: sliding faster

$$\frac{f_{\text{viscous}}}{\ell^2} \sim \eta \left[\frac{dv}{dz} + \frac{d}{dz}\left(\frac{dv}{dz}\right) \times \ell \right]$$

$$\sigma_{\text{shear}} = \frac{f_{\text{viscous}}}{\ell^2} \sim \eta \frac{dv}{dz}$$

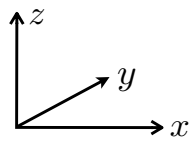
$\frac{dv}{dz}$ varies with z

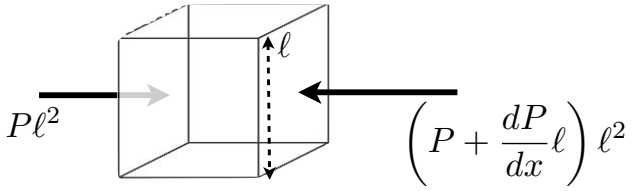
Layer below: sliding slower

$$\text{Net viscous force} = \eta \ell^3 \frac{d^2 v}{dz^2}$$

Net viscous force $= \eta \ell^3 \dfrac{d^2u}{dz^2}$

$\mathbf{v} = (u, v, w)$





Net pressure force $= -\dfrac{dP}{dx}\ell^3$

External (body) force $= f_x \ell^3$

$$\underbrace{\rho a}_{\frac{\text{mass}}{\text{vol}} \times \text{ accel.}} = \underbrace{-\frac{dP}{dx} + \eta \frac{d^2u}{dz^2} + f_x}_{\frac{\text{force}}{\text{vol}}}$$

$$\rho a = -\frac{dP}{dx} + \eta \frac{d^2u}{dz^2} + f$$

characteristic speed and length: U, L

Dimensionless variables:

$$\bar{x}, \bar{z} = \frac{x}{L}, \frac{z}{L}$$

$$\bar{u} = \frac{u}{U}$$

$$\bar{a} = \frac{a}{U^2/L}$$

$$\bar{P} = \frac{P}{\eta U/L}$$

$$\bar{f} = \frac{f}{\eta U/L^2}$$

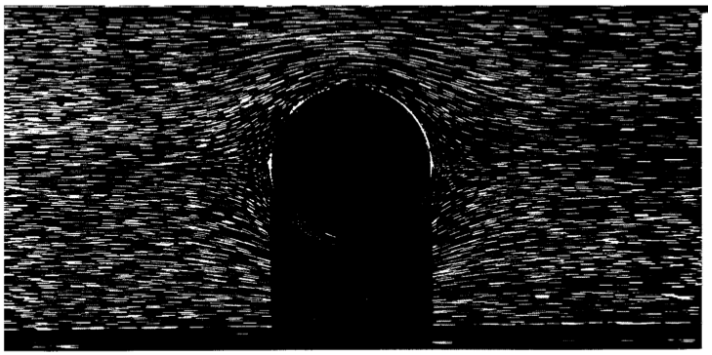
$$\mathrm{Re} \times \bar{a} = -\frac{d\bar{P}}{d\bar{x}} + \frac{d^2\bar{u}}{d\bar{z}^2} + \bar{f} = 0$$

$$\mathrm{Re} = \frac{\rho L v}{\eta}$$

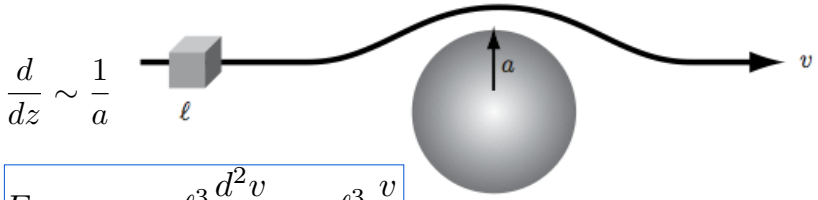
$$\mathrm{Re} \to 0 \Rightarrow -\frac{d\bar{P}}{d\bar{x}} + \frac{d^2\bar{u}}{d\bar{z}^2} + \bar{f} = 0$$

$$-\frac{dP}{dx} + \eta \frac{d^2u}{dz^2} + f = 0$$

$$-\nabla P + \eta \nabla^2 \mathbf{v} + \mathbf{f} = 0$$



$$f_{\text{inertial}} \sim \rho \ell^3 \frac{v^2}{a}$$

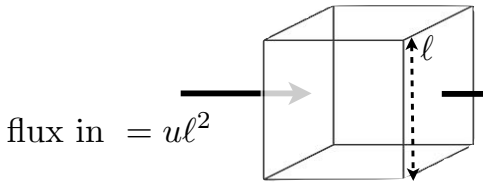


$$\frac{d}{dz} \sim \frac{1}{a}$$

$$F_{\text{viscous}} \sim \eta \ell^3 \frac{d^2 v}{dz^2} \sim \eta \ell^3 \frac{v}{a^2}$$

$$\text{Re} = \frac{\text{inertial}}{\text{viscous}} \sim \frac{\rho v^2 / a}{\eta v / a^2} \sim \frac{\rho v a}{\eta}$$

Incompressibility & continuity



flux in $= u\ell^2$ flux out $= \left(u + \dfrac{du}{dx}\ell\right)\ell^2$

$$\text{Net flux along } x \;= \frac{\partial u}{\partial x}\ell^3$$

$$\text{net flux } = 0 \Rightarrow \left(\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z}\right)\ell^3 = 0$$

$$\nabla \cdot \mathbf{v} = 0$$

Full equations for Stokes (Re = 0) flow

$$-\frac{dP}{dx} + \eta\frac{d^2u}{dz^2} + f_x = 0 \qquad -\nabla P + \eta\nabla^2\mathbf{v} + \mathbf{f} = 0$$

+ corresponding *y*, *z* equations

subject to

$$\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = 0 \qquad \nabla \cdot \mathbf{v} = 0$$

Just *looking* at gives lots of insight!

→ Tutorial problem 1, 2, 3

1. Linearity

Dimensionless variables:

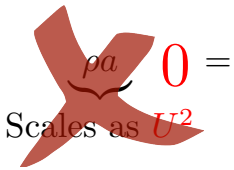
$$x, z = L\bar{x}, L\bar{z}$$

$$a = \frac{U^2}{L}\bar{a}$$

$$u = U\bar{u}$$

$$P = \frac{\eta U}{L}\bar{P}$$

$$f = \frac{\eta U}{L^2}f$$



$$\underbrace{-\frac{dP}{dx} + \eta\frac{d^2u}{dz^2} + f}_{\text{Scales as } U}$$

Everything scales as U as $\therefore$ as everything else.

One well known consequence:

Fluid exerts drag $\mathbb{F} = -6\pi\eta a\mathbf{v}$ on sphere

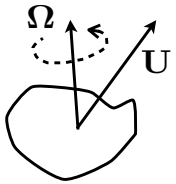
More generally

Drag force/torque linear in velocity/angular velocity

Drag on general body

3x3 matrix

$$\begin{pmatrix} \mathbb{F} \\ \mathbb{N} \end{pmatrix} = - \begin{pmatrix} \underline{\underline{A}} & \underline{\underline{B}} \\ \underline{\underline{B}}^{\mathrm{T}} & \underline{\underline{D}} \end{pmatrix} \begin{pmatrix} \mathbf{U} \\ \mathbf{\Omega} \end{pmatrix}$$



rotational-translational coupling

Sphere

$$\begin{pmatrix} \mathbb{F} \\ \mathbb{N} \end{pmatrix} = - \begin{pmatrix} 6\pi\eta a & 0 \\ 0 & 8\pi\eta a^3 \end{pmatrix} \begin{pmatrix} \mathbf{U} \\ \mathbf{\Omega} \end{pmatrix}.$$

General axi-symmetric body in suitable frame

$$\begin{pmatrix} \mathbb{F} \\ \mathbb{N} \end{pmatrix} = - \begin{pmatrix} A & B \\ B & D \end{pmatrix} \begin{pmatrix} \mathbf{U} \\ \mathbf{\Omega} \end{pmatrix}$$

$$\mathbb{F} = -A\mathbf{U} - \mathbf{\Omega}, \quad \mathbb{N} = -B\mathbf{U} - D\mathbf{\Omega}$$

$$A \sim \eta L$$
$$B \sim \eta L^2$$
$$D \sim \eta L^3$$

$$\begin{pmatrix} \mathbb{F} \\ \mathbb{N} \end{pmatrix} = - \begin{pmatrix} \underline{\underline{\mathbb{A}}} & \underline{\underline{\mathbb{B}}} \\ \underline{\underline{\mathbb{B}}}^{\mathrm{T}} & \underline{\underline{\mathbb{D}}} \end{pmatrix} \begin{pmatrix} \mathbf{U} \\ \mathbf{\Omega} \end{pmatrix}$$

The Resistance Matrix

(Inverse = Mobility Matrix)

General $\quad \begin{pmatrix} \underline{\underline{\mathrm{A}}} & \underline{\underline{\mathrm{B}}} \\ \underline{\underline{\mathrm{B}}}^{\mathrm{T}} & \underline{\underline{\mathrm{D}}} \end{pmatrix}$

$A \sim \eta L$

$B \sim \eta L^2$

$D \sim \eta L^3$

force ↔ velocity

Axisymmetric $\quad \begin{pmatrix} \underline{\underline{\mathrm{A}}} & \underline{\underline{\mathrm{B}}} \\ \underline{\underline{\mathrm{B}}} & \underline{\underline{\mathrm{D}}} \end{pmatrix}$

force ↔ angular velocity

Torque ↔ velocity

torque ↔ angular velocity

Everything moving in goo (= low Re) has one!

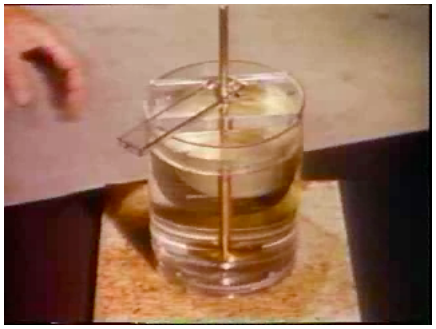
2. Reversibility

$$-\frac{dP}{dx} + \eta \frac{d^2u}{dz^2} + f_x = 0 \qquad -\nabla P + \eta \nabla^2 \mathbf{v} + \mathbf{f} = 0$$

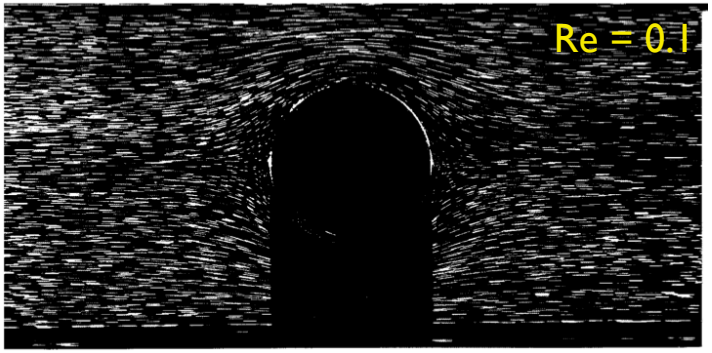
'Reversed flow field'

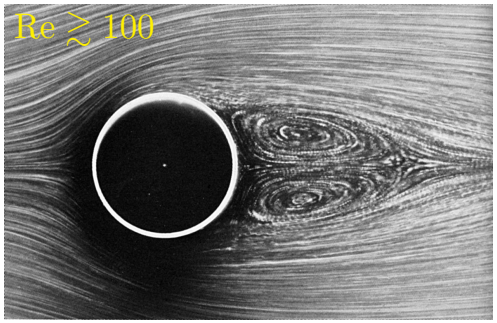
$$u \to -u \text{ etc.}$$
$$f_x \to -f_x \text{ etc.}$$
$$\frac{dP}{dx} \to -\frac{dP}{dx} \text{ etc.}$$

is also a solution



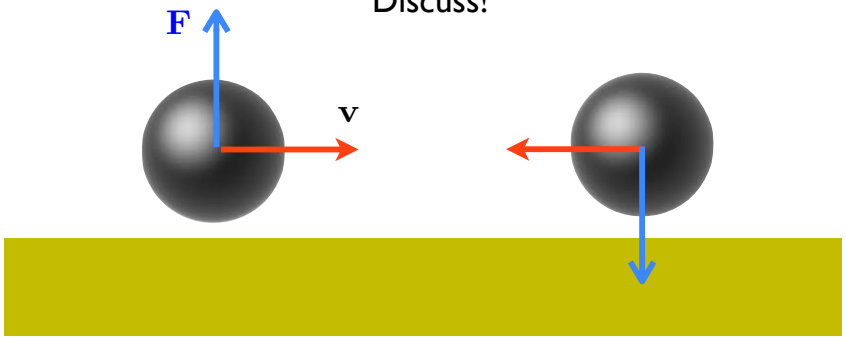
G. I. Taylor


Re = 0.1


Re $\gtrsim$ 100

Does the wall exert a lift force on the sphere?

Discuss!



Assume force **F**
Reverse **v** and **F** - still a solution

Can't both be true!
F = 0

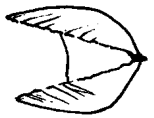
→ Tutorial problem 4

Reversibility ⇒

Scallop Theorem: reciprocal motion does not propel at low Re

E. M. Purcell, 'Life at Low Reynolds Number', *Am. J. Phys.* **45** (1977) 3-11

The Scallop Theorem



Section 1

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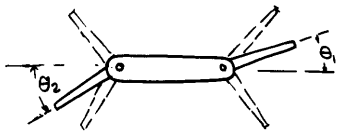
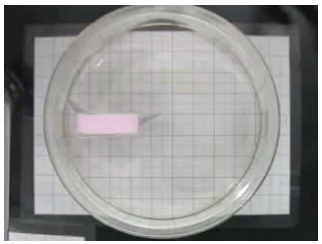
Microorganisms at low Re have to invent
non-reciprocating cyclical motions to propel



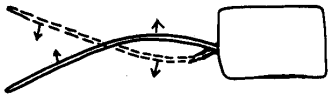
You can tell which way the movie is being played!



Brian Chan, MIY

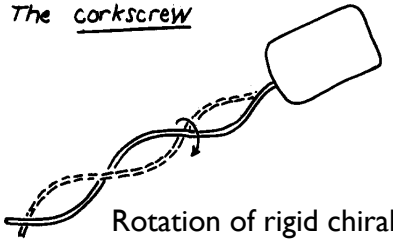
Lighthill, SIAM Review 1976

The flexible oar



travelling wave along flagellum

The corkscrew



Rotation of rigid chiral flagellum

The Journal of Experimental Biology 213, 1226-1234

doi:10.1242/jeb.039800

High-precision tracking of sperm swimming fine structure provides strong test of resistive force theory

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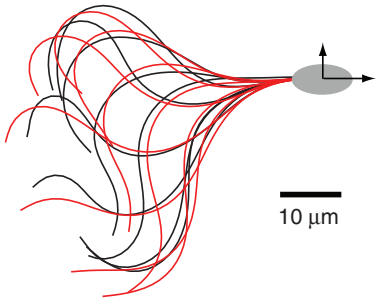
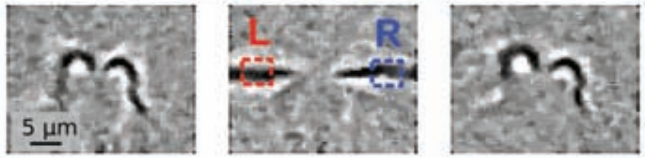
Accepted 2 December 2009

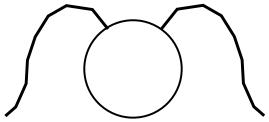


Bending waves along flagellum

Algae *Chlamydomonas reinhardtii*

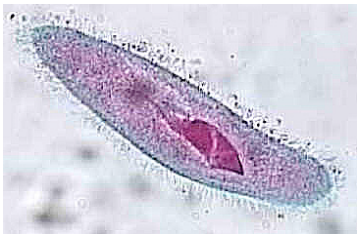


Polin et al., *Science* **325** (2009) 487

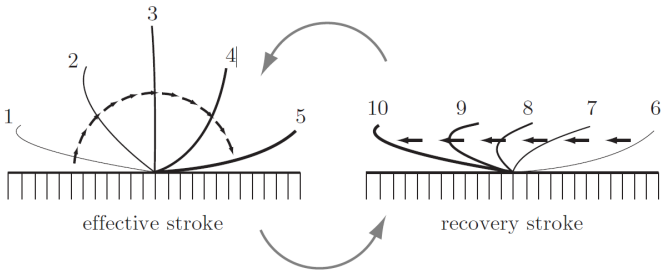


‘Breast stroke’

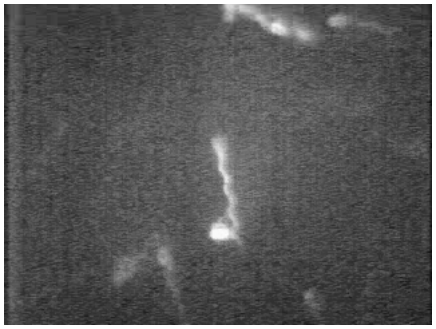
Paramecium: layer of beating cilia



http://www.youtube.com/watch?v=HXcEACQv5-8



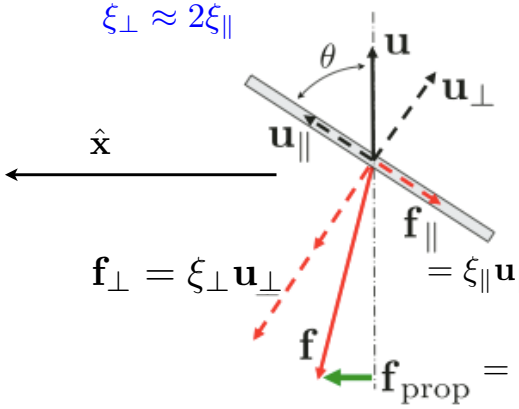
E. coli - rotating rigid helical flagalla



Linda Turner

All based long, thin filaments!

The importance of being anisotropic



Global requirement:
non-reciprocating

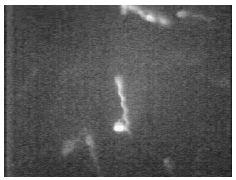
Local requirement:
drag anisotropy

Net propulsion from $u \sin\theta \cos\theta$

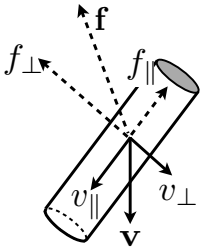
$(u, \theta) \to (-u, \pi - \theta)$  Finite average over cycle

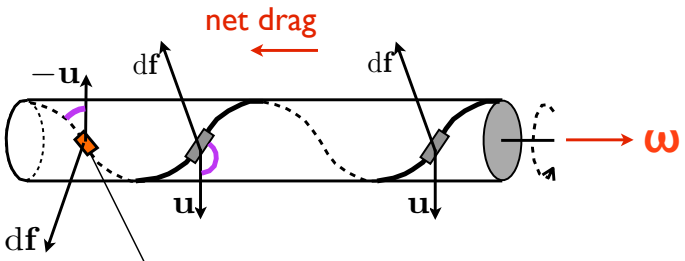
$(u, \theta) \to (-u, \theta)$  Zero average over cycle

Criterion: must be able to tell if movie is run backwards …
… i.e. non-time-reversible (= non-reciprocating)



Left-handed helix





$$(u, \theta) \rightarrow (-u, \pi - \theta)$$

negative rotational-translational coupling

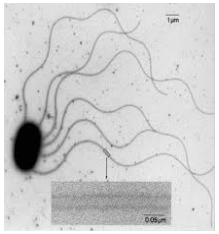
→ Tutorial problem 5

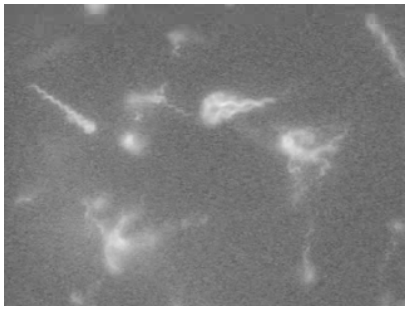
Section 1

1. Revision (low Re theory)
2. Introduction to swimming micro-organisms
3. Real vs. model *E. coli*
4. Detailed theory of model *E. coli*

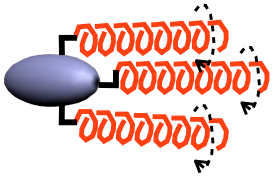
Wild-type *E. coli*

~ 10 flagella
CCW = bundle & propel
CW of one or more = unbundle & tumble



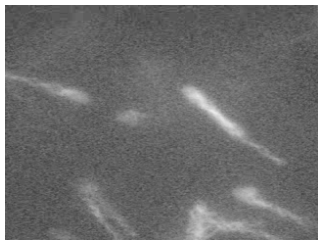


Linda Turner



‘hairy hippy’

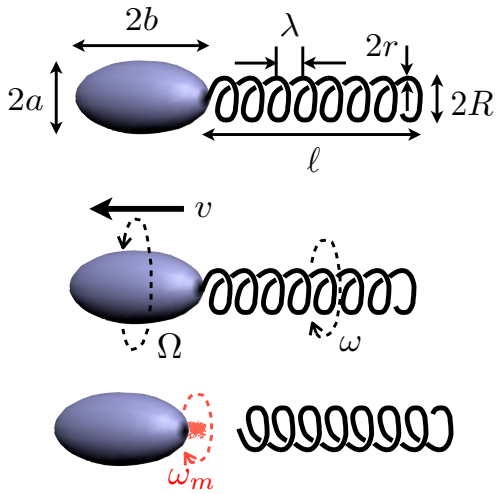
Smooth-swimming mutant



≈ 1s of movie

Purcell's *E. coli* model

Single 'effective' flagellum



Does it work?

$2a \sim 1\mu\text{m}$
$2b \sim 2\mu\text{m}$
$\ell \gtrsim 7\mu\text{m}$
$\lambda \sim 1.5\mu\text{m}$
$2R \sim 0.2\mu\text{m}$
$2r \sim 20\text{nm}$

$v \sim 20\mu\text{m/s}$
$\omega \sim 2\pi \times 10^2\text{Hz}$
$\Omega \sim 2\pi \times 10\text{Hz}$

Motor rotates at ω_m relative to stationary body

$\omega = \omega_m - \Omega$ or $\omega_m = \omega + \Omega$

Section 1

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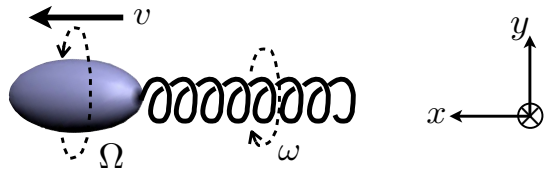
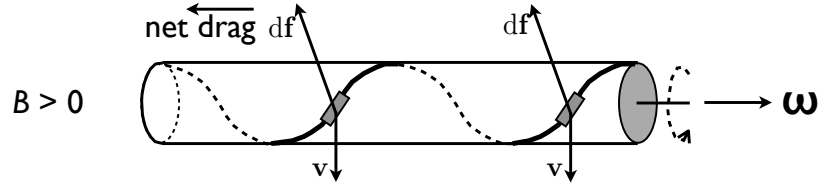


$$\begin{pmatrix} \mathbb{F}_b \\ \mathbb{N}_b \end{pmatrix} = -\begin{pmatrix} A_0 & 0 \\ 0 & D_0 \end{pmatrix}\begin{pmatrix} \mathbf{v} \\ \mathbf{\Omega} \end{pmatrix} \text{ and}$$

$$\begin{pmatrix} \mathbb{F}_f \\ \mathbb{N}_f \end{pmatrix} = -\begin{pmatrix} A & B \\ B & D \end{pmatrix}\begin{pmatrix} \mathbf{v} \\ \boldsymbol{\omega} \end{pmatrix}, \text{ with}$$

$A_0, D_0, A, D > 0$

$\mathbf{v} = (v, 0, 0)$, $\boldsymbol{\omega} = (-\omega, 0, 0)$, $\mathbf{\Omega} = (\Omega, 0, 0)$



$$\begin{pmatrix} \mathbb{F}_b \\ \mathbb{N}_b \end{pmatrix} = -\begin{pmatrix} A_0 & 0 \\ 0 & D_0 \end{pmatrix}\begin{pmatrix} \mathbf{v} \\ \boldsymbol{\Omega} \end{pmatrix} \text{ and}$$

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$A_0, D_0, A, B, D > 0$

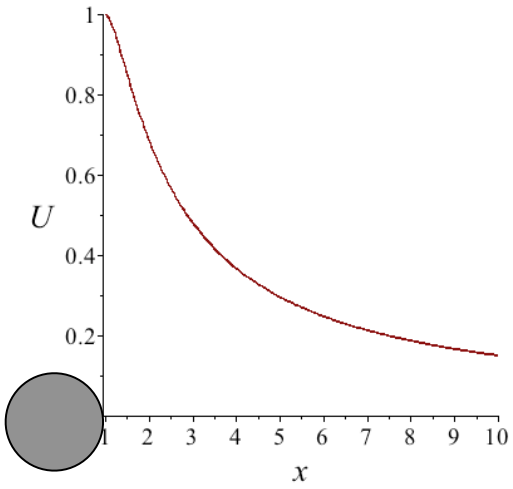
$\mathbf{v} = (v, 0, 0)$, $\boldsymbol{\omega} = (-\omega, 0, 0)$, $\boldsymbol{\Omega} = (\Omega, 0, 0)$

Force free : $-A_0 v - Av - B(-\omega) = 0$ or $(A_0 + A)v = B\omega$

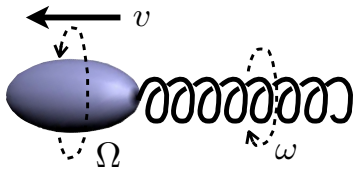
Torque free : $-D_0\Omega - Bv - D(-\omega) = 0$ or $D_0\Omega = -Bv + D\omega$

(Neglects hydrodynamic interaction between body and flagella!)

Decay of flow in ‘wake’ of sphere



$(A_0 + A)v = B\omega$ $\qquad$ $D_0\Omega = -Bv + D\omega$



$\omega_m = \omega + \Omega$

2 equations, 3 unknowns → need extra information!

Two equations alone: can eliminate one unknown …
… all relations are *linear*.

$$\Omega = \alpha v$$
$$\omega = \beta\Omega$$
$$v = \gamma\omega$$

$$v = \left[\frac{BD_0}{(A_0 + A)(D_0 + D) - B^2}\right]\omega_m$$

$$v = \left[\frac{BD_0}{(A_0 + A)(D_0 + D) - B^2} \right] \omega_m$$

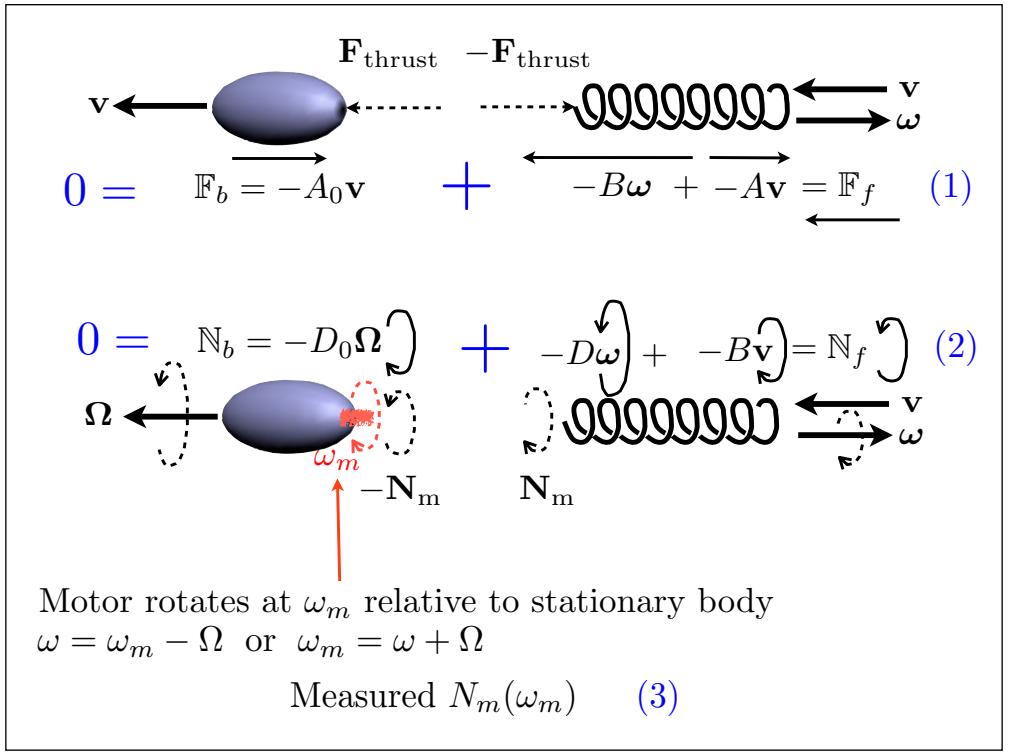
$B \neq 0$ and $D_0 \neq 0$ both crucial – generic feature

$B \neq 0$ and $D_0 \neq 0$ both crucial!

Exercise: discuss why ...

$$\begin{pmatrix} \mathbb{F}_b \\ \mathbb{N}_b \end{pmatrix} = - \begin{pmatrix} A_0 & 0 \\ 0 & D_0 \end{pmatrix} \begin{pmatrix} \mathbf{v} \\ \boldsymbol{\Omega} \end{pmatrix}$$

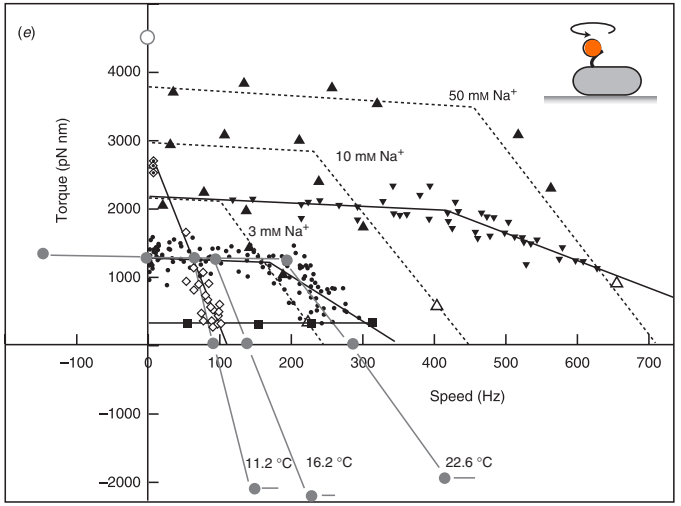
$$\begin{pmatrix} \mathbb{F}_f \\ \mathbb{N}_f \end{pmatrix} = - \begin{pmatrix} A & B \\ B & D \end{pmatrix} \begin{pmatrix} \mathbf{v} \\ \boldsymbol{\omega} \end{pmatrix}$$



Motor rotates at ω_m relative to stationary body

$\omega = \omega_m - \Omega$ or $\omega_m = \omega + \Omega$

Measured $N_m(\omega_m)$ (3)



Richard Berry, *Q. Rev. Biophys* (2008)

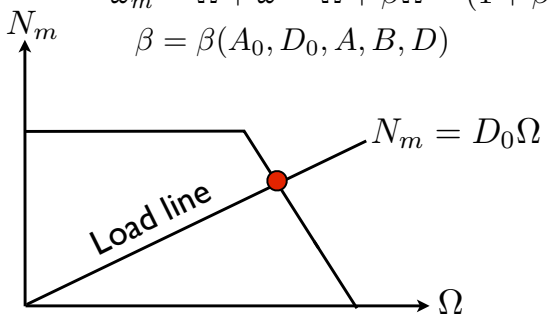
Force free : $-A_0 v - Av - B(-\omega) = 0$ or $(A_0 + A)v = B\omega$

Torque free : $-D_0\Omega - Bv - D(-\omega) = 0$ or $D_0\Omega = -Bv + D\omega$

$N_m(\omega_m)$

$\omega_m = \Omega + \omega = \Omega + \beta\Omega = (1 + \beta)\Omega$

$\beta = \beta(A_0, D_0, A, B, D)$



Completely specifies model *E. coli*, provided A_0, D_0, A, B, D are known

$$\begin{pmatrix} \mathbb{F}_b \\ \mathbb{N}_b \end{pmatrix} = -\begin{pmatrix} A_0 & 0 \\ 0 & D_0 \end{pmatrix}\begin{pmatrix} \mathbf{v} \\ \mathbf{\Omega} \end{pmatrix}$$

$$\begin{pmatrix} \mathbb{F}_f \\ \mathbb{N}_f \end{pmatrix} = -\begin{pmatrix} A & B \\ B & D \end{pmatrix}\begin{pmatrix} \mathbf{v} \\ \boldsymbol{\omega} \end{pmatrix}$$

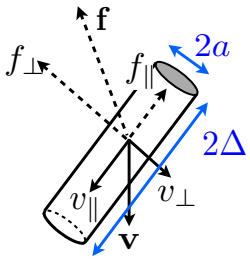
Ellipsoid $a, a \ll b$

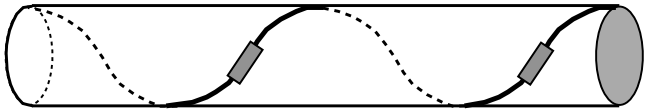
$$A_0 = \frac{4\pi\eta b}{\ln\left(\frac{2a}{b}\right) - \frac{1}{2}}$$

$$D_0 = \frac{16\pi\eta a^2 b}{3}$$

Not really valid for *E coli* with $b \approx 2a$n…
… but people use these anyway!

Much more interesting ...





Treat local bits of helix as slender cylinders and integrate

$$\xi u = \text{resistance/length}$$

$$\xi_\parallel = \frac{4\pi\eta}{2\ln\left(\frac{2\Delta}{a}\right) - 1}$$

$$\xi_\perp = \frac{8\pi\eta}{2\ln\left(\frac{2\Delta}{a}\right) + 1}$$

!!

$$\Delta/a \gg 1$$

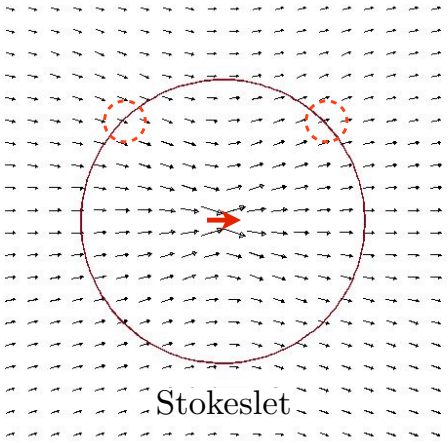
How come?

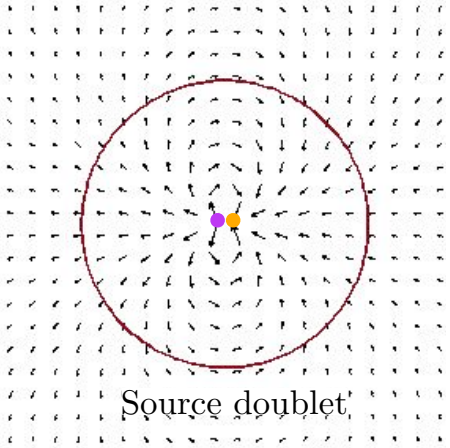
How do we get $F = 6\pi\eta va$ for a sphere being dragged with force F?

Solve Stokes problem requiring stick boundary condition on sphere surface

Want $\mathbf{v}(\mathbf{r}) = \mathbf{u_0} = (u, 0, 0)$ on sphere (radius a)

$$\mathbf{v} = \frac{F}{8\pi\eta}\left(\frac{x^2+r^2}{r^3}, \frac{xy}{r^3}, \frac{xz}{r^3}\right) \qquad \mathbf{v} = \frac{G}{4\pi}\left(\frac{1}{r^3} - \frac{3x^2}{r^5}, -\frac{3xy}{r^5}, -\frac{3xz}{r^5}\right)$$



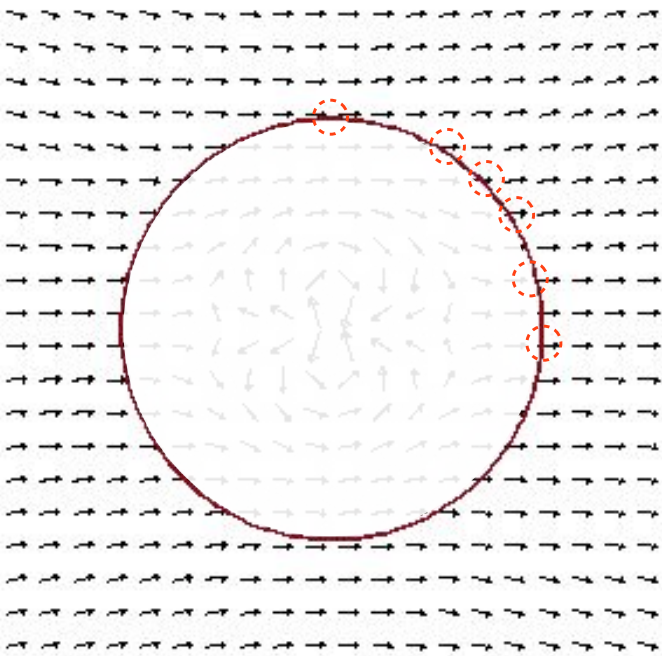


Point force @ origin

Source Sink point dipole @ origin

Exerts net force ***F*** on fluid

Exerts zero force on fluid



Suitable combination of Stokeslet and source doublet

$$\mathbf{v}_{SS} = \frac{F}{8\pi\eta}\left(\frac{x^2+r^2}{r^3}, \frac{xy}{r^3}, \frac{xz}{r^3}\right) \qquad \mathbf{v}_{SD} = \frac{G}{4\pi}\left(\frac{1}{r^3} - \frac{3x^2}{r^5}, -\frac{3xy}{r^5}, -\frac{3xz}{r^5}\right)$$

$$G = \frac{Fa^2}{6\eta}$$

$$\mathbf{v}_{SS}(r=a) + \mathbf{v}_{SD}(r=a) = \frac{F}{6\pi\eta a}(1,0,0)$$

Satisfies boundary condition for sphere translating with $\mathbf{v} = (u, 0, 0)$

Sphere exerts force $\mathbf{F} = 6\pi\eta a\mathbf{v}$ on fluid

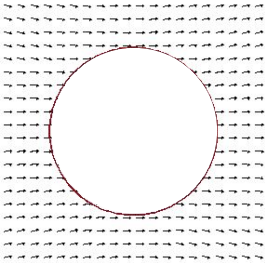
Fluid exerts drag $\mathbb{F} = -6\pi\eta a\mathbf{v}$ on sphere

Indeed $\mathbf{F} \propto \mathbf{v}$ (linearity)

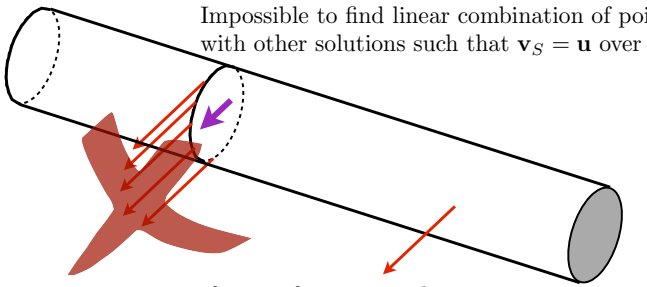
Another property of Stokes (low Re) flow

Uniqueness

A solution that satisfies boundary conditions is *the* solution.



is *the* solution of uniformly translating sphere in infinite fluid



Impossible to find linear combination of point force solution with other solutions such that $\mathbf{v}_S = \mathbf{u}$ over any cross section

for uniform translation at $\mathbf{u}$

$$\xi_{\parallel} = \frac{4\pi\eta}{2\ln\left(\frac{2\Delta}{a}\right) - 1} \qquad \xi_{\perp} = \frac{8\pi\eta}{2\ln\left(\frac{2\Delta}{a}\right) + 1}$$

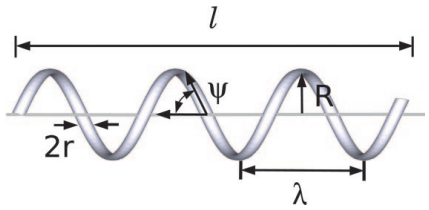
Lighthill

$c < 1$

$$\xi_{\parallel} = \frac{4\pi\eta}{2\ln\left(\frac{c\lambda}{a}\right) - 1} \qquad \xi_{\perp} = \frac{8\pi\eta}{2\ln\left(\frac{c\lambda}{a}\right) + 1}$$

Self consistent argument: $c \approx 0.18$

(Impose variation on force along cylinder and consider resulting flow)



$$A = \xi_\perp \ell \frac{1-\beta}{\sqrt{\beta}} \left(1 + \gamma_k \frac{\beta}{1-\beta}\right),$$

$$B = \xi_\perp \ell \left(\frac{\lambda}{2\pi}\right) \frac{1-\beta}{\sqrt{\beta}} (1-\gamma_k),$$

$$D = \xi_\perp \ell \left(\frac{\lambda}{2\pi}\right)^2 \left(1 + \gamma_k \frac{\beta}{1-\beta}\right) \frac{1-\beta}{\sqrt{\beta}}$$

$$\gamma_k = \xi_\parallel / \xi_\perp$$
$$\xi_\perp (1-\gamma_k) = \xi_\perp - \xi_\parallel$$

$\beta = \cos^2 \psi$ with $\psi = \tan^{-1}(2\pi R/\lambda)$ is the helix pitch angle

Section 2: Experimental tests

1. Coarse-grained description
2. Measuring the resistance matrix
3. Does it really fit?

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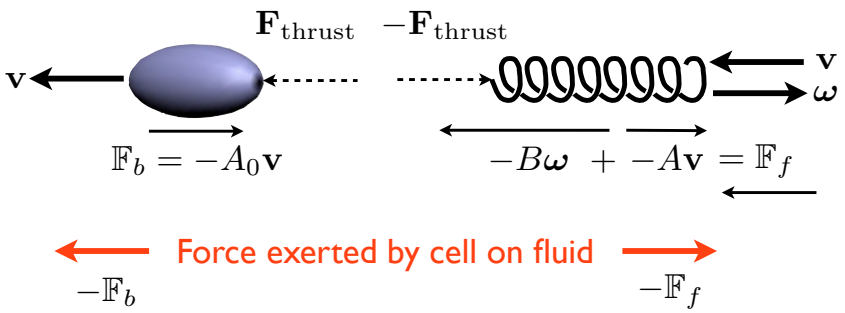
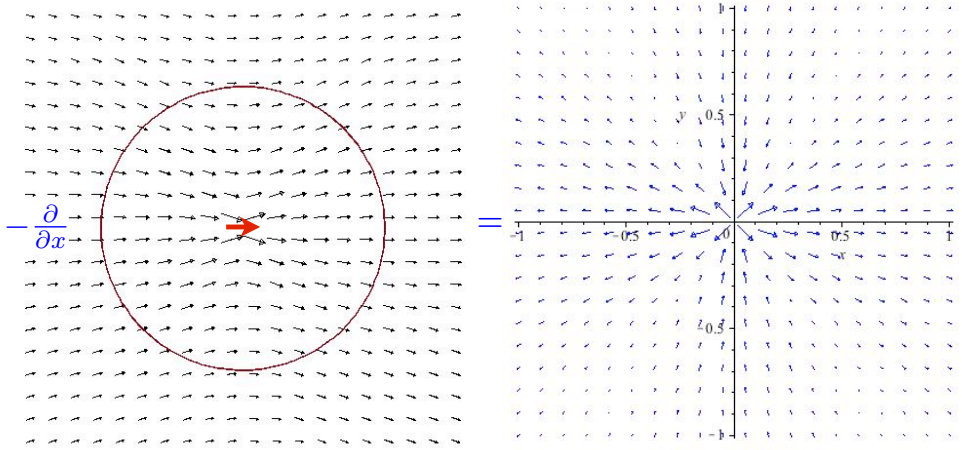


This is a force dipole

The dipolar flow field should be a good approximation in the far field ...

Pusher/extensile dipole



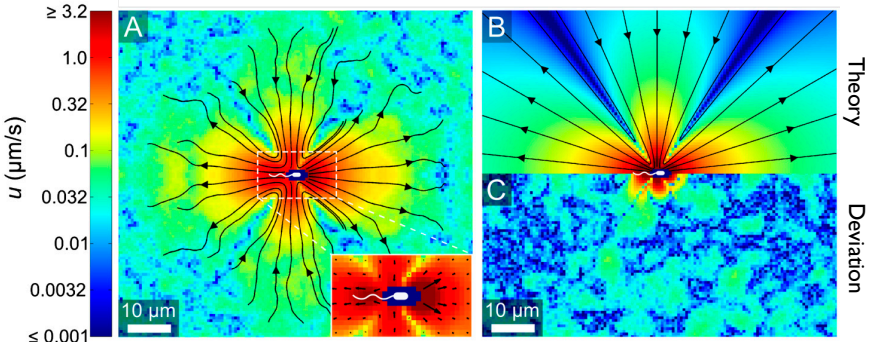
Point force @ origin

$$u \sim \frac{1}{r}$$

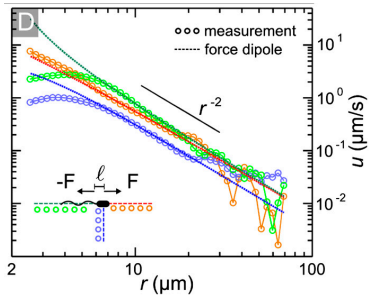
Point dipole @ origin

$$u \sim \frac{1}{r^2}$$

Is it true?

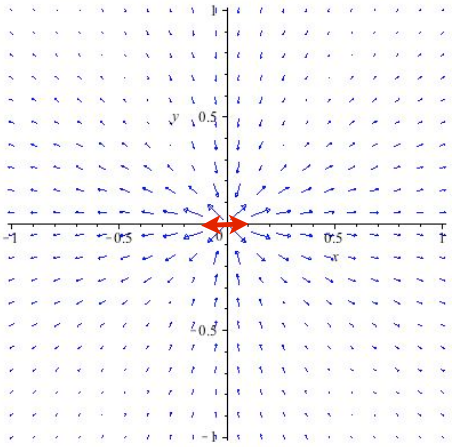


Drescher et al. PNAS**108** (2011)10940



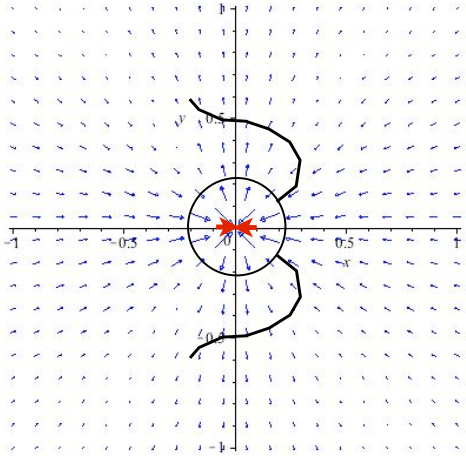
Two kinds of force dipole exist

Pusher/extensile



Point dipole @ origin

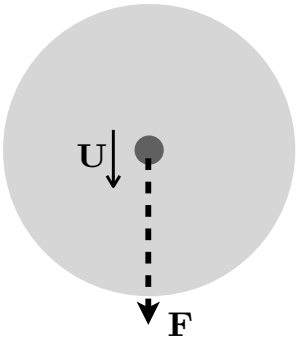
Puller/contractile



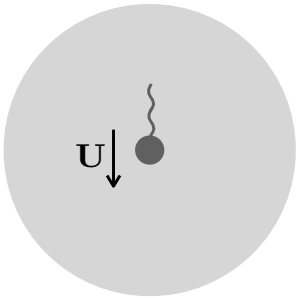
Point dipole @ origin

Isolated liquid drop with

dragged particle



self-propelled swimmer



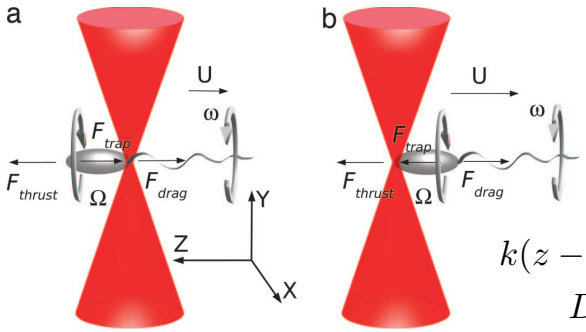
Discuss!

Section 2: Experimental tests

1. Coarse-grained description
2. Measuring the resistance matrix
3. Does it really fit?

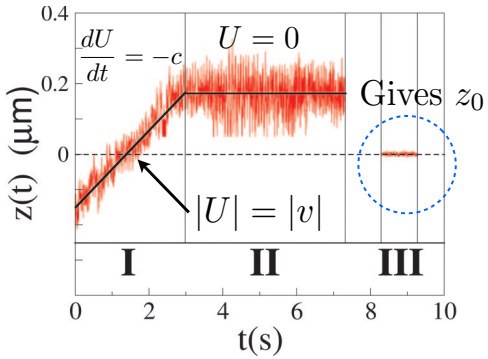
Chattopadhyay et al. *PNAS* 103 (2013) 13712–13717

We use measurements of swimming bacteria in an optical trap to determine fundamental properties of bacterial propulsion. In particular, we directly measure the force required to hold the bacterium in the optical trap and determine the propulsion matrix, which relates the translational and angular velocity of the flagellum to the torques and forces propelling the bacterium.



k from calibration
A_0, D_0 from ellipsoid
Ω, ω from power spec.

$$k(z - z_0) = (A + A_0)U + B\omega$$
$$D_0\Omega = -BU + D\omega$$



Regime I: $\frac{dz}{dt} = \frac{dz}{dU}\frac{dU}{dt} \Rightarrow A$

Regime II: $U = 0 \Rightarrow B, D$

Section 2: Experimental tests

1. Coarse-grained description
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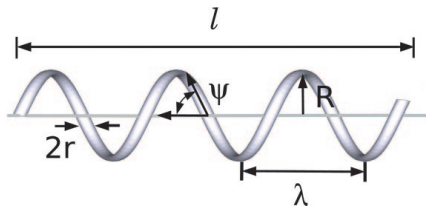
Their conclusion: 'it fits'



literature ψ, calculated A_0, D_0, measured A, B, D

$\rightarrow$ OK values for $\ell, \lambda, \xi_{\|}/\xi_{\perp}$

But ...

$$a = 20 \text{ nm}, c = 2.4$$

$$\xi_{\parallel} = \frac{4\pi\eta}{2\ln\left(\frac{c\lambda}{a}\right) - 1}$$

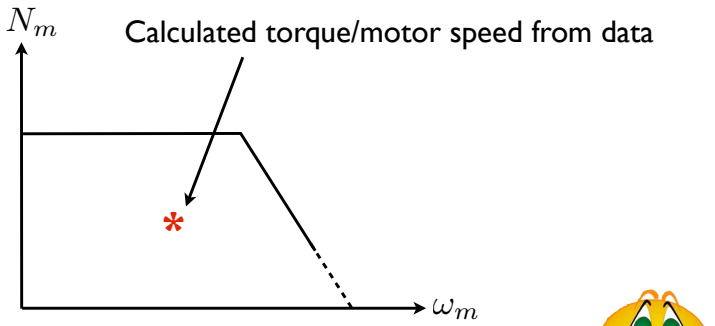
$$\xi_{\perp} = \frac{8\pi\eta}{2\ln\left(\frac{c\lambda}{a}\right) + 1}$$

Single flagellum: $a = 10$ nm
Lighthill: $c < 1$, perhaps 0.18

$c\lambda$ is locally straight!

Only used 2 equations ...

… need to test consistency with 3rd source of info.

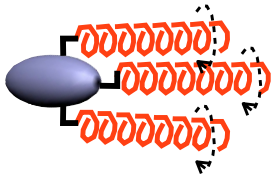


Other caveats:

- Head-tail HI neglected

- Resistive force theory neglects HI within flagellum
→ slender body theory

- Movement of hairy flagellum body is complex, so power spectrum may not give ω.



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On Torque and Tumbling in Swimming *Escherichia coli*[▽]†

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Bacteria swim by rotating long thin helical filaments, each driven at its base by a reversible rotary motor. When the motors of peritrichous cells turn counterclockwise (CCW), their filaments form bundles that drive the cells forward. We imaged fluorescently labeled cells of *Escherichia coli* with a high-speed charge-coupled-device camera (500 frames/s) and measured swimming speeds, rotation rates of cell bodies, and rotation rates of flagellar bundles. Using cells stuck to glass, we studied individual filaments, stopping their rotation by exposing the cells to high-intensity light. From these measurements we calculated approximate values for bundle torque and thrust and body torque and drag, and we estimated the filament stiffness. For both immobilized and swimming cells, the motor torque, as estimated using resistive force theory, was significantly lower than the motor torque reported previously. Also, a bundle of several flagella produced little more torque than a single flagellum produced. Motors driving individual filaments frequently changed directions of rotation. Usually, but not always, this led to a change in the handedness of the filament, which went through a sequence of polymorphic transformations, from normal to semicoiled to curly 1 and then, when the motor again spun CCW, back to normal. Motor reversals were necessary, although not always sufficient, to cause changes in filament chirality. Polymorphic transformations among helices having the same handedness occurred without changes in the sign of the applied torque.

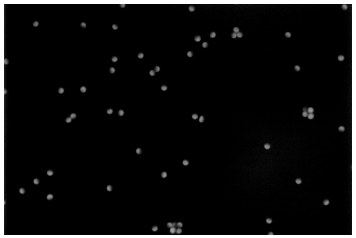
Single ‘effective flagellum’ model remains ill tested …

… may be necessarily non-self-consistent!

Other ways of testing Stokes propulsion in Newtonian fluids ...

Democracy at work

Tomorrow: one more *E. coli* swimming story, and then ...



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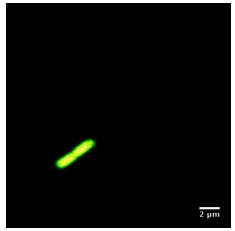

You vote!