Lecture 11

Life in the low-Reynolds number world

Sources:

Purcell – Life at low Reynolds number (Am. J. Phys 1977)
Nelson – Biological Physics (CH.5)

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Outline

I. Friction in fluids.

II. Low Reynolds-number world.

III. Biological applications.

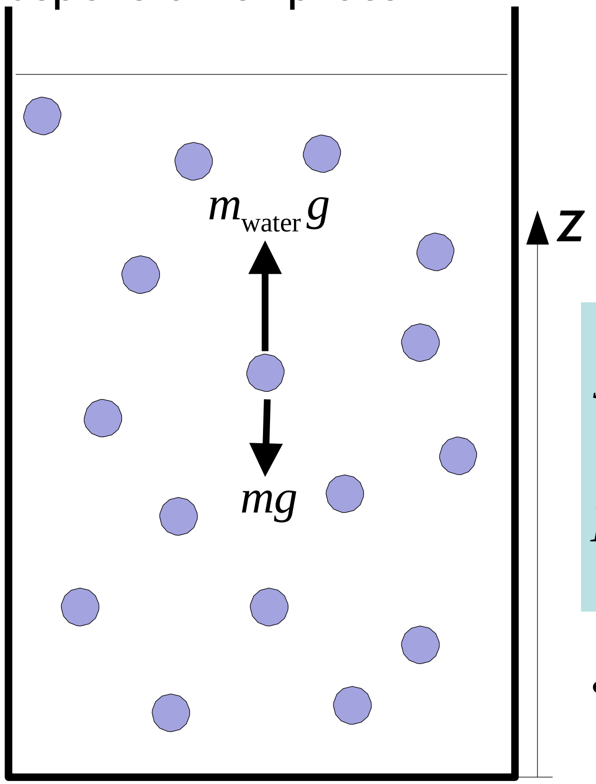
- Viscous friction dominates mechanics in the nanoworld.
- Friction is dissipative: converts ordered motion into thermal energy.
- Implications of symmetry.

- Biological Q: Why don't bacteria swim like fish?
- Physical idea: motion in the nanoworld have different symmetry than motion in the macroworld.

I. Friction in fluids

Small particles can remain in suspension indefinitely

Suspension of protein



Gravity: $mg = \rho V g$

Bouyancy force: $m_{\text{water}} g = \rho_{\text{water}} V g$

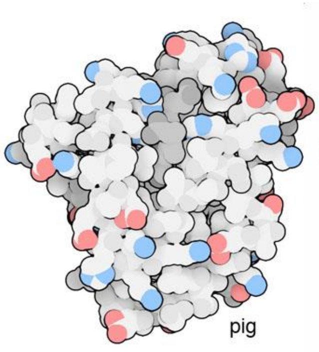
Net force: $m_{\text{net}} \mathrm{g} = \Delta\rho \mathrm{V g}$ (Archimedes' principle)

- What happens after a long time?

$$j = -\mu P \frac{dU}{dx} - D \frac{dP}{dx} = 0 \quad \text{(Smoluchowski's eq. for eqilibrium)}$$

$$P(x) \propto \exp\left[-\frac{m_{\text{net}} g z}{k_B T}\right] \quad \text{(Einstein's relation } k_B T = D/\mu\text{)}$$

- Example: Myoglobin:



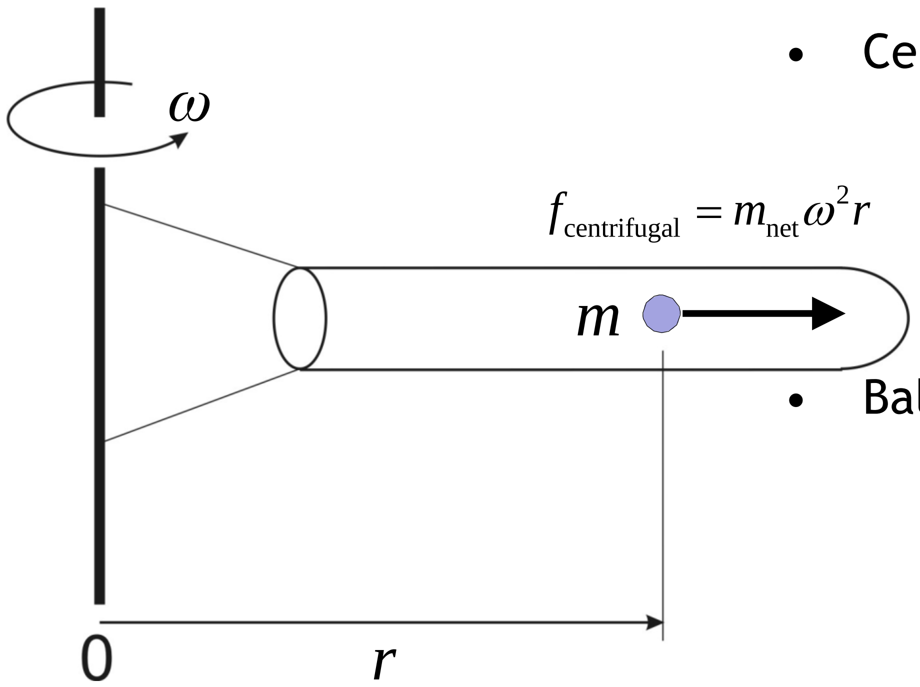
Myoglobin mass: $m = 1.7 \cdot 10^4 \text{ Da} = 2.7 \cdot 10^{-23} \text{ kg}$

net mass: $m_{\text{net}} \approx m/4 = 0.7 \cdot 10^{-20} \text{ kg}$

scale height $z_* = \dfrac{k_B T}{m_{\text{net}} g} = \dfrac{4.2 \cdot 10^{-23}}{0.7 \cdot 10^{-20} \times 10} = 60 \text{ m}$

- Density in test-tube is ~ constant.

Centrifuges can achieve a much higher g



- Centripetal acceleration is by frictional drag:

$$j_v = \mu P \frac{dU}{dr} = \mu f \cdot P(r) = \mu m_{\text{net}} \omega^2 P(r) r$$

- Balanced by diffusion current

$$j_D = -D \frac{dP(r)}{dr}$$

$$j = j_v + j_D = 0 \quad \rightarrow \quad \mu m_{\text{net}} \omega^2 P(r) r - D \frac{dP}{dr} = 0$$

$$P(r) \propto \exp\left(\frac{m_{\text{net}} \omega^2 r^2}{k_B T} \right)$$

- How long does it take to reach equilibrium?

Sedimentation time scale depends on solvent viscosity

- Sedimentation velocity (depends g not intrinsic property)

$$v_{\text{drift}} = \mu m_{\text{net}} g = \frac{m_{\text{net}} g}{\xi}$$

- Sedimentation time scale:

$$\tau = \frac{v_{\text{drift}}}{g} = \mu m_{\text{net}} = \frac{m_{\text{net}}}{\xi}$$

- Unit is Svedberg (10^{-13} sec)

- The sedimentation scale is determined by the size and mass of the particles and the viscosity of the surrounding fluid.

- For a sphere

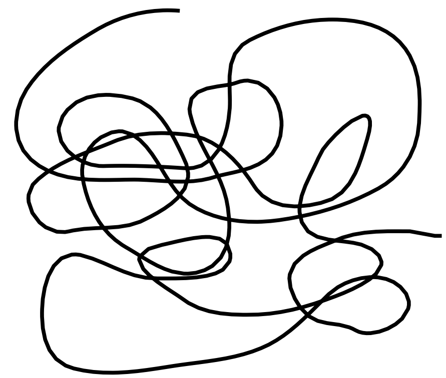
$$\xi = 6\pi\eta R \text{ where } \eta \text{ is the viscosity}$$

- The viscosity of water at room temperature is

$$\eta \approx 10^{-3}\ \text{Pa}\cdot\text{s} = 10^{-2}\ \text{poise}\ \ (\text{erg/cm}^3 \cdot s)$$

Rheology is useful to study macromolecules

- Example: polymer size scaling.
- Assuming random walk



$$R_g \sim m^p$$

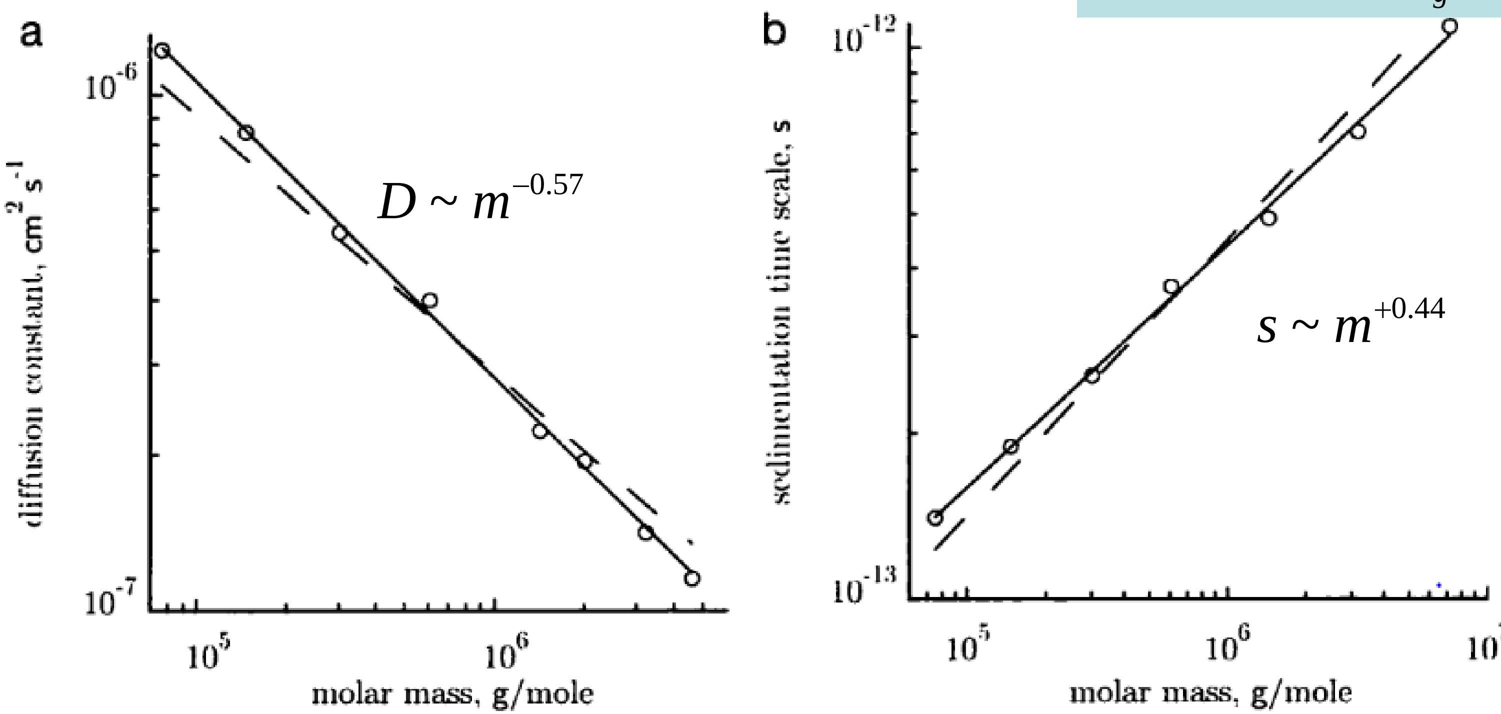
$$m_{\text{net}} \sim m$$

Random walk: $p = 0.5$

Self-avoiding: $p = 0.57$

$$D = \frac{k_B T}{\xi} = \frac{k_B T}{6\pi\eta R_g} \sim m^{-p}$$

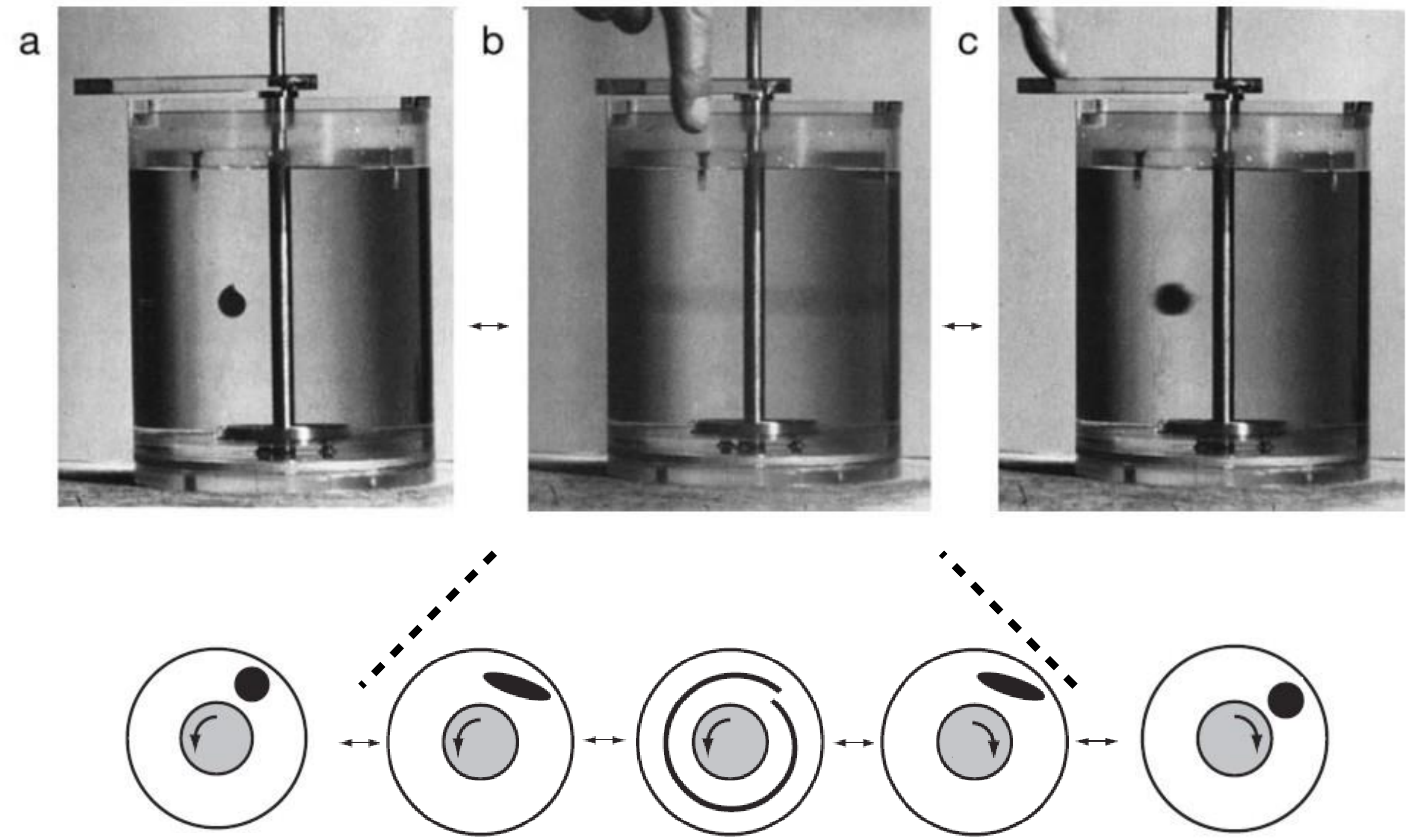
$$s = \frac{m_{\text{net}}}{\xi} = \frac{m_{\text{net}}}{6\pi\eta R_g} \sim \frac{m}{m^p} = m^{1-p}$$



Hard to mix a viscous liquid

- Experiment: ink in glycerin

Slowly…

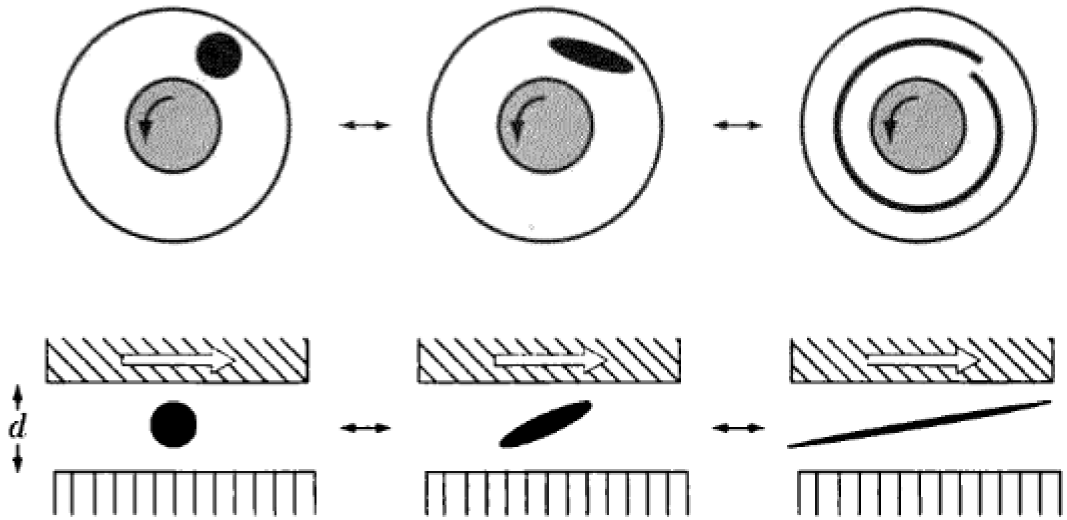


- The clockwise-counterclockwise experiment: blob will smear out but retracing make the blob reassemble into nearly original position and shape!

- That's not what happens when you stir cream into your coffee…

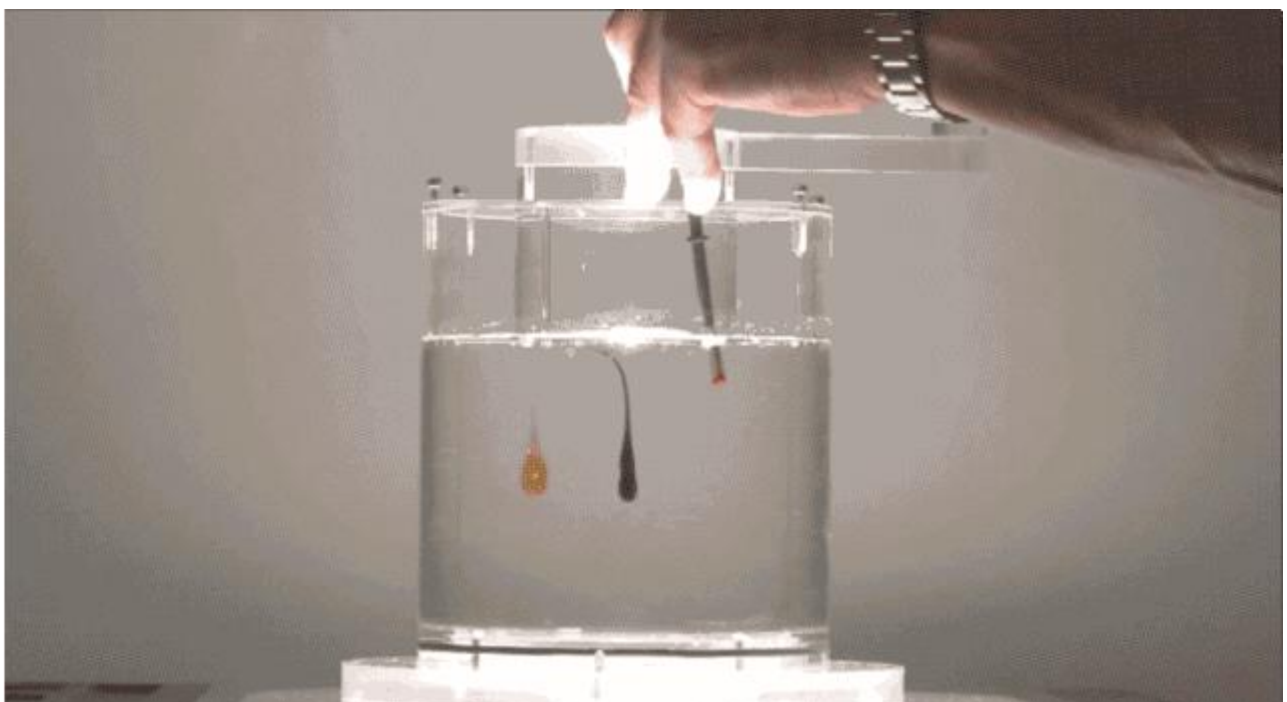
Does reversibility violates 2nd law of TD?

- Ink diffuses but very slowly: $D = \frac{k_B T}{\xi} \propto \frac{k_B T}{\eta}$
- So the blob cannot change much by diffusion $\eta \to \infty \quad \Rightarrow \quad D \to 0.$
- Stirring causes organized motion: fluid layers slide over one another.
- Ink molecules spread out but not randomly (because diffusion is too slow).
- Reversing the wall motion: fluid layers slide back and reassemble the blob.



- Such organized flow is called **laminar**.

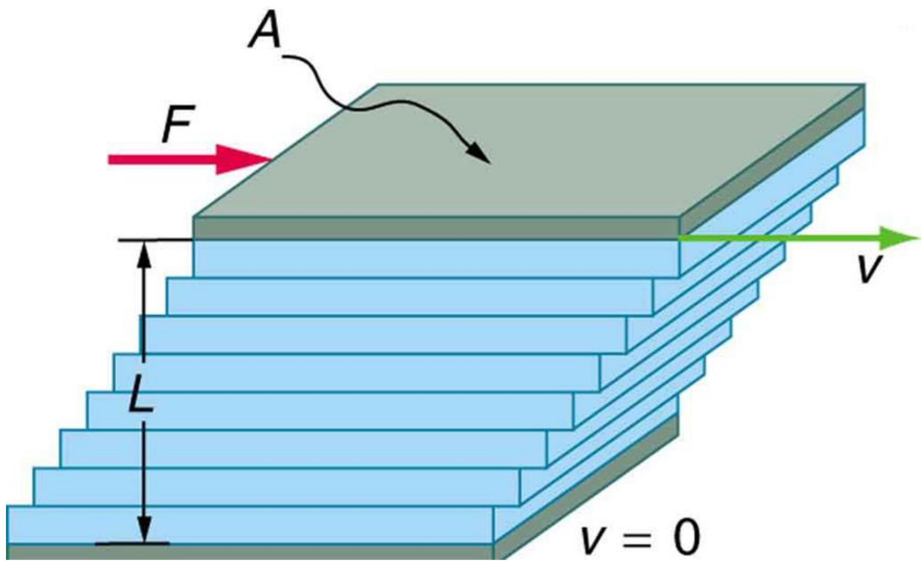
In RGB



II. Low Reynolds-number world

Quantifying the friction-dominated regime (laminar vs. turbulent)

Forces in laminar flow

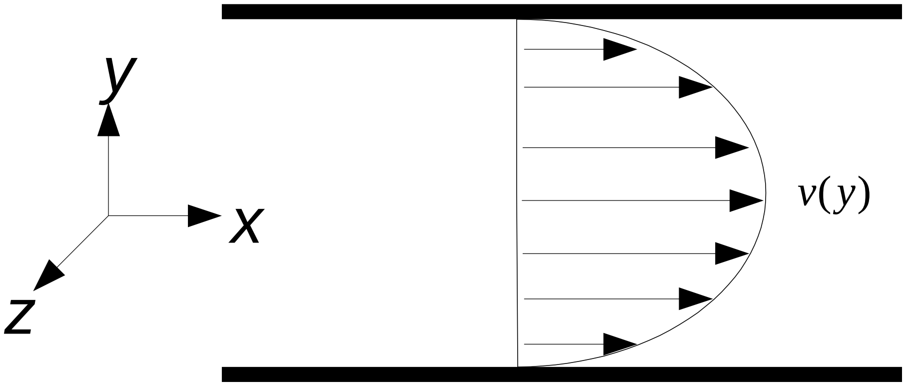


$$f = -\eta v \frac{A}{L}$$

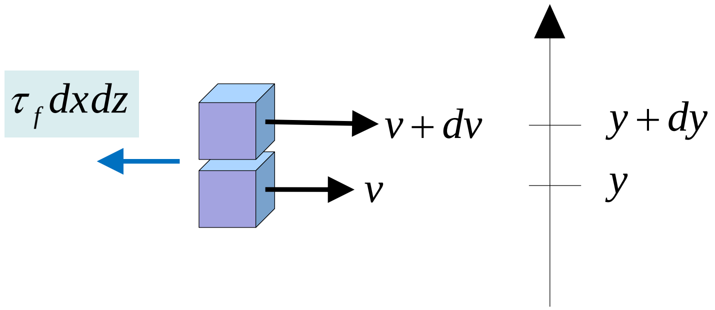
- Shear motion: moving plate feels resisting viscous force

  stationary plate feels opposite force (entraining force).
- Viscous force *f* is proportional to area *A*, and speed *v* but decrease with plate separation.
- Empirically, for small *v*, many fluids follow simple law:

Newtonian fluid



Uniform flow along *x*



Force applied on *y*+*dy* layer by *y* layer

$$\tau_f = -\eta \frac{dv}{dy}$$

(Newtonian viscous formula)

Coefficient of viscosity

Critical force demarcates the friction-dominated regime

- Intuitively, flow is laminar when viscosity η is large and turbulent if η is small. But "small" or "large" w.r.t. what?
- Dimensional analysis for Newtonian fluid:

$$[\eta] = \frac{\text{force}}{\text{velocity x length}} = \frac{M}{LT}; \quad [\rho] = \frac{M}{L^3}$$

- No dimensionless quantity from η and ρ.
- But we can make a **characteristic quantity**.

$$f_{\text{crit}} = \frac{\eta^2}{\rho} \quad \text{critical viscous force}$$

→ no intrinsic length scale: cannot tell "thick" from "thin" fluids.

Newtonian fluid is scale invariant.

- Situation dependent: fluid motion is viscous if

$$f < f_{\text{crit}} = \frac{\eta^2}{\rho}.$$

Aquatic cellular environment is viscous

- For macroscopic bodies and forces water is turbulent.
- For pN forces in the cell, water is viscous…

fluid	ρ_m, kg m^{-3}	η, Pa s	f_{crit}, N
air	1	$2 \cdot 10^{-5}$	$4 \cdot 10^{-10}$
water	1000	0.0009	$8 \cdot 10^{-10}$
olive oil	900	0.08	$7 \cdot 10^{-6}$
glycerine	1300	1	0.0008
corn syrup	1000	5	0.03

- For $f < f_{crit}$, fluid is thick: friction quickly damps out inertial effects. Flow is dominated by friction.

The Reynolds number quantifies the relative importance of friction and inertia

Flow past a sphere:

- Velocity changes direction during $\Delta t \sim R / v$.

$\rightarrow$ Acceleration magnitude $a \sim v / \Delta t \sim v^2 / R$

- Newton's law $f_{\text{ext}} + f_{\text{frict}} = f_{\text{tot}} = ma$

(f_{ext} is by fluid pressure)

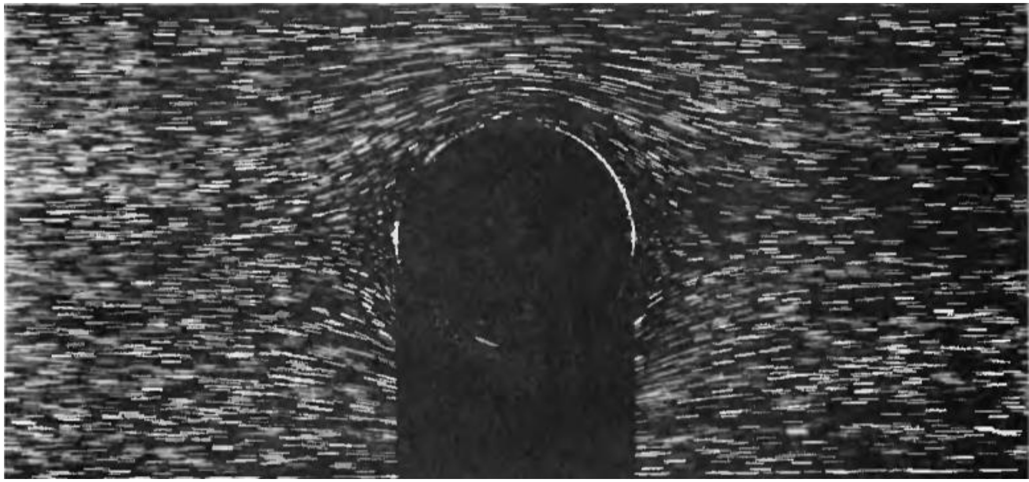
- $f_{\text{inertia}} = ma = \rho l^3 \dfrac{v^2}{R}$
- friction force: $\dfrac{f}{A} = -\eta \dfrac{dv}{dx}$

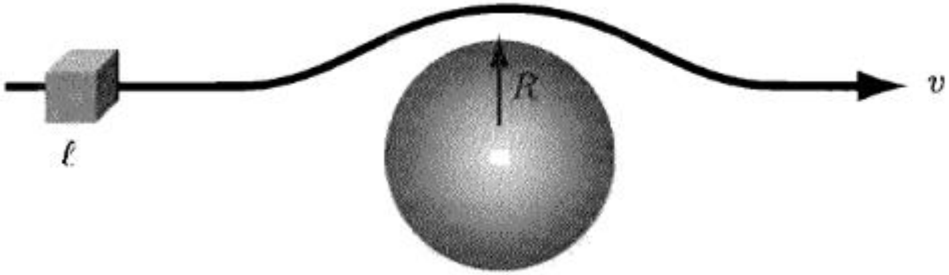
- Net force on fluid: $\Delta f = f(x_0 + l) - f(x_0)$

$$f_{friction} = \Delta f \sim l \frac{df}{dx} = \eta A l \frac{d^2 v}{dx^2} = \eta l^3 \frac{v}{R^2}$$

Reynolds number

$$\Re = \frac{f_{\text{inertia}}}{f_{\text{friction}}} = \frac{\rho l^3 v^2 / R}{\eta l^3 v / R^2} = \frac{\rho v R}{\eta}$$

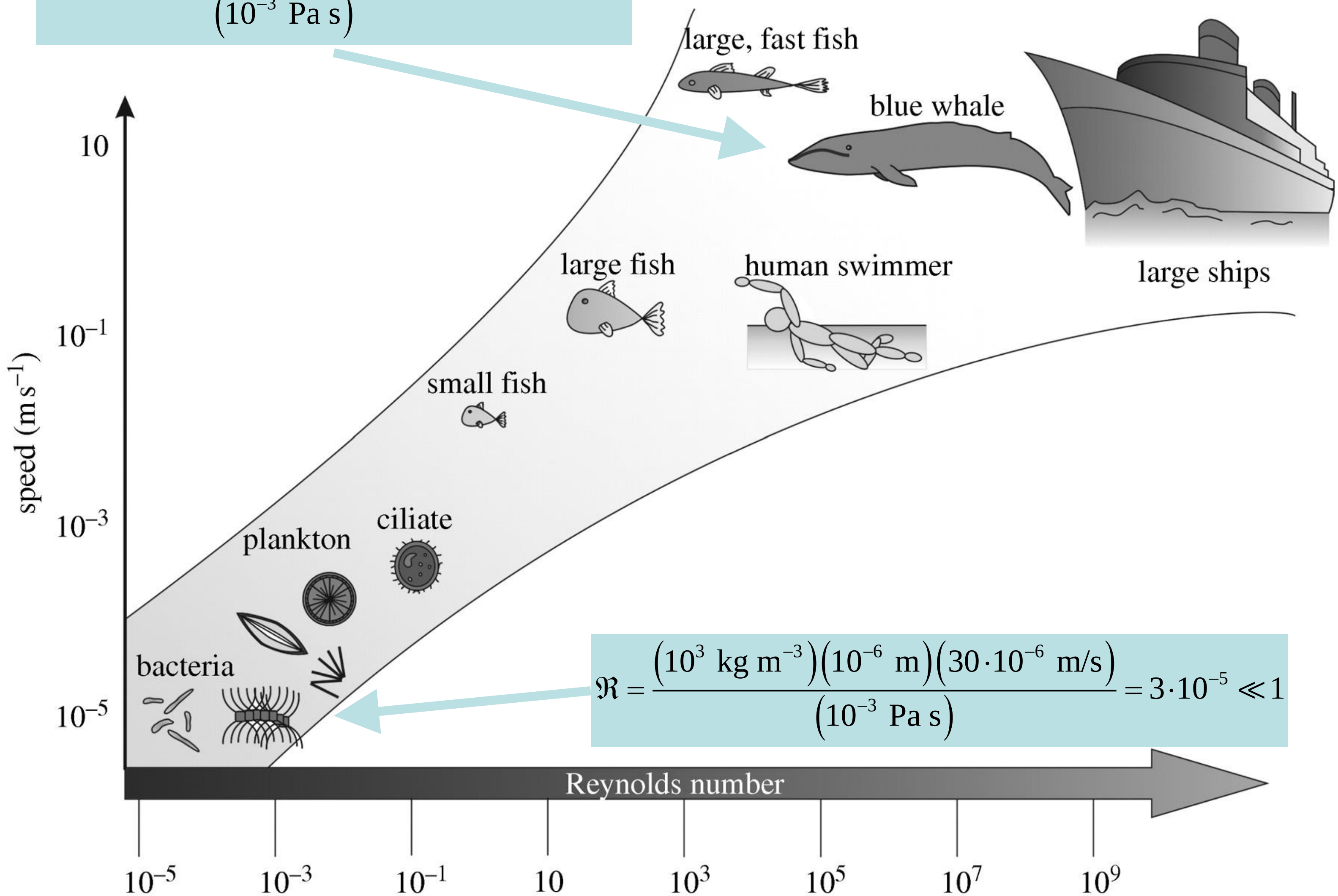




- Small Re: friction dominates; flow stops immediately when force stops ("creeping flow“).
- Big Re: inertial effects dominate, coffee keeps swirling; flow is turbulent.

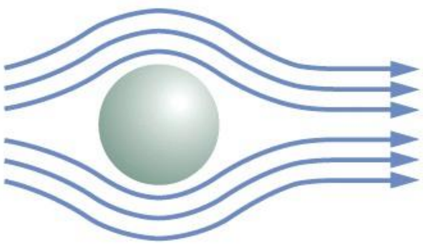
Microbiology is viscous (low Re)

$$\Re = \frac{\left(10^3 \text{ kg m}^{-3}\right)\left(30 \text{ m}\right)\left(10 \text{ m/s}\right)}{\left(10^{-3} \text{ Pa s}\right)} = 3 \cdot 10^8 \gg 1$$

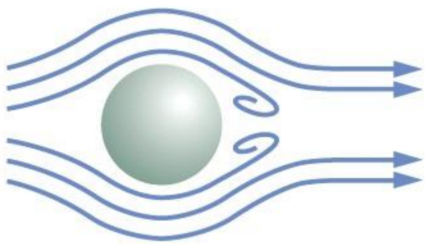


$$\Re = \frac{\left(10^3 \text{ kg m}^{-3}\right)\left(10^{-6} \text{ m}\right)\left(30 \cdot 10^{-6} \text{ m/s}\right)}{\left(10^{-3} \text{ Pa s}\right)} = 3 \cdot 10^{-5} \ll 1$$

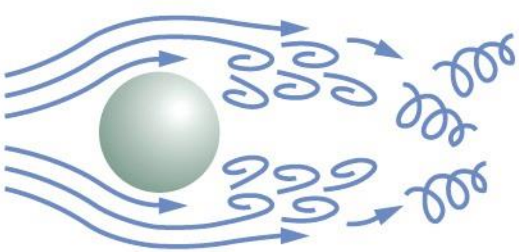
Tuning Re



Re < 10
Laminar flow



Re 10–40
Vortices form and are maintained



Re 40–20,000
Vortices form and are periodically shed

- Australian Pitch drop experiment running from **1927**

- Viscosity ~ 10^{12} of water

Time-reversal properties of a dynamical law signal its dissipative character

- Sheets move uniformly $\rightarrow$ forces balance out:

$$\frac{dv}{dx} = \text{const.} \;\rightarrow\; v = \frac{x}{d} v_0$$

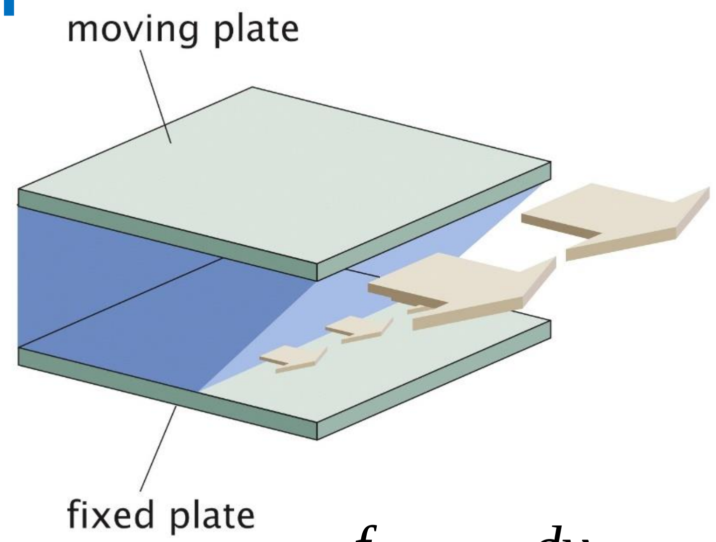
- Time depndent motion: $f \ll f_{\text{crit}} \rightarrow f_{\text{inertia}}$ negligible

$$v(x,t) = \frac{x}{d} v_0(t)$$

- Unmixing:

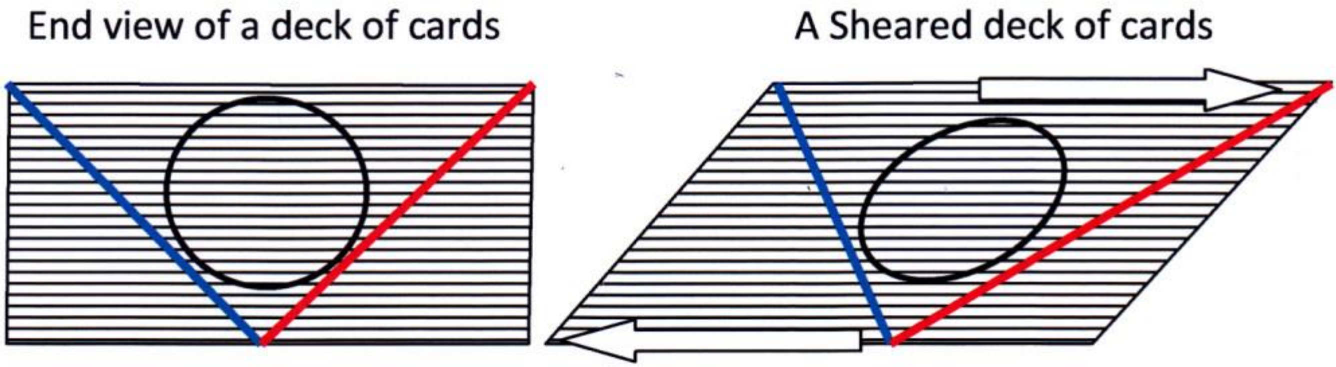
$$v_0 : \quad (x,y,z) \rightarrow \left(x + \frac{x}{d} v_0 t, y, z \right)$$

$$-v_0 : \quad \left(x + \frac{x}{d} v_0 t, y, z \right) \rightarrow \left(x + \frac{x}{d} v_0 t - \frac{x}{d} v_0 t, y, z \right) = (x,y,z)$$



friction force: $\dfrac{f}{A} = -\eta \dfrac{dv}{dx}$

- Once the top plate has returned to its initial position, each fluid element has also returned, regardless of the dynamics of the return stroke.



Time reversal: Newtonian mechanics

$$m\frac{dz^2}{dt^2} = f = -\frac{dU}{dz} = -mg$$

$$\begin{tikzcd}
\frac{dz^2}{dt^2} = -g \arrow[r, "\text{solution}"] \arrow[d, "="'] \arrow[dr, "\text{solution}"] & z(t) = v_0 t - \frac{1}{2} g t^2 \arrow[d] \\
\frac{dz^2}{dt^2} = -g \arrow[r, "\text{solution}"] & z(t) = -v_0 t - \frac{1}{2} g t^2
\end{tikzcd}$$

Time reversal:
$t \to -t$

- In Newtonian physics, the time-reversed process is a solution to the equations of motion with the ***same sign of force*** as the original motion.

- Time-reversed trajectory solves Newton's law with inverse v_0.

Time reversal: Diffusion

$$\frac{dc}{dt} = D\frac{d^2c}{dx^2} \xrightarrow{\text{solution}} c(x,t) = \frac{1}{\sqrt{4Dt}}\exp\left(-\frac{x^2}{4Dt}\right)$$

$\neq$

no solution

Time reversal:

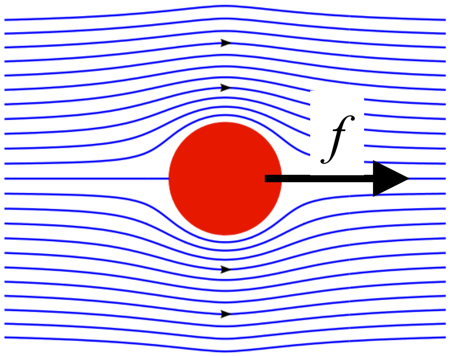
$t \rightarrow -t$

$$-\frac{dc}{dt} = D\frac{d^2c}{dx^2} \xrightarrow{\text{solution}} c(x,t) = \frac{1}{i\sqrt{4Dt}}\exp\left(-\frac{x^2}{4Dt}\right)$$

- Diffusion equation is not time invariant.
- Time-reversed solution does not solve original diffusion equation.

Viscous friction is not time reversal invariant

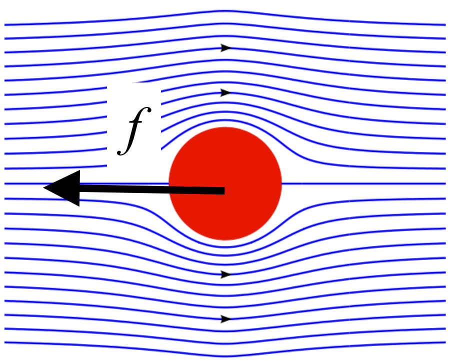
A ball in highly viscous fluid



$$\frac{dz}{dt} = \frac{f}{\xi}$$

solution:

$$z = z_0 + \frac{f}{\xi} t$$



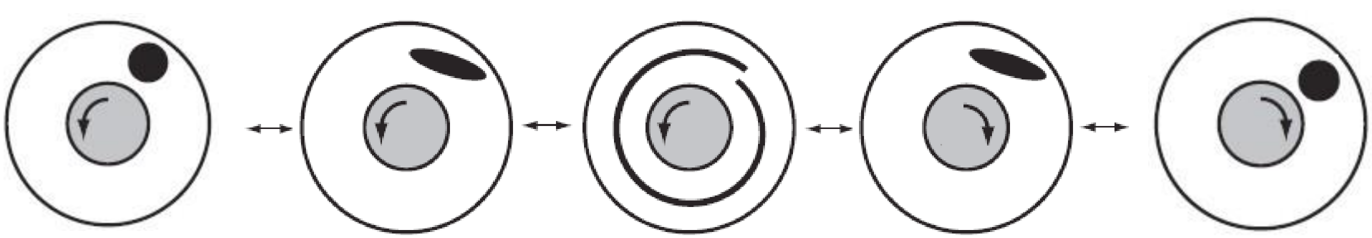
$$-\frac{dz}{dt} = \frac{f}{\xi}$$

solution:

$$z = z_0 - \frac{f}{\xi} t$$

Time-reversed solution does not solve original friction equation, unless ***force is inversed***

Frictional motion is irreversible because friction dissipates ordered motion into heat.



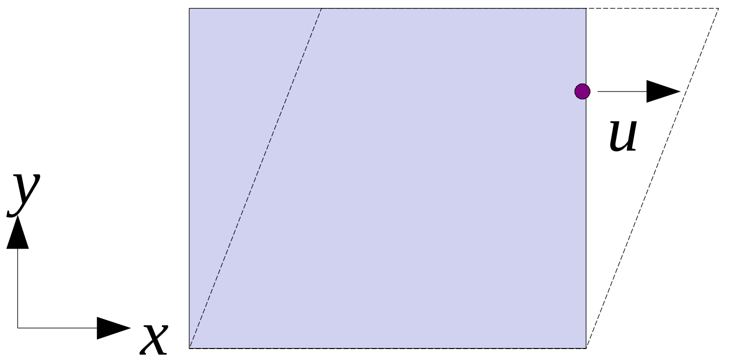
?

Fluids and solids differ in time-reversal symmetry

$$\frac{f}{A} = G\frac{du}{dy}$$

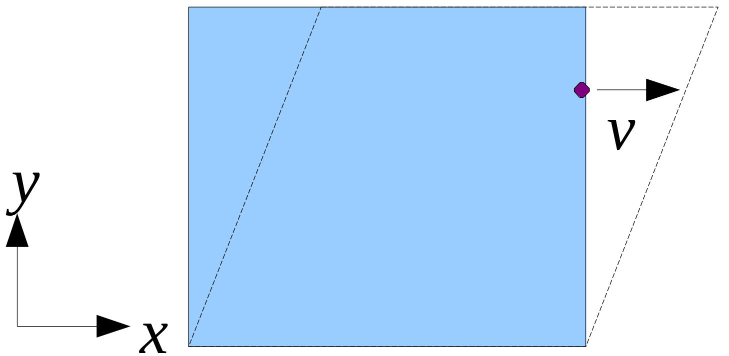
- No explicit time dependence: invariant.

(displacement)



- Solids have “memory” of position.

$$\frac{f}{A} = \eta\frac{d}{dy}\left(\frac{du}{dt}\right)$$



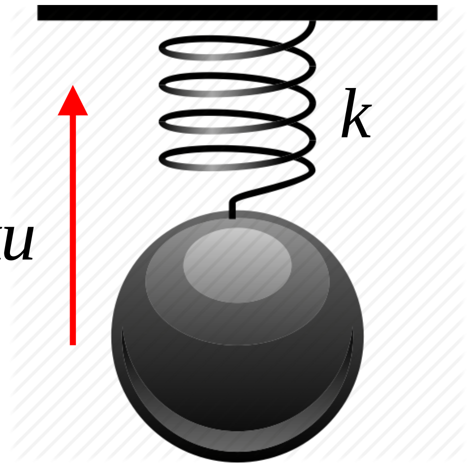
- Not invariant.

Fluids and solids differ in time-reversal symmetry

$$m\frac{d^2u}{dt^2} = -ku$$

- 2^{nd} order time derivative: invariant.

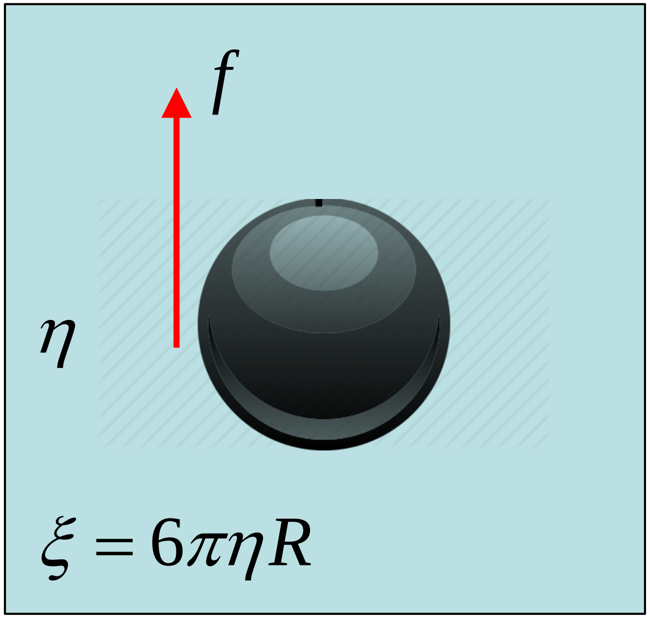
$$f = -ku$$



- Solids have “memory” of position.

$$\frac{du}{dt} = \frac{f}{\xi}$$

- 1^{st} order time derivative: Not invariant.



Viscous flow have other symmetry properties

Stokes flow:

$$\nabla p = \eta \nabla^2 v$$

The reversed flow with

$$v \to -v \qquad p \to -p$$

obeys the same equation.

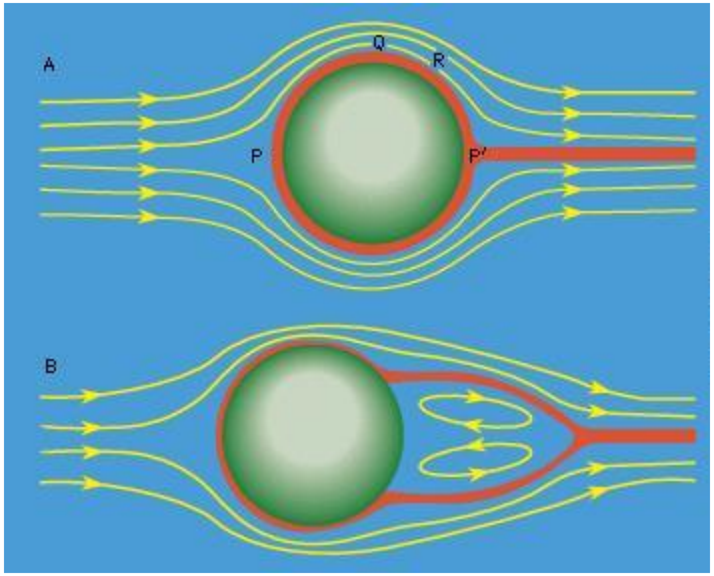
Low Re flow around a stationary object having a plane of symmetry is symmetric.

Proof: Symmetry plane $x = 0$.

- Flow reversal: $v(x, y, z) \to -v(x, y, z)$.
- Mirror symmetry:

$$v_x(x, y, z) \to -v_x(-x, y, z) = -v_x(x, y, z)$$

$$v_{y,z}(x, y, z) \to v_{y,z}(-x, y, z) = -v_{y,z}(x, y, z)$$

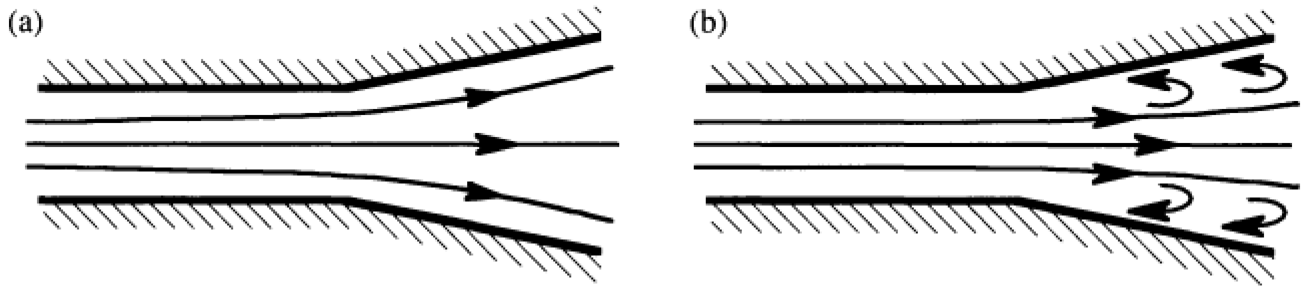


- Sensitive test for small Re flows

upon reversal, fluid follows the identical streamlines in the opposite direction.

Stokes flow:

$$\nabla p = \eta \nabla^2 v$$



- In low Re we can blow out a candle either by blowing or suction.
- In high Re, we cannot blow out a candle by suction

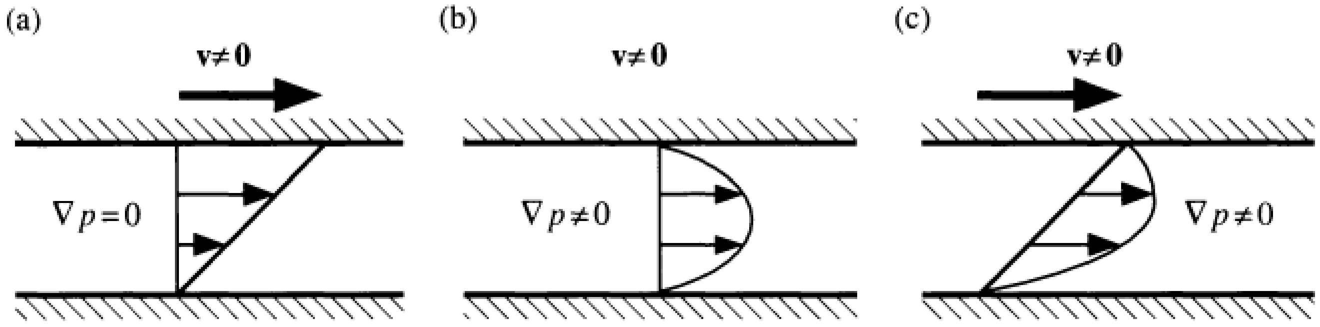
Streamlines are invariant to rate of flow

Stokes flow:

$$\nabla p = \eta \nabla^2 v$$

$$\nabla(\lambda p) = \eta \nabla^2 (\lambda v)$$

- Follows form linearity of the flow.
- No notion of explicit time.



$v_1(r,t)$ and $v_2(r,t)$ solutions

$\rightarrow \lambda_1 v_1 + \lambda_2 v_2$ is also a solution

with $\nabla p = \lambda_1 \nabla p_1 + \lambda_2 \nabla p_2$

III. Biological applications

Swimming and pumping

- In the low Re world: a motion can be canceled completely by applying minus the time-reversed force. What are the implications for microorganisms?
- Flapping back and forth returns every fluid element to its original position:

No net motion!

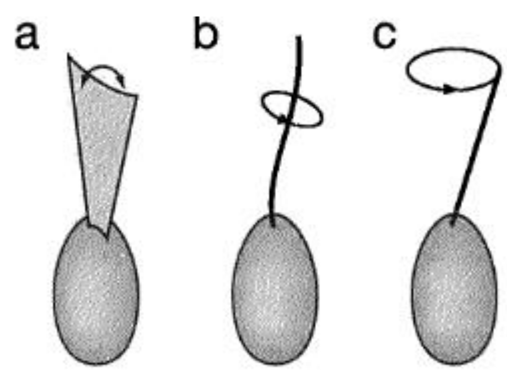
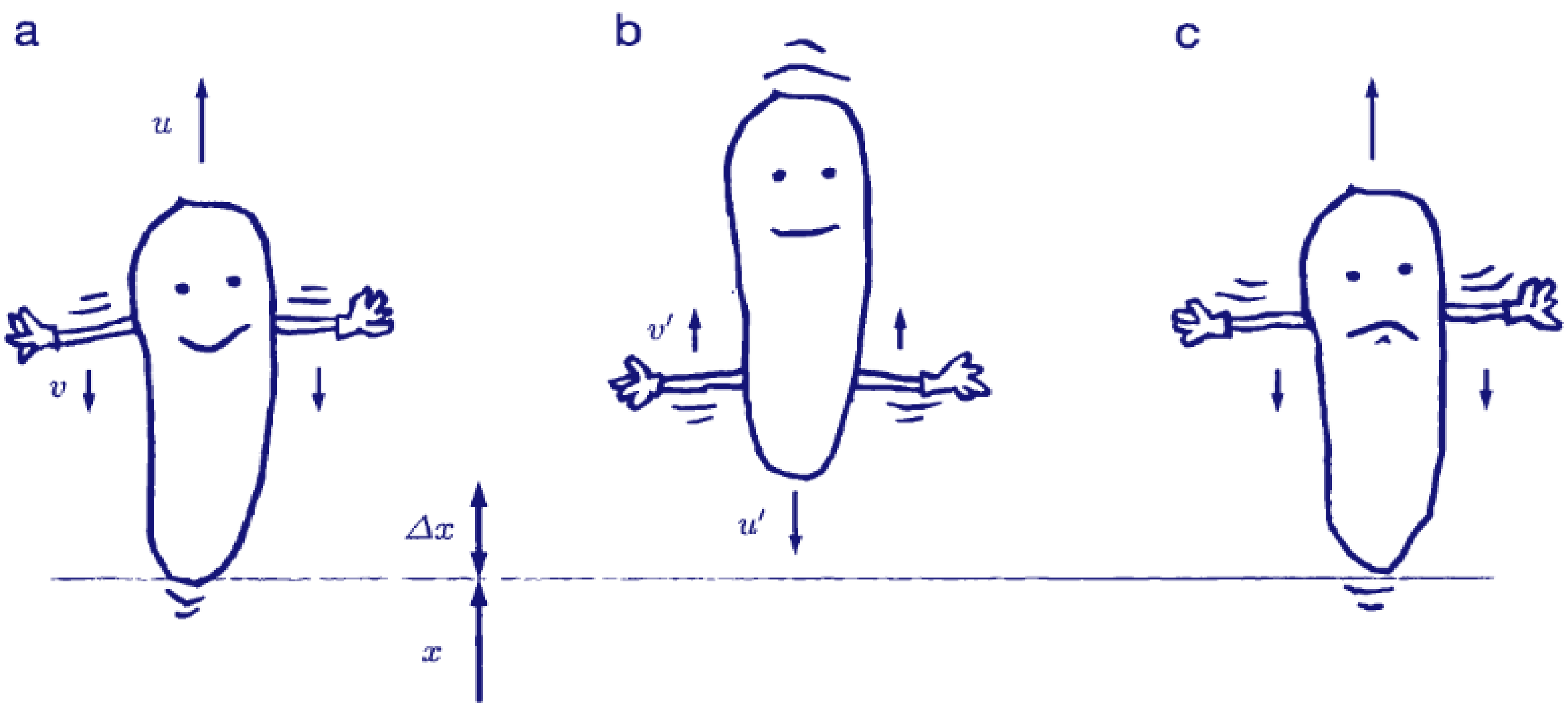


Figure 5.5: (Schematic.) Three swimmers. (a) The flapper makes reciprocal motion. (b) The twirler cranks a stiff helical rod. (c) The spinner swings a stiff, straight rod.

Swimming of microorganisms: reciprocal motion



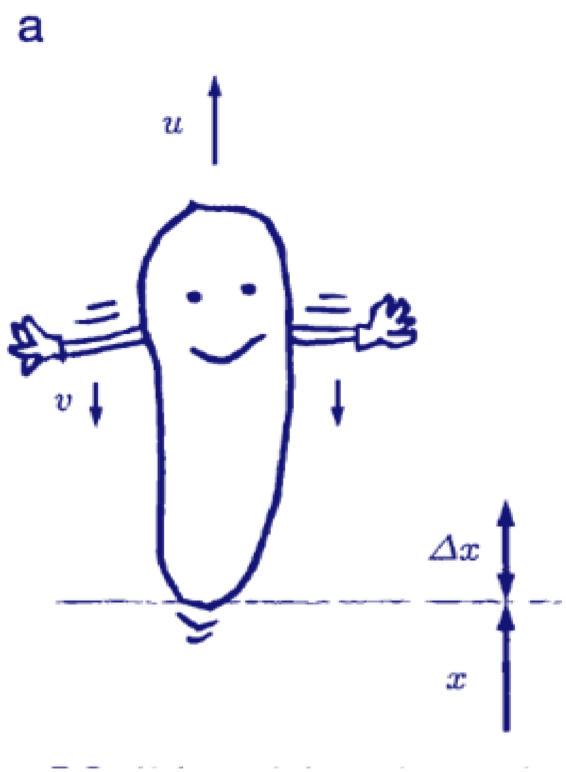
a. paddles move backward at speed v relative to the body → forward motion of the body at speed u relative to water.

b. paddles move forward at v' relative to the body → backward motion of body at u' relative to water.

c. Repeat…

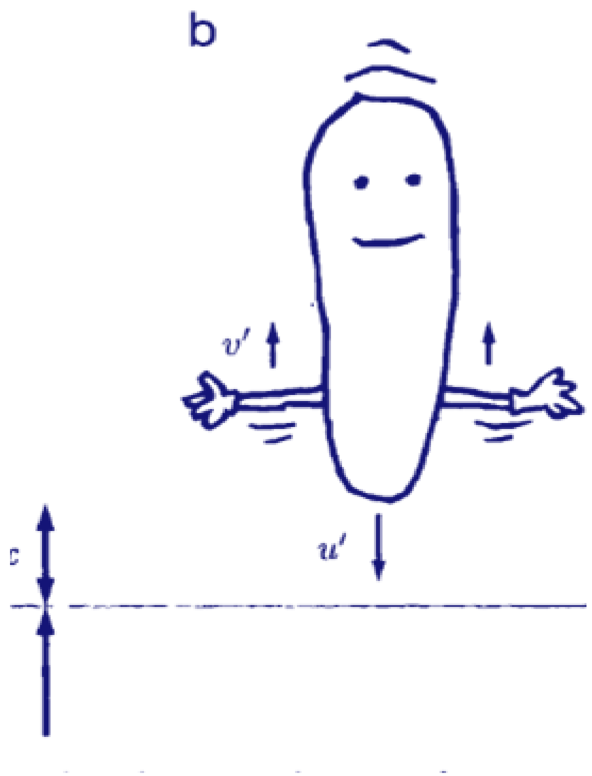
Any net motion?

[Cartoon by Jun Zhang.]



- relative velocity of paddles w.r.t. fluid: $v-u$
- drage force on paddles: $f_{\text{paddle}} = \xi_p (v-u)$
- drag force on body: $f_b = \xi_b u$
- force balance: $f_p = f_b$
- body velocity: $u = v \dfrac{\xi_p}{\xi_b + \xi_p}$

Total displacement: $\Delta x = ut = vt \dfrac{\xi_p}{\xi_b + \xi_p}$



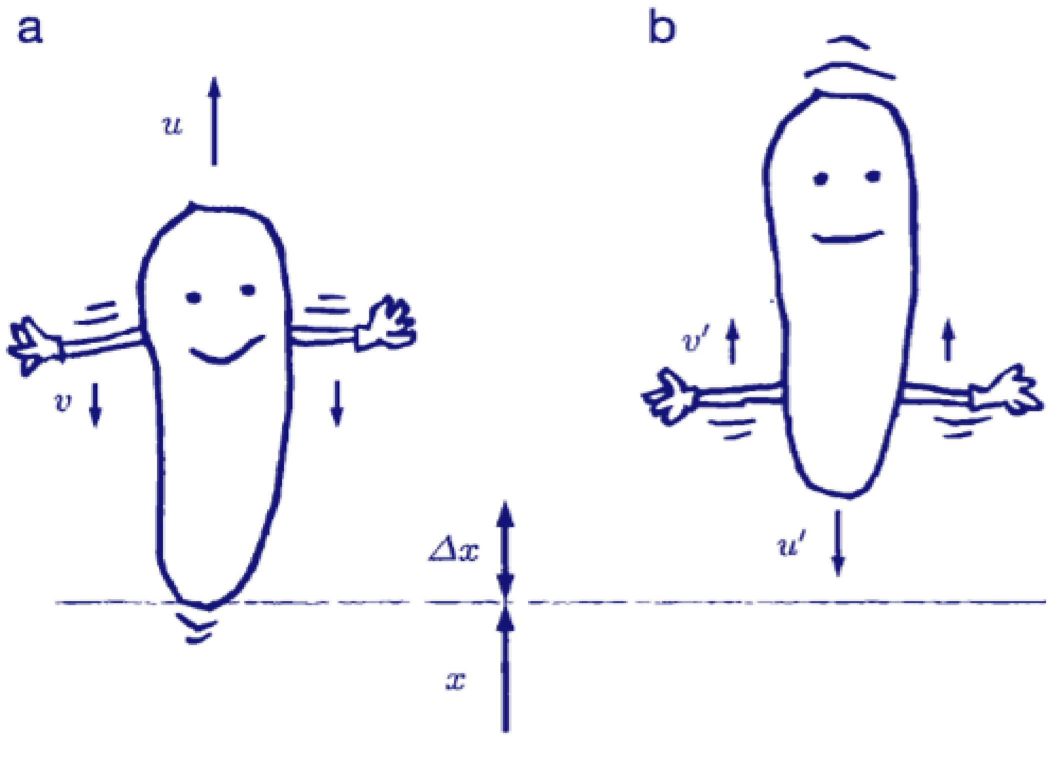
- Similarly: relative velocity of paddles w.r.t. fluid: $v' - u'$

- drage force on paddles: $f_{\text{paddle}} = \xi_p (v' - u')$

- drag force on body: $f_b = \xi_b u'$

- body velocity: $u' = v' \dfrac{\xi_p}{\xi_b + \xi_p}$

Total displacement: $\Delta x' = u't' = v't' \dfrac{\xi_p}{\xi_b + \xi_p}$



- In reciprocal motion the paddles return to their original position:

$$vt = v't'$$

- Hence:

$$\Delta x' = u't' = v't' \frac{\xi_p}{\xi_b + \xi_p} = vt \frac{\xi_p}{\xi_b + \xi_p} = ut = \Delta x$$

NO NET MOTION!

Scallop theorem forbids strictly reciprocal motion

- **Scallop theorem:**

  Strictly reciprocating motion won't work for swimming in the low-Reynolds world [Purcell (1977) Am. J. Phys.]

Navier - Stokes:

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

If $R \ll 1$:

Time doesn't matter. The pattern of motion is the same, whether slow or fast, whether forward or backward in time.

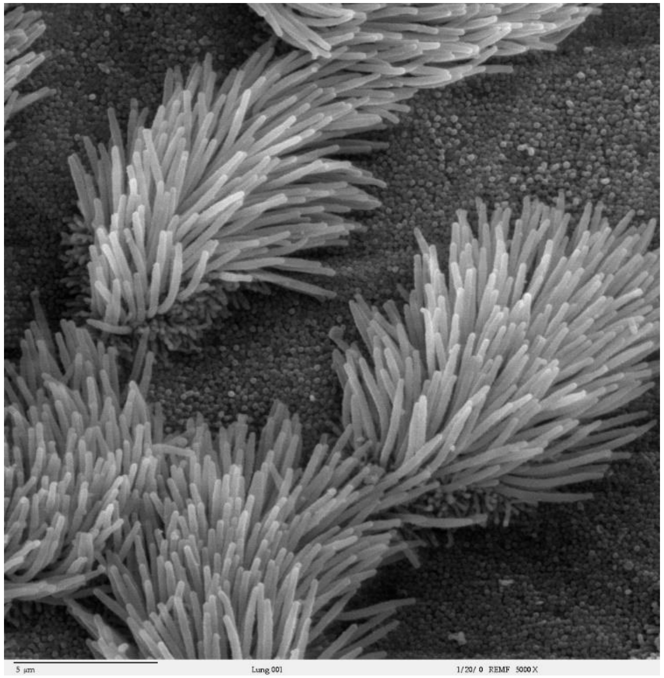
The Scallop Theorem

What other options a microorganism has?

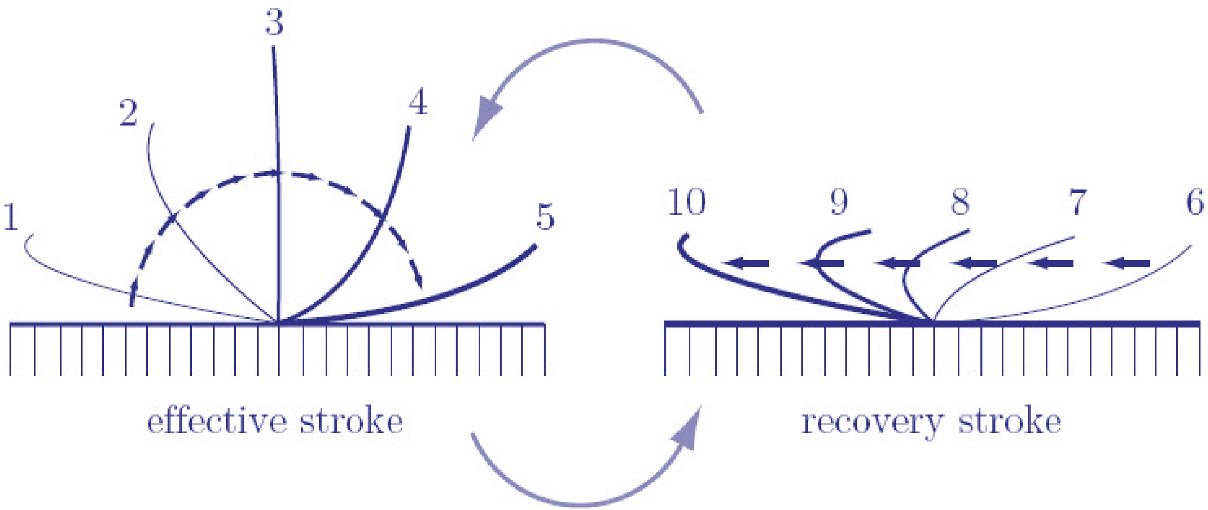
Motion must be periodic (to be repeated).

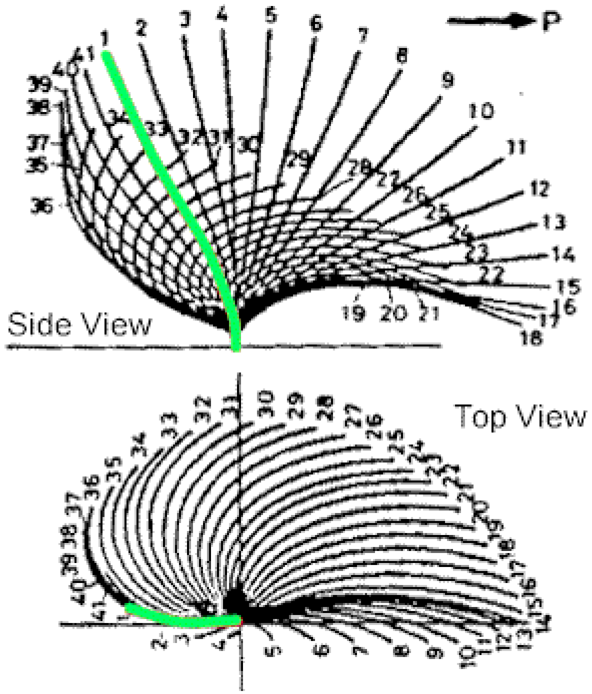
It can't be of the reciprocal.

Ciliary propulsion is periodic not reciprocal



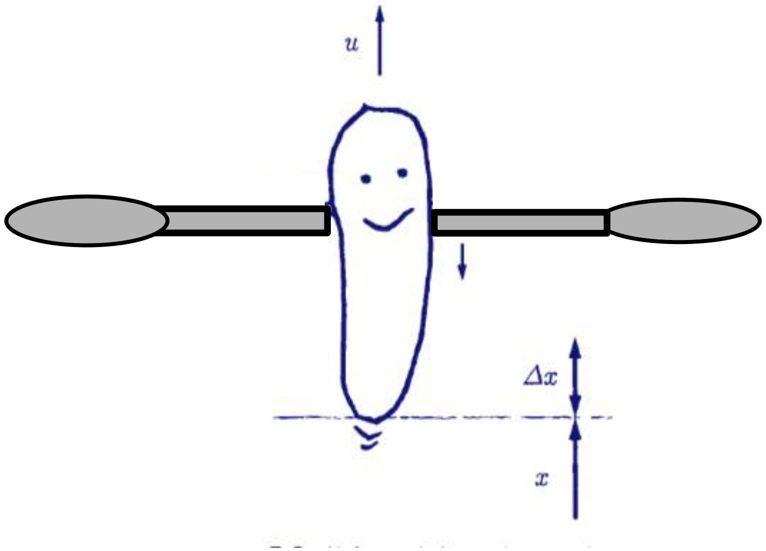
- Many cells use cilia to generate net thrust.
- Each cilium contains internal filaments and motors.
- Cilia can be used for translocation and pumping (in stationary cells).

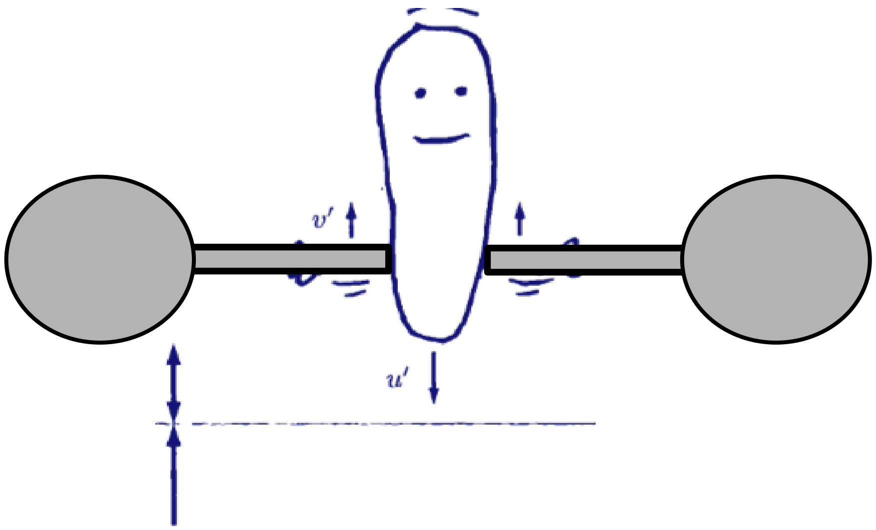




- The difference is in the additional degrees of freedom.

Net motion requires breaking the back and forth symmetry





Large drag in forward motion.

Displacement:

$$\Delta x = ut = vt\frac{\xi_p}{\xi_b + \xi_p} = \frac{vt}{1 + \xi_b / \xi_p}$$

Smaller drag in backward motion: $\xi'_p < \xi_p$

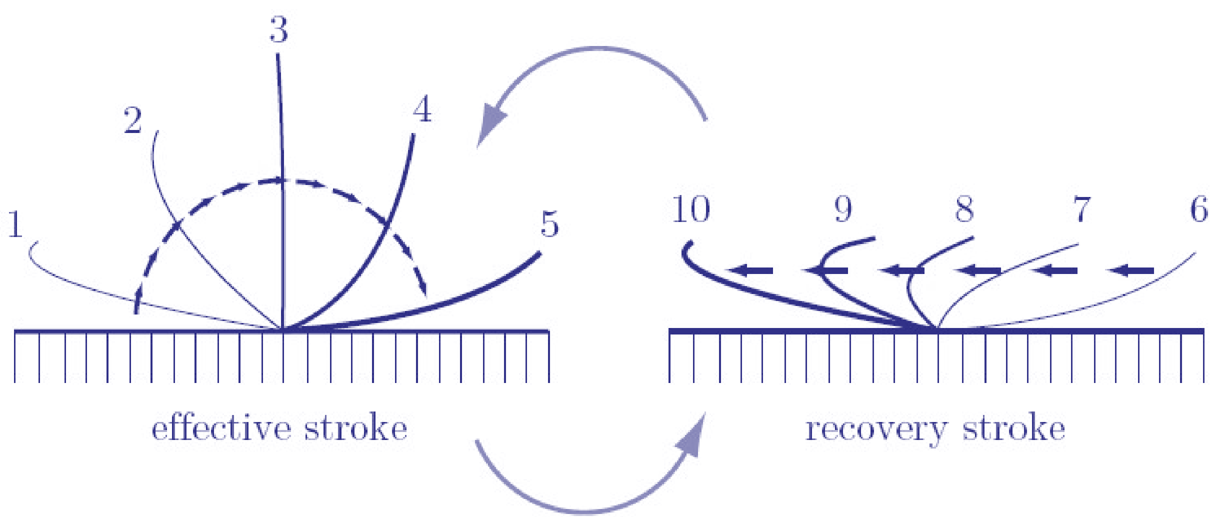
Displacement:

$$\Delta x' = u't' = v't'\frac{\xi'_p}{\xi_b + \xi'_p} = \frac{v't'}{1 + \xi_b / \xi'_p}$$

Total displacement:

$$\Delta x' - \Delta x = \frac{vt}{1 + \xi_b / \xi_p} - \frac{v't'}{1 + \xi_b / \xi'_p} = vt\frac{\xi_b\left(\xi_p - \xi'_p\right)}{\left(\xi_b + \xi_p\right)\left(\xi_b + \xi'_p\right)} > 0$$

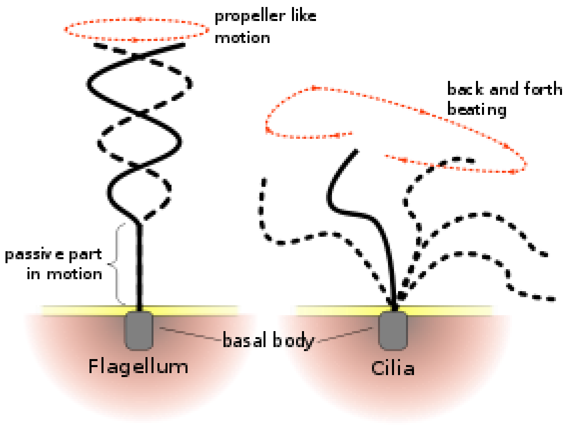
Cilia break symmetry by changing the direction of motion

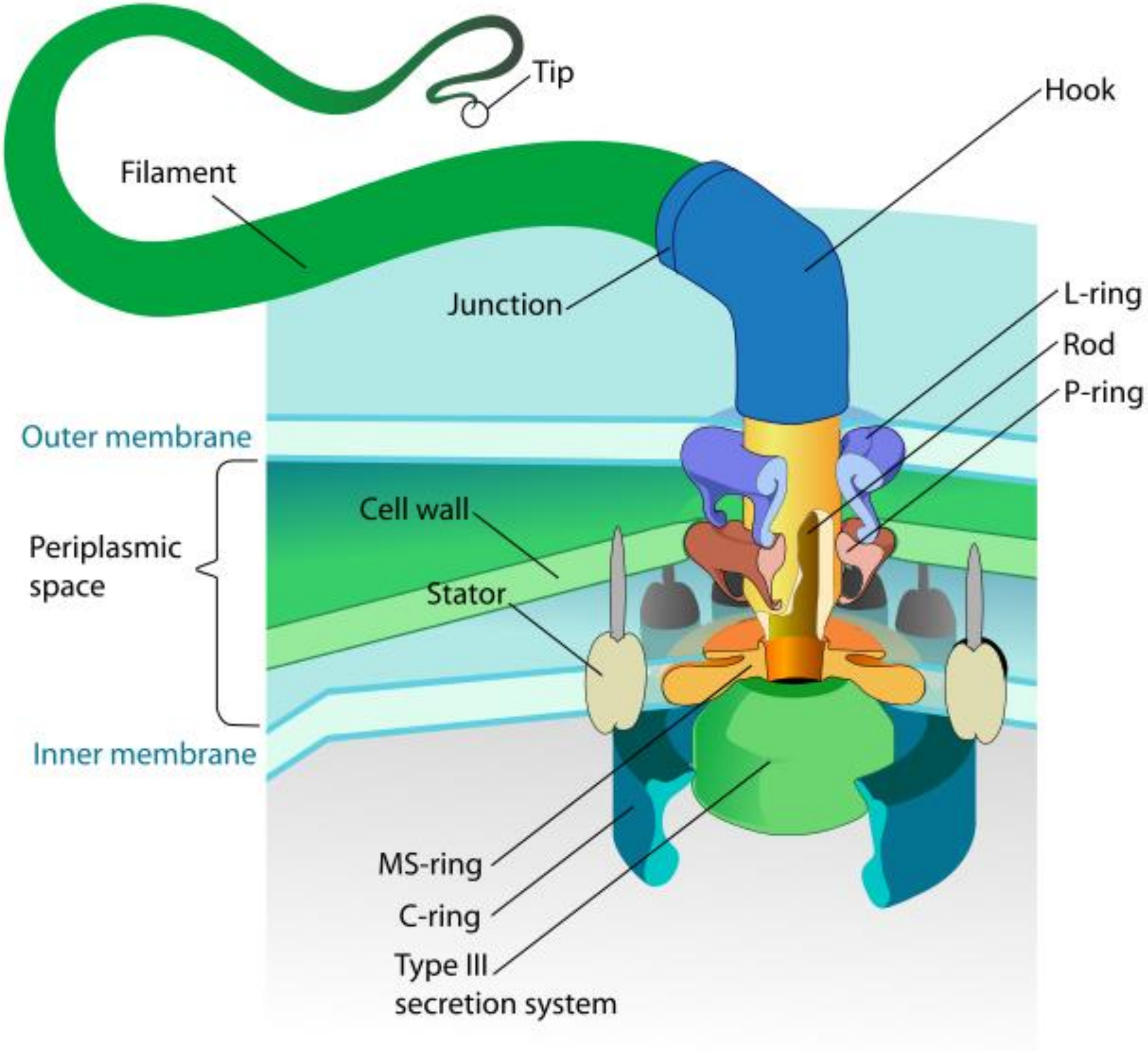


- Effective stroke: high drag (perpendicular)
- Recovery stroke: low drag (parallel)

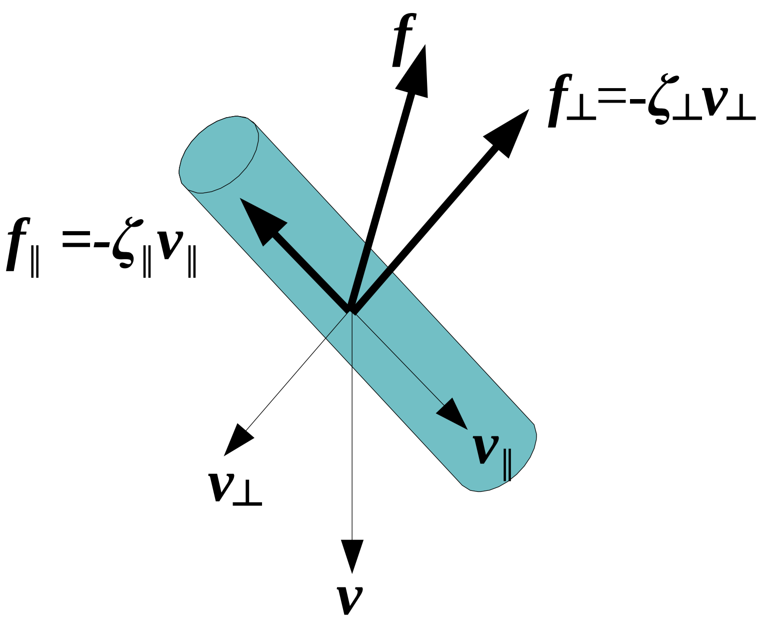
Figure 7: Flagellar movements that propel Chlamydomonas forward - up [6].

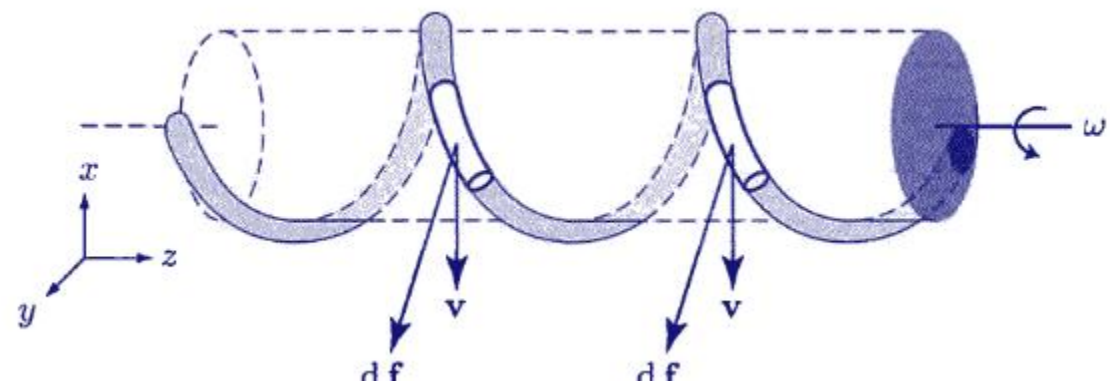
Bacteria use rotating flagella for locomotion





Flagella break shape symmetry for locomotion





$$\xi_\perp > \xi_\parallel$$

$$\rightarrow f = f_\perp + f_\parallel = \xi_\perp v_\perp + \xi_\parallel v_\parallel$$

f not parallel to v

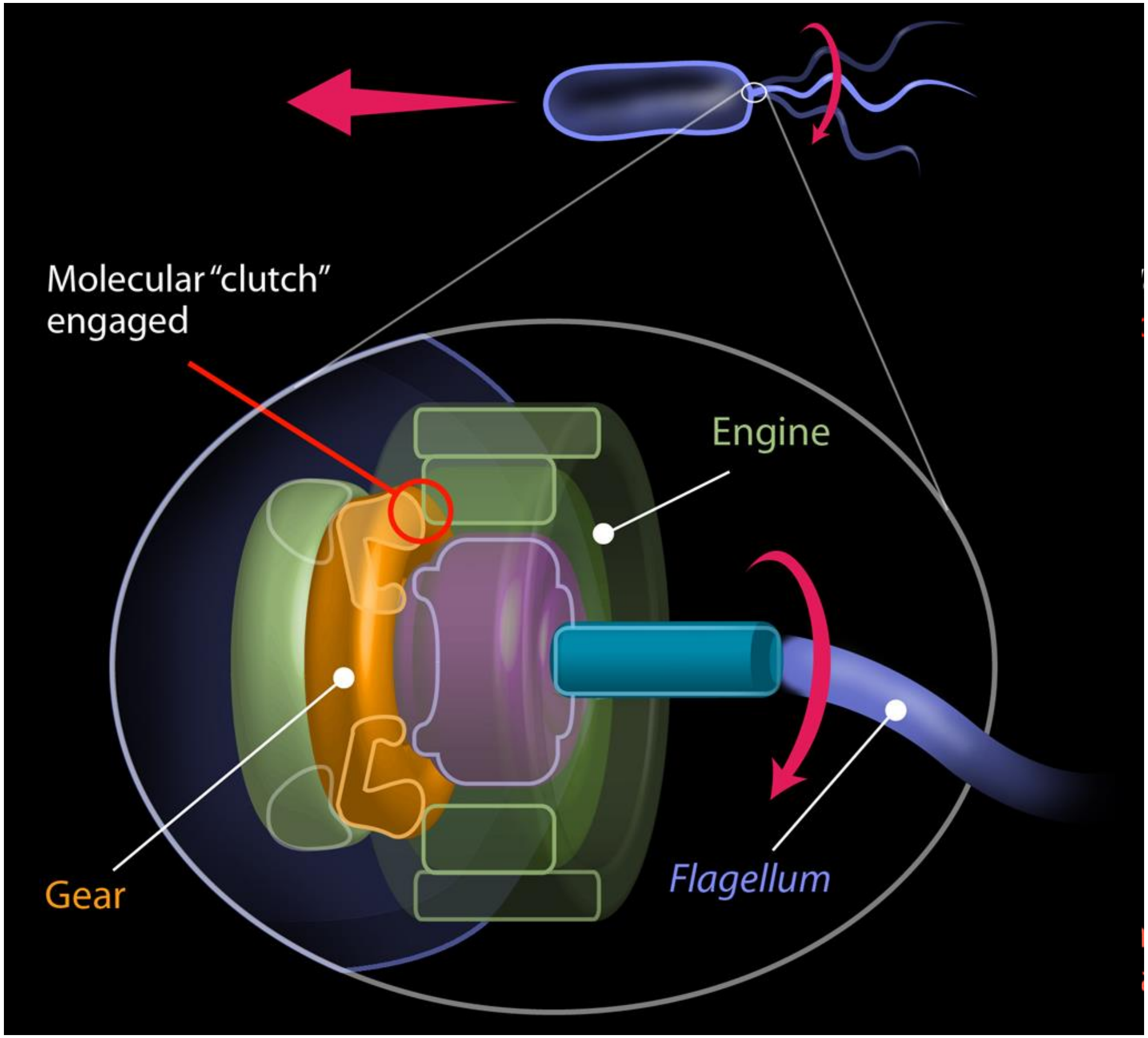
- The drag coefficients parallel and perpendicular to the cylinder (helix) are not equal.

→ Although the velocity is in y-x plane, there is a z-component of the force.

→ The net force on the helix is in z direction.

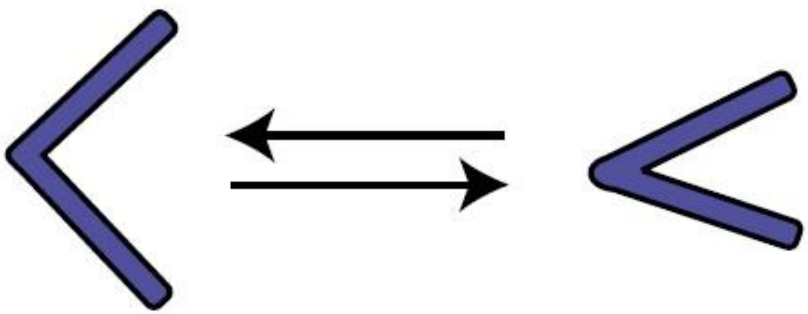
How bacteria avoid rotating by torque?

- Bacteria are large enough such that friction slows down rotation
- Bacteria may also have pairs of flagella rotating in opposite directions.



Two coupled scallops can move

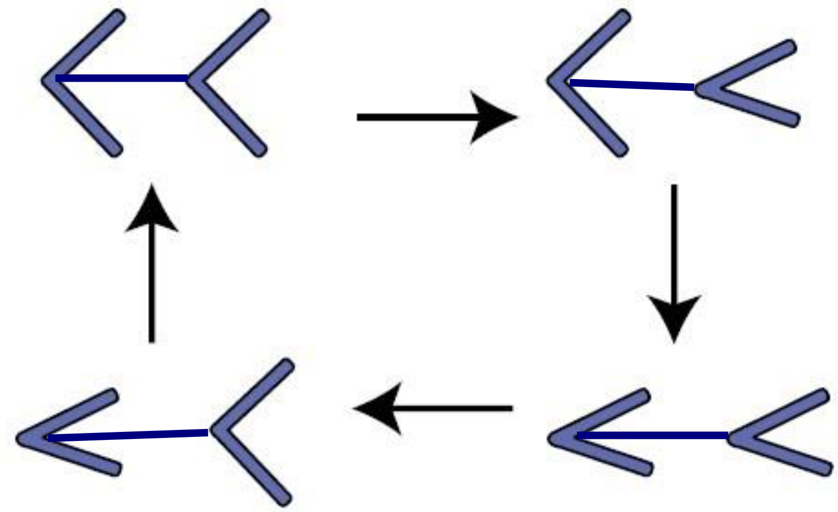
Single pair of paddles



Strictly reciprocal

→ No net motion

Dimer of 2 pairs of paddles



Single pair: strictly reciprocal

Dimer: nonreciprocal

→ Net motion!

[Lauga and Bartolo (2008) PRE]

Why should bacteria move and stir?

- Eating? It's anyhow hard to mix:

-- Only a few streamlines reach a moving object.

- Solution: use diffusion.

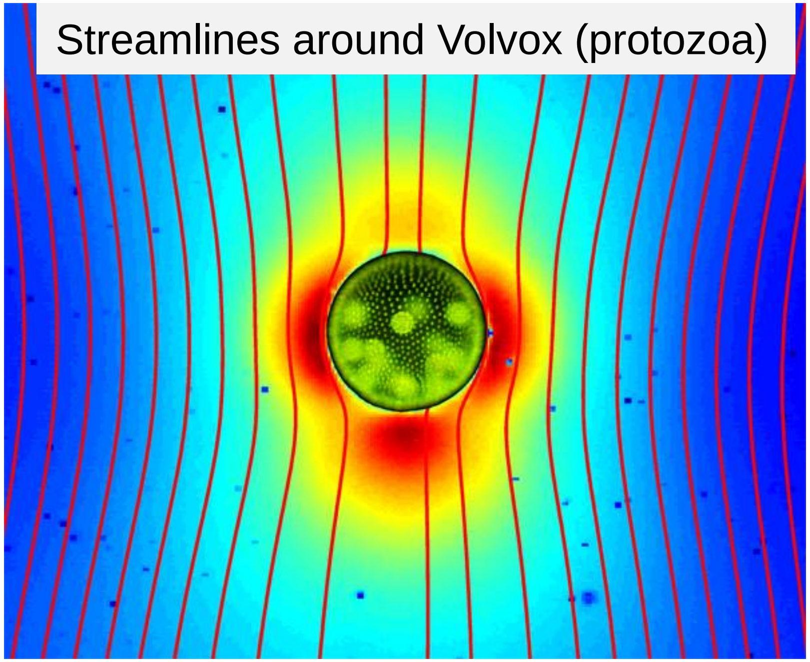
- Why stir?

-- Cilia of length d refreshes its volume every $t_{stir} = d/v$

-- diffusion time scale is $t_{diff} = d^2/D$

- Only if $t_{stir} < t_{diff}$ this is worthwhile.
- Peclet number:
- For D = 1000 μm²/s and d =1 μm, v = 1000 μm/s…

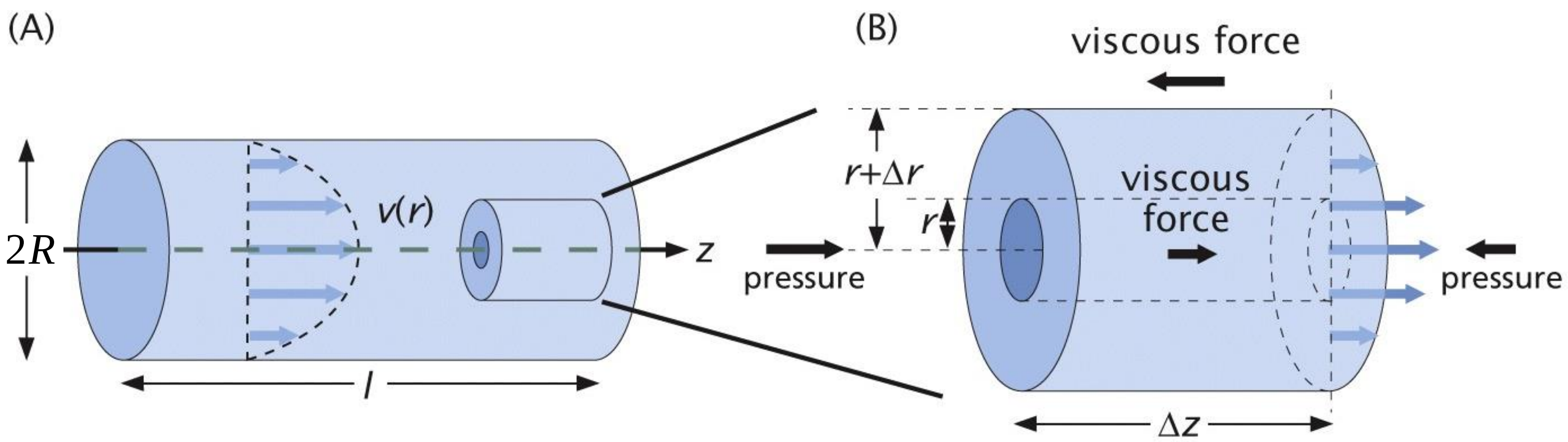
- Bacteria swim for other reasons, like food *gradient*…



Streamlines around Volvox (protozoa)

$$\mathrm{Pe} = \frac{t_{\mathrm{diffusion}}}{t_{\mathrm{stir}}} = \frac{d \cdot v}{D}$$

Vesicular delivery networks are essential for macroscopic organisms that cannot rely on diffusion



Constraints:

$v(R) = 0$ (non-slip)

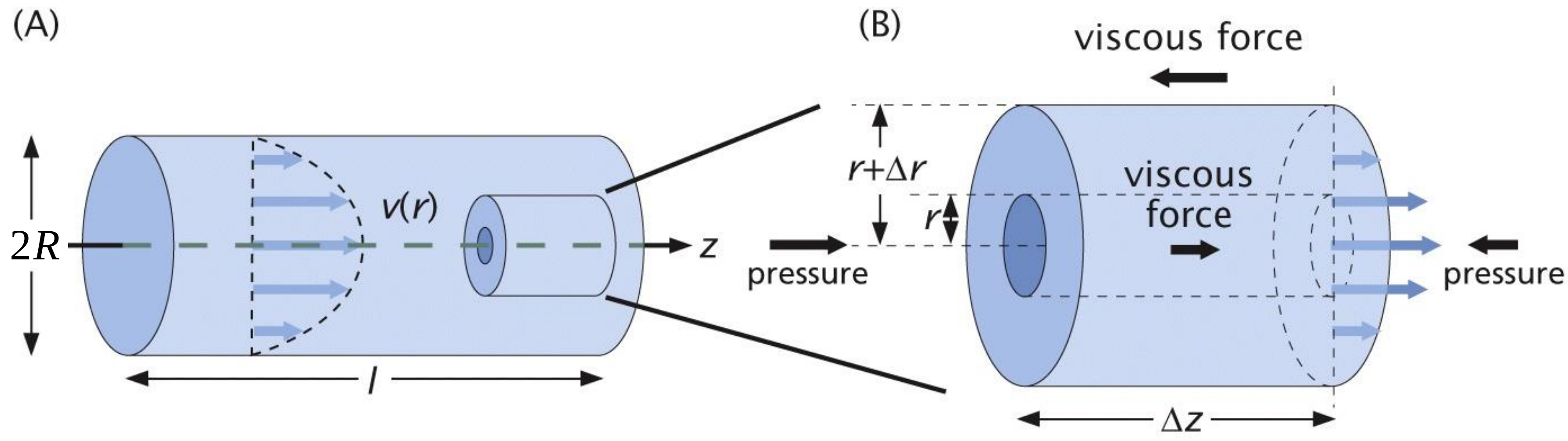
$v(0) < \infty$

$\rho = 10^3$ kg/m^3; $R = 10\ \mu m$

$v = 10$ cm/s ; $\eta = 10^{-3}$ Pa · s

$$\Re = \frac{\rho v R}{\eta} = \frac{10^3 \times 10^{-1} \times 10^{-5}}{10^{-3}} = 1 \text{ (within low Re)}$$

Balancing the forces:



- Pressure applies force: $df_p = (2\pi r dr)\, p$
- Viscous force from inner shell pushes shell forward:

$$df_{in} = -\eta[2\pi rL]\left.\frac{dv(r)}{dr}\right|_r \qquad (dv/dr<0)$$

- Viscous force from outer shell pulls shell backward:

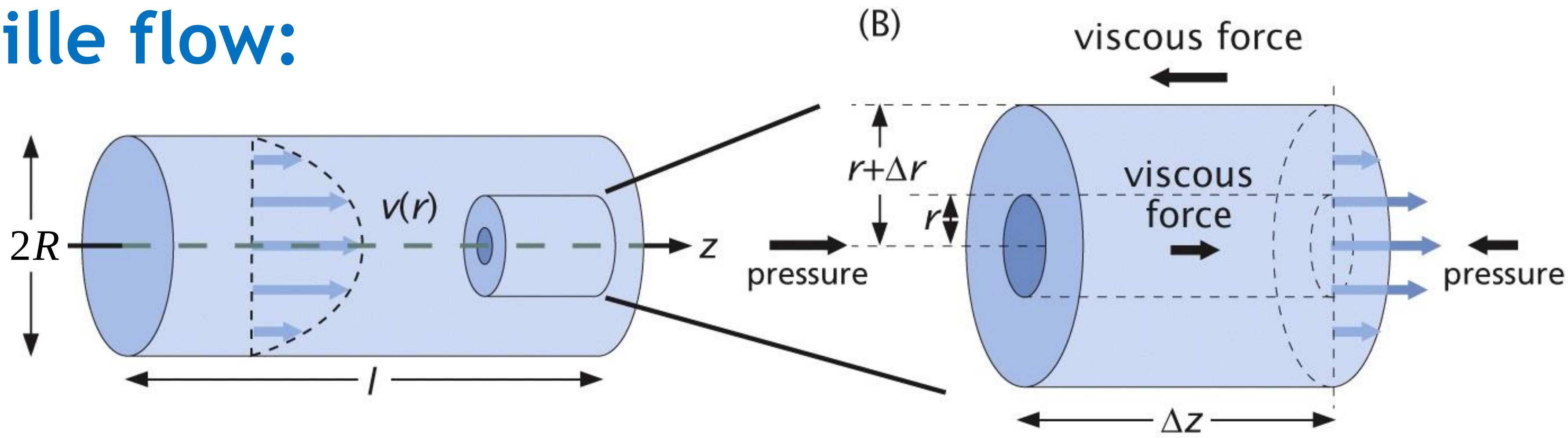
$$df_{out} = -\eta\left[2\pi(r+dr)L\right]\left.\frac{dv(r)}{dr}\right|_{r+dr} = -\eta\left[2\pi(r+dr)L\right]\left(\left.\frac{dv(r)}{dr}\right|_r + \left.\frac{d^2v(r)}{dr^2}\right|_r dr\right)$$

$$df = df_p + df_{in} + df_{out} =$$

$$(2\pi r)\, p dr + \eta[2\pi L]\frac{dv}{dr}dr + \eta[2\pi rL]\left(r\frac{d^2v}{dr^2}dr\right) = 0$$

$$df = 0 \quad \Rightarrow \quad \frac{p}{\eta L} + \frac{1}{r}\frac{dv}{dr} + \frac{d^2v}{dr^2} = 0$$

Poiseuille flow:



$$df = 0 \quad \Rightarrow \quad \frac{p}{\eta L} + \frac{1}{r}\frac{dv}{dr} + \frac{d^2 v}{dr^2} = 0$$

General solution:

$$v(r) = A + B \ln r + \frac{p}{4L\eta} r^2$$

Flux

$$Q = \int_0^R 2\pi r\, dr\, v(r) = \frac{\pi R^4 p}{8L\eta}$$

Boundary conditions:

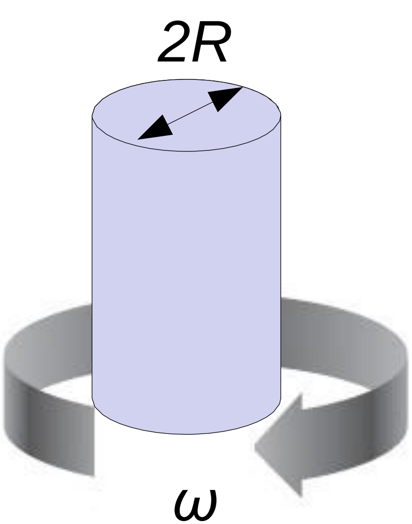
$$v(r) = \frac{p}{4L\eta}\left(R^2 - r^2\right)$$

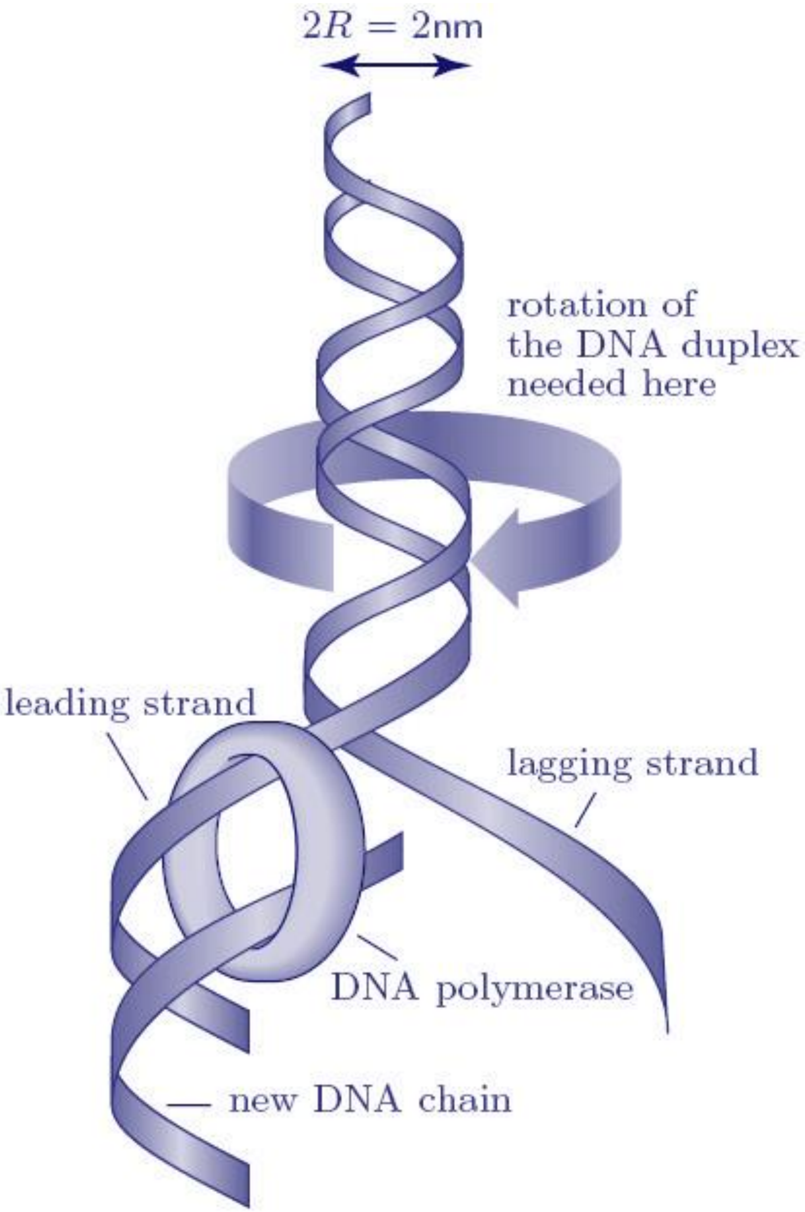
- The flow is laminar in most blood vessels in the human body except for the largest veins and arteries.
- Q ~ R^4 flow can be controlled by small variation of radius.

Viscous force at DNA replication fork

Since the two single strands cannot pass through each other, the original must continually rotate.

Would frictional force resisting this rotation be enormous?





Y-shaped junction

Viscous force at DNA replication fork

The torque scales like:

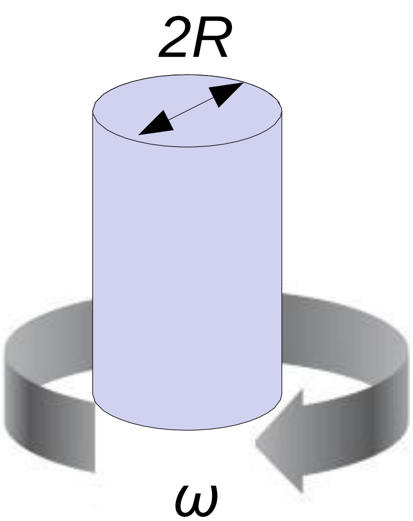
$\tau = r \times f = R \times \eta \omega R L$

The dissipation work

$P = \tau\omega = \eta\omega^2 R^2 L$

per turn of 2π:

$W = 2\pi\tau = 2\pi\eta\omega R^2 L$



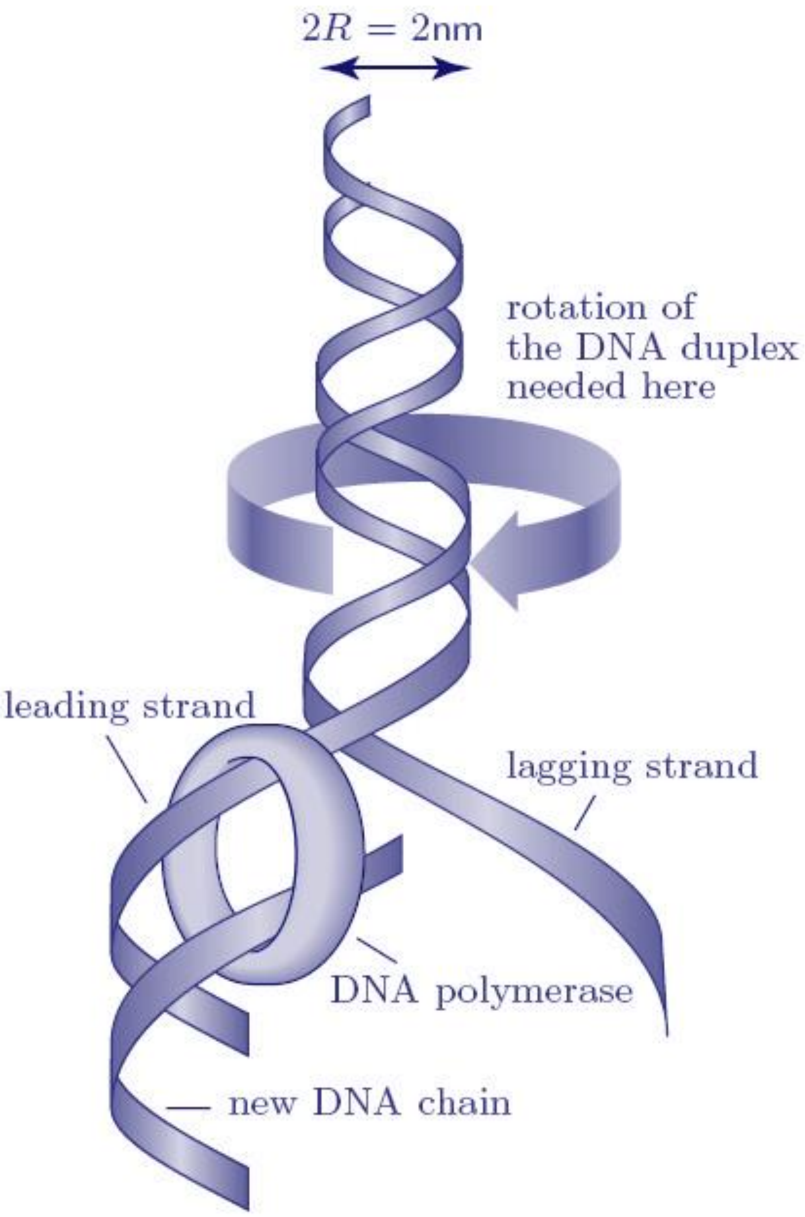
Replication rate: 1000 bp/s

DNA period: 10.5 bp/turn

$$\rightarrow \ \omega = 2\pi \frac{1000}{10.5} = 600 \text{ rad/s}$$

$$W = (2\pi)(600\ \mathrm{s}^{-1})(10^3 \mathrm{Pa\ s})(1\ \mathrm{nm}^2)L \sim 0.01\ \mathrm{L}\ \ k_B T / \mu m$$

- Small friction compared to energy consumed by DNA helicase which unzips DNA.



Y-shaped junction

Summary

$$\tau = \frac{v_{\text{drift}}}{g} = \mu m_{\text{net}} = \frac{m_{\text{net}}}{\xi}$$

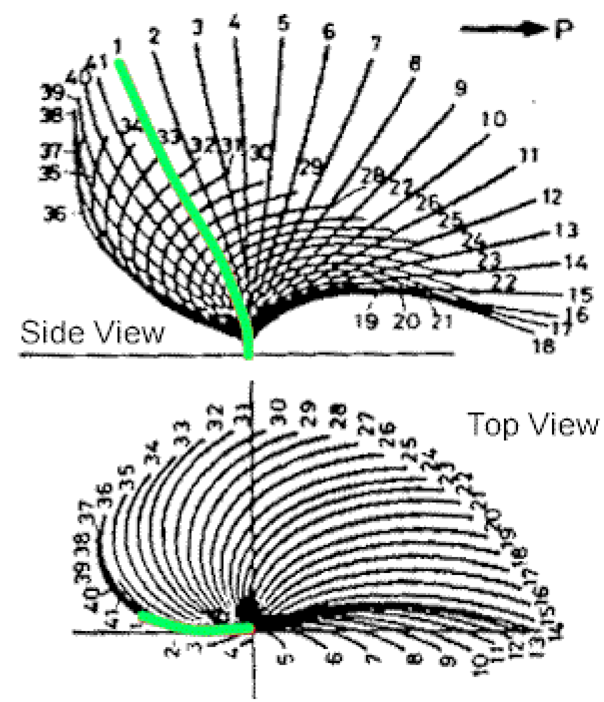
- Viscosity dominates the nano-world .
- Suspension is stabilized by diffusion at time scale:
- Hard to mix viscous fluids

Reynolds number

$$\Re = \frac{f_{\text{inertia}}}{f_{\text{friction}}} = \frac{\rho l^3 v^2 / R}{\eta l^3 v / R^2} = \frac{\rho v R}{\eta}$$

- Reynolds number:
  - Inertia/friction
  - Force/critical force
- Symmetry:
  - Newtonian dynamics: time-reversal invariant
  - Viscous friction: not time-reversal invariant
- Swimming of microorganisms:
  - Strictly reciprocal motion cannot translocate
  - Periodic but not reciprocal motion work

    in ciliary and flagellar propulsion



- Viscosity dominates flow in blood vessels.