

Lectures on Microswimmer Hydrodynamics

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Goals

1. Build intuition about low Re hydrodynamics
2. Introduce the theoretical framework for studying swimming at $Re=0$
3. Review some classic calculations

References

Swimming:

- Lauga + Powers, "The hydrodynamics of swimming microorganisms," *Rep. Prog. Phys.* 72 (2009) 096601.
- Lauga, "The fluid dynamics of cell motility," Cambridge University Press, 2020. Many details + insights!
- Purcell, "Life at low Reynolds number" *Am. J. Phys.* 45 (1977)3.

Stokes flow:

- Kim and Karrila, "Microhydrodynamics: principles and selected applications," Butterworth-Heinemann 1991.
- Guazzelli + Morris, "A physical introduction to suspension dynamics," Cambridge 2012.
- Graham, "Microdynamics, Brownian motion, and complex fluids," Cambridge 2018.

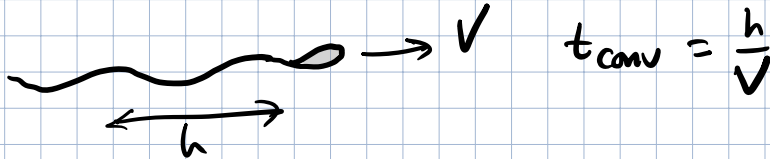
Lecture 1: Fundamentals Monday, 2-3:30 pm, 2022-07-25

outline for today

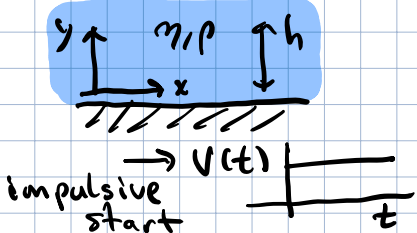
1. Properties of Stokes flow: linearity, reversibility, singular solutions
2. Hydrodynamic forces on a flagellum: RFT, SBT

- The Reynolds number in the context of swimming.

(i) time scales



How long before we can detect a change in the body shape a distance h away? To see how this time scale depends on h , idealize and solve Stokes' problem



$$\underline{u} = u_x(y, t)$$

$$\partial_t u_x = \nu \partial_y^2 u_x$$

$$t_{diff} \approx h^2 / \nu = \frac{h^2 \rho}{\eta}$$

$$\frac{t_{diff}}{t_{conv}} = \frac{\rho h V}{\eta} = Re \quad \text{Bacterium} \quad \begin{array}{l} \rho = 10^3 \text{ kg/m}^3 \quad h = 1 \mu\text{m} \\ V = 10 \mu\text{m/s} \quad \eta = 10^{-3} \text{ Pa}\cdot\text{s} \\ \Rightarrow Re = 10^{-5} \ll 1 \end{array}$$

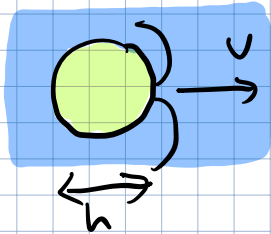
$Re = 0 \Rightarrow$ the flow instantly adjusts to changes in boundaries, such as the deformation of a swimmer. The transfer of information at low Re is fast because the shear stresses are large relative to inertial terms such as ρV^2 .

$$Re = 0 \Rightarrow \left. \begin{array}{l} -\nabla p + \eta \nabla^2 \underline{u} = 0 \\ \nabla \cdot \underline{u} = 0 \end{array} \right\} \text{Stokes equations}$$

Note $\nabla^2 \underline{\omega} = 0$ where $\underline{\omega} = \nabla \times \underline{u}$ is the vorticity. The vorticity adjusts instantaneously in Stokes flow. Of course, we know that it takes a certain time

for vorticity to spread, so the Stokes equations are only valid for length scales $\ll \sqrt{\nu t}$

(ii) Stopping distance



$$m a \sim \eta V h \quad \text{viscous drag}$$

$$a \sim \frac{\eta V h}{\rho_s h^3} = \frac{\eta V}{\rho_s h^2}$$

$$d \sim \frac{v^2}{a} \sim \frac{v^2 \rho_s h^2}{\eta v} = \frac{\rho_s}{\eta} \left(\frac{\rho_s h v}{\eta} \right) h = \frac{\rho_s}{\eta} Re h$$

At low Re , the stopping distance is a small fraction of the body length.

cf. large scale, using Bernoulli for drag:

$$m a \sim \rho v^2 h^2 \Rightarrow a \approx \rho / \rho_s \frac{v^2}{h}$$

$$d \sim \frac{v^2}{a} \sim \rho_s / \rho h$$

● Properties of Stokes flow

(i) Stokes equations = force balance

$$\underline{\underline{\sigma}} = \eta (\nabla \underline{v} + \nabla \underline{v}^T) - p \underline{\underline{I}}$$

$$(\nabla \underline{v})_{ij} = \frac{\partial v_i}{\partial x_j} = \partial_j v_i$$

$$\underline{v} = v_x \hat{x} + v_y \hat{y} = v_i \hat{e}_i$$

$$\underline{\underline{\sigma}} = \sigma_{xx} \hat{x} \hat{x} + \sigma_{xy} \hat{x} \hat{y} + \sigma_{yx} \hat{y} \hat{x} + \dots = \sigma_{ij} \hat{e}_i \hat{e}_j$$

$$Re=0 \Rightarrow \nabla \cdot \underline{\underline{\sigma}} + \underline{f}_{ext} = 0$$

$$\underline{F}_{hydro} = \int \underline{\underline{\sigma}} \cdot \hat{n} dA = \int \nabla \cdot \underline{\underline{\sigma}} dV = 0$$

in the absence of external forces (but see Volvox!)

The hydrodynamic forces & torques generally vanish at $Re=0$.

(ii) Uniqueness: the Stokes equations have a unique solution for a given boundary condition.

This fact can be proved using the reciprocal theorem: Given two solutions to Stokes equations for the same geometry but different boundary conditions, the 'mixed' rates of working are the same:

we'll
come back
to this

$$\rightarrow \int \underline{\underline{\sigma}}_1 \cdot \underline{\underline{\sigma}}_2 \cdot \hat{n} \, dA = \int \underline{\underline{\sigma}}_2 \cdot \underline{\underline{\sigma}}_1 \cdot \hat{n} \, dA$$

cf. Green's theorem in electrostatics, the Maxwell-Betti theorem in linear elasticity...

From the reciprocal theorem we can show that Stokes flow is the flow with minimum dissipation for given boundary conditions. And from the principle of minimum dissipation, we can deduce that the solution to Stokes equations is unique (see the Stokes flow references listed above)

iii) linearity \Rightarrow superposition is valid - we can get new solutions by adding up solutions.

Example: drag on a sphere



what force is required to steadily move the sphere at velocity v ?

As in electrostatics, we put singular solutions inside the sphere and adjust their strengths to satisfy the no-slip BC $\underline{v}(a\hat{r}) = v\hat{x}$.

point force at origin

\uparrow = "Stokeslet" $-\nabla p + \eta \nabla^2 \underline{v} + \underline{F} \delta(\underline{x}) = 0$

dimensional analysis or experience with electrostatics $\Rightarrow v \propto \frac{F}{\eta|\underline{x}|}$

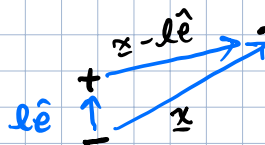
But $\underline{v} = \frac{-\underline{F}}{4\pi\eta|\underline{x}|}$ is not incompressible.

The full calculation yields $\underline{v}_{st} = \frac{1}{8\pi\eta} \left(\frac{\underline{I}}{|\underline{x}|} + \frac{\underline{x}\underline{x}}{|\underline{x}|^3} \right) \underline{F}$

The flow field falls off slowly, as $1/r$. This slow fall-off is the origin of the "hydrodynamic interaction"

The Stokeslet velocity is not constant at $r=a$. We add another singular solution - the potential dipole. We can get potential multipole solutions by differentiating the potential source

$$\underline{v}_Q = \frac{Q \underline{x}}{4\pi|\underline{x}|^3} = \frac{Q \hat{r}}{4\pi r^2}$$



$$\underline{v}_{\text{doublet}} \approx -l \hat{e} \cdot \underline{v} Q \propto \left(\frac{\mathbb{I}}{|\underline{x}|^3} - \frac{3\underline{x}\underline{x}}{|\underline{x}|^5} \right) \cdot Q \hat{e}$$

The potential dipole (also called the "source dipole" or "doublet") makes no contribution to the pressure - at $Re=0$, any potential flow yields zero pressure gradient:

$$\nabla \times \underline{v} = 0 \Rightarrow \nabla \times (\nabla \times \underline{v}) = 0$$

i.e. $-\nabla^2 \underline{v} + \nabla(\nabla \cdot \underline{v}) = 0$. Incompressibility $\Rightarrow \nabla^2 \underline{v} = 0$
 Stokes equations $\Rightarrow \nabla p = 0$.

Adding the Stokeslet and the doublet yields

$$\underline{v} = \frac{3a}{4} \underline{v} \cdot \left(\frac{\mathbb{I}}{|\underline{x}|} + \frac{\underline{x}\underline{x}}{|\underline{x}|^3} \right) + \frac{a^3}{4} \underline{v} \cdot \left(\frac{\mathbb{I}}{|\underline{x}|^3} - \frac{3\underline{x}\underline{x}}{|\underline{x}|^5} \right)$$

Exercise: calculate the pressure, the stress, and integrate to find $\underline{F} = 6\pi\eta a \underline{v}$

$$\text{Note } \underline{v} = \frac{\underline{F}}{8\pi\eta} \cdot \left(\frac{\mathbb{I}}{|\underline{x}|} + \frac{\underline{x}\underline{x}}{|\underline{x}|^3} \right) + \frac{a^2 \underline{F}}{24\pi\eta} \left(\frac{\mathbb{I}}{|\underline{x}|^3} - \frac{3\underline{x}\underline{x}}{|\underline{x}|^5} \right)$$

$$\rightarrow \underline{v}_{\text{st}} \text{ as } a \rightarrow 0$$

(iv) kinematic reversibility

$$-\nabla p + \eta \nabla^2 \underline{v} + \underline{f} = \underline{0}$$

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

$$\underline{v} = \underline{v}_s \text{ on boundaries}$$

Reversing \underline{v}_s and \underline{f} reverses \underline{v} and ∇p .

The streamlines of the flow stay the same; only the direction of flow changes.

See G.I. Taylor's demonstrations in the "Low Reynolds Number Flow" movie at ncfmf.html
National Committee for Fluid Mechanics Films.

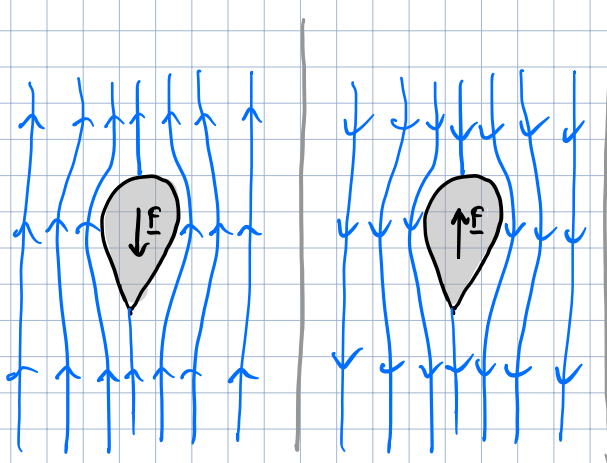
13:40 concentric cylinder demonstration of kinematic reversibility

26:45 model swimmers

The principle of kinematic reversibility is useful in situations with high symmetry.

Examples

①



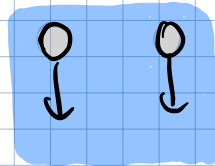
The forces required to keep the object fixed in the flow are the same! The streamlines are the same, with opposite direction.

②



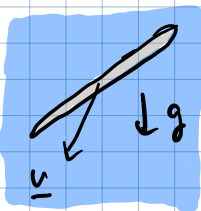
a sedimenting sphere near a wall falls straight down

③



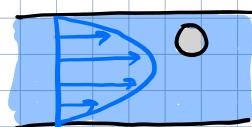
distance between two sedimenting spheres is maintained

④



a sedimenting rod falls without rotating

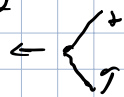
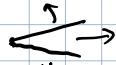
⑤



sphere in Poiseuille flow has no lateral drift

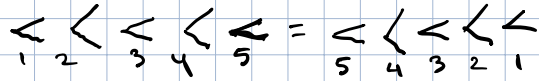
"Purcell's scallop theorem:" A reciprocal stroke leads to no net progress in one cycle.

But see Ludwig
"Zur Theorie der
Flimmerbewegung"
1930:

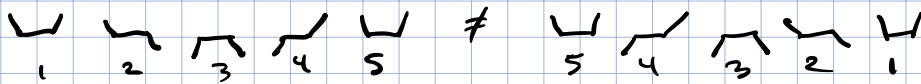


The hinge oscillates back and forth but makes no net progress - during the return stroke, each particle retraces the path it took on the power stroke.

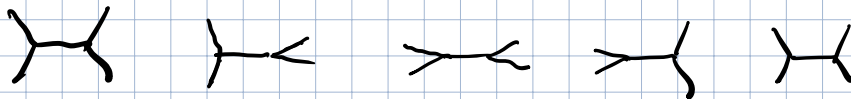
One way to see if a stroke pattern is reciprocal is to imagine taking a movie of it and then playing the movie backwards - if you can't tell if the movie is playing backward (you are allowed to speed up and slow down the movie), then the stroke is reciprocal, i.e. you pass through the same sequence of shapes in the opposite order.



Purcell proposed an idealized non-reciprocal sequence of shapes for the "minimal swimmer":

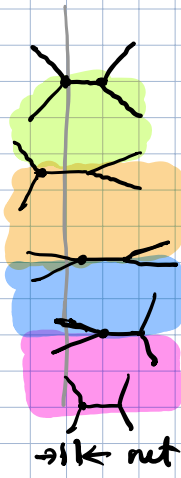
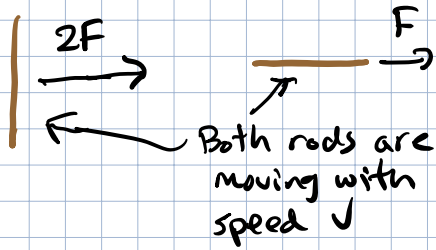


It's easier to analyze a variant that does not rotate as it goes through its cycle:



The key to deducing the direction the swimmer advances is that the drag on a thin rod is roughly twice as big if it is moved \perp to its

axis compared to moving || to its axis.



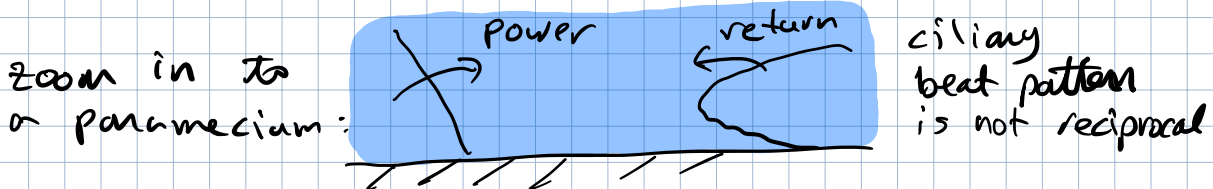
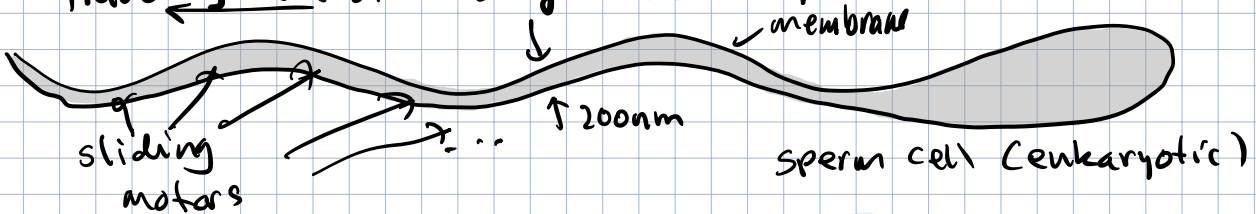
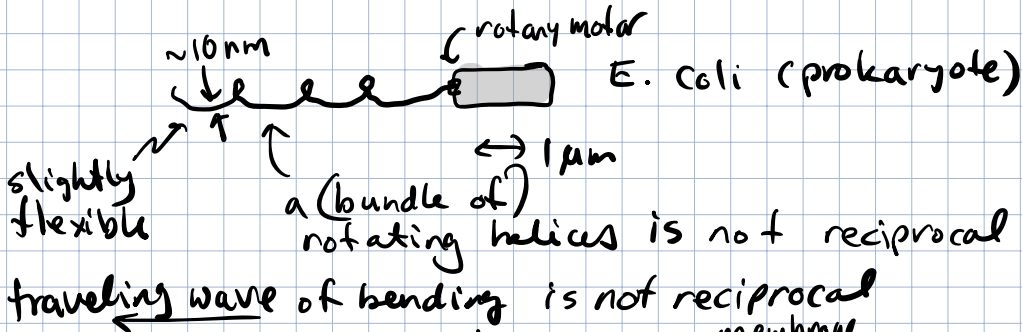
The second segment of the stroke more than recovers the distance lost on the first segment since the drag resisting the motion is smaller. Likewise, the distance lost on the 4th segment is smaller than the distance gained on the third due to the difference in drag.

→ net progress!

Proof of scallop theorem for a single hinge: $\langle \dot{\theta}(t) \hat{x} \rangle = 0$
 $\underline{v} = \dot{\theta} f(\theta) \hat{x}$ by linearity.
 $\int_0^T \underline{v} dt = \int_0^T \dot{\theta} f(\theta) dt \hat{x} = 0$ for periodic stroke.

● Models for rotating and beating flagella

Biological microswimmers evade the scallop theorem with non-reciprocal flagellum motions. Note that prokaryotic flagella and eukaryotic flagella are so different that they should have different names.



zoom in to a paramecium:

To calculate how fast a microorganism swims given its sequence of flagellum shapes requires us to calculate the hydrodynamic forces on a thin filament. We'll start with dimensional analysis:

Stokes drag on a sphere



$$F \sim \text{stress} \times \text{area}$$

$$\frac{\eta V}{a} \cdot a^2$$

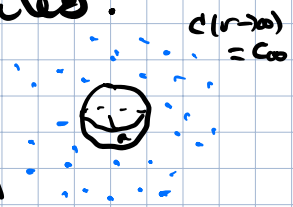
$F \sim \eta V a$ the drag force \propto linear size, not length.

Aside: We get the same result for a perfectly absorbing sphere in a field of diffusing molecules:

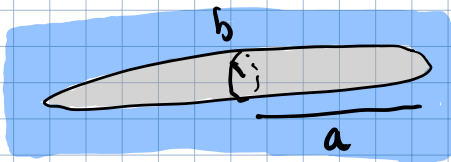
uptake rate = flux \times area

$$= D \frac{dc_0}{a} \cdot a^2 = D c_0 a$$

see Berg "Random walks in biology" Princeton 1993



Drag on a thin ellipsoid



$$F \sim \frac{\eta V}{b} \cdot ab \sim \eta V a$$

\therefore When $Re \ll 1$, the drag on a rod of length $2a$ is the same order of magnitude as the drag on a sphere of diameter $2a$!



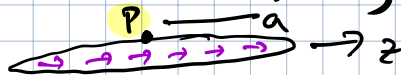
We can be a bit more quantitative by replacing the ellipsoid with a line of

Stokeslets. Note that there is a factor of 2 enhancement of flow along the axis of a Stokeslet relative to flow at the equator:

$$\begin{aligned} \tau 2v(r, \theta = \pi/2) \hat{z} &= \hat{z} \cdot (\mathbb{I} + \hat{r} \hat{r}) \cdot \hat{z} = 2 \\ \tau v(r, \theta = \pi/2) \hat{z} &= \hat{z} \cdot (\mathbb{I} + \hat{r} \hat{r}) \cdot \hat{z} = 1 \end{aligned}$$

$\hat{r} = \hat{z}$
 $\hat{r} = \hat{x}$

Very roughly, the velocity of a rod subject to force F along its axis is given by



$$v_z(P) \sim \sum \frac{F}{N} \frac{1}{\eta z} \sim \int_{-a}^a \frac{dz}{2a/N} \frac{F}{N} \frac{z}{\eta z} \sim \frac{F}{\eta a} \log \frac{a}{b}$$

P is a distance b away from the center line

Likewise, for dragging the rod along the \perp direction, the mobility is half as big:

$$v_z \sim \int_{-a}^a \frac{dz}{\frac{2a}{N}} \frac{F}{N} \frac{1}{\eta z} \sim \frac{F}{2\eta a} \log \frac{a}{b}$$

more careful calculations for a thin ellipsoid \Rightarrow

$$\underline{F} = (\zeta_{\perp} \underline{\sigma}_{\perp} + \zeta_{\parallel} \underline{\sigma}_{\parallel}) \cdot 2a$$

$$\zeta_{\perp} = \frac{4\pi\eta}{\log \frac{2b}{a} + \frac{1}{2}} \quad b \gg a$$

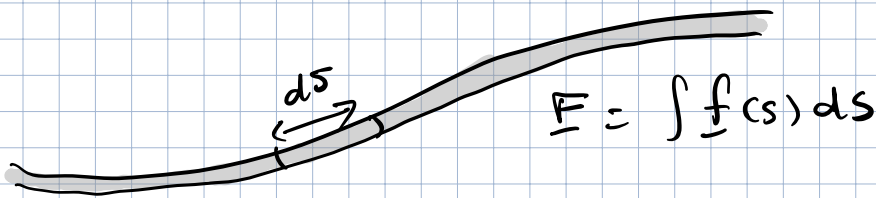
$$\zeta_{\parallel} = \frac{2\pi\eta}{\log \frac{2b}{a} - \frac{1}{2}}$$

These results are for a thin ellipsoid, which approximates a straight rod. We want the hydrodynamic forces on a curved or deforming rod. Simplest approach: use the coefficients we just derived as the force per unit length \underline{f} on a curved rod!

Gray + Hancock
1955

Resistive force theory

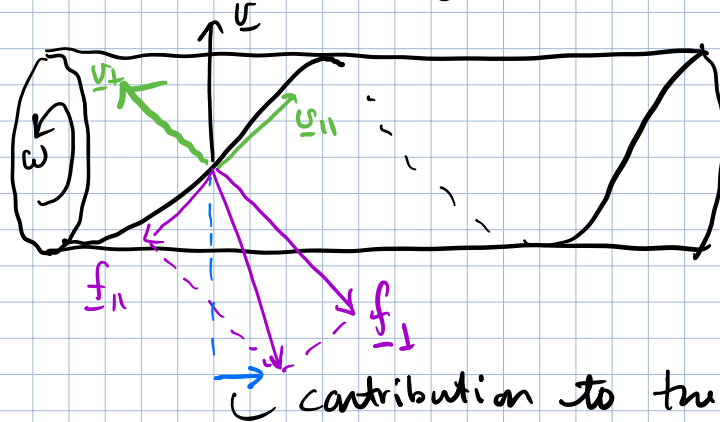
also "local drag theory"



$$\underline{f} = \zeta_{\perp} \underline{v}_{\perp} + \zeta_{\parallel} \underline{v}_{\parallel}$$

We can use resistive force theory to calculate the thrust induced by a rotating helix:

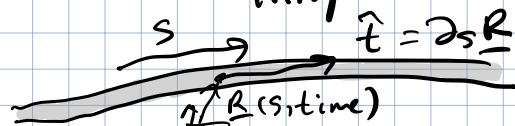
HC Berg
"Random walks in biology"



We have shown that a left-handed helix rotating counter-clockwise (when viewed outside the cell) delivers a positive thrust.

Comments: resistive force theory is OK for developing intuition and determining scaling relations. See the slides and Qian, Powers, Breuer Phy Rev Lett 2008 for a table-top elastohydrodynamics experiment that is accurately described by resistive force theory. Another interesting example is the migration of helices in the vorticity direction of a shear flow, with the sign given by the handedness of the helix (Marcos, Fu, Powers, Stoeber, Phy Rev Lett 2009).

But when the rod does not have gentle curvature, RFT becomes inaccurate. A better approach is slender-body theory. Just as we did for the sphere, we can add a line distribution of doublets to the line of Stokeslets at the center of a rod, and adjust the relative coefficients to enforce no-slip BC:

$$\underline{u}(s) = \frac{1}{4\pi\eta} \left(\underline{I} - \hat{t}\hat{t} \right) \cdot \underline{f}(s) + \frac{1}{8\pi\eta} \left(\frac{\underline{I}}{r} + \frac{\hat{r}\hat{r}}{r} \right) \cdot \underline{f}(s') ds'$$


The diagram shows a rod of radius $R(s, \text{time})$ along the s -axis. The unit tangent vector is $\hat{t} = \partial_s \underline{R}$. The distance from a point s' to a point s is r .

See Langa's book and references therein, especially Lighthill 1976, for the derivation.

Slender body theory is more accurate than resistive force theory, but we need to solve an integral equation to get $f(s)$ given $u(s)$. Once we have $f(s)$, we can calculate the flow anywhere.

In the slides we show a couple examples of the comparison between

RFT + SBT + experiments } Liu, Powers, Breuer
for a "swimming" helix } PNAS 2011

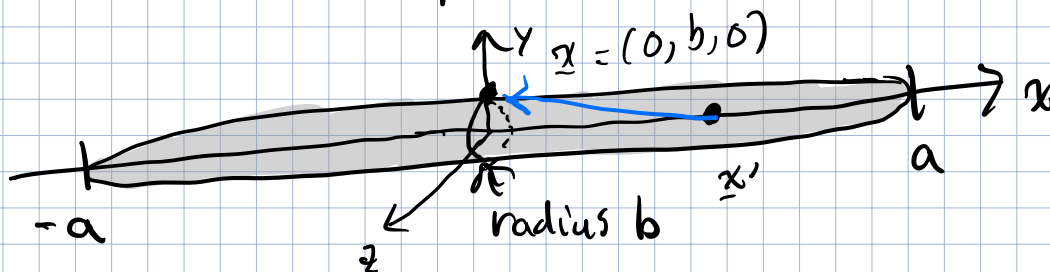
SBT + experiment for } Kim, Kim, Bird,
a rotating helical bundle } Park, Powers, Breuer
Expts in Fluids 2004

Appendix to lecture 1: A slightly less hand-wavy way to derive the resistance coefficients for a straight slender rod.

First, assume a uniform distribution of Stokeslets of unknown strength along the rod centerline. We don't expect this assumption be valid near the ends, but if the rod is

long and thin, we expect a small error. For a point \underline{x} on the rod surface,

$$\underline{v}(\underline{x}) = \frac{1}{8\pi\eta} \int \underline{G}(\underline{x} - \underline{x}') \cdot \underline{f} dx'$$



$$\text{where } G_{ij}(\underline{R}) = \frac{\delta_{ij} + \hat{R}_i \hat{R}_j}{|\underline{R}|}$$

Since the rod is slender, we may take $\hat{R} \approx \hat{x}'$. Then, since \underline{f} is constant,

$$\underline{v}(0, b, 0) = \frac{1}{8\pi\eta} (\underline{I} + \hat{x} \hat{x}) \cdot \underline{f} \int_{-a}^a \frac{dx}{\sqrt{b^2 + x^2}}$$

But $\int_{-a}^a \frac{dx}{\sqrt{b^2 + x^2}} = \int_{-a/b}^{a/b} \frac{dx}{\sqrt{1+x^2}} = 2 \operatorname{arctanh} \frac{a/b}{\sqrt{1+a^2/b^2}}$

$\approx 2 \operatorname{arctanh}(1 - \frac{1}{2} b^2/a^2)$ since $b \ll a$

$\approx \log \frac{1 + 1 - b^2/a^2}{1/2 b^2/a^2} \approx 2 \log \frac{2a}{b}$

Since $\underline{v}(0, b, 0)$ must be the velocity of the rod, we have $\underline{V} = \frac{\log(2a/b)}{4\pi\eta} (\underline{I} + \hat{x} \hat{x}) \cdot \underline{f}$

$$\text{i.e. } \boxed{\begin{matrix} \zeta_{\perp} \approx \frac{4\pi\eta}{\log \frac{2a}{b}} & \zeta_{\parallel} \approx \frac{2\pi\eta}{\log \frac{2a}{b}} \end{matrix}}$$

Lecture 2: Flows and stresses induced by

microswimmers

wed 11am - 12:30pm
2022-07-27

outline for today

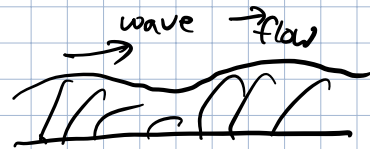
1. Taylor sheet + Lighthill squirmer - two classic models
2. The reciprocal theorem
3. More singular solutions
4. swimmer contribution to stress

● Taylor 1951 waving sheet - a highly idealized model for

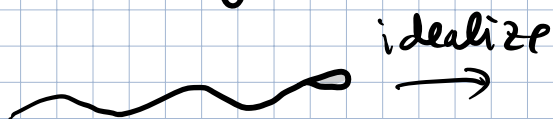
(i) undulating swimmers



(ii) transport of fluid by a carpet of cilia



Taylor's question: can we see in a simple model how drag leads to propulsion?



$$x_s = x$$

$$y_s = B \sin(kx - \omega t)$$

infinite sheet w/ transverse undulations

material points on the sheet move up and down in the swimmer frame

To find the swimming velocity V , impose no-slip BC on the sheet $\underline{v}(x_s, y_s) = \partial_t y_s \hat{y}$ and solve the Stokes equations.

$$\begin{aligned} \rightarrow v_x(y \rightarrow \infty) &= V \neq 0 \\ &\Rightarrow \text{swimming} \end{aligned}$$

If $v_x(y \rightarrow \infty) \neq 0$ in the frame of the swimmer (the frame in which material points on the body move up and down), then the sheet swims in the lab frame (where $\underline{v}(y \rightarrow \infty) = \underline{0}$).

Note that a shift in the origin of time is equivalent to a shift in the origin for x . Since the length is infinite, we conclude $\partial_t V = 0$. Also, replacing the amplitude B by $-B$ is a shift by one-half wavelength, which should not affect the speed. Thus

$$V(-B) = V(B).$$

Although the Stokes equations are linear, the boundary conditions are nonlinear - we have to solve a nonlinear problem to determine the swimming speed V . This situation is reminiscent of finding the eigenvalues of a matrix. To make analytic progress, Taylor expanded in powers of Bk .

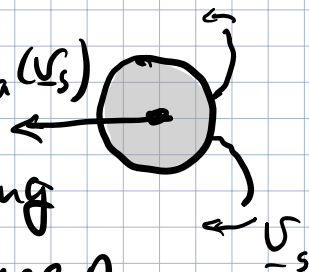
Linearity $\Rightarrow V \propto \omega$, or $V \propto c = \omega/k$.

Dimensional analysis $\Rightarrow V \propto c B^2 k^2$. The viscosity has dropped out because we assumed that the swimmer gait is prescribed, independent of the load.

Side comment: We can use linearity to see why swimming speed does not depend on viscosity in the prescribed swimmer problem. Let us consider a swimmer of finite size. We can find the swimming speed at an instant in time by adding two flows:

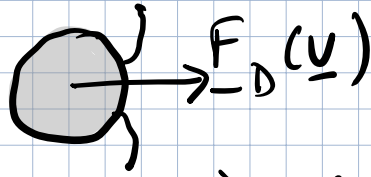
1. thrust flow: $F_a(\underline{v}_s)$

$F_a(\underline{v}_s)$ is the anchoring force required to keep the swimmer from moving at this instant.



2. drag flow

$\underline{F}_D(\underline{v})$ = drag force



required to drag frozen swimmer with velocity \underline{v} . Add the flows and forces,

$$\underline{F}_a(\underline{v}_s) + \underline{F}_D(\underline{v}_{\text{swim}}) = 0$$

to find $\underline{v}_{\text{swim}}$. Both \underline{F}_a and \underline{F}_D are proportional to η , so viscosity drops out.

If we accounted for the driving motors, or the filament elasticity, we could have $\underline{v}_{\text{swim}}$ depend on η .

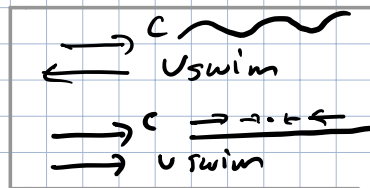
Back to Taylor's calculation: the key step is

to expand the boundary condition: $\underline{v} = \underline{v}^{(1)} + \underline{v}^{(2)}$;

$$\underline{v}(x, h_s) = \left[\underline{v}^{(1)} + h_s \partial_y \underline{v}^{(1)} + \underline{v}^{(2)} \right]_{(x, 0)} + \dots$$

solving $\Rightarrow v_{\text{swim}} = \frac{1}{2} c B^2 h^2$

If you think the direction of swimming (opposite the direction of



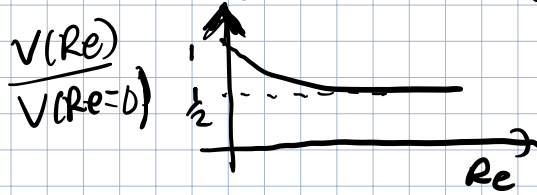
propagation of the transverse wave) is obvious, note that a longitudinal swimmer swims in the same direction as the propagating wave!

See slides - the swimming direction is determined by the 2nd order disturbance flow required to correct the error induced by the 1st order no-slip BC

Comments

- The Taylor sheet is useful studying how various physical effects alter the swimming speed:

- Langa 2007 viscoelastic effects
- Leshansky 2009 colloidal nature
- Tuck 1968 inertia slows the swimmer

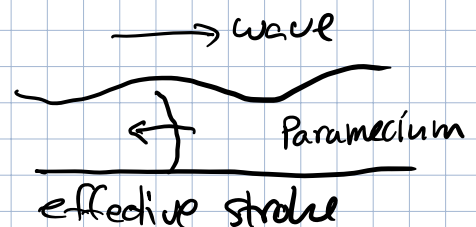
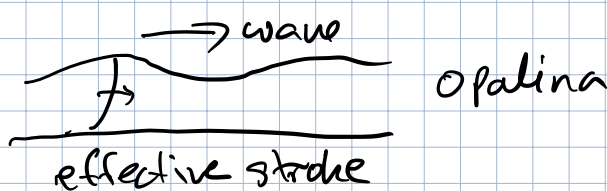


- Energy dissipated/area of sheet = $\eta \omega^2 b^2 k$.

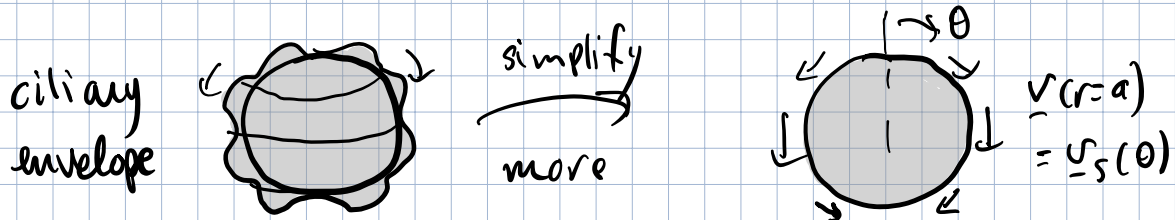
This value is less than the value found by Tuck at finite Re . Recall that for given boundary conditions, Stokes flow is the flow with minimum dissipation rate.

- We need both the longitudinal and transverse waves to model the motion of the tips of cilia in the ciliary envelope. Demanding the greatest flow for a given dissipation rate yields two solutions:

see
Langa book

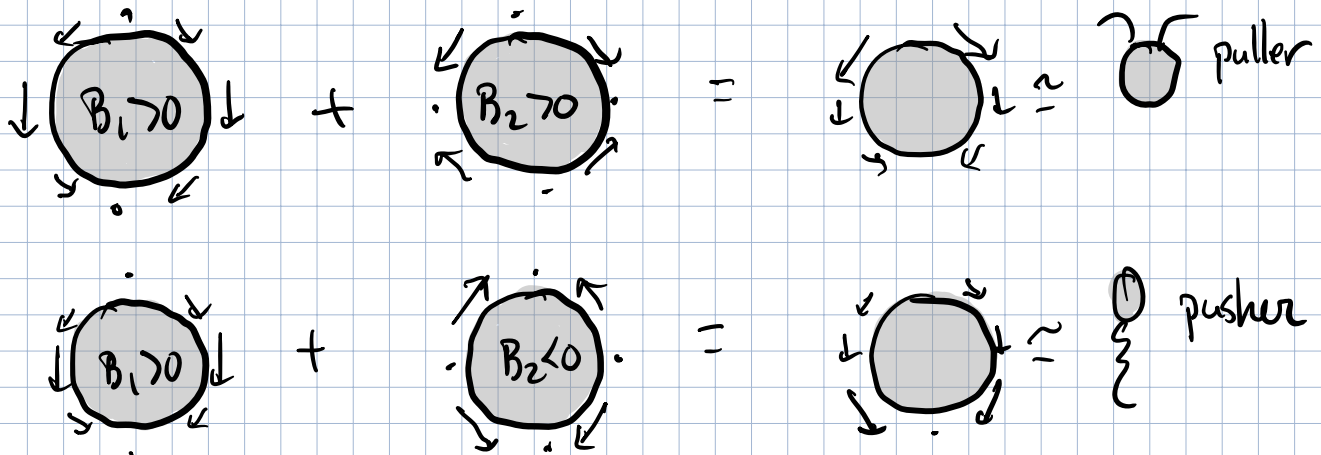


● Lighthill squirmer 1952 (Blake 1971)



Replacing the ciliary envelope with a sphere (with slip $B < 0$) is not such a big change since shape does not matter much at low Re .

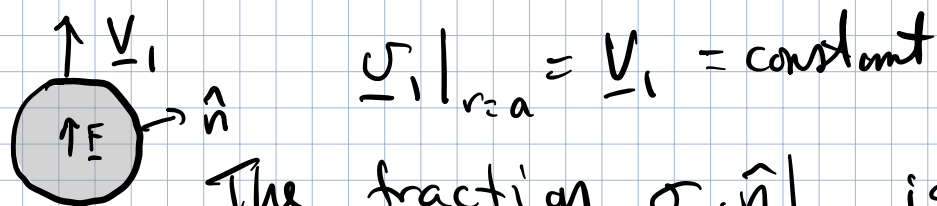
Simplest case: $\underline{v}_s = (B_1 \sin\theta + B_2 \sin\theta \cos\theta) \hat{\theta}$



We can solve the problem as Lighthill + Blake did by solving the Stokes equations in spherical coordinates by separation of variables. Or we can take a shortcut using the reciprocal theorem (Stone + Samuel PRL 1996)

$$\int \underline{\sigma}_1 \cdot \underline{\sigma}_2 \cdot \hat{n} dA = \int \underline{\sigma}_2 \cdot \underline{\sigma}_1 \cdot \hat{n} dA$$

Problem 1: Stokes drag



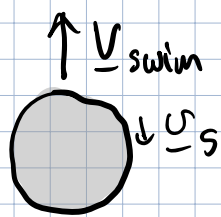
$$\underline{\sigma}_1|_{r=a} = \underline{V}_1 = \text{constant}$$

The traction $\underline{\sigma}_1 \cdot \hat{n}|_{r=a}$ is also constant! (Need to calculate to see this.)

$$\underline{\sigma}_1 \cdot \hat{n} = \frac{-6\pi\eta a \underline{V}_1}{4\pi a^2} \leftarrow \text{force the fluid exerts on the sphere}$$

$$= -\frac{3}{2}\eta/a \underline{V}_1$$

Problem 2: Swimmer problem



$$\underline{\sigma}_2|_{r=a} = \underline{V}_{\text{swim}} + \underline{\sigma}_s$$

$$\int \underline{\sigma}_2 \cdot \hat{n} dA = 0$$

Thus

$$\underline{V}_1 \cdot \int \underline{\sigma}_2 \cdot \hat{n} dA = \int (\underline{V}_{\text{swim}} + \underline{\sigma}_s) \cdot \underline{\sigma}_1 dA$$

$$-\underline{V}_{\text{swim}} \cdot 6\pi\eta a \underline{V}_1 = -\frac{3}{2}\eta/a \int \underline{\sigma}_s \cdot \underline{V}_1 dA$$

True for any \underline{V}_i . \therefore

$$\underline{V}_{\text{swim}} = -\frac{1}{4\pi a^2} \int \underline{u}_s \, dA$$

$$\underline{V}_{\text{swim}} = \frac{2}{3} B_1 \hat{z}$$

We found the swimming speed without calculating the entire flow field!

It is also instructive to calculate the flow field directly - the key step in determining the coefficients of the fundamental solutions is to demand that the total force vanishes. With no-slip, we find

$$\underline{u} = \underbrace{-\frac{2}{3} B_1 \hat{z}}_{\text{uniform}} - \underbrace{B_2 \frac{a^2}{r^2} P_2(\cos\theta) \hat{r}}_{\text{stresslet}} + \underbrace{\frac{2}{3} B_1 \frac{a^3}{r^3} (\hat{r} \cos\theta + \frac{1}{2} \hat{\theta} \sin\theta)}_{\text{potential dipole } \pm}$$

There is no stresslet because the force vanishes.

$$+ B_2 \frac{a^4}{r^4} \left[\hat{r} P_2(\cos\theta) + \hat{\theta} \sin\theta \cos\theta \right]$$

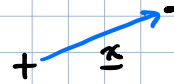
potential quadrupole \pm

As we saw last time, we get the potential multipoles by differentiating the source.

Let's verify that the terms above come from differentiating the source and the Stresslet.

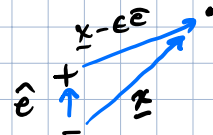
I find this easiest to do in Cartesian coordinates:
See Pozrikidis "Boundary integral and singularity methods for linearized viscous flow" Cambridge 1992.

source
$$v_i = \frac{x_i}{|x|^3} \sim 1/r^2$$



potential dipole
$$= -\hat{e} \cdot \nabla v_i \sim 1/r^3$$

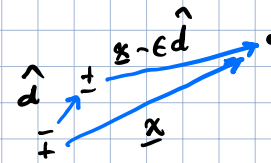
$$= -e_j \partial_j \frac{x_i}{|x|^3} = -e_j \left(\frac{\delta_{ij}}{|x|^3} - \frac{3x_i x_j}{|x|^5} \right)$$



potential quadrupole
$$= -\hat{d} \cdot \nabla (-\hat{e} \cdot \nabla v_i) \sim 1/r^4$$

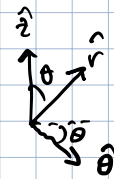
$$= e_j d_k \partial_k \left(\frac{\delta_{ij}}{|x|^3} - \frac{3x_i x_j}{|x|^5} \right)$$

$$= e_j d_k \left(\frac{15 x_i x_j x_k}{|x|^7} - \frac{3 \delta_{ik} x_j + 3 \delta_{jk} x_i + 3 \delta_{ij} x_k}{|x|^5} \right)$$



In our problem, the swimmer is axisymmetric, so $\hat{e} = \hat{d} = \hat{z}$. Thus the potential dipole is

$$\begin{aligned} \underline{v}^{\text{dipole}} &= \left[\frac{\hat{z}}{r^3} - \frac{3\hat{r}\hat{r}}{r^3} \right] \cdot \hat{z} = \frac{1}{r^3} (\hat{z} - 3\hat{r} \cos\theta) \\ &= \frac{1}{r^3} (\cos\theta \hat{r} - \sin\theta \hat{\theta} - 3\hat{r} \cos\theta) \\ &= -\frac{2}{r^3} (\cos\theta \hat{r} + \frac{1}{2} \sin\theta \hat{\theta}) \checkmark \end{aligned}$$



Likewise

$$\underline{v}^{\text{quad}} = \frac{15}{r^4} \hat{r} \cos^2\theta - \frac{3(\hat{r} + 2\cos\theta \hat{z})}{r^4}$$

so $\hat{r} \cdot \underline{v}^{\text{quad}} = \frac{15}{r^4} \cos^2\theta - \frac{3}{r^4} - \frac{6}{r^4} \cos^2\theta = \frac{9\cos^2\theta - 3}{r^4}$

$$= \frac{6}{r^4} \left(\frac{3}{2} \cos^2\theta - \frac{1}{2} \right) = \frac{6}{r^4} P_2(\cos\theta)$$

also $\hat{\theta} \cdot \underline{v}^{\text{quad}} = + \frac{6 \cos\theta \sin\theta}{r^4} \quad (\hat{\theta} \cdot \hat{z} = -\sin\theta)$

i.e.
$$\underline{v}^{\text{quad}} = \frac{6}{r^4} \left[P_2(\cos\theta) \hat{r} + \cos\theta \sin\theta \hat{\theta} \right] \checkmark$$

The remaining term, the stresslet, is part of the Stokeslet dipole:

$l \hat{d} \uparrow F \hat{e}$
 $\downarrow -F \hat{e}$

at $\underline{G} = \frac{1}{8\pi\eta} \frac{1}{|\underline{x}|} \left(\underline{\underline{I}} + \frac{\underline{x} \underline{x}}{|\underline{x}|^2} \right)$

Then $\sigma_i^{\text{Stokes dipole}} \equiv \sigma_i^{SD} = -l d_k \partial_k (G_{ij} F e_j)$
 $\equiv -l F G_{ijk}^{SD} e_j d_k$

where $G_{ijk}^{SD} = \frac{\partial_k}{8\pi\eta} \left(\frac{\delta_{ij}}{|\underline{x}|} + \frac{x_i x_j}{|\underline{x}|^3} \right) = \left[\frac{-\delta_{ij} x_k}{|\underline{x}|^3} + \frac{x_i \delta_{jk} + x_j \delta_{ik}}{|\underline{x}|^3} - \frac{3x_i x_j x_k}{|\underline{x}|^5} \right] / 8\pi\eta$

$G_{ijk}^{SD} = \left[\frac{x_i (\delta_{jk} - \frac{3x_j x_k}{|\underline{x}|^2})}{|\underline{x}|^3} + \frac{\delta_{ik} x_j - \delta_{ij} x_k}{|\underline{x}|^3} \right] / 8\pi\eta$

symmetric + traceless in jk
antisymmetric in jk

"stresslet"

"rotlet"

Examine the rotlet first. Consider the case $\hat{d} \perp \hat{e}$:

This is a point torque, with moment $l F \hat{d} \times \hat{e}$. The corresponding flow is

$$-\frac{l F}{8\pi\eta} \frac{e_j d_k}{r^3} (\delta_{ik} x_j - \delta_{ij} x_k) = -\frac{l F}{r^3} (d_i \hat{e} \cdot \underline{x} - e_i \hat{d} \cdot \underline{x}) \frac{1}{8\pi\eta}$$

But $(\hat{d} \times \hat{e}) \cdot \underline{x} = -\hat{d} \cdot \hat{e} \times \underline{x} + \hat{e} \cdot \hat{d} \times \underline{x}$

so $\underline{v} = \frac{(l \hat{d} \times F \hat{e}) \times \underline{x}}{8\pi\eta r^3} = \frac{\underline{M} \times \underline{x}}{8\pi\eta |\underline{x}|^3}$

Note $\underline{v}(r=a) = \frac{M \sin\theta}{8\pi\eta a^2} = \omega a \sin\theta$ satisfies no slip for a rotating sphere!

$$M = 8\pi\eta\omega a^3 \quad \text{torque required to rotate a sphere at rate } \omega.$$

The rotlet - the flow induced by a point force - is the same as the flow induced by the rotation of a sphere. The torque on our squirmer vanishes, so the rotlet does not enter.

Now turn to the symmetric part:

$$\underline{u}^{\text{stresslet}} = \frac{\underline{x}(-lF)}{8\pi\eta|\underline{x}|^3} \hat{e} \cdot \left(\underline{\mathbb{I}} - 3 \frac{\underline{x}\underline{x}}{|\underline{x}|^2} \right) \cdot \hat{d}$$

$$= -\frac{3\underline{x}}{8\pi\eta} \frac{lF}{|\underline{x}|^5} \left[|\underline{x}|^2 \frac{\hat{e} \cdot \hat{d}}{3} - \underline{x} \cdot \left(\frac{1}{2} \hat{e} \hat{d} + \frac{1}{2} \hat{d} \hat{e} \right) \underline{x} \right]$$

$$\text{or } \underline{u}^{\text{stresslet}} = -\frac{3}{8\pi\eta} \frac{\underline{x} \cdot \underline{\underline{S}} \cdot \underline{x}}{|\underline{x}|^5} \quad \text{where } \underline{\underline{S}} \equiv lF \left(\underline{\mathbb{I}} \frac{\hat{e} \cdot \hat{d}}{3} - \frac{1}{2} (\hat{e} \hat{d} + \hat{d} \hat{e}) \right)$$

$\underline{\underline{S}}$ is the "stresslet tensor" - we'll see in a moment that $\underline{\underline{S}}$ is the contribution of a swimmer to the average stress.

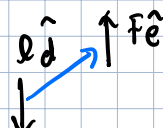
First check that it gives the term we found in the squirmer flow. Again, $\hat{d} = \hat{e} = \hat{z}$ for our squirmer:

$$\underline{u}^{\text{stresslet}} = -\frac{\underline{x} lF}{8\pi\eta|\underline{x}|^3} (1 - 3\cos^2\theta)$$

$$= \frac{lF}{4\pi\eta r^2} \hat{r} P_2(\cos\theta) \quad \checkmark$$

Summarize: We found that the Stokes dipole can be written as

$$\underline{U}^{SD} = \underbrace{-\frac{3}{8\pi\eta} \frac{\underline{x} \cdot \underline{S} \cdot \underline{x}}{|\underline{x}|^5}}_{\text{stresslet flow}} + \underbrace{\frac{\underline{M} \times \underline{x}}{8\pi\eta |\underline{x}|^2}}_{\text{rotlet flow = flow induced by a rotating sphere subject to torque } \underline{M}}$$

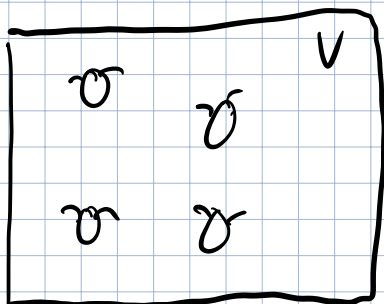
\hat{d} 
 where $\underline{S} = \ell F \left[\frac{\hat{d} \cdot \hat{e}}{3} \underline{I} - \frac{1}{2}(\hat{d} \hat{e} + \hat{e} \hat{d}) \right]$ stressed tensor
 $\underline{M} = \ell \hat{d} \times F \hat{e}$

In our case, $\hat{d} = \hat{e} = \hat{z}$, and the leading term in the far field is the stresslet.

- See the slides for the measurement of the far-field flow of a swimming *E. coli* bacterium and the comparison with a stresslet flow (Drescher, Dunkel, Cisneros, Ganguly, Goldstein PNAS 2011)
 - they used non-tumbling bacteria
 - they looked for events where bacteria swim in the focal plane
 - they tracked fluid tracers and averaged over many bacteria to get the time-averaged flow
 - $\ell \approx 2 \mu\text{m}$, $F \approx 0.4 \text{ pN}$
 - Near a surface there is an image stresslet below the surface, altering the form of the flowlines

Volvox is not neutrally buoyant - its flow field is given by a Stokeslet + stresslet + potential dipole. The Stokeslet dominates the far field, and the potential dipole is more dominant than the stresslet
 Drescher, Goldstein, Michel, Blin, Tuval PRL 200

- We close this lecture by sketching Batchelor's 1970 result that the particle contribution to the mean stress in a suspension is given by the stresslet/volume.



← dilute solution of swimmers

$$\Sigma_{ij} \equiv \int_V \sigma_{ij} dV / V$$

↑ includes the cell volumes

steps (See Lauga's book for details)

- write the volume as $V = V - V_{\text{swimmers}} + V_{\text{swimmers}}$
- use Stokes + integration by parts to write

$$\Sigma_{ij} = \frac{1}{V} \int_{V - V_{\text{swimmers}}} [-p \delta_{ij} + \eta (\partial_i u_j + \partial_j u_i)] dV + \frac{1}{V} \int_{V_{\text{swimmers}}} \sigma_{ij} dV$$

$\underbrace{\hspace{10em}}_{\text{mean swimmer stress}}$

let $V_0 = V_{\text{swimmers}}$

Here we summarize the main steps from Langa 2020:

$$\int_{V_{\text{swimmers}}} \sigma_{ij} dV = \int_{V_0} \left[\partial_k (\sigma_{ik} x_j) - \overset{\text{stress}}{(\partial_k \sigma_{ik})} x_j \right] dV = \int_{S_0} \sigma_{ik} x_j dS$$

hard to know
sum over surface of all swimmers
easier to know

Next, write the integral over $V-V_0$ in terms of

$$\underbrace{\partial_j U_i}_{\text{mean velocity gradient}} \equiv \frac{1}{V} \int_V \partial_j \sigma_i dV \underset{\text{entire volume}}{=} \frac{1}{V} \int_{V-V_0} \partial_j u_i dV + \int_{V_0} \partial_j u_i dV$$

$$= \frac{1}{V} \int_{V-V_0} \partial_j u_i dV + \frac{1}{V} \int_{S_0} u_i n_j dS$$

$$\therefore \Sigma_{ij} = -\frac{1}{V} \int_{V-V_0} p \delta_{ij} dV + \eta (\partial_i U_j + \partial_j U_i) + \Sigma_{ij}^s$$

$$\text{with } \Sigma_{ij}^s = \frac{1}{V} \int_{S_0} \left[\sigma_{ik} x_j n_k - \mu (\nu_i n_j + \nu_j n_i) \right] dS$$

$$= \left(\Sigma_{ij}^s - \frac{1}{3} \delta_{ij} \Sigma_{kk}^s \right) + \frac{1}{3} \delta_{ij} \Sigma_{kk}^s$$

$$\equiv \Sigma_{ij}^{s, \text{dev}} + \frac{1}{3} \delta_{ij} \Sigma_{kk}^s \quad \text{"dev" for deviatoric}$$

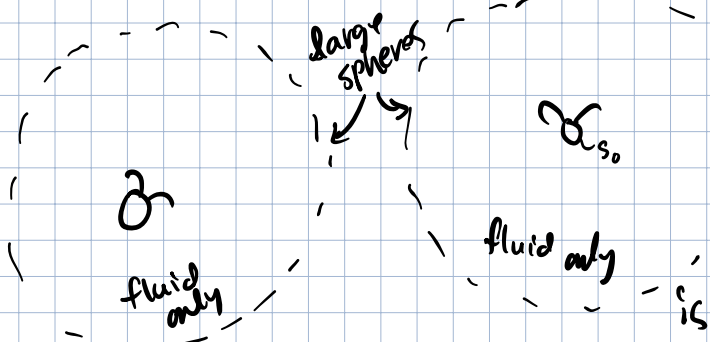
$$\Sigma_{ij}^{s, \text{dev}} = \frac{1}{V} \int_{S_0} \left[\sigma_{ik} x_j n_k - \frac{1}{3} \sigma_{kk} x_i n_k \delta_{ij} - \eta (\nu_i n_j + \nu_j n_i) \right] dS$$

Batchelor 1970

$$\Sigma_{ij} = -P \delta_{ij} + \eta (\partial_j U_i + \partial_i U_j) + \Sigma_{ij}^{s, \text{dev}} ; P = \frac{1}{V} \int_{V-V_0} p dV - \frac{1}{3} \Sigma_{kk}^s$$

key step: for a sufficiently dilute suspension, we may replace the integrals over the surfaces with integrals over large spheres - one surrounding

each swimmer, with only fluid between the swimmer's surface and its surrounding sphere.



We assume the dominant component of the flow at a sphere is the stresslet flow of the swimmer at the center of the sphere, and we disregard the contributions from swimmers outside a given sphere. Calculate! Starting from

$$v_i = -\frac{3}{8\pi\eta} x_i \frac{\sum_j S_{ij} x_j}{|\underline{x}|^3}, \text{ show } p = -\frac{3}{4\pi} \frac{x_i S_{ij} x_j}{|\underline{x}|^3} \text{ and}$$

$$\sigma_{ij} = \frac{3\eta k_B T}{4\pi} \left[\frac{\sum_k x_i x_j x_k x_k}{|\underline{x}|^3} - \frac{\delta_{ik} x_k x_j + \delta_{jk} x_k x_i}{|\underline{x}|^3} \right].$$

Then use Batchelor's formula to get

$$\sum_{ij}^{\text{dev}} = \sum_{ij} - \frac{1}{3} \delta_{ij} \sum_{ii} = \frac{1}{V} \sum_{\text{swimmers}} S_{ij}$$

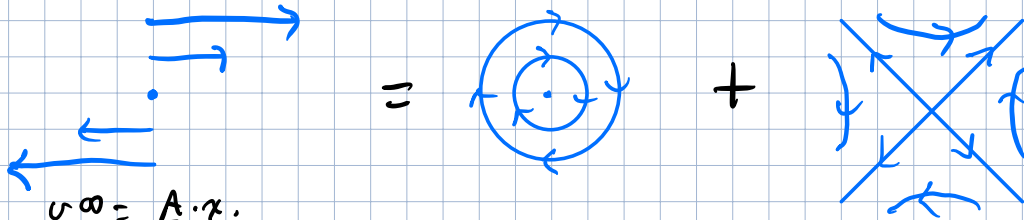
or $\sum_{ij}^{\text{dev}} = \frac{n}{N} \sum_{\text{swimmer}} S_{ij}$

$n = \text{swimmer concentration}$
 $N = \# \text{ swimmers}$

- Batchelor's formula applies to passive and active suspensions. As an application, consider a dilute suspension of passive spheres in a shear flow, and calculate

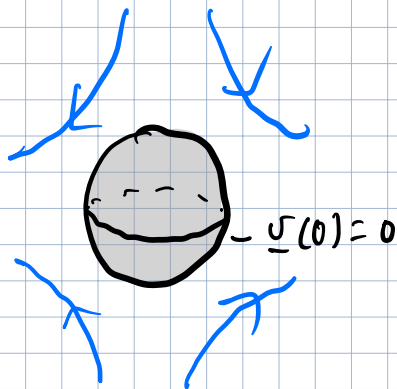
their contribution to the shear viscosity.

shear flow = rotation + extensional flow



$$\underline{v}^\infty = \begin{pmatrix} 0 & \dot{\gamma} \\ 0 & 0 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 0 & \dot{\gamma}/2 \\ -\dot{\gamma}/2 & 0 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} 0 & \dot{\gamma}/2 \\ \dot{\gamma}/2 & 0 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

Solve flow around a sphere with $\underline{v} \rightarrow \underline{v}^\infty$ as $r \rightarrow \infty$. The rotating part does not lead to a stresslet and \therefore does not contribute to the mean stress. Solve for a



sphere in an extensional flow to find

$$\underline{v} = \underline{v}^\infty - \frac{5}{2} a^3 \underline{x} \frac{\underline{x} \cdot \underline{E}^\infty \cdot \underline{x}}{|\underline{x}|^5} + \text{potential quadrupole}$$

(where $\underline{E}^\infty = \frac{1}{2} \underline{A} + \frac{1}{2} \underline{A}^T$)

$$\text{cf. } \frac{-3}{8\pi\eta} \frac{\underline{x} \cdot \underline{S} \cdot \underline{x} \cdot \underline{x}}{|\underline{x}|^5} = -\frac{5}{2} a^3 \frac{\underline{x} \cdot \underline{E}^\infty \cdot \underline{x} \cdot \underline{x}}{|\underline{x}|^5}$$

$$\Rightarrow \underline{S} = \frac{20}{3} \pi \eta a^3 \underline{E}^\infty$$

The contribution to the stress is
therefore $\underline{\underline{\Sigma}} = \frac{20}{3} \pi \eta a^3 n \underline{\underline{E}}^\infty$

Defining the volume fraction as

$$\phi = \frac{4}{3} \pi a^3 \cdot n, \text{ we find } \underline{\underline{\Sigma}} = \frac{5}{2} \eta \phi \underline{\underline{E}}^\infty.$$

Total viscosity
in the dilute
limit

solvent viscosity
↓

$$\eta = \eta_0 + \eta_p = \eta \left(1 + \frac{5}{2} \phi \right)$$

Einstein 1908

only accurate for
 $\phi \leq 0.03$

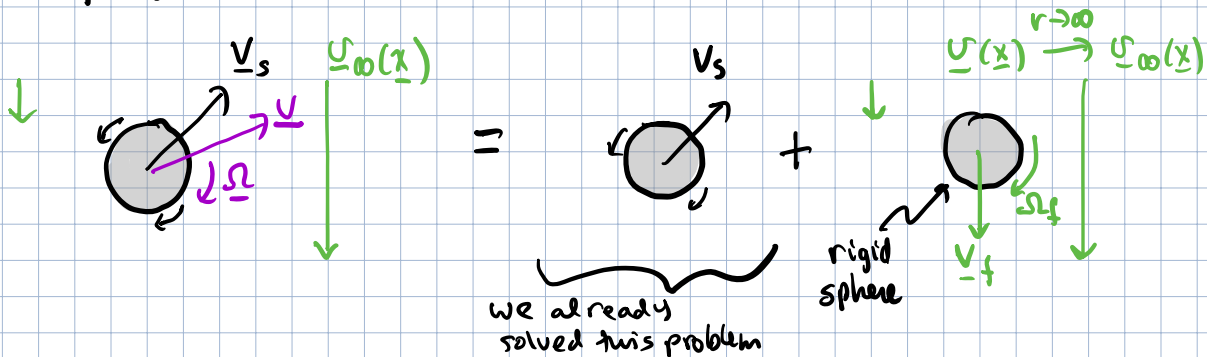
Lecture 3: Interactions + collective motion at $Re=0$

Thursday 11am - 12:30pm 2022-07-28

outline for today

1. swimmers in an external flow
2. interaction between swimmers (dilute case)
3. linear stability analysis of isotropic state

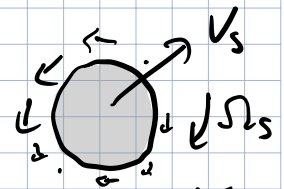
● How does a squirmer swim in an externally imposed flow?



$$\underline{V} = \underbrace{\underline{v}_s}_{\text{"swimmer"}} + \underbrace{\underline{v}_f}_{\text{"flow"}}$$

$$\underline{\Omega} = \underline{\Omega}_s + \underline{\Omega}_f$$

we've only looked at swimmers that don't rotate as they swim, but in general, there could be rotation, say if one side beats more than the other



Last time I just stated the solution to the problem of a force-free and torque-free sphere in a (linear) external flow. It turns out that the reciprocal theorem

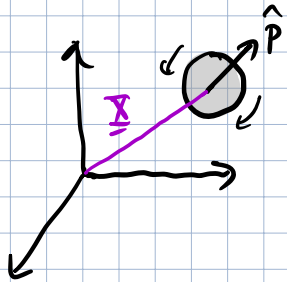
Leads to simple formulas for the linear and angular velocity of a rigid sphere in flow. These formulas are called "Faxén's laws." To derive them, take problem #1 to be a translating, rotating sphere with $\underline{u} \rightarrow 0$ as $r \rightarrow \infty$. Let problem #2 be the disturbance flow $\underline{u} - \underline{u}^\infty$ of the problem we want to solve. Then we can show that

$$\underline{V}_f = \underline{u}^\infty(\underline{0}) + \frac{a^2}{6} \nabla^2 \underline{u}^\infty \Big|_{\underline{0} \leftarrow \text{sphere center}}$$

$$\underline{\Omega}_f = \frac{1}{2} \nabla \times \underline{u}^\infty \Big|_{\underline{0}} \quad (\text{see any of the Stokes flow books})$$

The background flow \underline{u}^∞ advects the sphere like a point particle at the center of the sphere, with a finite-size correction whenever the background streamlines are sufficiently curved. If the scale of variation l of \underline{u}^∞ is large compared to the swimmer size a , then we may neglect the correction. Indeed a/l is typically small for swimmers. Note that $\nabla^2 \underline{u}^\infty = 0$ for linear flows: shear, rigid-body rotation, and pure extension. Note also that a sphere in steady linear flow rotates at a constant rate, half the vorticity.

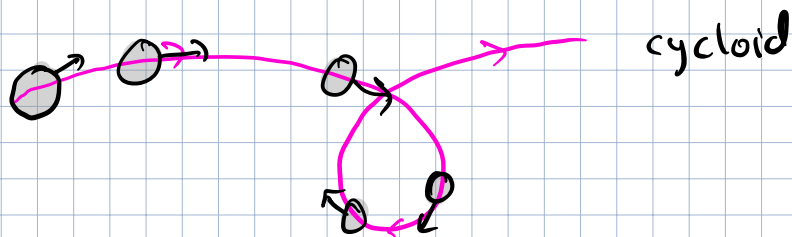
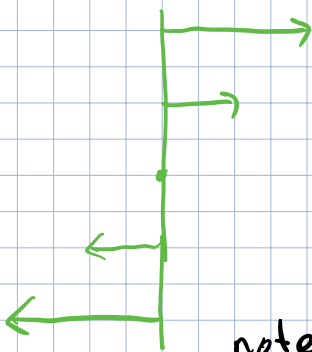
We can use these results to solve for (deterministic) swimmer trajectories:



$$\dot{\underline{x}} = \underline{v}_s + \underline{v}_\omega |_{\underline{x}} + \frac{a^2}{6} \nabla^2 \underline{v}_\omega |_{\underline{x}}$$

$$\dot{\hat{p}} = \left(\underline{\Omega}_s + \frac{1}{2} \nabla \times \underline{v}_\omega |_{\underline{x}} \right) \times \hat{p}$$

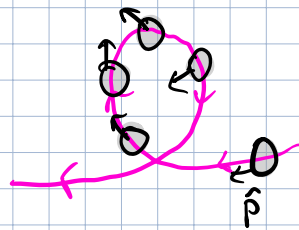
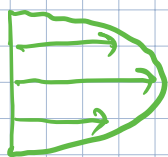
These trajectories can be found analytically for some simple flows, such as simple shear



cycloid

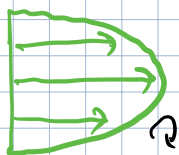
note: noise alters the trajectory, damping out the oscillations e.g. ten Hagen, Wittkoski + Löwen 2011

Poiseuille flow



upstream "swinging"

\hat{p} oscillates between two extremes



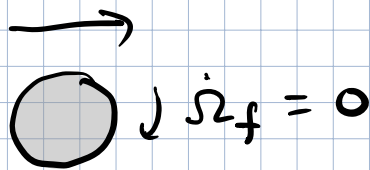
down stream "tumbling"

Zöttl + Stark 2012

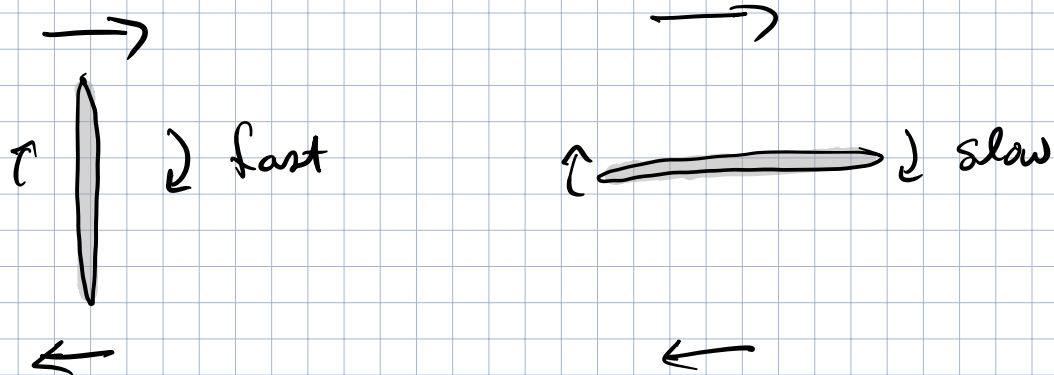
Rusconi et al. 2012: Noise \Rightarrow a single *E. coli* can switch between upstream and downstream trajectories

See Junot, Figueroa-Moreals et al. 2019 EPL 3D tracking of *E. coli* in Poiseuille flow. *E. coli* are more like rods than spheres - role of Jeffrey orbits.

Spheres rotate steadily in constant shear



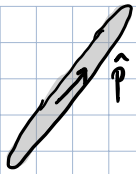
Rods have a time-dependent rotation rate



- The orbit of a rod in shear is called a Jeffrey orbit.

Exercise: Using resistive force theory with

$S_{\perp} = 2S_{\parallel}$, impose zero total hydrodynamic force and torque on a thin rod in



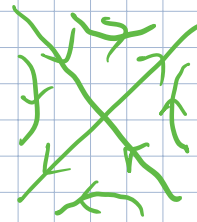
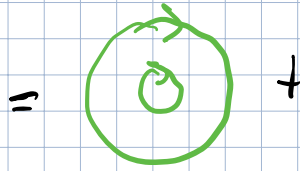
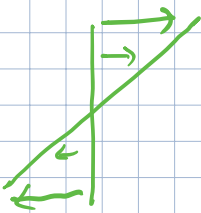
a linear flow $\underline{v} = \underline{A} \cdot \underline{x}$ (A_{ij} constant)
and show that

$$\dot{p}_i = \frac{1}{2} (\underline{\omega} \times \hat{p})_i + (\delta_{ij} - p_i p_j) E_{jk} p_k$$

$\omega = \nabla \times v$ $E_{jk} = \frac{1}{2} (\partial_j v_k + \partial_k v_j)$

or $\dot{p}_i = W_{ij} p_j + (\delta_{ij} - p_i p_j) E_{jk} p_k$

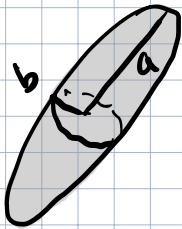
$$W_{ij} = \frac{1}{2} (\partial_j v_i - \partial_i v_j)$$



one component
of rotation
is like Faxén
for a sphere

one component
is time-dependent

1922 Jeffery - exact result for an ellipsoid

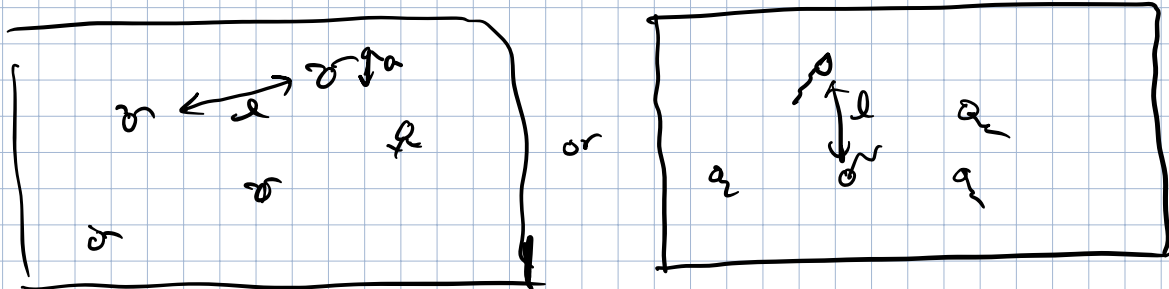


$$\dot{p}_i = W_{ij} p_j + B (\delta_{ij} - p_i p_j) E_{jk} p_k$$

$$B = \frac{r^2 - 1}{r^2 + 1} \quad r = \frac{a}{b} \quad \begin{array}{l} r=1 \text{ sphere} \\ r \gg 1 \text{ rod} \end{array}$$

This formulas have many applications -
see Langa's book. We'll use it to
study the linear stability of a collection
of swimmers.

- Last topic: a minimal continuum model for a dilute suspension of swimmers.



We'll use distribution functions as is commonly done in polymer physics e.g. Doi + Edwards "Theory of polymer dynamics" 1988

Dilute limit \Rightarrow each swimmer sees only the stresslet of the other swimmers, leading to reorientation as well as an active stress that drives flow

$$\Phi(\underline{x}, \hat{p}, t) d^3x d\Omega = \# \text{ swimmers in volume } d^3x \text{ about } \underline{x} \text{ and solid angle } d\Omega \text{ about } \hat{p}$$

not momentum!

$$\# \text{ density } n(\underline{x}, t) = \int \Phi d\Omega$$

$$\frac{\partial \Phi}{\partial t} + \frac{\partial}{\partial x_i} J_{x_i} + \left(\frac{\partial}{\partial \hat{p}_i} \right) J_{\hat{p}_i} = 0$$

$$\left(\frac{\partial}{\partial \mathbf{p}}\right)_i = (\delta_{ij} - p_i p_j) \frac{\partial}{\partial p_j}$$

Φ can change because particles move due to swimming, flow, or Brownian motion

$$\underline{I}_x = v \hat{p} \Phi + \underline{v}(x, t) \Phi - D \frac{\partial \Phi}{\partial x}$$

likewise, Φ can change due to

rotational swimming motion, flow, or Brownian motion

$$\underline{I}_{\hat{p}} = \underline{\Omega} \times \hat{p} \Phi + \left[\underline{\omega} + B(\mathbb{I} - \hat{p} \hat{p}^T) \cdot \underline{E} \cdot \hat{p} \right] \Phi - D_r \frac{\partial \Phi}{\partial \hat{p}}$$

We neglect rotation from swimming and Brownian motion: $\underline{\Omega} = 0$, $D = 0$, $D_r = 0$ (for illustration purposes).

Recall

$$v_i = -\frac{3}{8\pi\eta} \frac{x_i x_j S_{jk} x_k}{|x|^5}$$

$$S_{ij} = \mathcal{P} \left(\frac{1}{3} \delta_{ij} - p_i p_j \right)$$

$\mathcal{P} \gtrless 0$ pushers pullers

$$\sum_{ij} s_{ij}^{\text{dev}} = \int \Phi(x, \hat{p}, t) S_{ij} d\Omega \quad \text{from Batchelor}$$

$$= -\mathcal{P} \int \Phi (p_i p_j - \frac{1}{3} \delta_{ij}) d\Omega$$

$$\equiv \mathcal{P} n Q_{ij}$$

$$Q_{ij} = S (p_i p_j - \frac{1}{3} \delta_{ij})$$

nematic order-parameter tensor for the swimmers

The flow obeys

- the stresslet flow has
nematic symmetry $\hat{p} \mapsto -\hat{p}$

$$-\nabla P + \eta \nabla^2 \underline{v} - \rho \nabla \cdot (\eta \underline{Q}) = 0$$

assume uniform concentration for today:

$$-\nabla P + \eta \nabla^2 \underline{v} - a \nabla \cdot \underline{Q} = 0 \quad a = \rho n$$

$$\partial_t \Phi + \frac{\partial}{\partial x_i} \left[v p_i \Phi + \underline{v}_x \cdot \Phi \right] + \left(\frac{\partial}{\partial \hat{p}} \right)_i \left\{ \left[W_{ij} p_j + B(\delta_{ij} - p_i p_j) E_{jk} p_k \right] \Phi \right\} = 0$$

the swimmers
are advected
by the flows from
the otters - we
neglect the finite-
size corrections like what
we saw in Faxén's
law.

for orientation effects,
we treat the flow induced
by the swimmers as
a linear flow

Linear stability analysis of the isotropic
state with zero mean velocity

Saintillan +
Shelley PRL 2008

$$\Phi = \frac{n_0}{4\pi} + \Phi_1 = \frac{n_0}{4\pi} + \tilde{\Phi}(\underline{k}) e^{i\underline{k} \cdot \underline{x} + \sigma t}$$

$$\underline{v} = \tilde{v}(\underline{k}) e^{i\underline{k} \cdot \underline{x} + \sigma t}$$

linearize

$$\partial_t \Phi_1 + v \hat{p} \cdot \frac{\partial}{\partial \underline{x}} \Phi_1 - 3B \hat{p} \cdot \underline{E}_1 \cdot \hat{p} \Phi_0 = 0$$

$$-\nabla P_1 + \eta \nabla^2 \underline{v}_1 - \rho \nabla \cdot \int \Phi_1 \hat{p}' \hat{p}' d\Omega' = 0$$

(we absorbed the isotropic part
of \underline{Q}_1 into P_1)

Now use the $e^{i\mathbf{k}\cdot\mathbf{x} + \sigma t}$ dependence

$$\nabla \cdot \underline{v}_1 = 0 \Rightarrow P_1 = -\rho \hat{k} \cdot \int \tilde{\Psi} \hat{p}' \hat{p}' d\Omega' \cdot \hat{k}$$

solve Stokes to get

$$\underline{v}_1 = -i \frac{\rho}{\eta k} (\mathbb{I} - \hat{k} \hat{k}) \int \tilde{\Psi} \hat{p}' \hat{p}' d\Omega' \cdot \hat{k}$$

calculate $\underline{\underline{\epsilon}}_1 = \frac{1}{2} (i\mathbf{k} \underline{\underline{\sigma}} + i\underline{\underline{\sigma}} \mathbf{k})$

and find

$$(\sigma + i\mathbf{k} \cdot \hat{p} V) \tilde{\Psi} = \frac{3B\rho}{\eta} \hat{p} \cdot \hat{k} \hat{p} \cdot (\mathbb{I} - \hat{k} \hat{k}) \int \tilde{\Psi} \hat{p}' \hat{p}' d\Omega' \cdot \hat{k}$$

\underline{v}_1 is along \hat{k}_\perp

This suggests $\tilde{\Psi} = \hat{p} \cdot \hat{k} \hat{p} \cdot \hat{k}_\perp f(\mathbf{k} \cdot \hat{p})$

Let's just get the $k \rightarrow 0$ limit of the growth rate σ : $\tilde{\Psi} \xrightarrow{k \rightarrow 0} \hat{p} \cdot \hat{k} \hat{p} \cdot \hat{k}_\perp \Gamma$

where Γ is a constant.

Thus

$$\sigma = \frac{n_0 \rho B}{5\eta}$$

in the limit of $k \rightarrow 0$

- spherical swimmers $B=0$ are neutrally stable
- elongated swimmers $B>0$ are

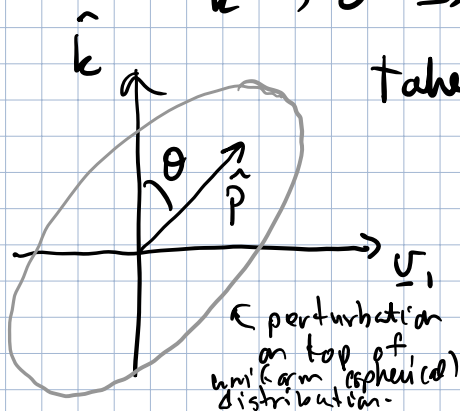
(of course we must check $k \neq 0$ to make this statement) \rightarrow stable if they are pullers $P < 0$

unstable if they are pushers $P > 0$

• $\sigma(k=0)$ is independent of swimming velocity V , so active extensile nematics undergo are also unstable, as we saw in the complementary approach (dynamics of \underline{v} and \underline{Q}) taken by Julia Yeomans and Suzanne Fielding in their lectures. See e.g. the supplementary material to Soni, Pelcovits, Powers PRL 2018 or the more complete treatment in Santhosh et al. J Stat Phys 2020.

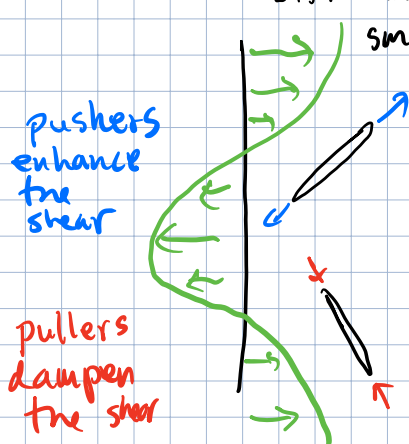
• Interpretation:

$$k \rightarrow 0 \Rightarrow \tilde{\Psi}_1 \propto \hat{p} \cdot \hat{k} \hat{p} \cdot \hat{k}_\perp \propto \sin 2\theta$$



take $\hat{k} \parallel p_z$ axis, $\tilde{v}_1 \parallel p_x$ axis

\tilde{v}_1 and $\tilde{\Psi}$ have a relative factor of $i \Rightarrow$ they are out of phase by $\pi/2$.



} alignment
 } no alignment
 } alignment

spherical swimmers don't align

Conclusions

- We developed the physical framework for studying the hydrodynamics of propulsion mechanisms used by microorganisms, including the basics of how flow affects swimmers and how they affect each other through hydrodynamics.
- These simple calculations can be extremely helpful before any attempts of doing numerical computation, which is inevitably required because of nonlinearities.
- There is still plenty of room to apply these approaches to problems in marine biology, reproduction, and infectious diseases.