The Hydrodynamics of Active Matter

Julia Yeomans
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Lecture 1: The mathematics and physics of bacterial swimming

1. Low Re and the Stokes equations
2. The Scallop theorem
3. Dipolar flow fields
4. Multipole expansion for the Stokes equations

Lecture 2: Applications

1. Swimming in Poiseuille flow and ...taxis
2. Stirring by microswimmers

Lecture 3: Continuum models of dense active matter

Lecture 4: Active turbulence and lyotropic active nematics
Phase portrait of a pendulum

\[ \ddot{\psi} + \sin \psi = 0. \]

\[ \dot{x} = -\sin \psi, \quad \dot{\psi} = x \]
The cell (indicated by the black arrow) moves in a sinusoidal trajectory (discussed below) as shown in the stroboscopic image. The observed trajectories are well fitted by sine waves, and the frequency and amplitude of oscillations are shown in Fig. 2. Increasing velocities result in increasing frequency and decreasing amplitude of the trajectories.

Oscillatory trajectories at a range of flow velocities are recorded. A suspension of T. brucei, which was taken with fluorescently labeled trypanosome, is included in the cell suspension as tracers for flow. It can be readily appreciated that this oscillatory behavior is a direct consequence of the interplay between the Poiseuille flow field and the active motion of the trypanosome. Increasing velocities result in increasing frequency and decreasing amplitude of oscillations. Increasing velocities result in increasing frequency and decreasing amplitude of oscillations.

Intriguingly, when we observe the cells at lower magnification, they are able to swim the width of the channel, whereas a dead cell stays at the top channel wall. A cell moving in pressure-driven flow through a microfluidic channel is carried by the flow. (1164)

The cell's actual trajectory is superimposed to the overlay of all frames in the montage, clearly showing the cell moving toward and away from boundaries in the same lateral position and is carried by the flow. The average flow velocities either by measuring Simpsons, illustrates that a swimming cell appears to move laterally across the width of the channel, while an immotile cell is able to turn within the channel, as applicable to the motion of microswimmers in parabolic flow. All observations are recorded only for cells in the middle plane (of the same length scale as the entity). Considering the effect of flow on the swimming speed of cells, the trypanosome's ability to swim is much higher than their own velocity, live trypanosomes, illustrates that a swimming cell appears to move laterally across the width of the channel, while an immotile cell is able to turn within the channel, as applicable to the motion of microswimmers in parabolic flow. All observations are recorded only for cells in the middle plane (of the same length scale as the entity). The swimmer is constrained to propel itself clearly continues to play a role in its behavior relative to the fluid, and may be a generic feature of self-propelled microorganisms that can be deconstructed into physical terms.

Typannosome

Uppaluri Biophys J (2012)
Poiseuille flow and notation

\[ \mathbf{v}_f = v_f (1 - x^2) \hat{Z} \]

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\[ \hat{e} = -\sin \psi \hat{x} - \cos \psi \hat{z}, \]

speed \[ v_0 \]
Swimmer model

\[ \hat{e} = -\sin \psi \hat{x} - \cos \psi \hat{z}, \]

\[ \frac{d}{dt} \mathbf{r} = v_0 \hat{e} + \mathbf{v}_f, \quad \frac{d}{dt} \hat{e} = \frac{1}{2} \Omega_f \wedge \hat{e}. \]
Swimmer model

direction

\[ \hat{\mathbf{e}} = -\sin \psi \hat{\mathbf{x}} - \cos \psi \hat{\mathbf{z}}, \]

speed \( v_0 \)

\[
\frac{d}{dt} \mathbf{r} = v_0 \hat{\mathbf{e}} + \mathbf{v}_f, \quad \frac{d}{dt} \hat{\mathbf{e}} = \frac{1}{2} \Omega_f \wedge \hat{\mathbf{e}}.
\]

NB scale time with \( v_0 \)
\[ \hat{e} = -\sin \psi \hat{x} - \cos \psi \hat{z}, \]
\[ \mathbf{v}_f = v_f (1 - x^2) \hat{z} \]

\[ \frac{d}{dt} \mathbf{r} = \hat{e} + \frac{\mathbf{v}_f}{v_0} \]

x-component
\[ \frac{d}{dt} x = -\sin \psi \]

z-component
\[ \frac{d}{dt} z = -\cos \psi + \frac{v_f}{v_0} (1 - x^2) \]
\[ \Omega_f = \nabla \wedge \mathbf{v}_f = (0, 2xv_f, 0) \]
\[ \dot{\hat{e}} = -\sin \psi \hat{x} - \cos \psi \hat{z}, \]
\[ \frac{d}{dt} \hat{e} = \frac{1}{2v_0} \Omega_f \wedge \hat{e}. \]
\[ -\cos \psi \psi = -\frac{xv_f \cos \psi}{v_0} \]
\[ \dot{\psi} \sin \psi \psi = \frac{xv_f \sin \psi}{v_0} \]
\[
\frac{d\psi}{dt} = \frac{v_f}{v_0} x \\
\frac{d}{dt} x = -\sin \psi \\
\frac{d}{dt} z = -\cos \psi + \frac{v_f}{v_0}(1 - x^2)
\]
\[
\frac{d\psi}{dt} = \frac{v_f}{v_0} x
\]

\[
\frac{d}{dt} x = -\sin \psi
\]

\[
\ddot{\psi} + \frac{v_f}{v_0} \sin \psi = 0.
\]

\[
\frac{d}{dt} z = -\cos \psi + \frac{v_f}{v_0} (1 - x^2)
\]
Trajectories correspond to the circling solution of the pendulum and typical trajectories the swimmer performs a tumbling motion (vorticity rotates the swimmer a way from the centerline). The arrows indicate the orientation vector which corresponds to the oscillating solution of the mathematical pendulum two swimming states exist. The flow vorticity rotates the upstream oriented microswimmer always towards the center. Hence, the swimmer performs a swinging motion between the walls with maximum amplitudes (c)–(e) sketch of trajectories in the channel for helical motion (d) and tumbling motion (e). Note the various scales which is the equation of motion of the mathematical pendulum.

When the upstream oriented swimmer moves exactly in the center of the channel (stable fixed point), the Hamiltonian is immediately write down the 2D Hamiltonian with the channel wall, the swimmer crashes into the wall at crossing the centerline. So, for a nonzero azimuthal component, Eqs. (3)–(5) and (6) do not L_\text{const} = \frac{\sin \phi}{\sin \theta}, whereas it tumbles close to the wall for v_f > H_\text{const} = \frac{\cos \phi}{\cos \theta}. For a nonzero azimuthal component, Eqs. (3)–(5) give the intersection curve) for

\[ x(t) = \sin \left( \frac{\omega t}{2} \right), \]

\[ z(t) = \cos \left( \frac{\omega t}{2} \right), \]

where \( \omega \) is the angular frequency of the oscillation.

A careful analysis reveals the following. The swimmer in the direction. Because of this constant the swimmer always enters a swinging motion between

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frames in the montage, clearly showing the cell moving toward and away from the top panel, the cell's actual trajectory is superimposed to the overlay of all frames in the montage. (1)

The cell (indicated by the black arrow) is a cell moving in pressure-driven flow through a microfluidic channel. Despite the channel flow velocity of 1.6 mm/s, which is much higher than their own velocity, live trypanosomes, illustrated in Fig. 2a, are able to swim the width of the channel, whereas a dead cell stays immotile (Fig. 2b).

Intriguingly, when we observe the cells at lower magnification, we see that the trypanosomes oscillate in a regular manner, as applicable to the motion of microswimmers in parabolic flow. All observations are recorded only for cells in the middle plane (of the same length scale as the euille flow field and the active motion of the trypanosome, which is a direct consequence of the interplay between the Pois-sion ratio of the swimmer and the flow velocity, as shown in previous work (11,25–27). The oscillatory trajectories at a range of flow velocities are fitted to sine waves, and the frequency and amplitude of oscillations are shown in Fig. 3. A suspension of Polystyrene beads (Polysciences, Eppelhem Germany), 1 μm in diameter, are mixed with the sample and then injected into the channel at a sufficient dilute concentration of polystyrene beads, 1 μm in diameter, in a microfluidic channel with radius R and an immotile cell (m) and a live cell (m).

Although several studies have shown that deformable vesicles and cells display oscillatory movements in pressure-driven flow (20,25,26), both fluorescently labeled trypanosomes and immotile cells are used as tracers for flow. To investigate the behavior of trypanosomes, both live and immotile, in flow, we begin with a geometry of equal height and width of 23 mm, which was taken with fluorescently labeled trypanosome suspension injection, as shown in Fig. 4. A suspension of trypanosomes, illustrates that a swimming cell appears to move downstream with the flagellum end leading (though they do not necessarily progress upstream due to the flow) from one wall to another in a sine wave trajectory, as shown in Fig. 2c. The trajectory in (1) is superimposed to the overlay of all frames in the montage. (1)

The trajectory in Fig. 2c is fitted to sine waves, and the frequency and amplitude of oscillations are shown in Fig. 3. Oscillatory trajectories at a range of flow velocities are fitted to sine waves, and the frequency and amplitude of oscillations are shown in Fig. 3. Oscillatory trajectories at a range of flow velocities are fitted to sine waves, and the frequency and amplitude of oscillations are shown in Fig. 3. Oscillatory trajectories at a range of flow velocities are fitted to sine waves, and the frequency and amplitude of oscillations are shown in Fig. 3. Oscillatory trajectories at a range of flow velocities are fitted to sine waves, and the frequency and amplitude of oscillations are shown in Fig. 3.
what is missing?

3D interactions with walls swimmer size and shape fluctuations
alignment with a given direction

gravitaxis – like to swim upwards

chemotaxis – follow a chemical gradient

magnetotaxis – follow a magnetic field

rheotaxis – shear + gravity

phototaxis – follow light

Why can’t you trust an atom?
They make up everything.
\[
\frac{d\hat{e}}{dt} = \frac{1}{2} \{\Omega_f \wedge \hat{e} + \frac{1}{\beta} (\hat{z} - (\hat{z} \cdot \hat{e})\hat{e})\}
\]

\[
\sin \theta = \beta \Omega
\]
Thin layers of phytoplankton are important hotspots of ecological activity that are found in the coastal ocean, meters beneath the surface, and contain cell concentrations up to two orders of magnitude above ambient concentrations. Current interpretations of their formation favor abiotic processes, yet many phytoplankton species found in these layers are motile. We demonstrated that layers formed when the vertical migration of phytoplankton was disrupted by hydrodynamic processes, yet many phytoplankton species found in these layers are motile. We demonstrated that the coupling between active microorganism motility and ambient fluid motion can shape the macroscopic features of the marine ecological landscape. Photosynthetic organisms known as thin layers. These results reveal that the coupling between active motility and shear. This mechanism, which we call gyrotactic trapping, can be responsible for the thin layers of phytoplankton commonly observed in the ocean. These results reveal that the coupling between active motility and ambient fluid motion can shape the macroscopic features of the marine ecological landscape. Photosynthetic organisms known as thin layers.
was parabolic, stabilizing gravitational torque that acts to orient the associated shear. Corresponding profile of measured flow velocities triggered layer formation by exposing toxic raphidophyte (Fig. 1B). We demonstrated that gyrotactic trapping can disrupt vertical migration direction sin θ. (Inset) Thin layers of 

\[ \text{Phytoplankton Layers} \]

\[ \text{Chlamydomonas nivalis} \]

is a classic model for photosynthetic organisms known as thin layers. (Fig. 2A). The dynamics revealed the occurrence throughout the body density (\( \rho \)), and internal concentrations essential for the survival of some phytoplankton species found in these layers are grazing, enhance zooplankton and fish mortality. Thin layers can disrupt vertical migration direction sin θ. (Inset) Thin layers of toxic phytoplankton species found in these layers are grazing, enhance zooplankton and fish mortality.

\[ \text{Fig. 1.} \]

Experimental apparatus and the deterioration in swimming direction result from shape or sensing. When considering the vorticity component of fluid viscosity, and gyrotactic reorientation time scale, \( \text{gyrotaxis} (S < S_{CR}) \) to torques. Cells \( |S| < S_{CR} \) tumble (Fig. 1B). We demonstrated that gyrotactic trapping can be responsible for the thin layers of phytoplankton species found in these layers are grazing, enhance zooplankton and fish mortality. Thin layers can disrupt vertical migration direction sin θ. (Inset) Thin layers of toxic phytoplankton species found in these layers are grazing, enhance zooplankton and fish mortality.

\[ \text{Fig. 2.} \]

Formation of a thin layer. (\( |S| > S_{CR} \)) Multiple-iso of thin phytoplankton species found in these layers are grazing, enhance zooplankton and fish mortality. Thin layers can disrupt vertical migration direction sin θ. (Inset) Thin layers of toxic phytoplankton species found in these layers are grazing, enhance zooplankton and fish mortality.

\[ \text{Fig. 3.} \]

\[ \text{Chlamydomonas nivalis} \]

is the motile phytoplankton accumulates where shear varying shear generated a depth-accumulated phytoplankton layers contain elevated amounts of photosynthetic organisms known as thin layers. (\( |S| > S_{CR} \)) iso of thin phytoplankton species found in these layers are grazing, enhance zooplankton and fish mortality. Thin layers can disrupt vertical migration direction sin θ. (Inset) Thin layers of toxic phytoplankton species found in these layers are grazing, enhance zooplankton and fish mortality.
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Stirring by microswimmers

Do microswimmers stir the fluid they swim in?

Why do microswimmers stir the fluid they swim in?

How do microswimmers stir the fluid they swim in?
Swimmers enhance diffusion

Leptos et al., PRL 103 (2009)
Stirring by microswimmers

Do microswimmers stir the fluid they swim in?

Why do microswimmers stir the fluid they swim in?

How do microswimmers stir the fluid they swim in?
Where does bad light end up?
In a prism.

Multipole flow fields

Dipole flow field
Multipole flow fields

Dipole flow field

dipole loop
Multipole flow fields

Dipole flow field

Dipole loop

Quadrupole loop
Enhanced diffusion and loops

Entrainment
Swimmer re-orientations
Entrainment

Dipole flow field
Boundary element simulations

Solve Stokes equations, no slip on swimmer surface, swimmer force and torque free

Swimmer radius 1; swimmer velocity 1; ~10 rotations of tail to advance one body length

Net tracer displacement along z – deviations from the z-direction very small

Swimmer moves from z= -1000 to z= +1000, and extrapolate to infinite swimmer path
Darwin drift
Darwin drift

Total fluid volume moved by swimmer

Darwin drift:
\[
 u_D = \frac{4\pi Q_\perp}{V} - u_*, \\
 u_* = u_s + u_{\text{wake}}
\]

\[
 Q_\perp = -\frac{1}{2} \int_S f_z \rho^2 dS
\]

Darwin
Benjamin
Eames
Belcher
Hunt
Gobby
Dalziel
Leshansky
Pismen
Comparison of analytic and numerical results for the Darwin drift

Table 1. Base parameters: $L_\parallel/L_\perp = 2$, $\lambda = 2$, $L = 10$, $a = \lambda/2\pi$.

<table>
<thead>
<tr>
<th>Shape</th>
<th>$Q_\perp/V$</th>
<th>$v_D$ (from equation)</th>
<th>$v_D$ (from simulations)</th>
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</thead>
<tbody>
<tr>
<td>Base</td>
<td>-0.15</td>
<td>-6.10</td>
<td>-6.11</td>
</tr>
<tr>
<td>$L_\parallel/L_\perp = 0.5$</td>
<td>-0.68</td>
<td>-12.74</td>
<td>-12.78</td>
</tr>
<tr>
<td>$L_\parallel/L_\perp = 3.5$</td>
<td>-0.08</td>
<td>-5.24</td>
<td>-5.33</td>
</tr>
<tr>
<td>$L = 5$</td>
<td>-0.17</td>
<td>-6.36</td>
<td>-6.30</td>
</tr>
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<tr>
<td>$\lambda = 3.5$</td>
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</tr>
<tr>
<td>$\lambda = 8$, $L = 20$</td>
<td>0.58</td>
<td>3.04</td>
<td>3.07</td>
</tr>
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Darwin drift:

\[
Q_\perp = -\frac{1}{2} \int_S f_z \rho^2 dS
\]

\[
v_D = \frac{4\pi Q_\perp}{V} - v_*,
\]

\[
v_* = v_s + v_{\text{wake}}
\]
Darwin drift
Comparison of analytic and numerical results for the Darwin drift

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Darwin drift:

$$Q_{\perp} = -\frac{1}{2} \int_{S} f_z \rho^2 dS$$
$$v_D = \frac{4\pi Q_{\perp}}{V} - v_*$$
$$v_* = u_s + v_{wake}$$
Entrainment

Tracer moves in loops far from swimmer
Entrainment close to the swimmer

Volume of fluid moved by the swimmer:

Darwin drift:

\[ v_D = \frac{4\pi Q}{V} - v_* , \]
\[ v_* = v_s + v_{wake} \]

\[ D_{entr} \approx \frac{1}{6} n V a \left( \frac{4\pi}{3} a^3 \right) \]
?? enhanced diffusion and loops ??

Entrainment

Swimmer re-orientations
### Bacterial Olympics: 100 micrometres

<table>
<thead>
<tr>
<th>Rank</th>
<th>Bacterial Type</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>E. coli chimera</td>
</tr>
<tr>
<td>2</td>
<td>E. coli</td>
</tr>
<tr>
<td>3</td>
<td>V. alginolyticus (puller)</td>
</tr>
<tr>
<td>4</td>
<td>V. alginolyticus (pusher)</td>
</tr>
<tr>
<td>5</td>
<td>P. aeruginosa</td>
</tr>
<tr>
<td>6</td>
<td>R. sphaeroides</td>
</tr>
<tr>
<td>7</td>
<td>R. rubrum</td>
</tr>
<tr>
<td>8</td>
<td>Y. enterocolitica</td>
</tr>
</tbody>
</table>

Judith Armitage, Oxford biophysics
Random reorientations

Lin, Thiffeault, Childress JFM (2011)
Random reorientations

Lin, Thiffeault, Childress JFM (2011)
Diffusion constant for random reorientations

Dipolar swimmer 3D

\[ D_{rr} = \frac{4\pi}{3} \kappa_m n V a^4 \]

- Independent of swimmer run length for dipolar swimmers in 3D
- Distribution of tracer run lengths converges to a Gaussian

Dipolar swimmer, d=3

\[
\frac{D_{rr}}{D_{entr}} \approx \frac{\tilde{\kappa}^2 n V a^4}{n V a^4} \sim \tilde{\kappa}^2
\]
What is missing?

Swimmer-swimmer interactions
Fluctuations
Diffusion in films
Experiments

Diffusion of particles in an active suspension has contribution from entrainment, random swimmer reorientations and thermal fluctuations.
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