Lecture 3: Bacterial Swimming

- Introduction
- Bacterial swimming
- Near surface accumulation
- Circular trajectories near interface
- Trapping of swimming bacteria at the air-water interface
Abundance of microbes at the interface

Biofilm: Bacteria mats near Grand Prismatic Spring in Yellowstone

Steps flagellated bacteria take to form biofilm

Jay X Tang, Brown University
Various species of motile bacteria
Bacterial motion driven by rotation of flagellar motor


Swimming direction

Google images
Life cycle of *Caulobactor crescentus*

Yves Brun, Indiana University
From swimming to attachment and adhesion

• **Body parts**
  - Cell body
  - Flagellum
  - Pilus
  - Holdfast
  - Stalk

• **Physics**
  - Swimming hydrodynamics
  - Electrostatics (DLVO)
    (Jucker et. al., 1998; Vigeant et al., App. Env Microbio., 2002; G. Li, LK Tam & J. X. Tang, PNAS, 2008)
A reversible motor powers bacterial swimming

Biochemistry, 3rd Ed., Voet & Voet, John Wiley & Sons

Jay X Tang, Brown University
Uni-flagellated bacteria are efficient swimmers

*C. crescentus*, movies taken by Guanglai Li, Brown Univ.


Jay X Tang, Brown University
The essential physics of bacterial swimming

• There two essential properties of a bacterial flagellum:
  – A rotary flagellar motor
  – A helical flagellar filament

• The next two slides explain the basic hydrodynamics that enable swimming of flagellated bacteria.
Asymmetric drag and vector analysis

G. Li & J. X. Tang, PRE, 2004;

Biological Physics, by Philip Nelson, 2004, W.H. Freeman

Jay X Tang, Brown University
A helical propeller
Specific topics

• I. Near surfaces accumulation
  – steric confinement & effects of collision
  – near surface drag, lubrication force

• II. Near surface swimming path
  – observation and analysis of circular trajectories
  – coupling between Brownian motion and hydrodynamics

• *** Swimming path at the air/water and oil/water interface
  – trapped at the surface
  – effects of surface tension, surface viscosity, and hydrophobicity

Implications: chemotaxis, bacterial adhesion, differentiation, biofilm formation, etc.

Jay X Tang, Brown University
Topic I. Near surface accumulation of micro-swimmers

Berke et al. 2008, Phys Rev Lett (Lauga)

Rothschild, 1963, Nature

Li & Tang, 2009, Phys Rev Lett
Visualizing how bacteria hit a surface

Ming-ming Wu, Cornell Univ.
What happens after a swimmer hits a surface
How fast to become parallel to surface

Force and torque balance
\[ F_p \cos \theta + F_{\parallel} \cos \theta + F_{\perp} \sin \theta = 0 \]
\[ \Gamma = 0 \]

Hydrodynamic force and torque

\[
\begin{pmatrix}
F_{\parallel} \\
F_{\perp} \\
\Gamma
\end{pmatrix}
= \begin{pmatrix}
-A_{11} & 0 & 0 \\
0 & -A_{22} & A_{23} \\
0 & A_{32} & -A_{33}
\end{pmatrix}
\begin{pmatrix}
V_{\parallel} \\
V_{\perp} \\
\Omega
\end{pmatrix}
\]

\[ V_{\parallel} = V_x \cos \theta \quad V_{\perp} = V_x \sin \theta \]

Results

\[ \Omega = \frac{A_{23} \sin \theta \cos \theta}{A_{33}(A_{11} \cos^2 \theta + A_{22} \sin^2 \theta) - A_{23}^2 \sin^2 \theta} \frac{F_p}{F_p} \]
Simulating a microswimmer confined in a thin layer

Simplified Model

Equations of Motion

\[
\Delta y = V \sin \phi \Delta t + \zeta \sqrt{2D_t \Delta t}
\]

\[
\Delta \phi = \zeta \sqrt{2D_r \Delta t}
\]

Simulated Path

Density distribution

Jay X Tang, Brown University
Comparison with Experiments

Guanglai Li & J. X. Tang, Phys Rev Lett, 2009, 103:078101

Jay X Tang, Brown University
Summary of Topic I

Surface sets initial angle

Swimming under the influence of rotational Brownian motion

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Specific Topic II

Near surface swimming path

- Observation and analysis of circular trajectories
- Coupling between Brownian motion and hydrodynamics

Implications on
- chemotaxis
- bacterial adhesion
- differentiation
- biofilm formation

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Swimming in circles near a surface boundary

E. coli  Frymier, PNAS 1995

Vibio. alginolyticus  Goto, Biophys. 2005

C. crescentus  Li, PNAS 2008

H. pylori  Celli, PNAS 2009

Jay X Tang, Brown University
The hydrodynamic basis of circular trajectory of near surface swimming
Trajectories Observed by TIRF

\[ I_z = I_0 e^{-z/d_p} \]
Force and Torque Analysis

\[
A\begin{pmatrix} U_1 \\ U_2 \\ U_3 \\ \Omega_1 \\ \Omega_2 \\ \Omega_3 \end{pmatrix} + B\begin{pmatrix} U_1 \\ U_2 \\ U_3 \\ \Omega_1 \\ \Omega_2 - \omega \\ \Omega_3 \end{pmatrix} + \begin{pmatrix} 0 \\ F_{\text{dlvo}} \cdot \sin \theta \\ F_{\text{dlvo}} \cdot \cos \theta \\ T_{\text{dlvo}} \\ 0 \\ 0 \end{pmatrix} + \begin{pmatrix} f_1 \\ f_2 \\ f_3 \\ t_1 \\ t_2 \\ t_3 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}
\]

dlvo (Derjaguin, Landau, Verwey and Overbeek Theory)

Jay X Tang, Brown University
Curvature and Swimming Speed vs Distance—Comparison between Measured and Simulated Data

Measured by TIRF microscopy

Simulated

Jay X Tang, Brown University
Role of Brownian Motion on Foraging

Guanglai Li, LK Tam & J. X. Tang, PNAS, 2008, 105:18355
Open Puzzle: Why are circular path noted only for backward swimmers?

A schematic comparison between forward and backward swimming near a surface

Jay X Tang, Brown University
Summary of Topic II

Brownian motion varies distance to surface

Drag sensitive to distance

Jay X Tang, Brown University
Topic III: Swimming at the air/water interface

Mike Morse, Huang, Li, Maxey & Tang, Biophys. J. (2013), 105:21-28
Analysis of trajectories at the air surface

Two types of swimming trajectories at the liquid/air interface: 
~40% straight swimmers & ~60% circular swimmers
Manipulation of swimming at the air/water interface

**Hypothesis:** bacteria tend to get trapped at the air/water surface due to its large surface tension. Adding surfactant, which reduces the surface tension, might release them from the surface.

**Experiment:** Add Triton, a non-ionic surfactant and observe!

Jay X Tang, Brown University
Molecular Layer of Triton onto the Surface Leads to Full Release of Trapped Bacterial Swimmers from the Liquid-Water Interface

Chemical Structure of Triton-100

Molecular weight: 625 Dalton
Molecular Length: ~3 nm

Swimming cells are trapped at the air surface of growth medium but not minimal salt solution.

Orange data: minimal salt solution

Blue data: growth medium containing Bactotrypton and Yeast Extract
Effects of selected organic materials in growth medium on trapping of the swimming cells at the surface

<table>
<thead>
<tr>
<th>Condition</th>
<th>Percentage of trapped cells</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minimal salt solution</td>
<td>4.0+-2.4</td>
</tr>
<tr>
<td>Growth medium</td>
<td>59.7+-5.9</td>
</tr>
<tr>
<td>Growth medium + surfactant</td>
<td>6.8+-1.3</td>
</tr>
<tr>
<td>Minimal salts + Yeast Extract</td>
<td>15.9+-1.6</td>
</tr>
<tr>
<td>Minimal salts + Bactotrypton</td>
<td>25.6+-2.3</td>
</tr>
</tbody>
</table>

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Circular trajectories of opposite handedness at the air/liquid surface

Contradictory recent reports on E. coli

- Lemelle, Pallierne, Chatre & Place, J. Bacteriology, 192:6307, 2010.
  - CW and CCW circles
  - Condition: growth medium

  - CW circles only, opposite to near solid surface
  - Condition: motility buffer

Take home message:
SURFACE CHEMISTRY MATTERS
Observation of swimming at the water/oil interface

- The forward swimmers move in tight, clockwise circles (radius under 2 um)
- They tend to be terminally trapped
- The strains that switch motor rotation directions can escape while backing off

Unpublished work-M. Morse & J. X. Tang
Flagellar motor switching is a first passage time process

Morse, Bell, Li & Tang, Phys. Rev. Lett., 2015
Concluding Remarks

• Swimming microbes tend to accumulate near a confining surface subsequent to collision.

• The accumulation facilitates biological functions such as nutrient foraging, adhesion, and biofilm formation.

• Adsorption of large organic molecules at the air/water interface causes the swimming microbes to be trapped. The trapped swimmers can be released by surfactants, which some microbes secrete.

• Detailed experiments and analysis of low Reynold # hydrodynamics and surface physics/chemistry are required to explain various bacterial properties at interfaces.
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Key Refs


