Mechanics of cell-motility and self-propulsion in viscous fluids

A. DeSimone
SISSA
International School for Advanced Studies, Trieste, Italy

http://people.sissa.it/~desimone/LectureNotes/

XXXVI Summer School on Mathematical Physics, Ravello, September 2011
Motility

Motility is the capability of exhibiting directed, purposeful movement.

Motile cells provides fascinating examples of motility at microscopic scales (1-50 μm)

Tumor cells
(crawling on a solid surface)

Sperm cells
(swimming in a fluid)

Bacteria
(swimming in a fluid)
Need better understanding of underlying mechanisms

Control mechanisms and interactions with surroundings to enhance (infertility) or reduce (metastasis) motility

Engineer self-propelled artificial micro-motile systems (nano-robots inside the human body for diagnostics and therapy)

We are currently unable to obtain self-propulsion at microscopic scales artificially

Maybe we can learn from Nature? (bio-mimetic or bio-inspired design)

Using Nature as a template is sometimes naive (airplanes don’t flap their wings)
Microscopic bio-swimmers: bacteria and cells

Euglenoids

Two movies of metaboly in Eutreptiella sp.

Escherichia Coli (E. Coli)

One movie of swimming in Anisonema sp.
Man made micro-swimmers: micro-robots

red blood cell + flexible magnetic filament


polymer film + muscle cells

3. Types of molecular motors

Cells generally store chemical energy in two forms: high-energy chemical bonds, such as the phosphahtyric bonds in ATP (adenosine triphosphate); and asymmetric ion gradients across membranes, such as the electrical potential seen in nerve cells. These sources of chemical energy drive all cell processes, from metabolism through DNA replication. The subset of cell proteins and macromolecular complexes that convert chemical energy into mechanical force are generally called *molecular motors*. Their astonishing variety reflects the diversity of cell movements necessary to life.

Known biological molecular motors may be divided into five general groups: (1) rotary motors, (2) linear stepper motors, (3) assembly and disassembly motors, (4) extrusion nozzles, and (5) prestressed springs. All of the various cell movements already described are performed by ensembles of molecular motors that fall into these categories (see table 1). Coordinated actions of many small individual components can give rise to large-scale (cellular or organismal) movements. Because the molecular motor appears to be the fundamental unit of biological motility, much experimental and theoretical effort has focused on understanding these motor elements.

Linear stepper motors. They drive sliding among adjacent fibers causing muscle contraction, bending of flagella, ...
**Cell Motility**

Table 1. Cell movements and their molecular mechanisms.

<table>
<thead>
<tr>
<th>Cell movement</th>
<th>Cell structure needed</th>
<th>Molecular motor</th>
<th>Motor category</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Movements through liquid</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bacterial swimming</td>
<td>Flagella (bacterial)</td>
<td>Flagellar rotor (MotA/MotB)</td>
<td>Rotary</td>
</tr>
<tr>
<td>Eukaryotic swimming</td>
<td>Cilia, flagella (eukaryotic)</td>
<td>Dynein</td>
<td>Linear stepper</td>
</tr>
<tr>
<td>Metaboly</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td><strong>Movements on solid surfaces</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amoeboid motility (crawling)</td>
<td>Lamellipodia, filopodia, pseudopodia</td>
<td>Actin</td>
<td>Assembly/disassembly</td>
</tr>
<tr>
<td>Bacterial gliding</td>
<td>Junctional pore complex</td>
<td>Myosin (several)</td>
<td>Linear stepper</td>
</tr>
<tr>
<td>Parasite gliding</td>
<td>Pellicle</td>
<td>Slime extrusion nozzle</td>
<td>Extrusion</td>
</tr>
<tr>
<td>Bacterial twitching</td>
<td>Type IV pili</td>
<td>Myosin (class XIV)</td>
<td>Linear stepper (probably)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pilus base motor (PilT)</td>
<td>Assembly/disassembly?</td>
</tr>
<tr>
<td><strong>Intracellular movements</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chromosome segregation</td>
<td>Mitotic spindle</td>
<td>Kinesin (several), dynein</td>
<td>Linear stepper</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tubulin</td>
<td>Assembly/disassembly</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Kinesin (several), dynein</td>
<td>Linear stepper</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Myosin (class V, class VI, others?)</td>
<td>Linear stepper</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Actin</td>
<td>Assembly/disassembly</td>
</tr>
<tr>
<td>Organelle transport</td>
<td>Microtubule arrays</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Actin gels</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Actin comets</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Rapid cell shape changes</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Muscle contraction</td>
<td>Sarcomere</td>
<td>Myosin (class II)</td>
<td>Linear stepper</td>
</tr>
<tr>
<td>Cytokinesis</td>
<td>Division furrow</td>
<td>Myosin (class II)</td>
<td>Linear stepper</td>
</tr>
<tr>
<td>Stalked ciliate recoil</td>
<td>Spasmone</td>
<td>Spasmin</td>
<td>Prestressed spring</td>
</tr>
<tr>
<td>Acrosome extension (Thyone)</td>
<td>Acrosomal vesicle</td>
<td>Actin</td>
<td>Assembly</td>
</tr>
<tr>
<td>Acrosome extension (Limulus)</td>
<td>Acrosomal bundle</td>
<td>Actin</td>
<td>Prestressed spring</td>
</tr>
</tbody>
</table>

Motility at microscopic scales. Antonio DeSimone, SISSA (Trieste, ITALY)
Actin-based motility

- fibroblasts
- neuronal growth cones
- listeria
- macrophages
- cancer cells
- keratocytes

Ravello course on motility at microscopic scales. Antonio De Simone, SISSA (Trieste, ITALY)
Actin polymerization at the leading edge drives motility of crawling cells*

(* metastatic tumor cells, immune system response ...)

Protrusion

Governed by a large number of well identified bio-chemical reactions mediated by actin-binding proteins

Motility at microscopic scales. Antonio DeSimone, SISSA (Trieste, ITALY)
Long range order: where from?

Long range order at the μm scale of the cell (the front is flat)
emerging from uncoordinated growth at the nm scale of the individual filaments.

Hypothesis:
self-organized growth is orchestrated by long range mechanical interactions mediated by the membrane.

After all, it’s filaments pushing against the membrane (Mogilner, Theriot, Keren, Marenduzzo, Prost, Sykes, Plastino...)

Pollard & Earnshaw, 2002

Motility at microscopic scales. Antonio DeSimone, SISSA (Trieste, ITALY)
Gathering of facts: 1. F vs V relation


Growth velocity rather insensitive to opposing force, up to a stall force.
Fact 2. Filament orientation

Actin filaments symmetrically oriented with respect to the protrusion direction.
A mechanical model for the active layer at the leading edge (2d horizontal slice)

An “active” layer of growing actin network between the plasma membrane (above) and the previously grown, immobilized network (entanglements, crosslinks, and adhesion to substrate mediated by molecular clutches, below)

Motility at microscopic scales. Antonio DeSimone, SISSA (Trieste, ITALY)
The model. 1: growth and branching events

Starting from a set of fixed “seeds”, at each time step $i$ a random filament grows at its barbed end, and a branch originates at a random location with probability $Pb$. (growth and branching)

At exposed pointed ends, filaments get depolymerized at speed $D$. (depolymerization)

Growth events that would lead to overlap with existing filaments are not allowed. (steric hindrance)

Contact among filaments and between filaments and membrane explicitly accounted for.
The model. 2: mechanical stresses

Stresses are computed by minimizing total elastic energy at each growth step

\[ \varepsilon_{\text{actin}} = \sum \frac{1}{2} E_a \varepsilon_a^2 l_a, \quad \varepsilon_{\text{membrane}} = \sum \frac{1}{2} E_m \varepsilon_m^2 l_m, \quad \varepsilon_{\text{bending}} = \sum \kappa \rho_m^2 d, \quad \varepsilon_{\text{contact}} = \sum_{h,k \neq h} \psi(d_{hk}). \]

\[ \varepsilon_i = \varepsilon_{\text{actin}} + \varepsilon_{\text{membrane}} + \varepsilon_{\text{bending}} + \varepsilon_{\text{contact}} - L_i^{\text{ext}}, \quad \{u_{\text{eq}}\}_i = \arg \min_{\{u\}_i} \varepsilon_i(\{u\}_i). \]

Monomers with stress exceeding threshold (filam. rupture bend. mom.) are cleaved away; equilibrium states are computed iteratively until no monomer exceed the critical stress.
Results

Growth periods alternate with retractions (avalanches of local rupture events).

Sustained growth when structures fit for pushing (uniform stress distribution thanks to mutual support between neighbors) emerge spontaneously (evolution: mutation through random growth and branching; selection: through failure of overstressed filaments).

Active sites for growth and branching are localized near the membrane.
Self-organization of the orientation (optimal shape design ?)

Flexible filaments: large deformations (elastic deflections compensate misalignment)

Stiff filaments: selection (cleavage of misoriented filaments)

Motility at microscopic scales. Antonio DeSimone, SISSA (Trieste, ITALY)
Growth velocity depends only weakly on the opposing force, up to stall force when growth becomes impossible.

Growth against higher values of opposing force requires higher density of actin monomers.
Mechanical self-organization: summary


• Mechanical stresses may govern the emergence of long range order through the following evolutionary scheme:
  - Filaments that try to grow alone break and depolymerize away.
  - Only when filaments happen to grow cooperatively they can support each other and manage to push the membrane without being crushed.

• Accumulation of mechanical stresses in randomly growing, breakable filaments that push against the membrane. This simple model exhibits (“explains”) :
  - Characteristic F vs V and the ability of the network to self-organize its orientation,
  - ....
## Appendix: values of material parameters

<table>
<thead>
<tr>
<th>parameter</th>
<th>description</th>
<th>value</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>$d$</td>
<td>actin filament thickness</td>
<td>7 nm</td>
<td>[8, 9]</td>
</tr>
<tr>
<td>$\beta$</td>
<td>characteristic angle of the truss structure</td>
<td>60°</td>
<td></td>
</tr>
<tr>
<td>$a$</td>
<td>monomer edge length</td>
<td>$d \cos(\beta/2)$</td>
<td></td>
</tr>
<tr>
<td>$\theta$</td>
<td>initial orientation of seeds</td>
<td>$\pm 30^\circ$</td>
<td></td>
</tr>
<tr>
<td>$\varphi$</td>
<td>branching angle</td>
<td>60°</td>
<td>[5, 10, 11]</td>
</tr>
<tr>
<td>$P_b$</td>
<td>branching probability</td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>$D$</td>
<td>depolymerization speed</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>$\xi$</td>
<td>filament persistence length</td>
<td>$10^3 d$</td>
<td>[4, 12]</td>
</tr>
<tr>
<td>$F_r$</td>
<td>filament rupture force</td>
<td>100 pN</td>
<td>[1]</td>
</tr>
<tr>
<td>$f_e$</td>
<td>edge rupture force</td>
<td>$F_r/2$</td>
<td></td>
</tr>
<tr>
<td>$E_m$</td>
<td>membrane stretching stiffness</td>
<td>2 $F_r$</td>
<td>[13, 14]</td>
</tr>
<tr>
<td>$k$</td>
<td>membrane bending stiffness</td>
<td>0.1 $F_r \cdot d^2$</td>
<td>[11]</td>
</tr>
<tr>
<td>$c$</td>
<td>contact stiffness</td>
<td>30 pN·nm</td>
<td></td>
</tr>
<tr>
<td>$\delta$</td>
<td>contact length</td>
<td>0.5$a$</td>
<td></td>
</tr>
</tbody>
</table>

$d = 7$ nm

$F_r$ in the range between 100 and 600 pN
Lecture 3: zero Re hydrodynamics

E.M. Purcell:
Life at low Reynolds numbers,
Am. J. Physics, 1977
From Navier-Stokes to Stokes

Navier-Stokes

\[ \rho \left( \frac{\partial \mathbf{v}}{\partial t} + (\mathbf{v} \cdot \nabla) \mathbf{v} \right) = -\nabla p + \eta \Delta \mathbf{v} \]
\[ \text{div} \mathbf{v} = 0 \]

Non-dimensionalization

\[ x_* = \frac{x}{L}, \quad t_* = \frac{t}{T}, \quad p_* = \frac{p}{V \eta}, \quad u_* = \frac{v}{V} \]

Stokes

\[ \sigma Re \frac{\partial u_*}{\partial t_*} + Re (u_* \cdot \nabla) u_* - \Delta u_* + \nabla p_* = 0, \]
\[ \text{div}_* u_* = 0 \]
\[ -\eta \Delta v + \nabla p = 0 \]
\[ \text{div} \mathbf{v} = 0 \]

All inertial effects neglected, formal limit.
Reynolds Number (Re)

\[ \text{Re} = \frac{VL\rho}{\eta} \]

Velocity (typical order of magnitude) \( V \)
Diameter (typical length scale) \( L \)
Mass density of the fluid \( \rho \)
Viscosity of the fluid \( \eta \)

For water at room temperature \( \rho/\eta = 10^6 \text{ (m}^2\text{s}^{-1})^{-1} \).

Re is a dimensionless measure of relative importance of inertia vs. viscosity

Orders of magnitude for swimmers:

Men, tuna, sharks: \( L=1\text{m}, V=1-10 \text{ ms}^{-1} \) \( \text{Re}=10^6-10^7 \)
Bacteria: \( L=1\times10^{-6}\text{m}, V=1-10\times10^{-6} \text{ ms}^{-1} \) \( \text{Re}=10^{-6}-10^{-5} \)
G.I Taylor and low Re flows

National Committee for Fluid Mechanics Films:
http://web.mit.edu/hml/ncfmf.html

G.I. Taylor’s movie on low Re flows:
http://modular.mit.edu:8080/ramgen/ifluids/Low_Reynolds_Number_Flow.rm

Modern classical physics through the work of G.I. Taylor:

One scientist’s work provides material for an entire course, covering topics ranging from hydrodynamic stability and turbulence to electrohydrodynamics and the locomotion of small organisms.
-- Michael P. Brenner and Howard A. Stone

http://www.deas.harvard.edu/brenner/taylor/physic_today/taylor.htm

Ravello course on motility at microscopic scales. Antonio DeSimone, SISSA (Trieste, ITALY)
Flow past a sphere (Stokes formula)

Re = 0

Drag = 6πμRV (Stokes, 1851)

Re > 250

Ravello course on motility at microscopic scales. Antonio DeSimone, SISSA
Resistance matrix for ellipsoidal shapes

The resistance matrix $k$ reflects the symmetries of $\Omega$. If $\Omega$ is symmetric, then the eigenvectors of $k$ are along the axes of symmetry.

Sphere

$$k = 6\pi I \mu \ I = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

Prolate ellipsoid of revolution

$$I_a = \begin{bmatrix} 2 \alpha & 0 & 0 \\ 0 & 2 \beta & 0 \\ 0 & 0 & \gamma \end{bmatrix}$$

$$k = 6\pi I \mu \ I = \begin{bmatrix} 2\alpha & 0 & 0 \\ 0 & 2\beta & 0 \\ 0 & 0 & \gamma \end{bmatrix}$$

As $a \rightarrow 10$, $e(1, \infty)$

As $b \rightarrow 0$, $e(1, 1/2)$
Gel electrophoresis of DNA and RNA
Viscous drag on a filament

Apply result first $\frac{s_a}{s_b} = \frac{1}{2}$ of $a \rightarrow b \rightarrow 0$ to the case of finite $a$ and $b \rightarrow 0$

So by thin cylinder, $\varepsilon'' = \frac{1}{2} \varepsilon' < \varepsilon'$, falling at 45° from axis.

Since $\varepsilon'' < \varepsilon'$, $F$ has a net positive component along $e$

If motion along the vertical is permissible, get a propulsive component along $e$

If force (gravity) is permissible at steady state $F$ must balance gravity, vertical

Then

$\varepsilon'' \sqrt{\varepsilon''} = \varepsilon' \sqrt{\varepsilon'} \Rightarrow \sqrt{\varepsilon'} = \frac{\varepsilon'}{\varepsilon''} \sqrt{\varepsilon''} > \sqrt{\varepsilon'}$

and the object will slide laterally towards $e$
Lecture 4: from mobility to motility

Swimming: a definition
the ability to advance in water
by performing a cyclic shape change (a stroke)
in the absence of external propulsive forces

It’s a control problem:
Can we reach B from A (with B≠A)
by executing (periodic) shape changes
(or by prescribing suitable internal forces)?
Two conceptual ingredients

1. How does the surrounding medium react (namely, which forces does it exert?) to shape changes of the swimmer?
   
   (equations of motion of the surrounding medium)

2. How does the swimmer move in response to the forces that the surrounding medium applies to it?
   
   (equations of motion of the swimmer)
Outer Stokes problem

Find $u$ induced in the fluid surrounding swimmer $\Omega$ by its shape changes:

\[-\eta \Delta u + \nabla p = 0 \quad \text{on } \mathbb{R}^3 \setminus \Omega,\]

\[\text{div}(u) = 0 \quad \text{on } \mathbb{R}^3 \setminus \Omega,\]

\[u = v_{\text{Dir}} \quad \text{on } \partial \Omega\]

\[u \to 0 \quad \text{at infinity.}\]

\[\sigma \cdot n = DN_{\Omega} [v_{\text{Dir}}] \quad \text{viscous “reactive” force p.u. area on } \partial \Omega\]
Equation of motion = Self-propulsion

The motion of the swimmer induced by its shape changes is a-priori unknown.

Equations of motion:

\[ m \ (x_c)_{tt} = F_{\text{tot}} \]

\[ 0 = F_{\text{tot}} \quad \text{neglecting swimmer’s inertia} \]

\[ 0 = F_{\text{ext}} + F_{\text{visc}} \]

\[ 0 = F_{\text{visc}} \quad \text{self-propulsion} \]

Similarly, total viscous torque = 0.
Life at low Reynolds numbers

in a flow regime obeying Stokes equations, a scallop cannot advance through the reciprocal motion of its valves

whatever forward motion will be produced by closing the valves, it will be exactly canceled by a backward motion upon reopening them (see Marta’s talk)

G.I. Taylor, 1951

H. Berg, 1973

(eukariotic flagella) (cilia) (bacterial flagella)
A. Najafi and R. Golestanian:
Simple swimmer at low Reynolds numbers: three linked spheres,
PRE 69, 062901 (2004)

Mathematical swimming in a nutshell

\[ \xi_1 = x^{(2)} - x^{(1)} \]

\[ \xi_2 = x^{(3)} - x^{(2)} \]

\[ c = \frac{1}{3} \sum_{i=1}^{3} x^{(i)} \]

Swimming is ..... executing cyclic shape changes

\[ \Delta c = \int_0^T \dot{c} dt \neq 0 \]

producing net positional change after one period

under no external force (self-propulsion)

\[ f^{(1)} + f^{(2)} + f^{(3)} = 0 \]
Positional change from shape change (axisym.)

\[
0 = i \cdot \int_{\partial \Omega} DN_\xi[v_{\text{Dir}}] \, dA
\]

\[
= \varphi_1(\xi, \xi') \dot{\xi}_1 + \varphi_2(\xi, \xi') \dot{\xi}_2 + \varphi_3(\xi, \xi') \dot{c}
\]

by transl. inv.

Then \( \dot{c} \) is uniquely determined and depends linearly on \( \dot{\xi}_1 \) and \( \dot{\xi}_2 \)

\[
\frac{dc}{dt} = V_1(\xi) \frac{d\xi_1}{dt} + V_2(\xi) \frac{d\xi_2}{dt}
\]

nonlinear dep. on \( \xi \)!

\[
V_i(\xi) = -\varphi_i(\xi) / \varphi_{n+1}(\xi)
\]

Dirichlet data on \( \partial \Omega \)

\( DN_\xi[v_{\text{Dir}}] = \sigma \, n \) surface force on \( \partial \Omega \)
Swimming with one formula

\[ \Delta c = \int_0^T \dot{c} \, dt = \int_0^T (V_1 \frac{d\xi_1}{dt} + V_2 \frac{d\xi_2}{dt}) \, dt = \int_\omega \text{curl} \, V \, d\xi_1 d\xi_2 \]

(notice that it’s entirely geometric!)

Swimming rests on the differential form \( V_1 d\xi_1 + V_2 d\xi_2 \) not being exact.

\[ V(\xi) \] summarizes hydrodynamic interactions and swimming capabilities of a swimmer.

Swimming = Controllability ; Optimal Swimming = Optimal Control
Controllability (see Jerome’s talk)

Nonholonomic motion planning vs. steering a control system

\[
\begin{align*}
\dot{\xi}_1 &= u_1 \\
\dot{\xi}_2 &= u_2 \\
\dot{c} &= V_1(\xi) u_1 + V_2(\xi) u_2
\end{align*}
\]

\[
\dot{q} = \frac{d}{dt} \begin{bmatrix} q_1 := \xi_1 \\ q_2 := \xi_2 \\ q_3 := c \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} V_1(q_1, q_2) \\ V_2(q_1, q_2) \end{bmatrix}
\]

\[
[g_1, g_2] = \left( \frac{\partial}{\partial q} g_2 \right) g_1 - \left( \frac{\partial}{\partial q} g_1 \right) g_2 = \begin{bmatrix} 0 \\ 0 \\ \text{curl} V(q_1, q_2) \end{bmatrix}
\]

\[
\text{det} [g_1 | g_2 | [g_1, g_2]](q_1, q_2, q_3) = \text{curl} V(q_1, q_2) \neq 0
\]

The three-sphere swimmer is globally controllable (Lie-bracket generating or totally nonholonomic control system)

Ravello course on motility at microscopic scales. Antonio DeSimone, SISSA (Trieste, ITALY)
Swimming at max efficiency (geodesic strokes)  
(strokes of max Lighthill efficiency)

Rescale to unit time interval. Minimize expended power

\[ \int_0^1 \int_\Omega \sigma \mathbf{n} \cdot \mathbf{v} \, dt = \int_0^1 \int_{\partial \Omega} D N_\xi [\mathbf{v}_{\text{Dir}}] \cdot \mathbf{v}_{\text{Dir}} \, d\mathbf{A} dt = \int_0^1 G(\xi) \dot{\xi} \cdot \ddot{\xi} \, dt \]

stroke “length”

at given \[ \Delta c = \int_0^1 V(\xi) \cdot \ddot{\xi} = \int_\omega \text{curl} V(\xi) \, d\xi \]

enclosed area

Euler-Lagrange eqn.

\[-\frac{d}{dt}(G \dot{\xi}) + \frac{1}{2} \left( \frac{\partial_1 G}{\partial_2 G} \dot{\xi} \cdot \ddot{\xi} \right) + \lambda \text{curl} V(\xi) \dot{\xi}^\perp = 0 \]

Optimal paths are sub-riemannian geodesics.  
Optimal strokes exist.  
They can be computed numerically.
Three sphere swimmers: a race

Ravello course on motility at microscopic scales. Antonio DeSimone, SISSA (Trieste, ITALY)
Optimal stroke

Level curves of curl $V(\xi_1, \xi_2)$

Optimal stroke maximizes flux of curl $V$ at given energy input, or minimizes power consumption at given flux of curl $V$
Summary and perspectives

- Self-propulsion yields the key equation(s) giving positional change from shape change
- Swimming problem as a problem of controllability
- Optimal strokes of low Re swimmers computable; sub-riemannian geodesics

- The picture is qualitatively similar for general swimmers with finitely many shape dofs.
  (6 ODEs rather than 1 equation of motion. But: rotations !)
- What about the genuinely infinite-dimensional case?

- What is the biological function of metaboloy motion (swimming ???)
- Is there something being optimized by the stroke of this micro-organism?

Ravello course on motility at microscopic scales. Antonio DeSimone, SISSA (Trieste, ITALY)
Lecture 6: the infinite-dimensional case

G.I. Taylor:
Analysis of the swimming of microscopic organisms,

G. Gray and G.J. Hancock:
The propulsion of sea-urchin spermatozoa,

Taylor’s swimming sheet

\[ h = b \sin(kx - \omega t), \]

Wave vector: \( k \mathbf{e}_x \)

Wave speed: \( \omega / k \)

Solve for the fluid velocity \( \mathbf{u} \) in the surrounding fluid. No-slip plus fluid at rest at infinity.

BCs in a frame moving with the sheet:

\[ \mathbf{u}(x, h(x, t)) = -b \omega \cos(kx - \omega t) \mathbf{e}_y, \]

\[ \lim_{y \to \infty} \mathbf{u}(x, y) = -\mathbf{U}. \]

where \( \mathbf{U} \) is the swimming speed of the sheet.

Wave travels to the right

Transversal (bending/shape) wave:

sheet moves to the left

Longitudinal (stretching) wave:

sheet moves to the right

(see Ezio’s talk on Monday)
Swimming direction from drag anisotropy (heuristics)

\[ h = b \sin(kx - \omega t), \]

Since \( \xi \perp > \xi \parallel \)
net force towards **left**

Wave travels to the **right**

Transversal (bending/shape) wave: **sheet moves to the left**

If the sheet is blocked: **the sheet pumps fluid towards right**
Gray-Hancock beating flagellum

Local drag approximation (??) or “resistive force theory”

\[ f = -\xi || u || - \xi \perp u \perp , \]

Eq. of motion:

\[ F_{\text{head}} + \int f = 0 \]

Solve for the unknown swimming velocity:

Average over one period of oscillation:

Remark: get back Taylor’s formula with \( L > > a \) (head radius) and \( \xi \perp = 2 \xi || \) (??)
Resistive force theory works surprisingly well

\[ \xi_{\perp} = 1.8 \xi_{\parallel} \]

Generic swimming blob

Velocity at points of swimmer:

\[ \mathbf{V}_t^{\text{rigid}} [\dot{y}_t, \omega_t] + \mathbf{V}_t^{\text{shape}} [\dot{s}_t, s_t^{-1}] \]

Polar Decomposition

\[ \nabla \varphi_t(x_0) = R_t \, U_t = \nabla r_t \, \nabla s_t (x_0) \]

Eq. of motion: total viscous force and torque = 0

\[
\begin{bmatrix}
F_t^{\text{visc}} \\
M_t^{\text{visc}}
\end{bmatrix} = - \begin{bmatrix}
K_t & C_t^T \\
C_t & J_t
\end{bmatrix}
\begin{bmatrix}
R_t & 0 \\
0 & R_t^T
\end{bmatrix}
\begin{bmatrix}
\dot{y}_t \\
\omega_t
\end{bmatrix} + \begin{bmatrix}
F_t^{\text{shape}} \\
M_t^{\text{shape}}
\end{bmatrix}
\]

Data are infinite dimensional, while the unknowns are finite dimensional.

Theorem: for any suff. smooth (Lip w/r to t) \( s_t \)
there exist a unique (AC w/r to t) rigid motion \( r_t \) generated by \( s_t \)
(see also Jerome’s talk)

Ravello course on motility at microscopic scales. Antonio DeSimone, SISSA (Trieste, ITALY)
References


- G. Galdi, A. Bressan et al., M. Tucsnak et al., (Function spaces, Well-posedness, Control)