The interactions and effects of fluid and body elasticity on locomotion at the micro-scale

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Joint work with Robert Guy, UC Davis
Micro-organisms move in complex environments at very small scales

- Chlamydomonas, Sperm, C. Elegans, bacteria
- Swim in a variety of media: water, cervical mucus, soil
  - Focus on fluids with elasticity
- Gait changes are observed as fluid changes
  - Can be functionally important
  - Focus on undulatory waving sheets
- How does fluid elasticity effect swimming speed?
  - Many different results in literature
  - Incomplete picture, complicated problem
  - Nonlinear interactions of fluid, body, gait…
Motivation: Sperm Gait in Different Fluids

In fresh water, sperm have a progressive movement, which is typical in most biological fluids. However, when placed in a viscoelastic fluid, the sperm adopt a more complex gait, indicated by the increased number of bends and twists in their movement patterns.

In hyperactivated solutions, the sperm exhibit a more aggressive and rapid swimming pattern, characterized by quick and rapid changes in direction, which is crucial for their ability to penetrate through the viscoelastic media.


Is there a functional significance to these shapes and shape changes?
## Some Results on Locomotion in Complex Fluids

<table>
<thead>
<tr>
<th>Citation</th>
<th>Result</th>
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<tr>
<td>1979 Chaudhury (JFM) Asymptotic analysis, infinite sheet, 2\textsuperscript{nd} order fluid</td>
<td>Speed Up</td>
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<td>1998 Fulford, Katz, Powell (Biorheology) Resistive force theory, general linear fluid, shear thinning</td>
<td>Speed Up</td>
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<tr>
<td>2007 Lauga (PoF) Asymptotic analysis, infinite small amp., wavy sheet, Oldroyd-B</td>
<td>Slow Down</td>
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<td>2007,2009 Fu, Powers, Wolgemuth (PRL,PoF) Asymptotic analysis, UCM/ OB, helical</td>
<td>Slow Down</td>
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<td>2010 Teran, Fauci, Shelley (PRL) Simulation, finite length, undulatory, Oldroyd-B</td>
<td>Speed Up (Local max)</td>
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<td>2011 Shen, Arratia (PRL) Experiment, C. elegans (undulatory)</td>
<td>Slow Down</td>
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<td>2011 Liu, Powers, Breuer (PNAS) Physical Experiment, helices</td>
<td>Speed Up</td>
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<tr>
<td>2013 Espinosa-Garcia, Lauga, Zenit (PoF) Physical experiment, flexible tail</td>
<td>Speed Up (monotonic)</td>
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<tr>
<td>2013 Dasgupta, Liu,Fu,Berhanu,Breuer,Powers, Kudrolli (PRE) Physical experiment, “infinite sheet” (cylinder)</td>
<td>Depends on rheology</td>
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<td>2013 Spagnolie, Liu, Powers (PRL) Simulation, helices, Oldroyd-B</td>
<td>Speed Up</td>
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<td>2013 Montenegro-Johnson,Smith,Loghin (PoF) Simulation, Carreau fluid</td>
<td>Depends on stroke</td>
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<td>2014 Riley, Lauga: Asymptotic analysis, flexible wave sheet</td>
<td>Speed Up</td>
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Oldroyd-B Model for Viscoelasticity

- Stokes Equations with extra stress due to polymer stress: \( \tau_p \)

\[
\Delta u - \nabla p + \xi \nabla \cdot \tau_p + f = 0, \\
\nabla \cdot u = 0, \\
\text{De}(\partial \tau_p/\partial t + u \cdot \nabla \tau_p - \nabla u \tau_p - \tau_p \nabla u^T) + \tau_p = \dot{\gamma}
\]

- Deborah number: \( De = \frac{\text{relaxation time}}{\text{flow time scale}} \)

\( De \) is a measure of elasticity of the fluid

\( De \to 0 \) recover Newtonian fluid

\( De \to \infty \) recover neo-Hookean elastic solid

- Oldroyd-B model can also be derived from dilute suspension of dumbbells connected by linear springs
1. Asymptotic analysis: infinite length, small amplitude
   • 2007, Lauga: Always slow down

\[ \beta = 2/3 \]

\[ \frac{U_{ve}}{U_N} = \frac{1 + \beta De^2}{1 + De^2}, \quad \beta = \frac{\eta_s}{\eta_p + \eta_s} < 1 \]
1. Asymptotic analysis: infinite length, small amplitude
   • 2007, Lauga: Always slow down

2. Simulations: finite length, large amplitude
   • 2011, Teran-Fauci-Shelley: Non-monotonic speed up
Undulatory Swimmers in viscoelastic fluid

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3. Biological experiment (C. Elegans): finite length, large amplitude
   - 2011, Shen-Arratia: Always slow down
Undulatory Swimmers in viscoelastic fluid

Kicker
Teran, Fauci, Shelley (2010)

Thomases, Guy (2014)

Burrower
Shen and Arratia (2011)

Thomases, Guy (2014)

Our Soft Kicker
TFS Simulation

Our Stiff Burrower

SA Experiment
Undulatory Swimmers in viscoelastic fluid

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3. Biological experiment (C. Elegans): finite length, large amplitude
   • 2011, Shen-Arratia: Always slow down

2014, Thomases-Guy: The gait is really important!
1. Asymptotic analysis: infinite length, small amplitude
   • 2007, Lauga: Always slow down

2. Simulations: finite length, large amplitude
   • 2011, Teran-Fauci-Shelley: Non-monotonic speed up

3. Biological experiment (C. Elegans): finite length, large amplitude
   • 2011, Shen-Arratia: Always slow down

4. Physical experiment: finite length, large amplitude
   • 2013, Espinosa-Garcia, Lauga, Zenit: Monontonic speed up
4. Physical experiment: finite length, large amplitude
   • 2013, Espinosa-Garcia, Lauga, Zenit:
     BIG Monontonic speed up
Model Equations

- **Fluid-Equations** – Stokes-Oldroyd-B model
  \[ \Delta u - \nabla p + \xi \nabla \cdot \tau_p + f = 0, \]
  \[ \nabla \cdot u = 0, \]
  \[ \text{De} \left( \frac{\partial \tau_p}{\partial t} + u \cdot \nabla \tau_p - \nabla u \tau_p - \tau_p \nabla u^T \right) + \tau_p = \dot{\gamma} \]

- **Structure Equations** – penalty method (Immersed Boundary)
  \[ X_t = \int_{\text{fluid}} \delta(x - X(s,t))u(x,t)dx \]
  \[ f_{\text{struct}} = \int_{\text{body}} \delta(x - X(s,t))F(s,t)ds \]
  \[ F = \frac{\delta E}{\delta X} \]
  \[ E = E_b + E_s \]
  \[ E_s, \text{stiff penalty for stretching} \]
  \[ \text{“easy” to enforce} \]
  \[ E_b = \frac{B}{2} \int_{\text{worm}} (\kappa - \kappa_0(s,t))^2 ds \]
  Prescribed body moments along the swimmer

- **Rigid body**: \( B \gg 1 \) - realized shape is very close to prescribed shape
- **Flexible body**: \( B \approx 1 \) - elastic forces and viscous forces are of the same scale and resultant shape is result of fluid-structure interaction
Speed dependence on frequency is related to swimmer body stiffness

Stokes (Newtonian) Fluid

- $B = 1.0$
- $B = 10.0$

- soft
- stiff
Fluid elasticity measured with Deborah number

Change the Deborah number by changing the fluid or changing the period of oscillation

\[ De = \frac{\lambda}{T} = \frac{\text{Viscoelastic relaxation time}}{\text{Period of oscillation}} \]

- Numerical Simulations: Scale time by the period and thus change the relaxation time (Teran-Fauci-Shelley, Thomases-Guy)
- Biological experiment: (Shen-Arratia) Cannot control period and must change fluid (relaxation time)

- Physical model: E-L-Z (2013)
- Changed the period

\[ De = \frac{\lambda}{T} = \frac{\text{Viscoelastic relaxation time}}{\text{Period of oscillation}} \]
aka large amplitude tail, flexible body (B~1) 

Vary De “two ways” 

\[ De = \frac{\lambda}{T} = \frac{\text{Viscoelastic relaxation time}}{\text{Period of oscillation}} \]

Deborah number alone is not the whole story!
Speed dependence on body stiffness

(a) very soft, $B = 0.1$

(b) moderately soft, $B = 1.0$

(c) stiff, $B = 10.0$

Espinosa-Garcia et al., 2013

Thomases, Guy, 2014

Teran et al., 2010
Elasto-hydrodynamics

- Balance of viscous drag force with elastic rod force

\[ \xi \frac{\partial y}{\partial t} = -B \frac{\partial^4 y}{\partial s^4} \]

- Define a dimensionless (inverse) body relaxation time, \( G \):

\[ G = \frac{T}{B^{-1} \xi L^4} = \frac{\text{Period of oscillation}}{\text{beam memory time}} \]

\( (G = Sp^{-4}, \text{ sperm number}) \)
Elastic induced shape changes

• Elastic induced shape changes depend on $G$ and $De$

• Small amplitude theory: shape changes first order in amplitude, swimming speed is second order

• Use linear viscoelasticity

• Obtain a complex drag coefficient, depends on fluid

$$\zeta_{viscoelastic} = \frac{1 + \eta_p/\eta_s + 2\pi i De}{1 + 2\pi i De} \zeta_{viscous}$$

• Solve for shape changes as a function of driving curvature

• Can we do analysis for LARGE AMPLITUDE?
Large Amplitude: Motion of curvature deviations

- Drive our system with prescribed target curvature
- Derive PDE for \textit{curvature deviations} (good approximation for small amplitude or high stiffness limit)

\[ c_t \approx -Gc_{ssss} - \frac{\partial \kappa_0}{\partial t} \]

- Solve for shape as a function of prescribed curvature

\[ \alpha_k = \alpha_k^\infty \left(1 - \left(1 - \frac{G \mu_k}{\zeta ve \cdot 2\pi i}\right)^{-1}\right) \]

resulting shape (amplitude)    prescribed shape (amplitude)

\[ \zeta ve = \left(\frac{1 + \eta_p / \eta_s + 2\pi i De}{1 + 2\pi i De}\right) \zeta vis \]
Consider a flexible beam that does not translate horizontally, prescribe target curvature:

\[ \kappa_0(s,t) = A \sin(\omega t) \]

\[ A = 0.5 \quad A = 4.0 \]
Emergence of three regimes, a very soft regime where the amplitude is always boosted, a moderately soft regime with a non-monotonic response, and a stiff regime with no amplitude boost.
What about swimming?

Theoretical swimming speed in viscous fluid can be computed:

\[ \kappa_0(s,t) = \alpha_1 \cos\left(\frac{2\pi t}{T} + \phi_1\right)\psi_1(s) + \alpha_2 \cos\left(\frac{2\pi t}{T} + \phi_2\right)\psi_2(s) \]

\[ \langle U \rangle \propto \left(\frac{\zeta_\perp}{\zeta_\parallel} - 1\right) \frac{1}{LT} \int_0^T \int_0^L y_x y_t \, ds \, dt \]

\[ \langle U \rangle \propto \alpha_1 \alpha_2 \sin(\phi_2 - \phi_1) \]
Shape Comparisons: simulation and theory
(Low amplitude is spot on)

Like the flexor the theory predicts the shape changes very well!
Theoretical vs. simulation swimming speed

Theory – Speed changes due to shape changes

\[ \propto \alpha_1 \alpha_2 \sin(\phi_2 - \phi_1) \]

Simulations include other fluid effects

Stroke induced swimming speed

Stokes-normalized swimming speed

- **very soft**, \( G = 0.1 \)
- **moderately soft**, \( G = 1.0 \)
- **stiff**, \( G = 10.0 \)

High-low amplitude speed ratio

- **High amp**
- **Low amp**
What is the “fluid” effect? i.e. minus shape changes

Data collapses for low amplitude

This effect is likely to be sensitive to specifics of the stroke

Something else is going on in the high amplitude case

Ratio of speed to stroke induced speed

Very soft, \( G = 0.1 \)

Moderately soft, \( G = 1.0 \)

Stiff, \( G = 10.0 \)
Theory ignores nonlinear elasticity effects

De = 4.0

Softest, $G=0.1$

Moderate, $G=1.0$

Stiffest, $G=10.0$

Target stroke not achieved. Effectively low amplitude and low polymer stress.

Target stroke strongly enforced. Large polymer stress as a result.
Look at a measure of amplitude along side stress ratios

It is only in the high amplitude and high De regime where very large stresses develop
Some conclusions

- Espinosa-Garcia, Lauga, Zenit result has $G \approx 0.43$, soft regime, expect speed ups

- Another numerical group reported only slow-downs, 2016, Salazar, Roma, Ceniceros, $G \approx 7.7B$, stiff regime ($L = 0.6$, $G \sim B/L^4$), expect slow downs

- Essential to report body relaxation time:
  - 2007 Lauga – small amplitude, large $G$, always slow down
  - 2014 Riley, Lauga – small amplitude, vary $G$, speed up possible
  - 2010 Teran, Fauci, Shelley – large amplitude, small $G$, sometimes speed up
  - 2011 Shen, Arratia- large amplitude (head), large $G$, always slow down
  - 2013 Espinosa-Garcia, Lauga, Zenit – large amplitude, small $G$, always speed up
  - 2016 Salazar, Roma, Ceniceros, large $G$, always slow down
Some questions

- Away from the tail: linear elastic fluid assumption valid?
- What causes the large tail stresses?
- What is the effect on swimming from the large tail (or head) stresses?