Sperm Navigation in Complex Environments

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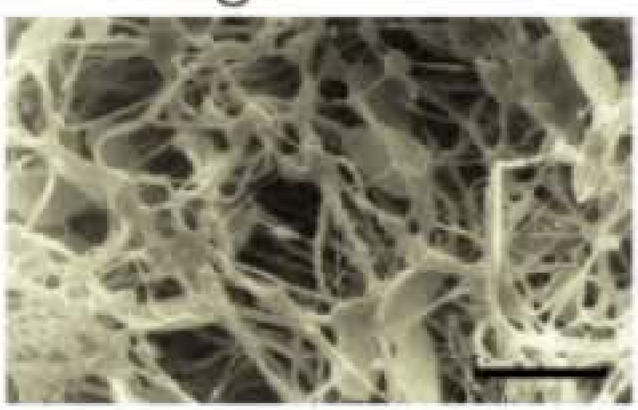
Fluid Resistance & Flagellar Waveforms

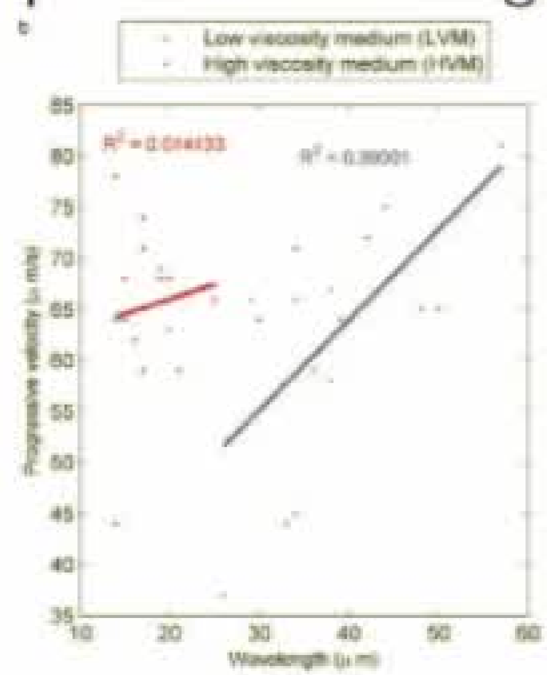
- How are emergent waveforms of elastic structures affected by the properties of the surrounding fluid?
- Fluid in the reproductive tract: changes viscosity, proteins, hormones, cellular debris, mucus (viscoelastic?)

Vaginal fluid



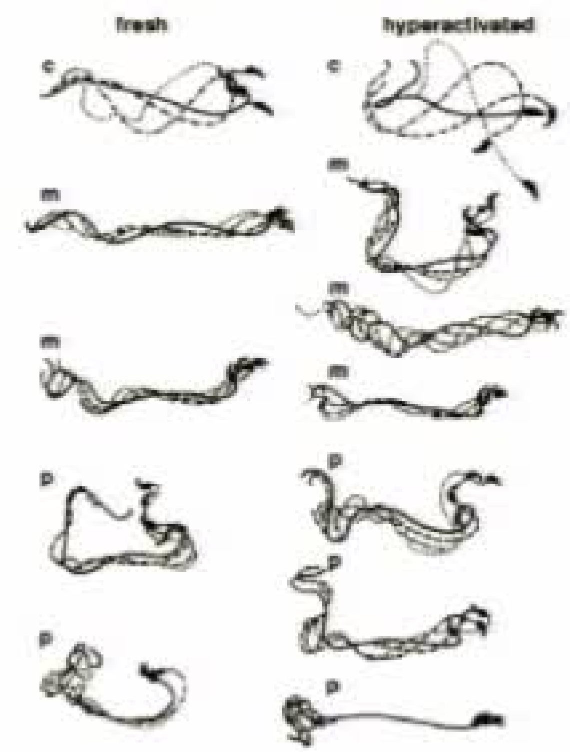
Ruttlant et al. Reprod Dom Anim (2005).

Speed & Wavelength



Smith *et al.* Cell Motil Cyto (2009).

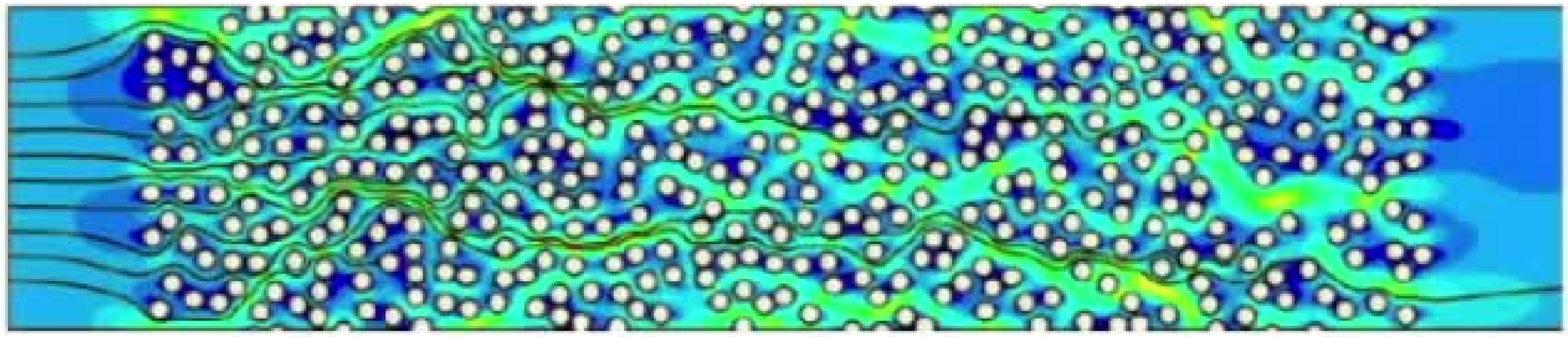
Beat Patterns



Suarez and Dai. Biol Reprod (1992).

Fluid Models

- Stokes: purely viscous, homogeneous, linear.
- Non-Newtonian: shear thinning fluids or viscoelastic models.
- Mixture models: two phases, fluid and solid.
- Porous media: solid matrix with interconnected voids (pores).



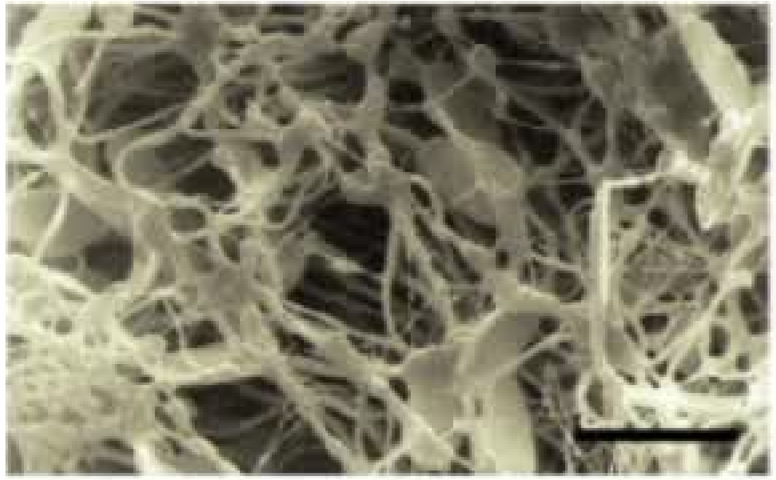
Porous Media (http://www.hans-hermann.ethz.ch)

Brinkman Model

- Brinkman Equation: effective medium approach modeling Stokes flow through sparse, stationary objects (Cortez, Leshansky, Siddiqui)

$$\nabla p = \mu \Delta \mathbf{u} - \mu \alpha^2 \mathbf{u} + \mathbf{F}, \qquad \nabla \cdot \mathbf{u} = 0$$

where $\alpha = 1/\sqrt{\gamma}$ is friction or resistance, γ is the permeability



Ruttlant *et al.* 2005.

- Assume pores are large enough for sperm to swim through
- Two phase fluid with stationary solid volume fraction

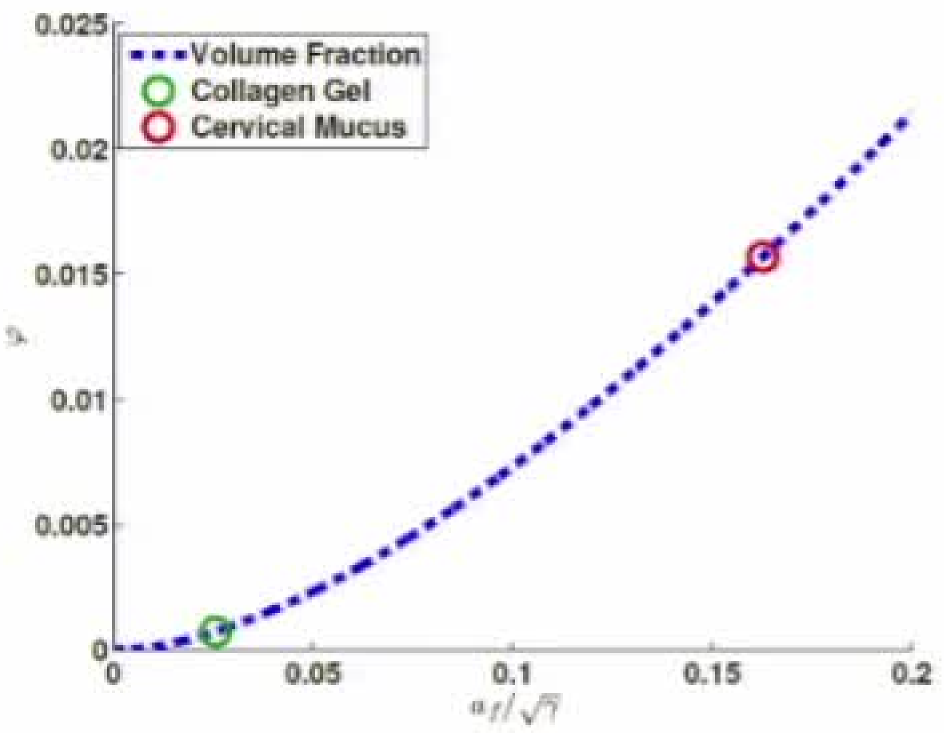
Permeability and Resistance

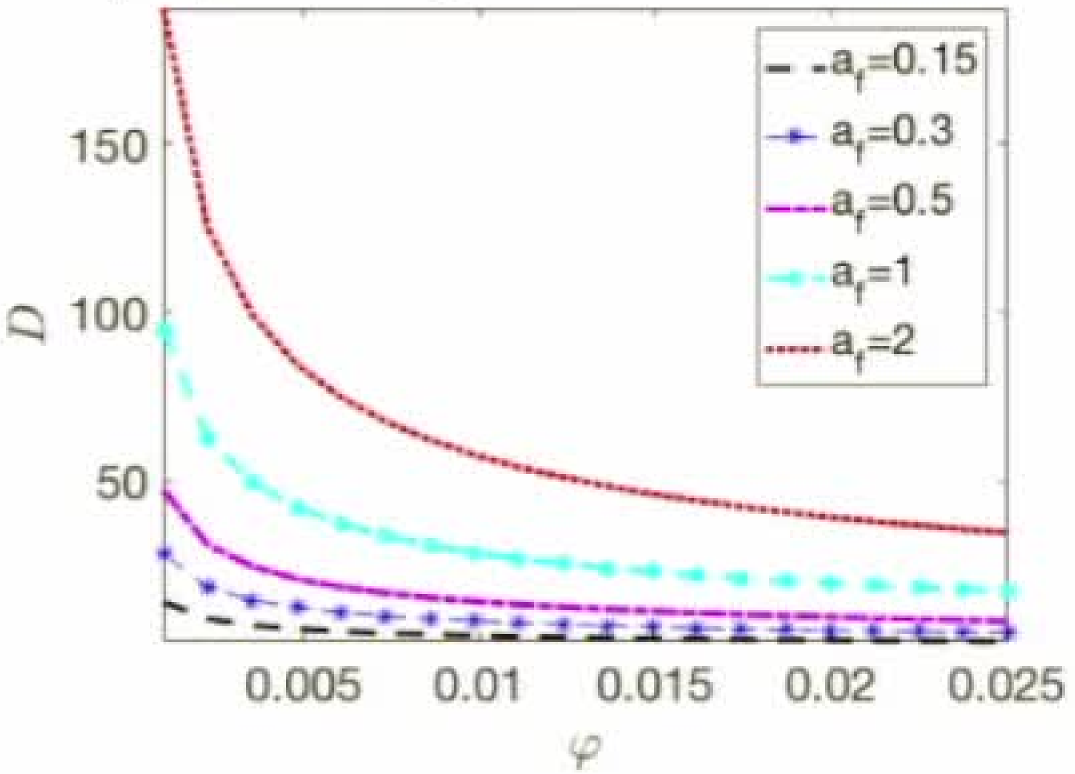
- Assuming randomly oriented fibers (Spielman and Goren, 1968):

$$\frac{a_f^2}{\gamma} = 4\varphi\left[\frac{1}{3}\frac{a_f^2}{\gamma} + \frac{5}{6}\frac{a_f}{\sqrt{\gamma}}\frac{K_1\left(a_f/\sqrt{\gamma}\right)}{K_o\left(a_f/\sqrt{\gamma}\right)}\right]$$

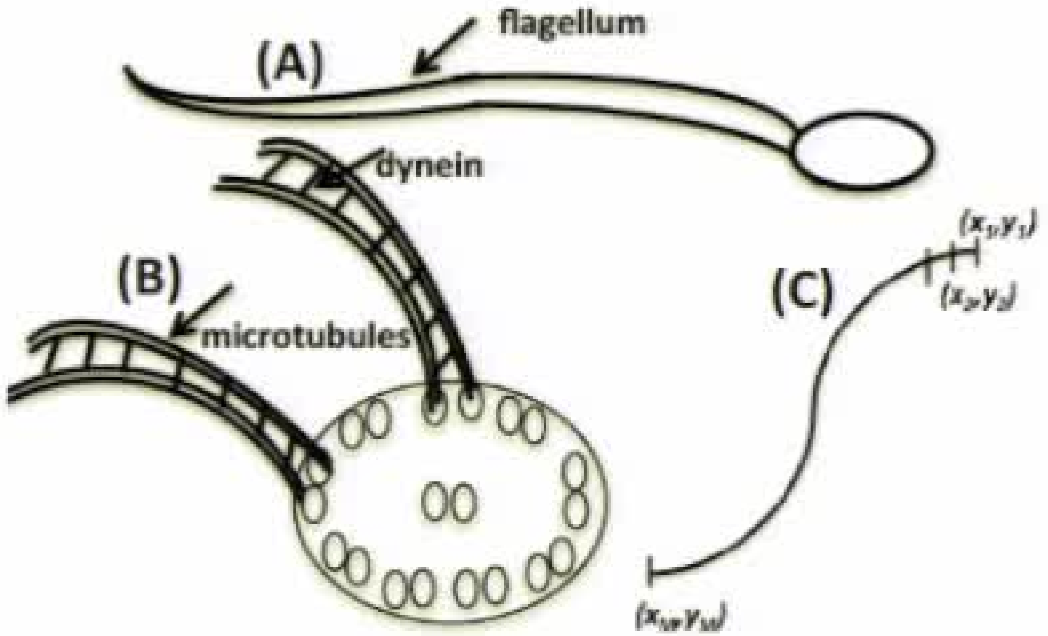
γ=permeability, φ=volume fraction of fibers, a_f=fiber radius, and $\alpha = 1/\sqrt{\gamma}$

- Average fiber separation D: $D \approx 2a_f\left[\frac{1}{2}\sqrt{\frac{3\pi}{\varphi}} - 1\right]$





Computational Models for Swimmers



- **Immersed Boundary Approach**: fluid coupled with elastic structure
- Flagellar centerline $\mathbf{X}(s,t)$
- Assume planar bending
- Structure - M points

- Velocity of structure: $\partial \mathbf{X}(s,t)/\partial t = \mathbf{u}(\mathbf{X}(s,t))$
- Utilize regularized fundamental solutions to have a Lagrangian method:

$$\mathbf{u}(\mathbf{y}_k) = \sum_{i=1}^{M} [\mathbf{f}_i H_1^\varepsilon + [\mathbf{f}_i \cdot (\mathbf{y}_k - \mathbf{x}_i)](\mathbf{y}_k - \mathbf{x}_i)\ H_2^\varepsilon]$$

which can then be written as $\mathcal{U} = \mathcal{A}\mathcal{F}$ for forces $\mathbf{F}_i = \mathbf{f}_i \psi_\varepsilon$

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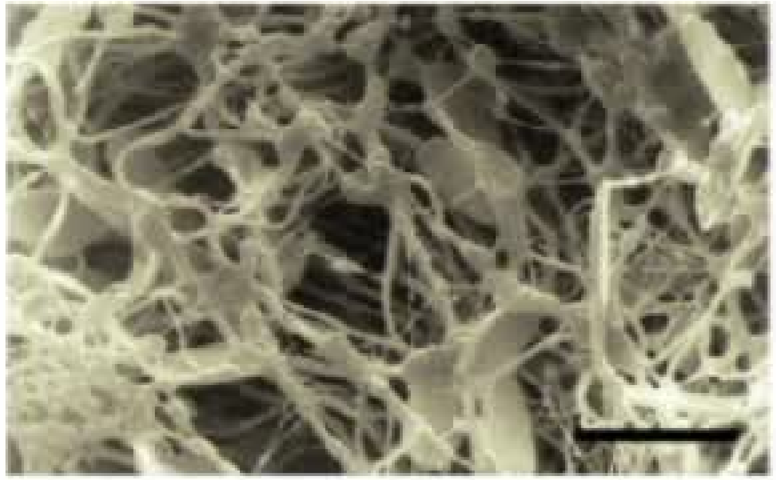

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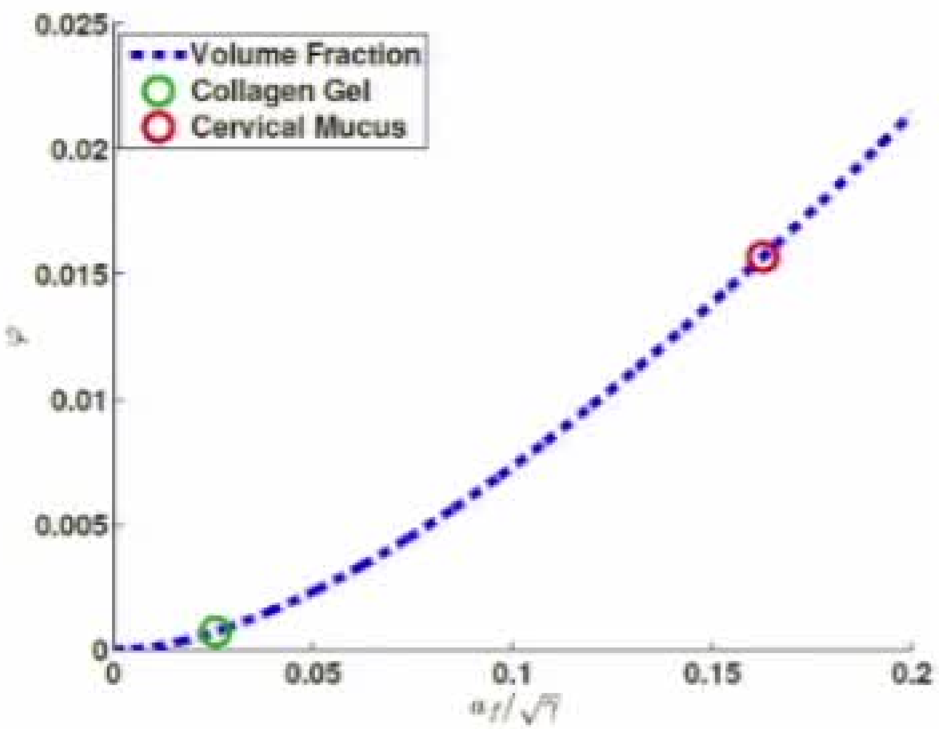

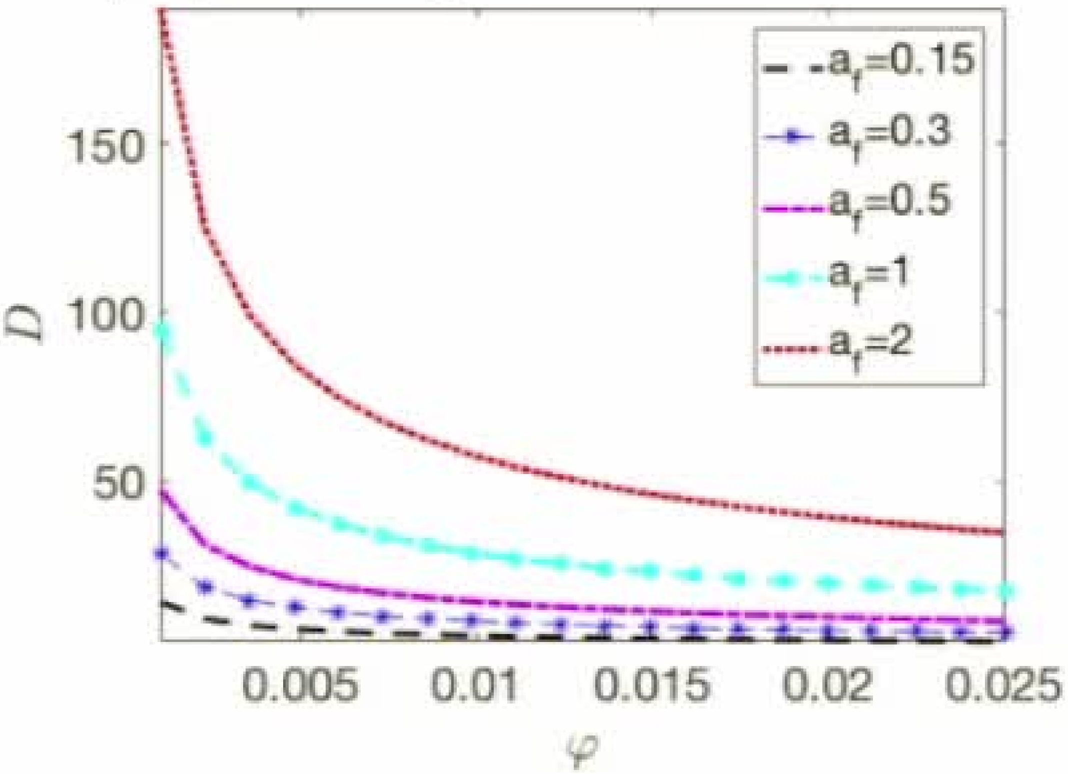

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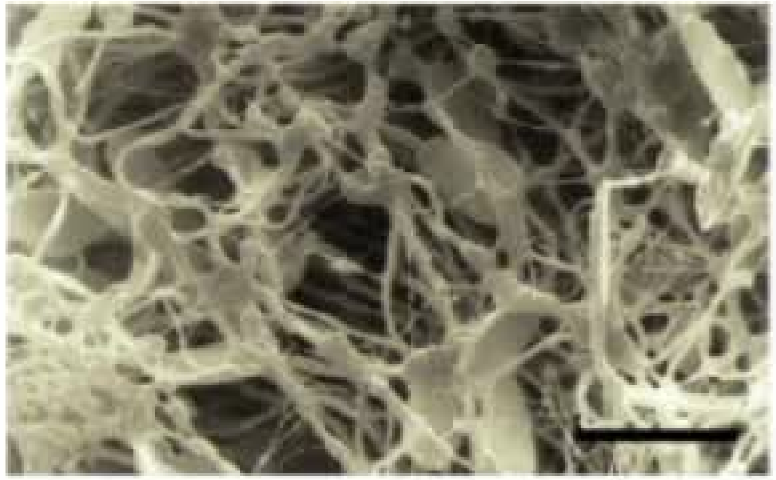

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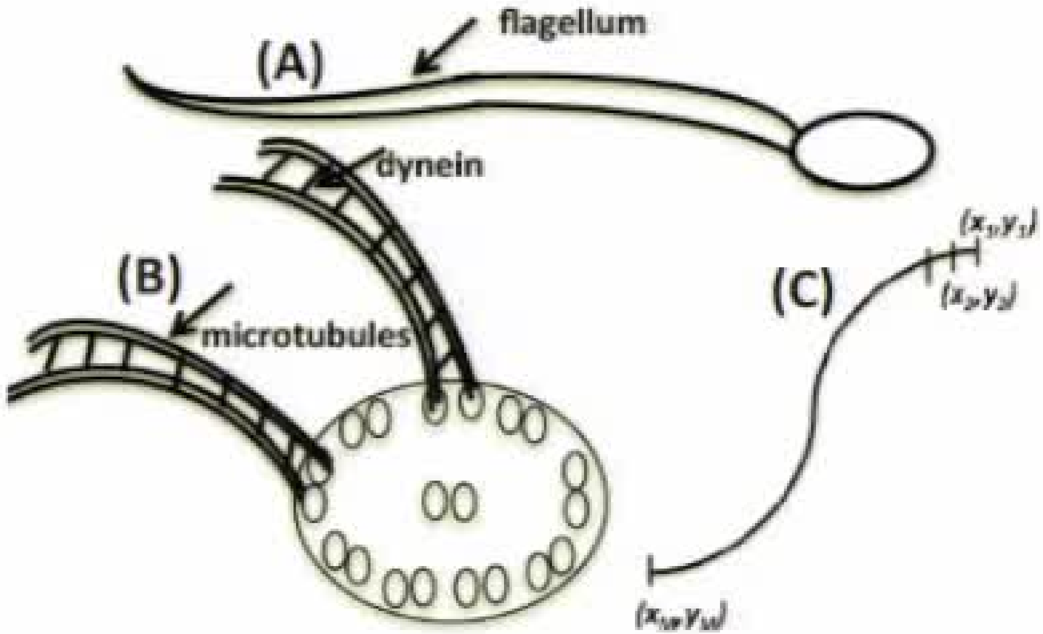

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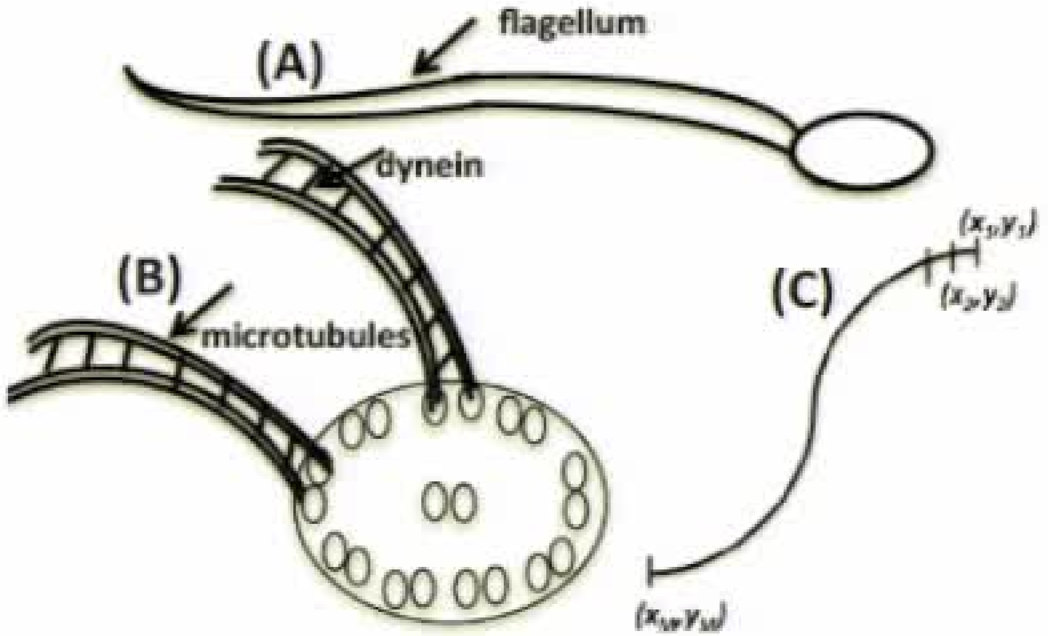

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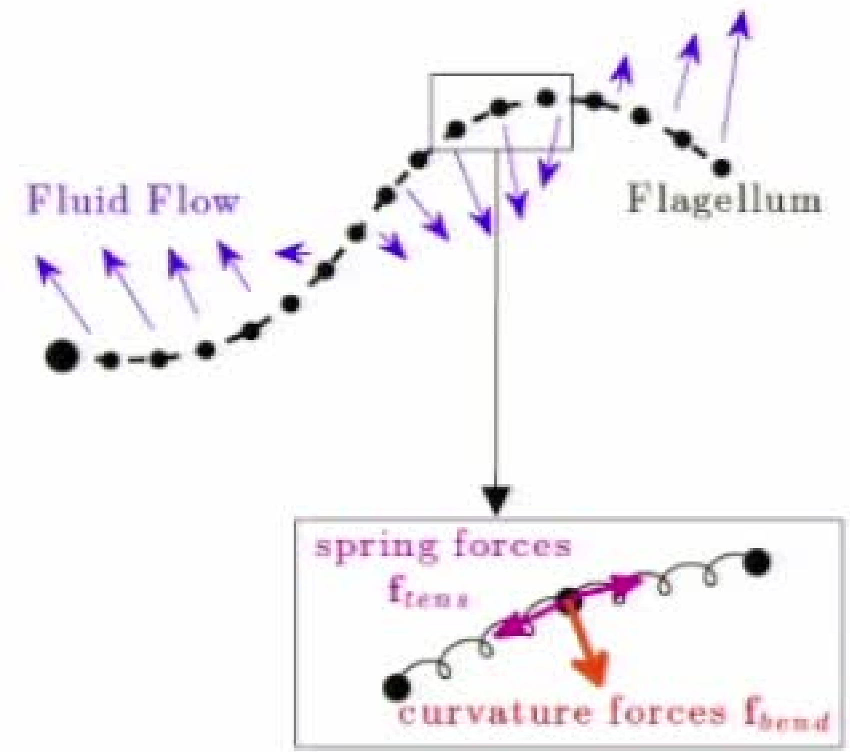
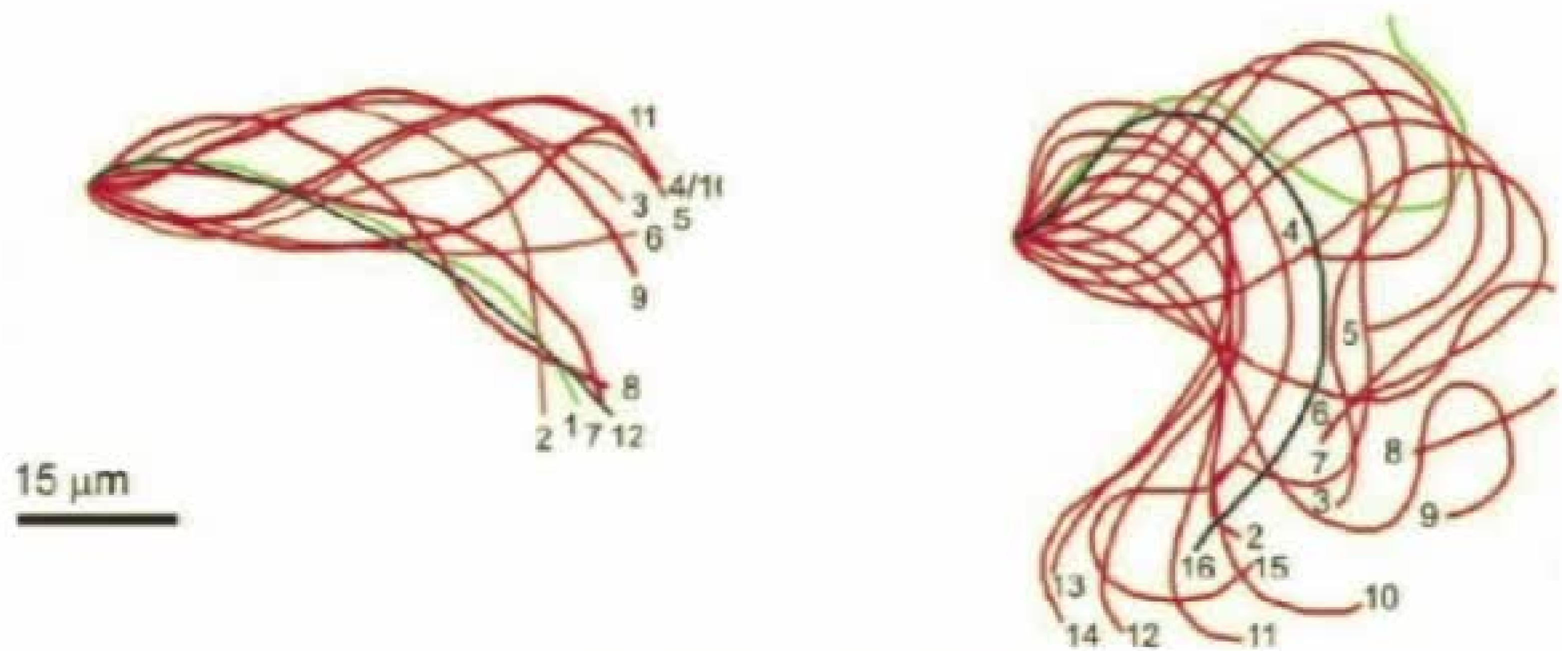
Forces

- Force per unit length of filament $\mathbf{X}(s,t)$:

$$\mathbf{f} = -\frac{\partial}{\partial \mathbf{X}} \left(E_{tens} + E_{bend}\right)$$

- $E_{tens} = S_1 \int \left[\left\| \frac{d\mathbf{X}}{ds} \right\| - 1 \right]^2 ds$
- $E_{bend} = S_2 \int \left[\frac{\partial \Theta}{\partial s} - \zeta(s,t) \right]^2 ds$





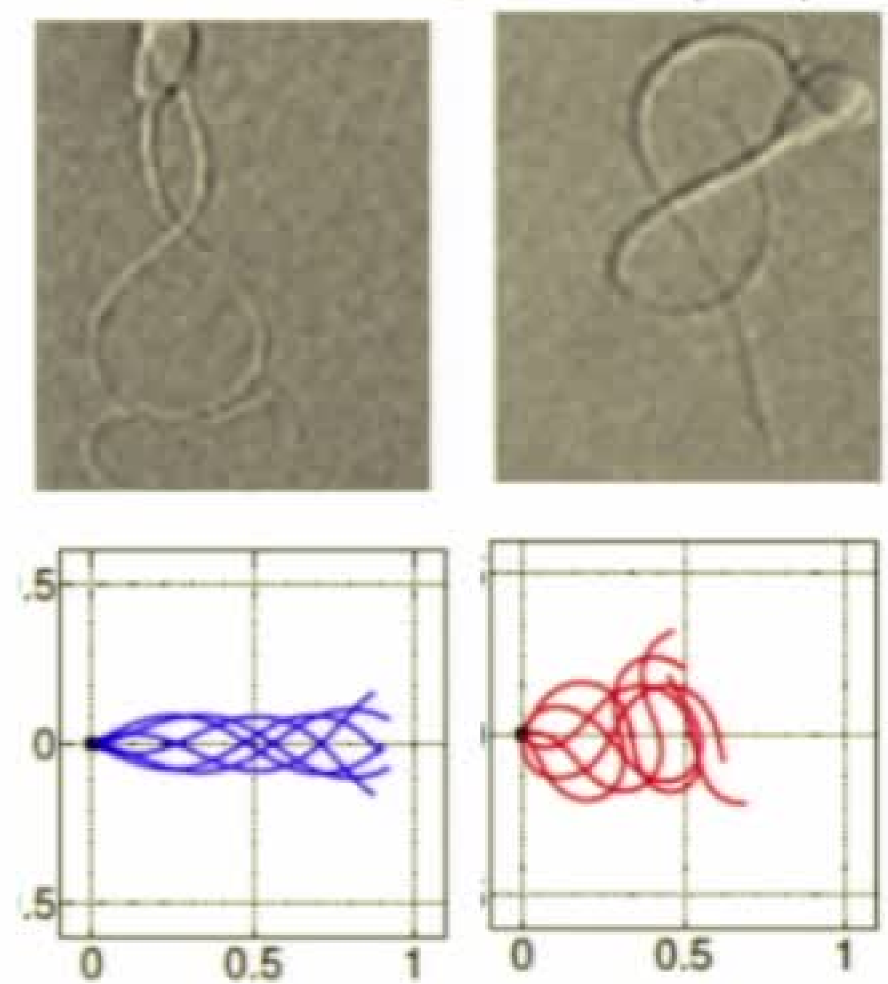
Carlson et al. PNAS (2003).

Curvature Model - $\zeta(s,t) = -k^2 b \sin(ks - \omega t)$

- **Constant amplitude** b,
  activated motility
- **Highly Asymmetric amplitude** b,
  hyperactivated motility:

$$b = \begin{cases} b_{A,1} & -k^2 \sin(ks - \omega t) > 0 \\ b_{A,2} & -\kappa^2 \sin(ks - \omega t) < 0 \end{cases}$$

Ho and Suarez. *Reproduction* (2001).



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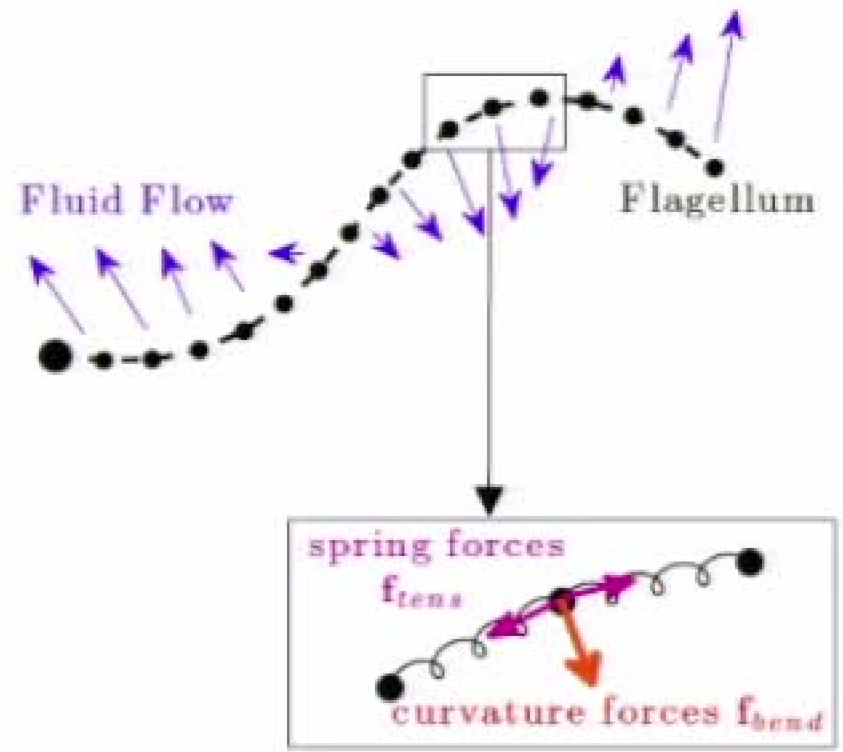

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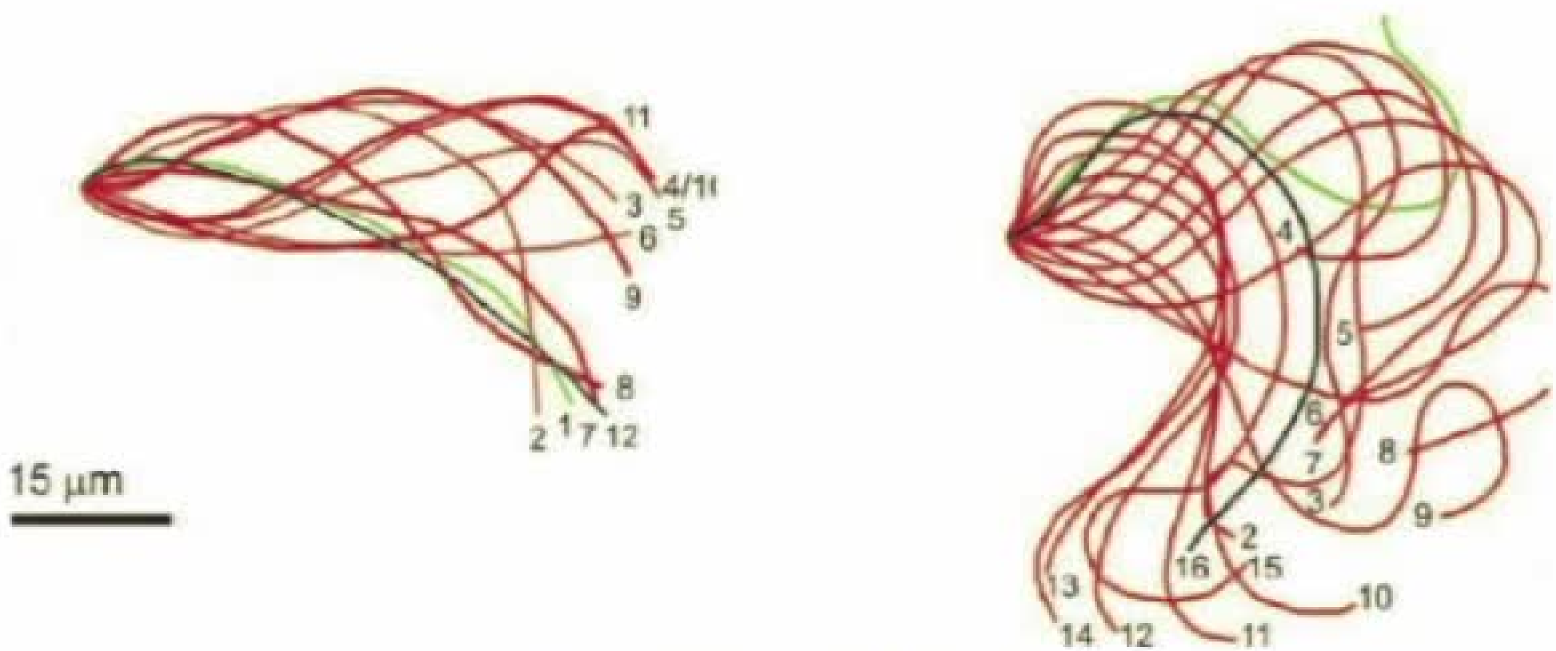

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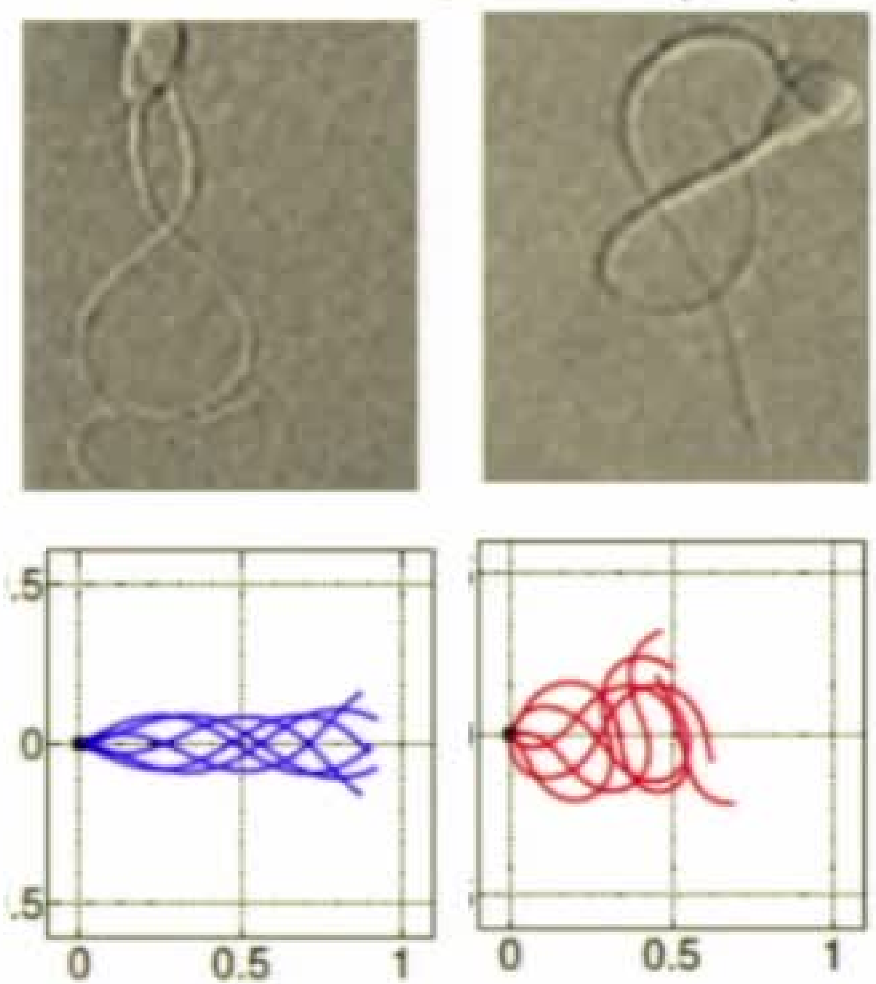

Symmetric Waveforms

$\overline{\alpha} = 0$

poster

poster

$\overline{\alpha} = 10$

poster

From asymptotic analysis (Leshansky 2009)

$$u_\infty = \frac{b^2 k\omega}{2}\sqrt{1 + \left(\frac{\overline{\alpha}}{k}\right)^2}$$

Olson and Leiderman. 2016. *Phys Fluids.*

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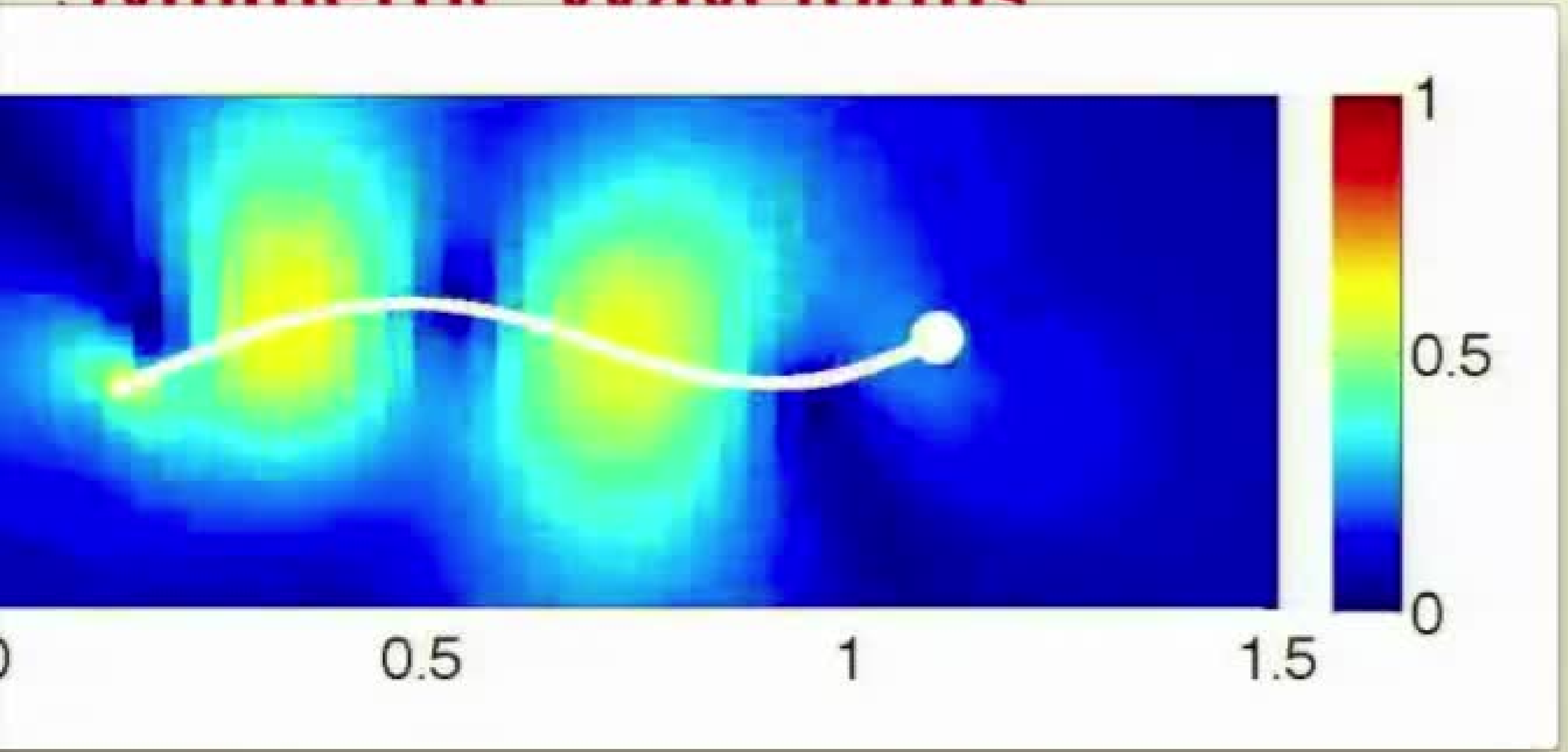

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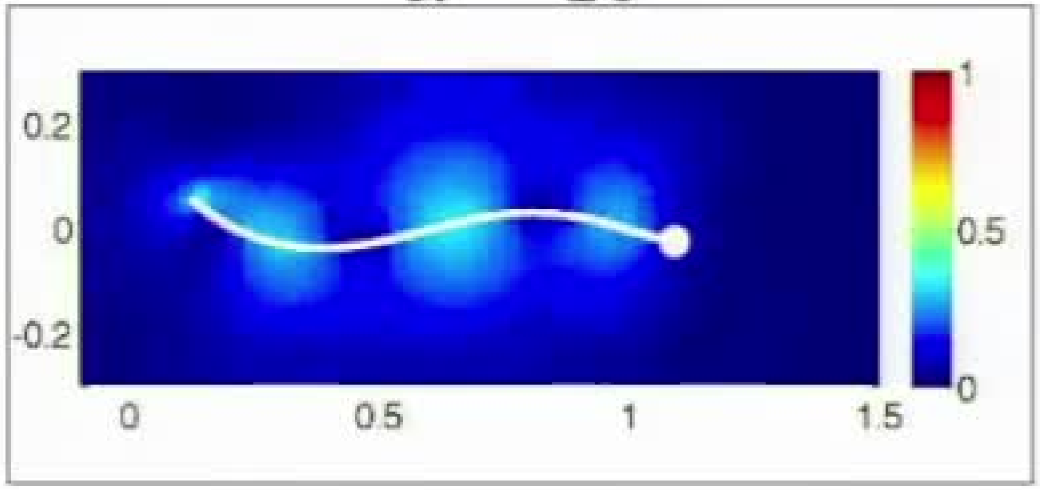

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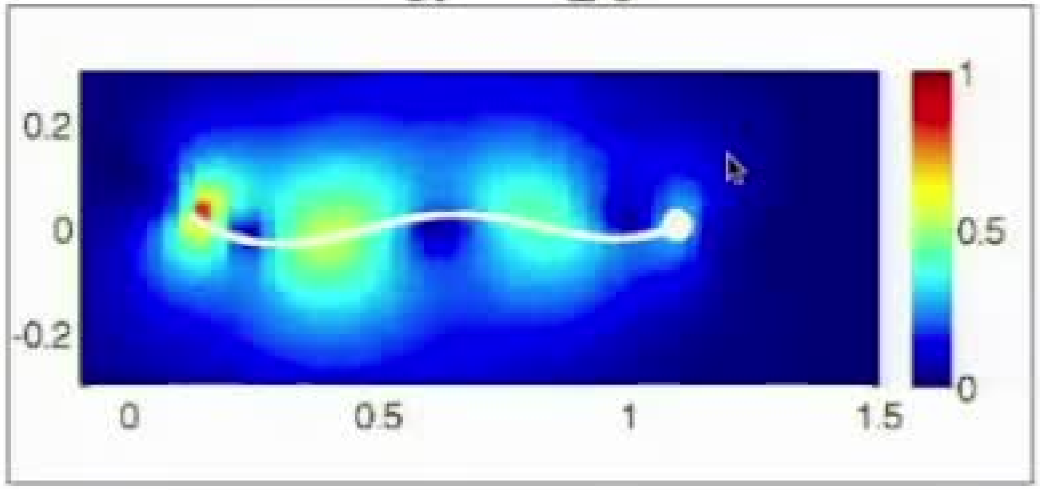

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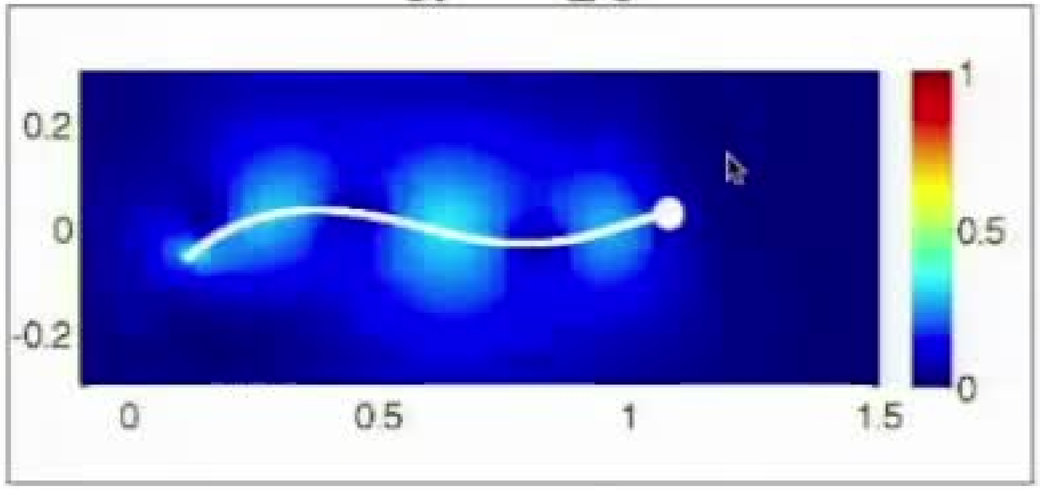

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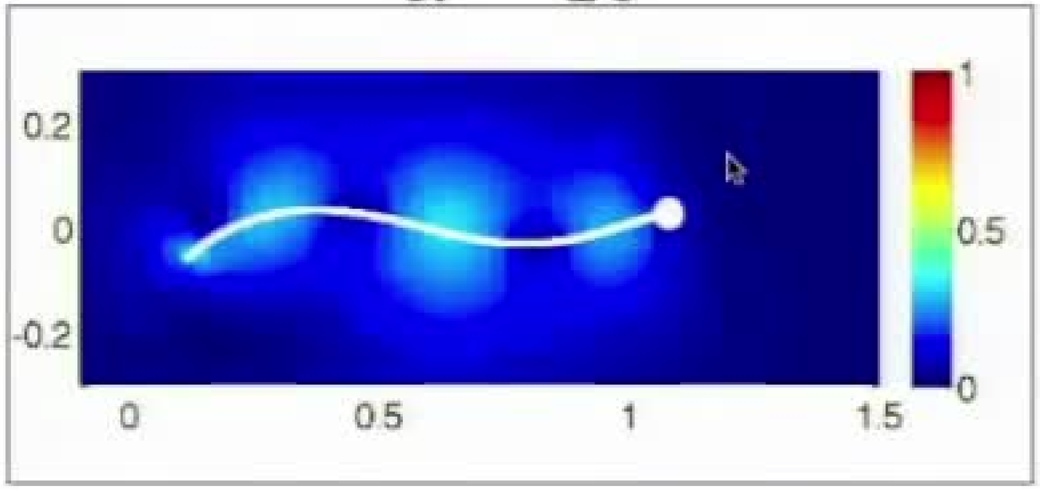

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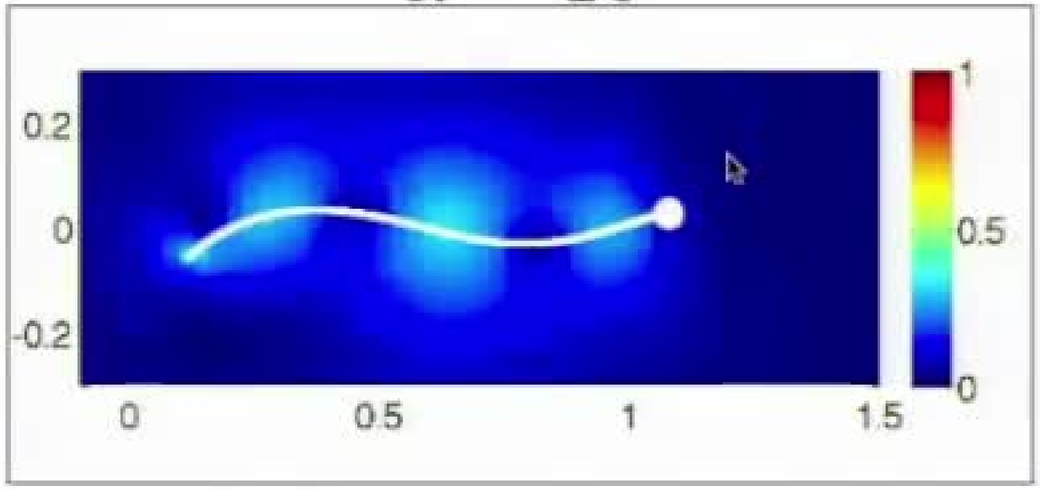

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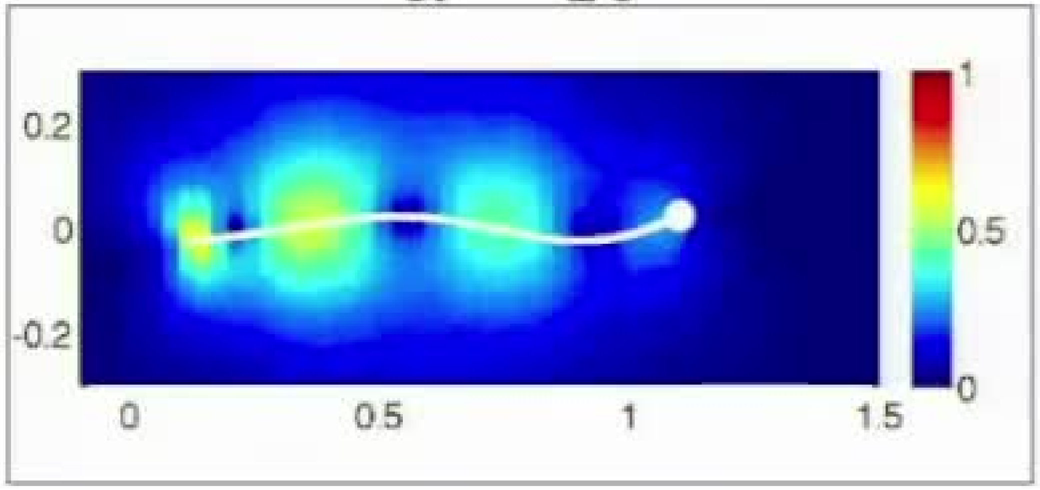

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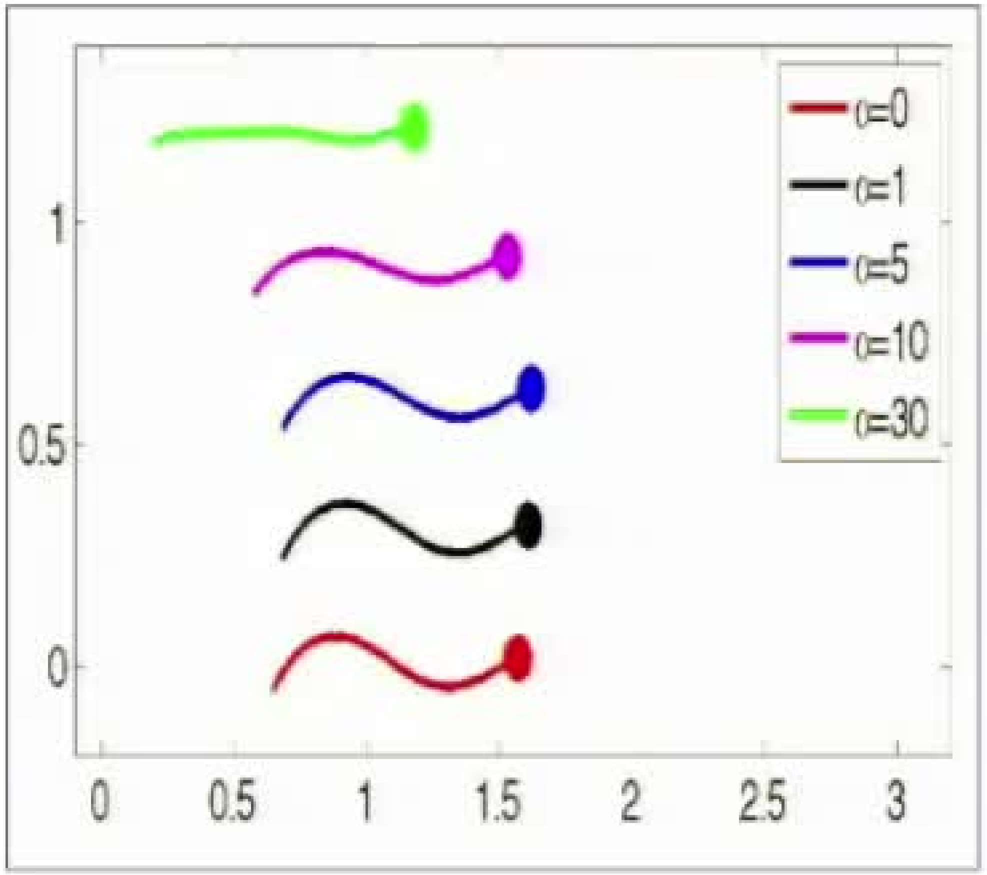

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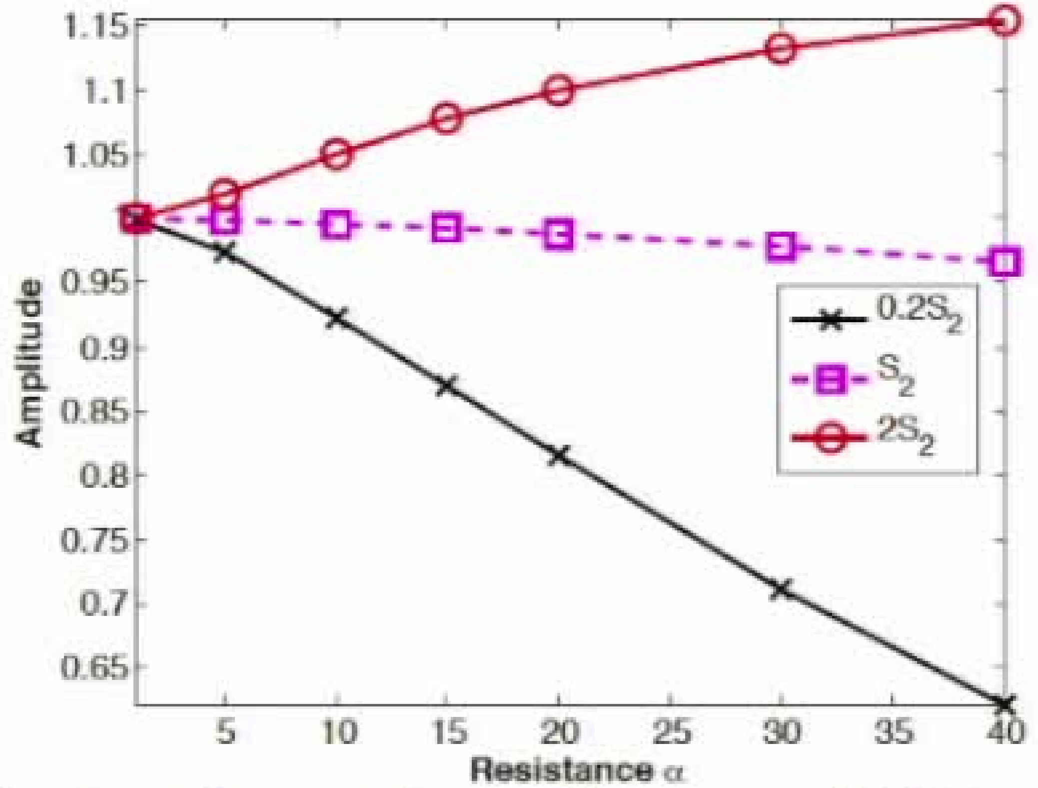
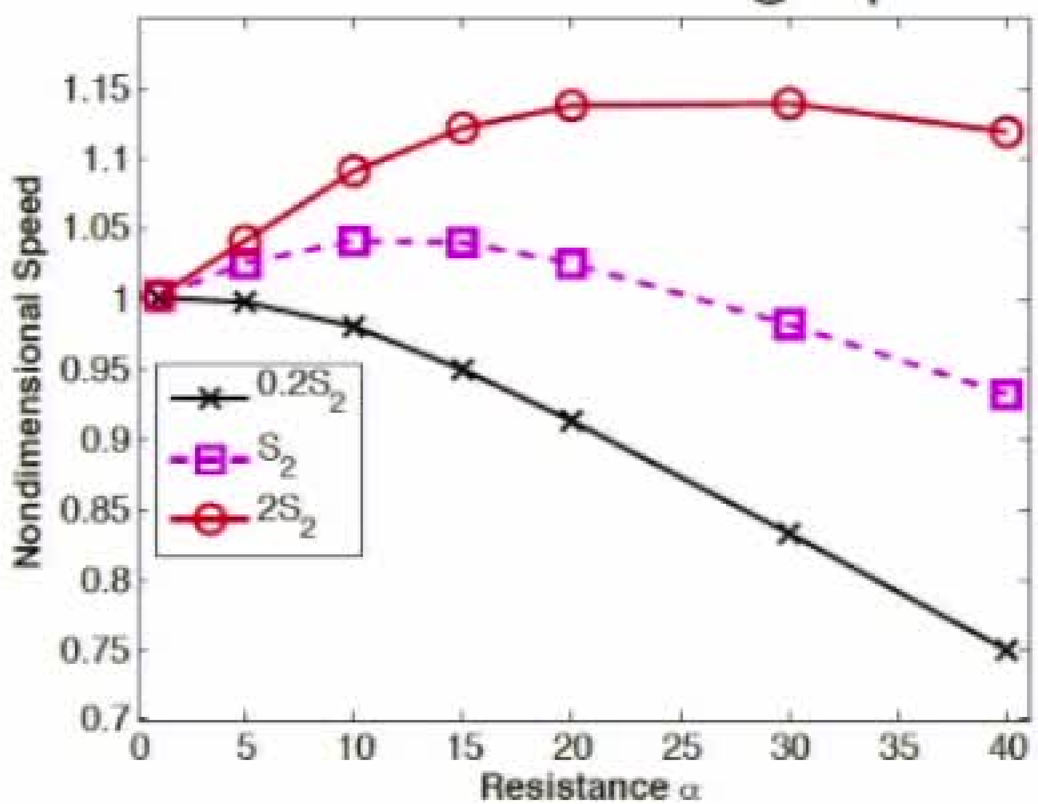




Infinite length swimmer (2D - sheet):

- Swimming speed enhanced with Brinkman model (relative to Stokes)

Leshansky. Phys Rev E (2009).

- Stationary limit of two phase fluid enhances swimming speed

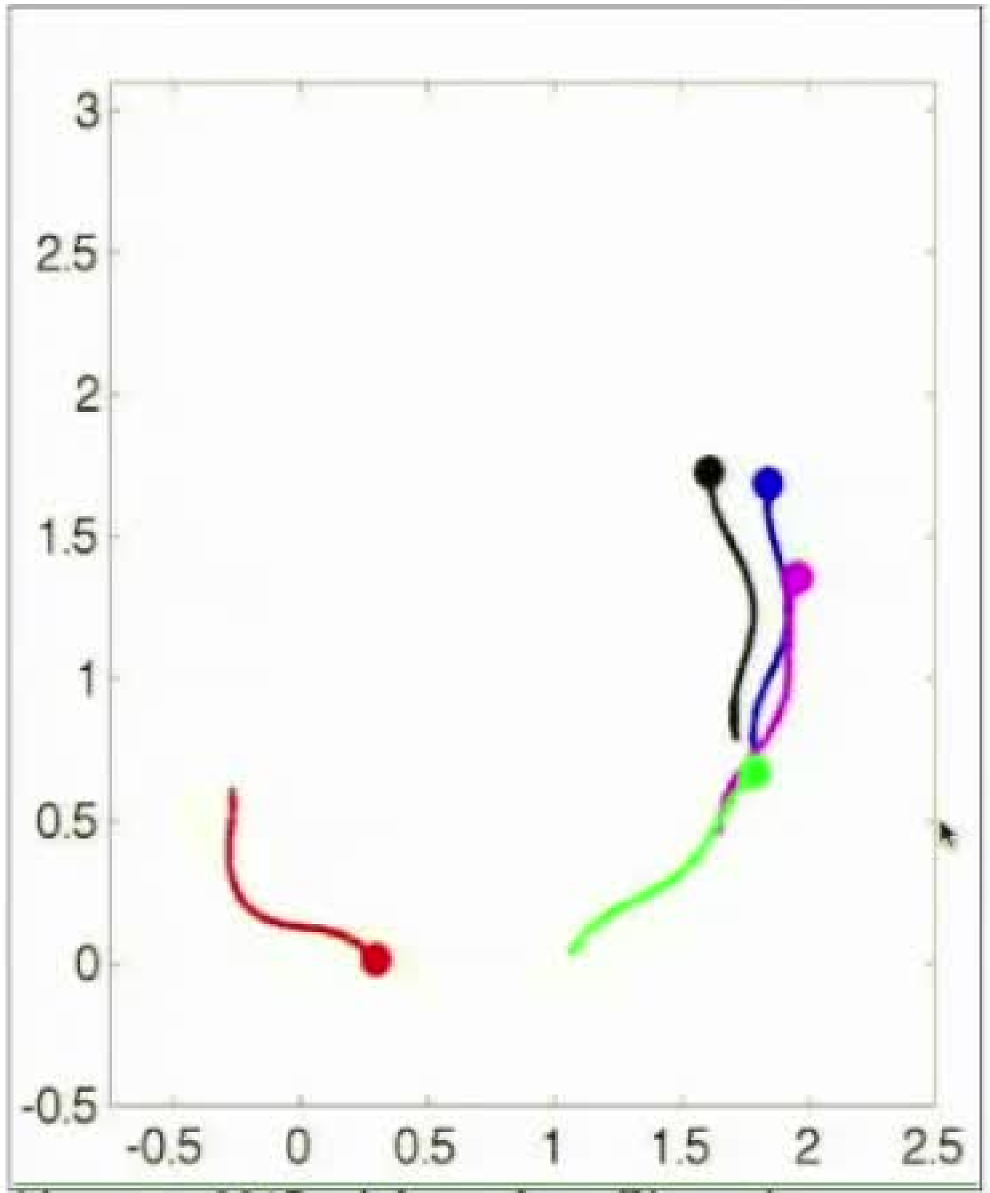
Fu et al. EPL (2010).

Finite length swimmer (3D - planar):

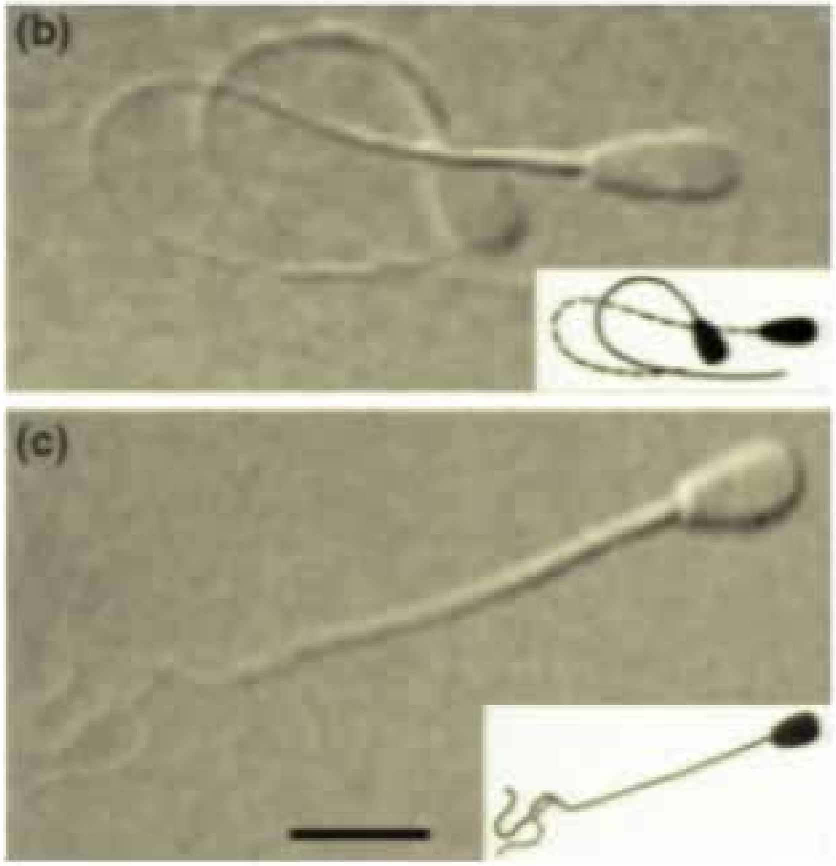
- Non-monotonic swimming speed with Brinkman model

Cortez et al. JCP (2010).

Asymmetric Waveforms - Trajectories



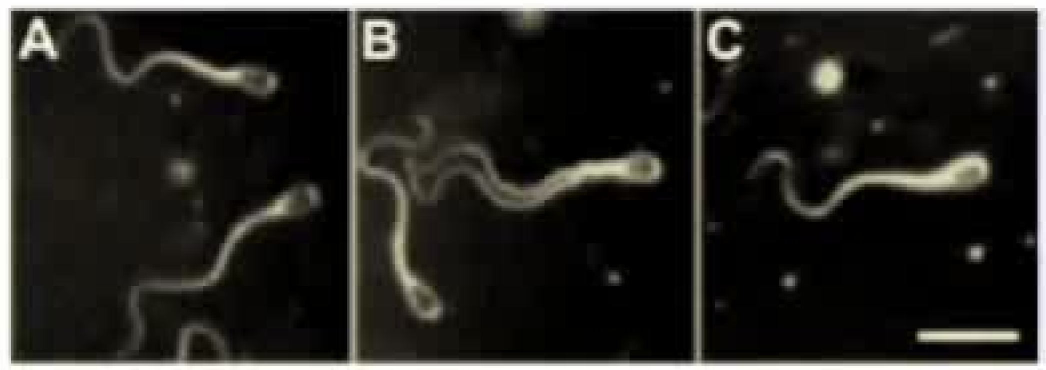
Olson and Leiderman. 2015. *J Aqua Aero Biomech.*



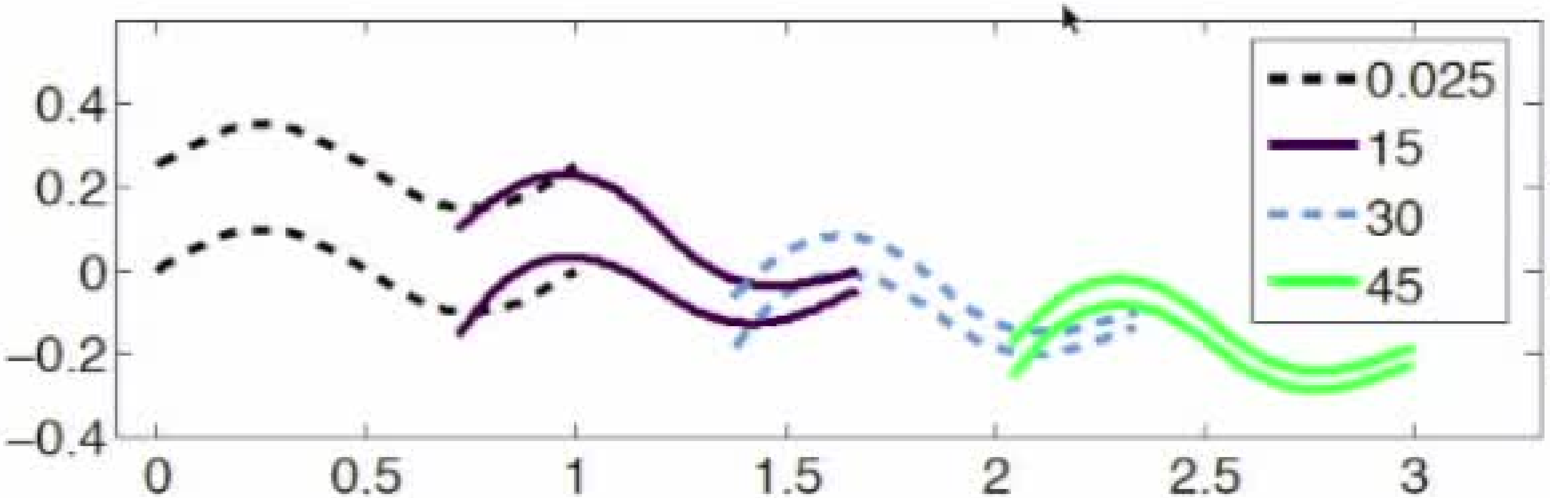
Ho and Suarez. 2001. *Reproduction.*

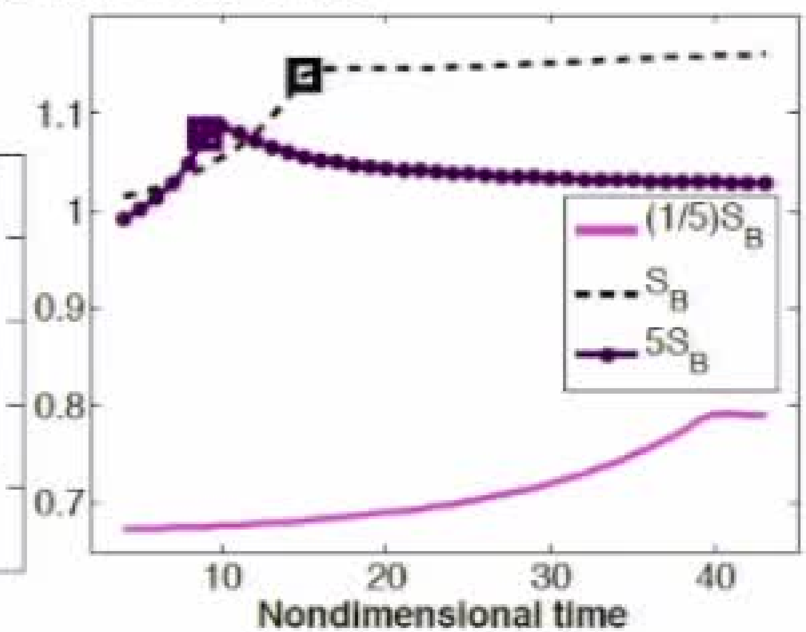
Synchronization & Attraction

- Analysis: decreased energy dissipation when beating is in phase (Taylor 1951, Elfring and Lauga 2011)
- Our model: each flagellum is given a *different* time dependent *preferred curvature*



Woolley, Crockett, Groom, and Revell. 2009. J Exp Biol 212:2215–2223.





Olson and Fauci. 2015. *Phys Fluids.*

Symmetric Waveforms - Attraction

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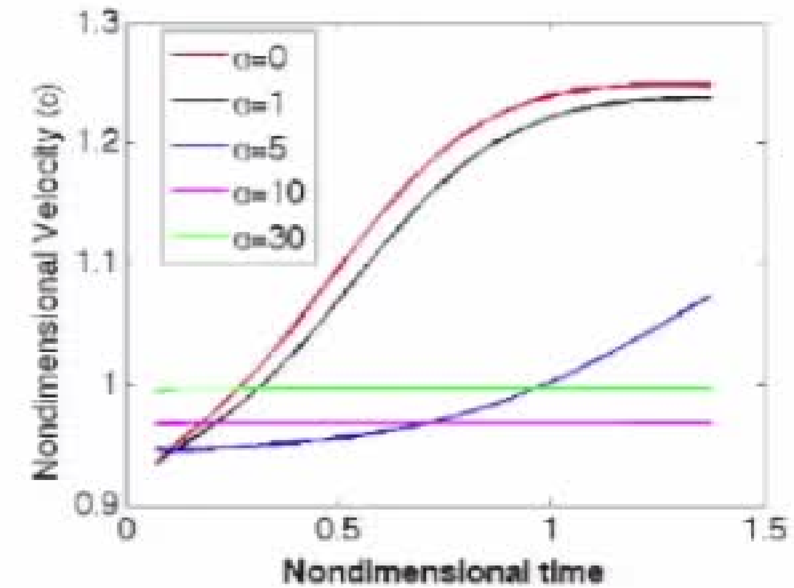
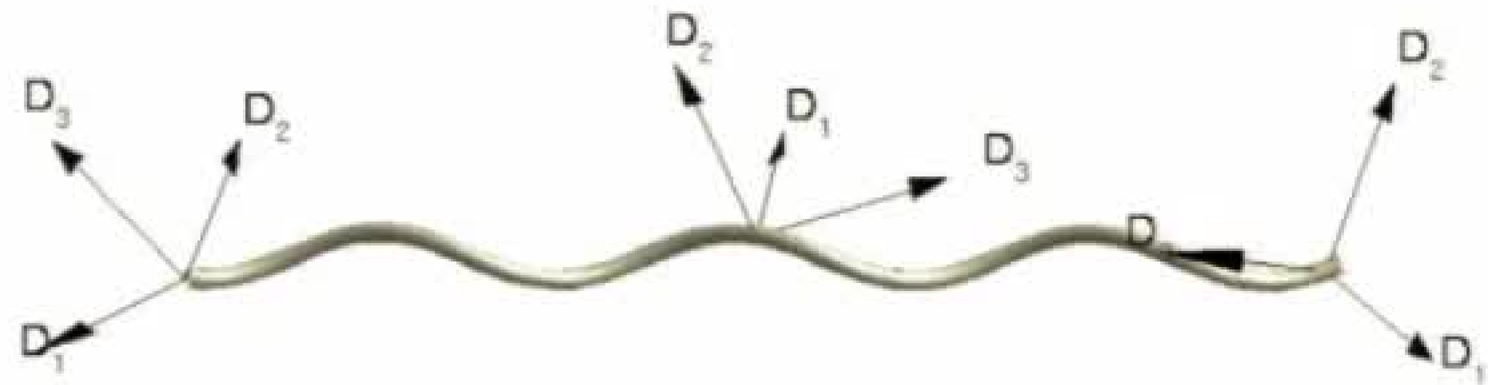
Olson and Leiderman. 2016. *Phys Fluids*.

Normalized Swimming Speed



Kirchhoff Rod Model

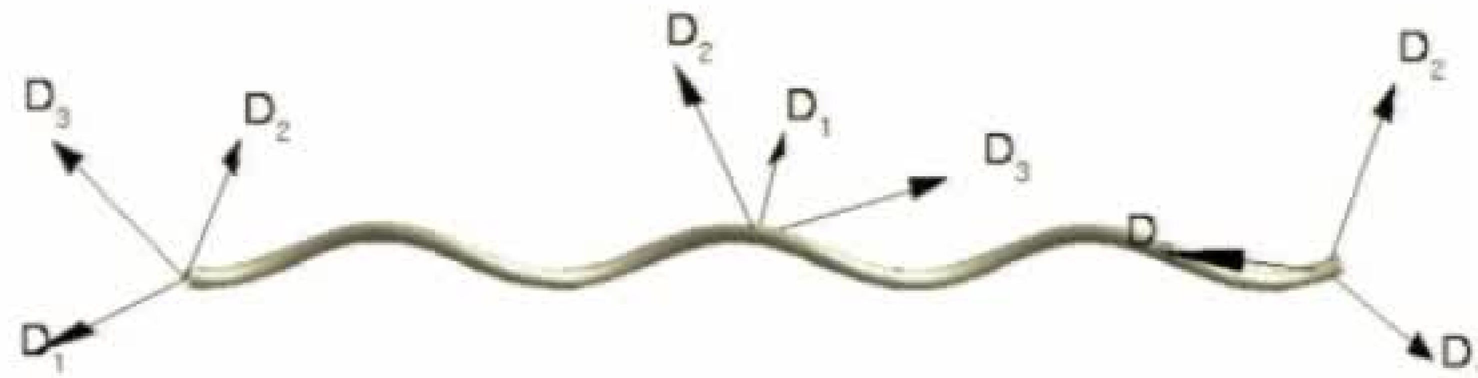


- Rod in terms of space curve $\mathbf{X}$ and associated triad $\{\mathbf{D}^1, \mathbf{D}^2, \mathbf{D}^3\}$
- $\mathbf{n}$ and $\mathbf{f}$ are applied torque and force density wrt ds
- Ω_i are preferred curvature and twist

$$E = \frac{1}{2}\int_0^L \Bigg[\underbrace{a_1\left(\frac{\partial \mathbf{D}^2}{\partial s}\cdot \mathbf{D}^3 - \Omega_1\right)^2 + a_2\left(\frac{\partial \mathbf{D}^3}{\partial s}\cdot \mathbf{D}^1 - \Omega_2\right)^2}_{\text{Bending}} + \underbrace{a_3\left(\frac{\partial \mathbf{D}^1}{\partial s}\cdot \mathbf{D}^2 - \Omega_3\right)^2}_{\text{Twisting}}\Bigg]\, ds$$

$$+ \frac{1}{2}\int_0^L \Bigg[\underbrace{b_1\left(\frac{\partial \mathbf{X}}{\partial s}\cdot \mathbf{D}^1\right)^2 + b_2\left(\frac{\partial \mathbf{X}}{\partial s}\cdot \mathbf{D}^2\right)^2}_{\text{Shear}} + \underbrace{b_3\left(\frac{\partial \mathbf{X}}{\partial s}\cdot \mathbf{D}^3 - 1\right)^2}_{\text{Extension/Compression}}\Bigg]\, ds$$

Kirchhoff Rod Model



- Rod in terms of space curve $\mathbf{X}$ and associated triad $\{\mathbf{D}^1, \mathbf{D}^2, \mathbf{D}^3\}$
- $\mathbf{n}$ and $\mathbf{f}$ are applied torque and force density wrt ds
- Ω_i are preferred curvature and twist

$$E = \frac{1}{2}\int_0^L \Bigg[\underbrace{a_1\left(\frac{\partial \mathbf{D}^2}{\partial s}\cdot \mathbf{D}^3 - \Omega_1\right)^2 + a_2\left(\frac{\partial \mathbf{D}^3}{\partial s}\cdot \mathbf{D}^1 - \Omega_2\right)^2}_{\text{Bending}} + \underbrace{a_3\left(\frac{\partial \mathbf{D}^1}{\partial s}\cdot \mathbf{D}^2 - \Omega_3\right)^2}_{\text{Twisting}}\Bigg] ds$$

$$+ \frac{1}{2}\int_0^L \Bigg[\underbrace{b_1\left(\frac{\partial \mathbf{X}}{\partial s}\cdot \mathbf{D}^1\right)^2 + b_2\left(\frac{\partial \mathbf{X}}{\partial s}\cdot \mathbf{D}^2\right)^2}_{\text{Shear}} + \underbrace{b_3\left(\frac{\partial \mathbf{X}}{\partial s}\cdot \mathbf{D}^3 - 1\right)^2}_{\text{Extension/Compression}}\Bigg] ds$$

Brinkman fluid with Kirchhoff rod

$$\nabla p = \mu \Delta \mathbf{u} - \mu \alpha^2 \mathbf{u} + \mathbf{f}_0 \psi_\varepsilon + \frac{1}{2} \nabla \times \mathbf{n}_0 \psi_\varepsilon$$

- Define $\Delta G_\varepsilon = \psi_\epsilon$ and $(\Delta - \alpha^2) B_\varepsilon = G_\varepsilon$
- Take divergence and use incompressibility to get: $p = \mathbf{f}_0 \cdot \nabla G_\varepsilon$
- Substituting the pressure back into the Brinkman equation:

$$\mu \mathbf{u} = (\mathbf{f}_0 \cdot \nabla) \nabla B_\varepsilon - \alpha^2 \mathbf{f}_0 B_\varepsilon - \mathbf{f}_0 G_\varepsilon - \frac{1}{2} \alpha^2 \nabla B_\varepsilon \times \mathbf{n}_0 - \frac{1}{2} \nabla G_\varepsilon \times \mathbf{n}_0$$

- Angular velocity is $\boldsymbol{\omega} = \frac{1}{2} \nabla \times \mathbf{u}$:

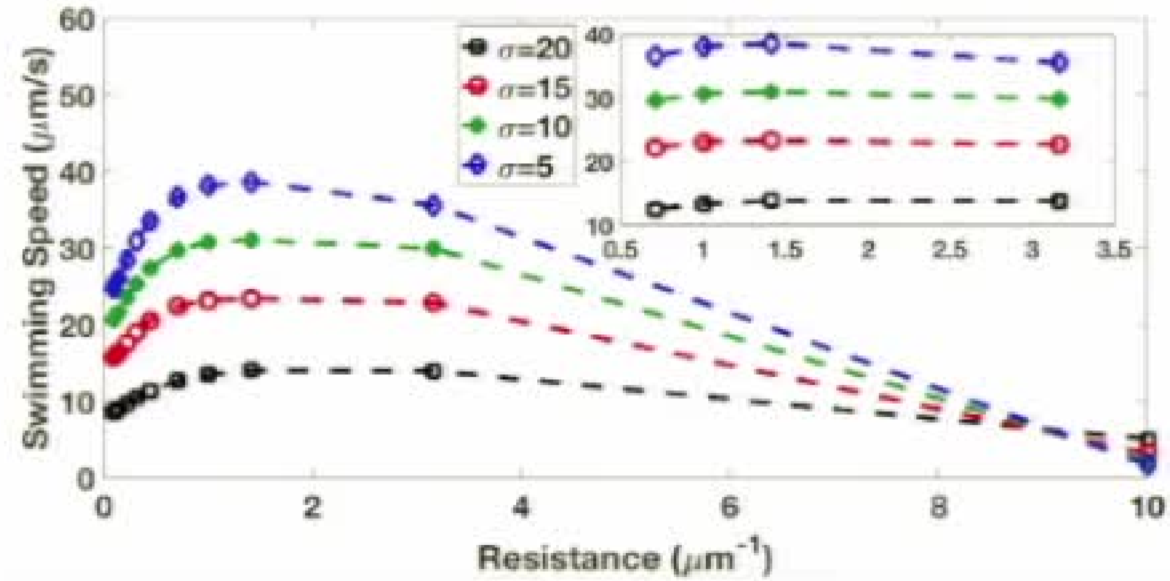
$$\begin{aligned} \mu \boldsymbol{\omega} &= \frac{1}{2} \alpha^2 \mathbf{f}_0 \times \nabla B_\epsilon + \frac{1}{2} \mathbf{f}_0 \times \nabla G_\epsilon - \frac{1}{4} \alpha^2 (\mathbf{n}_0 \cdot \nabla) \nabla B_\epsilon \\ &\quad + \frac{1}{4} \alpha^2 \Delta B_\epsilon \mathbf{n}_0 - \frac{1}{4} (\mathbf{n}_0 \cdot \nabla) \nabla G_\epsilon + \frac{1}{4} \Delta G_\epsilon \mathbf{n}_0 \end{aligned}$$

Brinkman - 3D Swimming

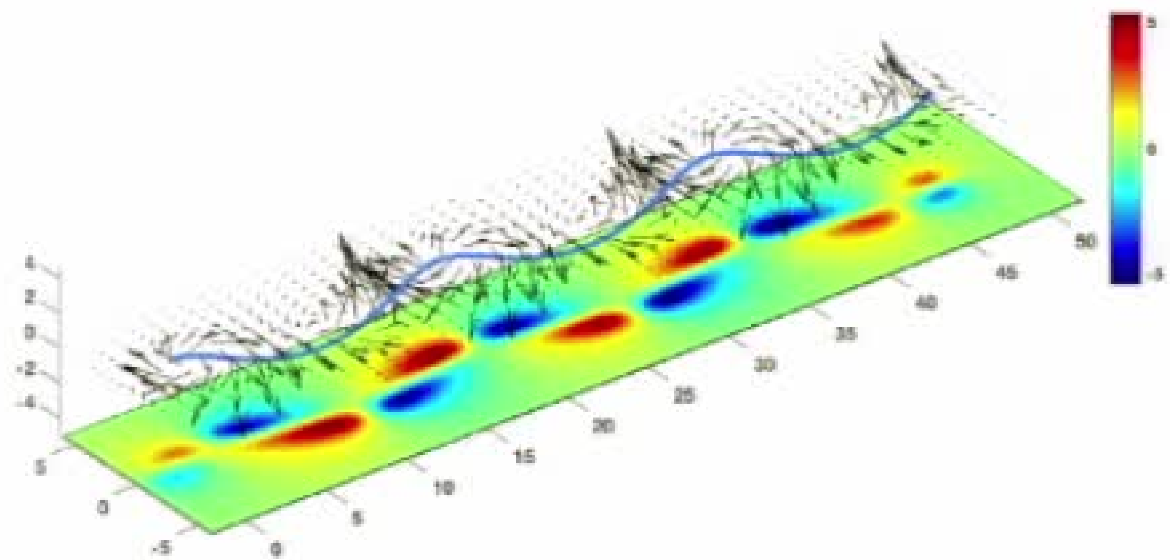
$\alpha = 1/\sqrt{\gamma}$

poster

Planar: $\Omega_1 = -bk^2 \sin(ks + \omega t)$,
$\Omega_2 = \Omega_3 = 0$



Helix: $\Omega_1 = \kappa \cos(\tau(s - Ut))$,
$\Omega_2 = -\kappa \sin(\tau(s - Ut))$, $\Omega_3 = 0$



Ho, Leiderman, and Olson. *In Review.*

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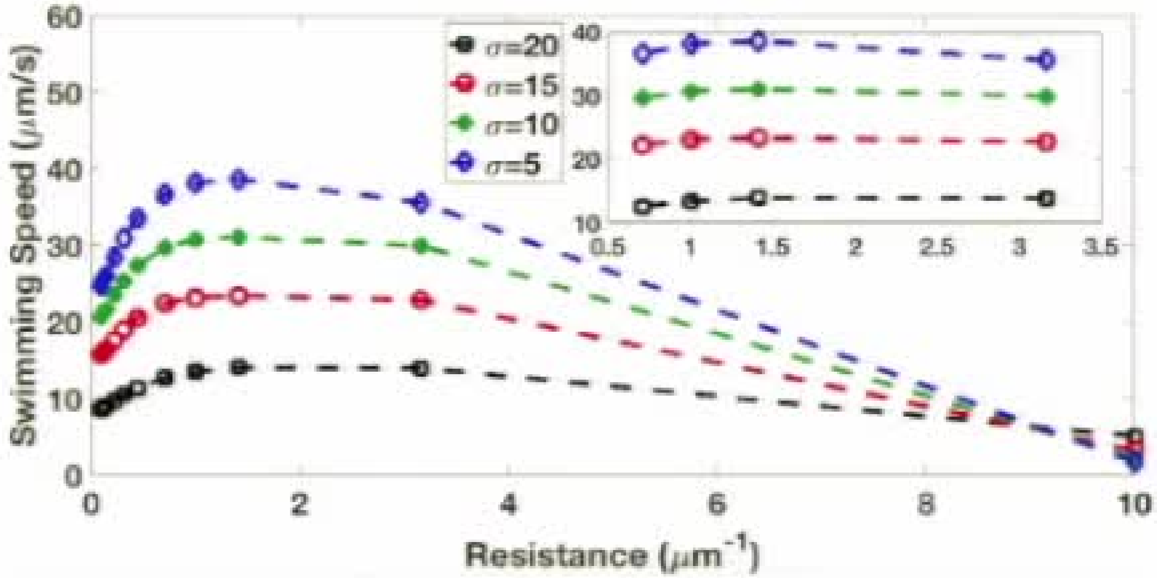

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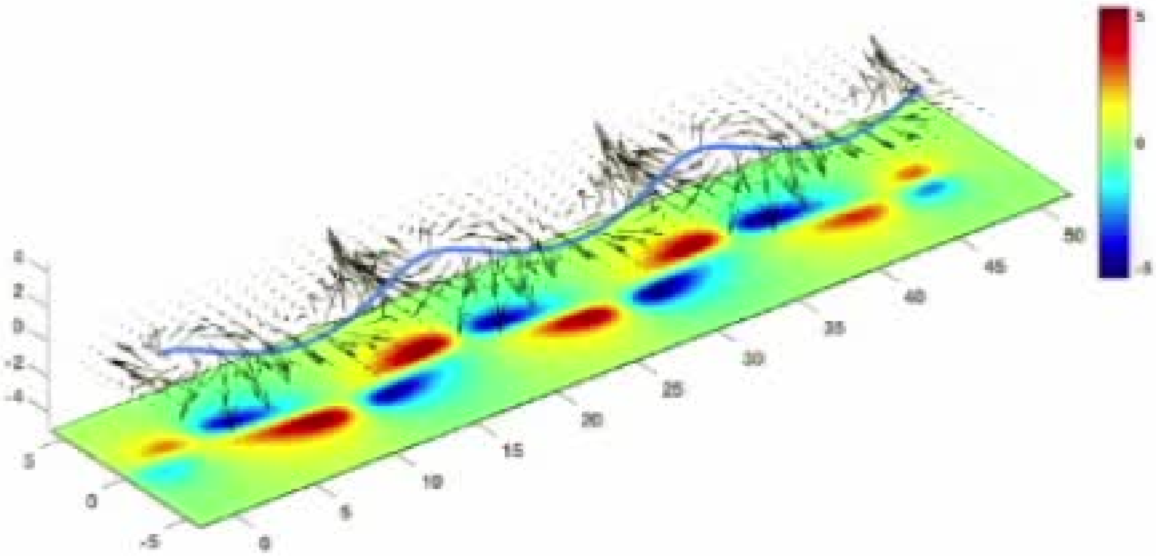

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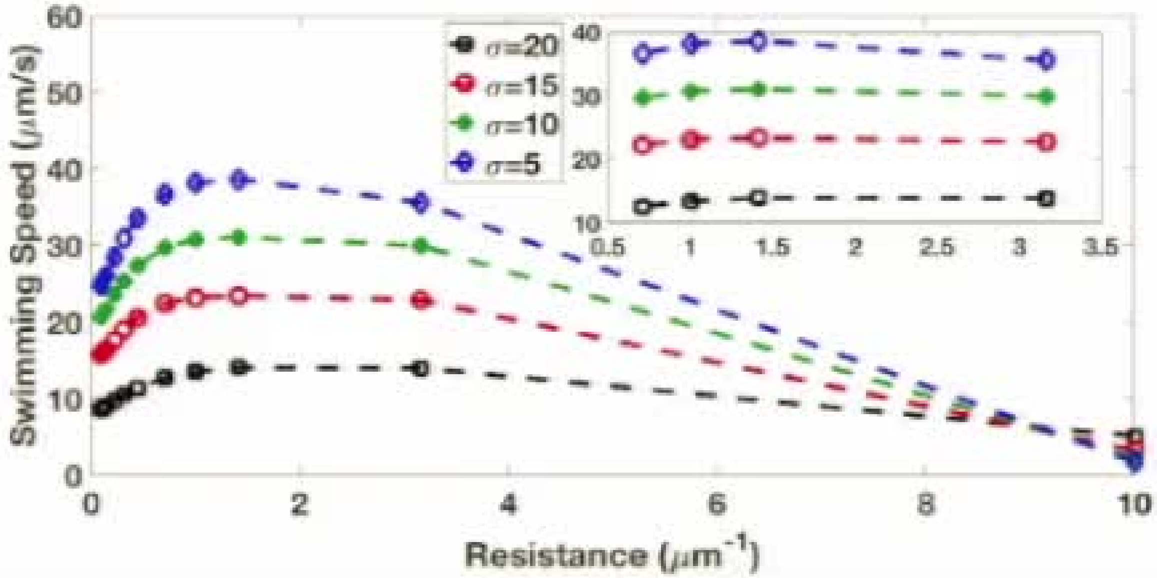

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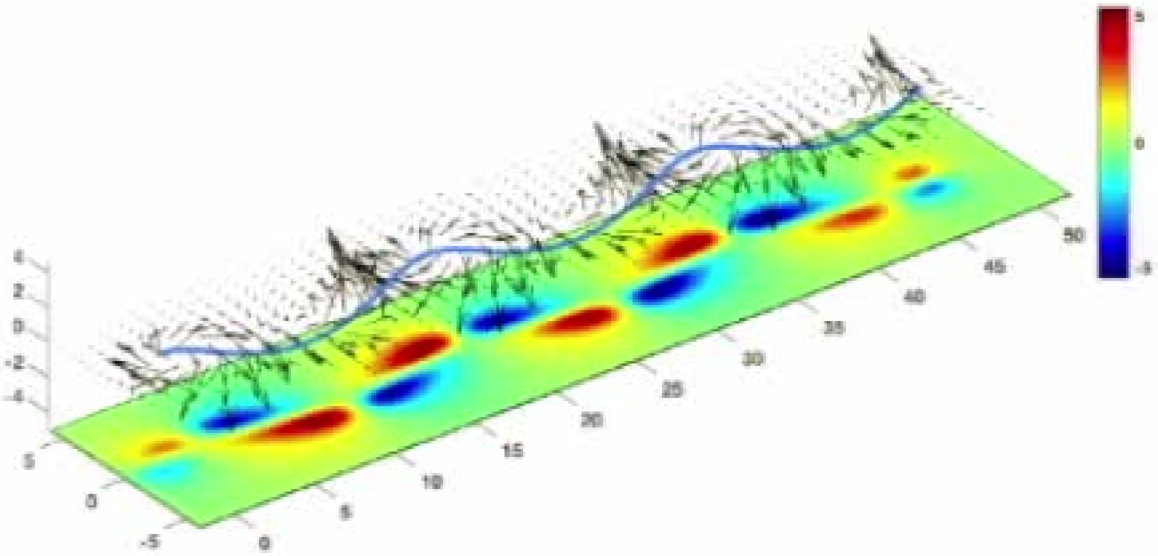

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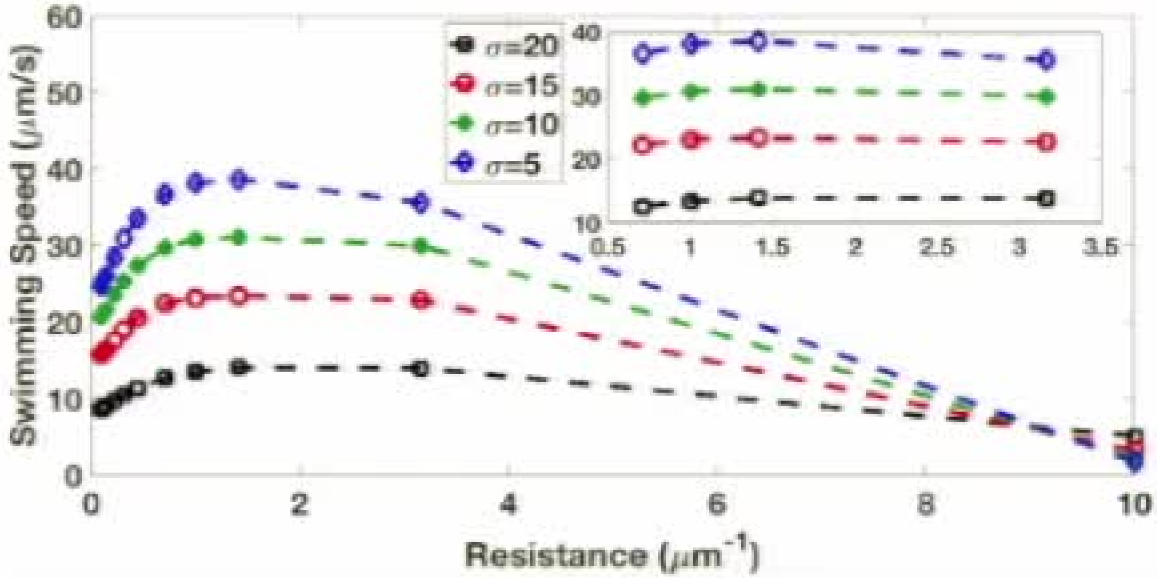

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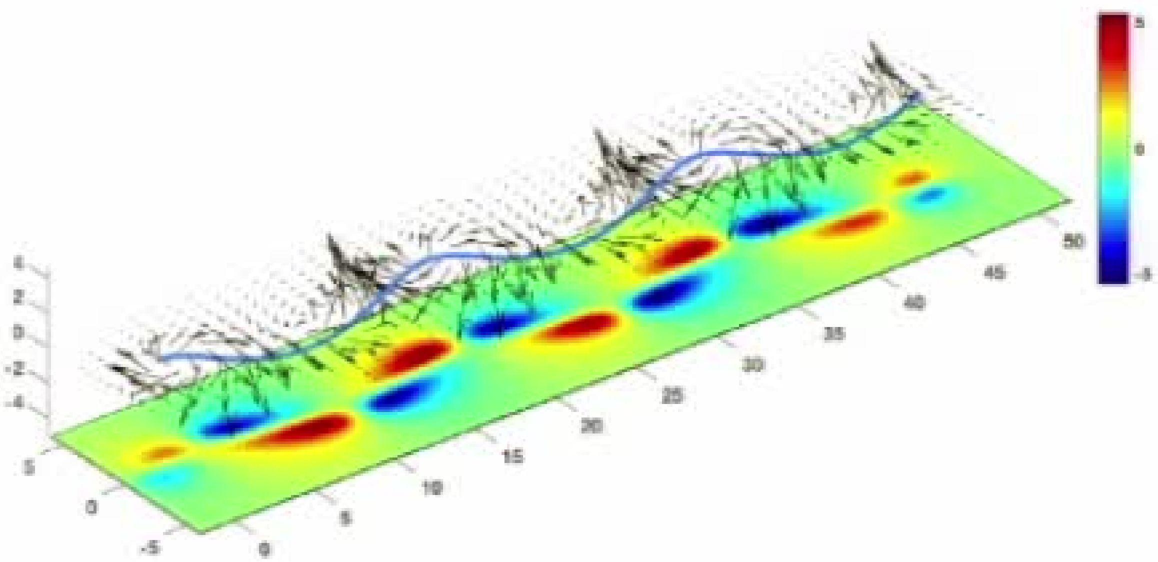


Ho, Leiderman, and Olson. *In Review.*

Brinkman - Propulsion

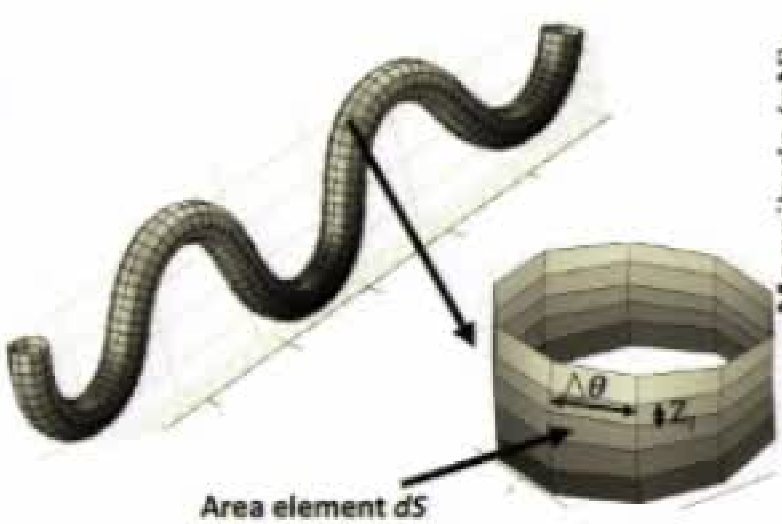
- $\hat{\mathbf{n}}$ is the unit outward normal and $\mathbf{\Lambda} = \mu(\nabla \mathbf{u} + \nabla \mathbf{u}^T)$ is the fluid stress
- Drag forces:

$$\mathbf{F}_{drag} = \int_{\Omega} \hat{\mathbf{n}} \cdot \mathbf{\Lambda} dS,$$

- Propulsive forces

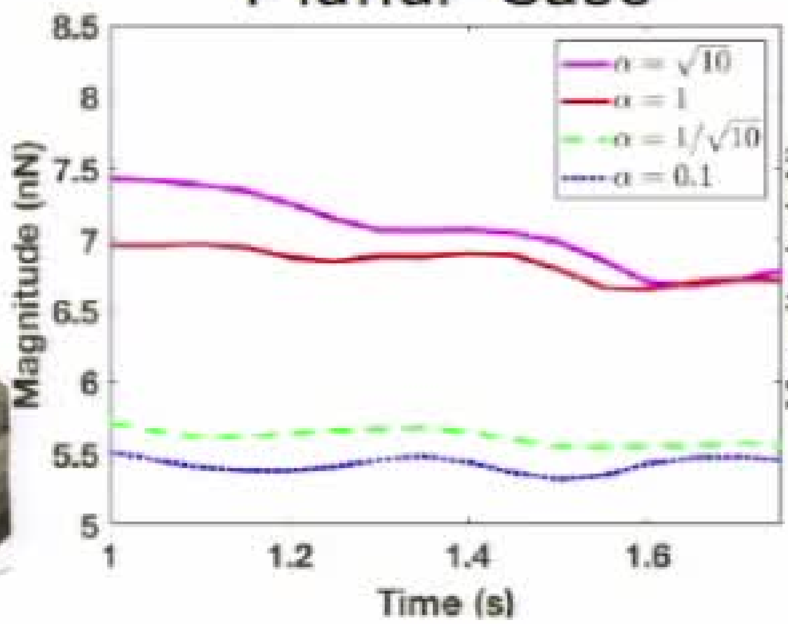
$$\mathbf{F}_{prop} = -\mathbf{F}_{drag} = -\sum_{i=1}^{N-1} \sum_{j=1}^{N_\theta} (\hat{\mathbf{n}})_{ij} \cdot (\mathbf{\Lambda})_{ij} Z_i \triangle\theta$$

Surface Elements

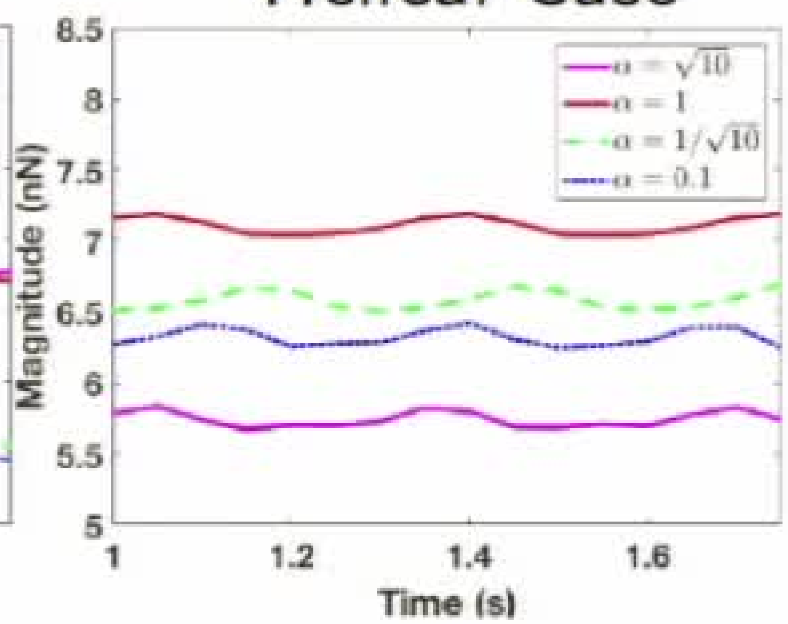


Ho, Leiderman, and Olson. *In Review.*

Planar Case

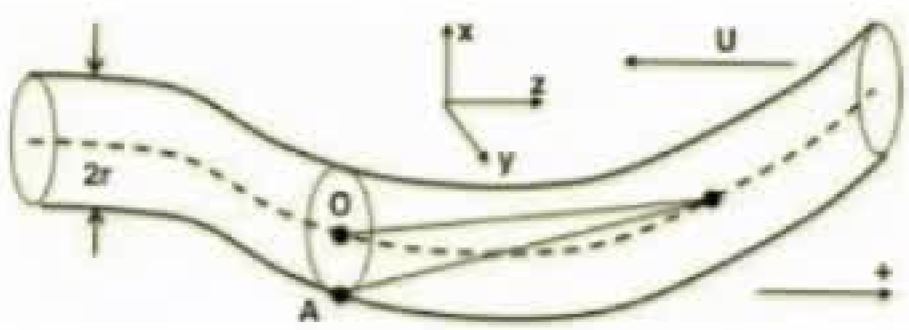


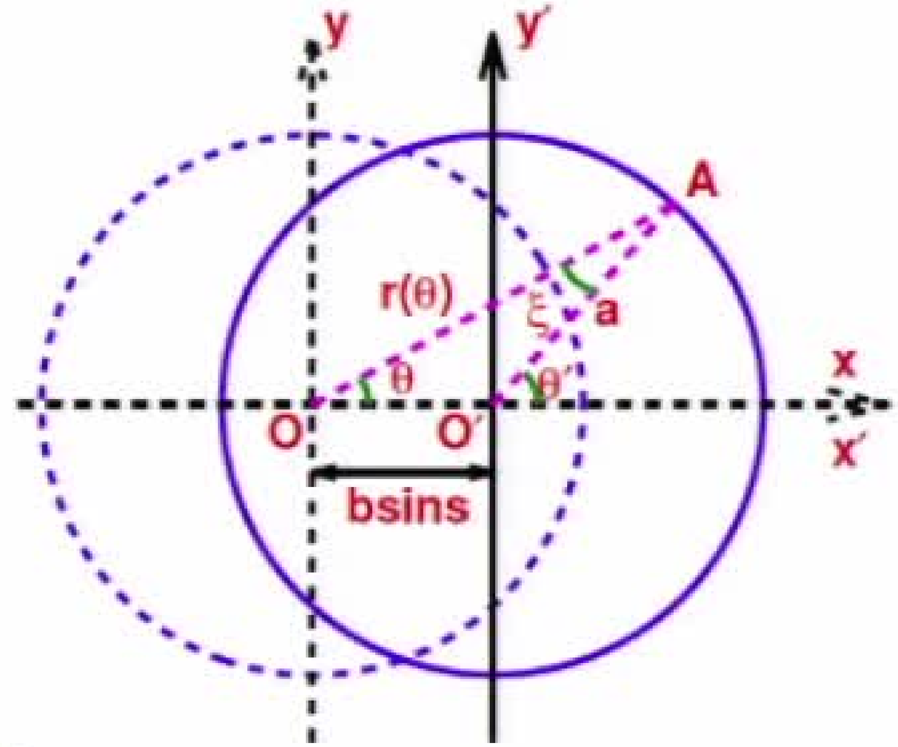
Helical Case



Brinkman - Infinite Cylinder

How do our numerical results compare with asymptotic swimming speeds?





- $b=$ amplitude, $a=$ radius, $U=$ wavespeed
- $k=$ is the wavenumber, $k = 2\pi/\lambda$ for $\lambda =$ wavelength
- $s = k(z + Ut)$
- Time-dependent position of the cylinder: $r = a + b \sin s \cos \theta$

Ho, Leiderman, Olson. Phys Rev E (2016).

Brinkman - Propulsion

- $\hat{\mathbf{n}}$ is the unit outward normal and $\boldsymbol{\Lambda} = \mu(\nabla\mathbf{u} + \nabla\mathbf{u}^T)$ is the fluid stress
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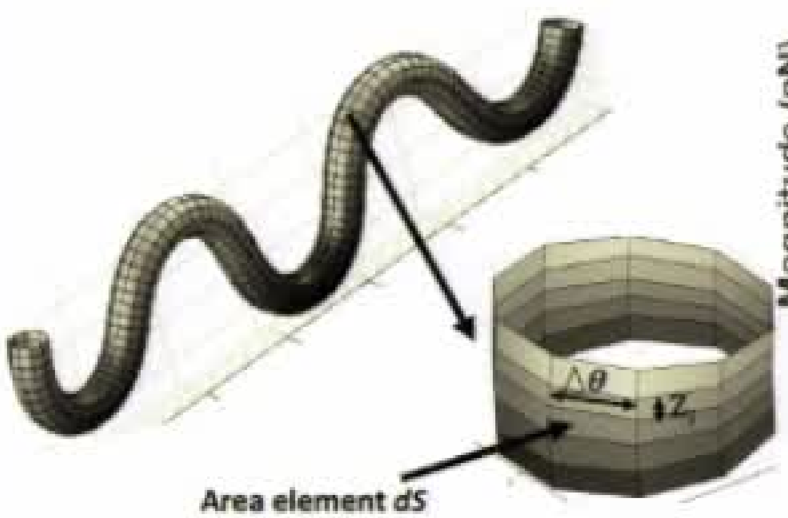
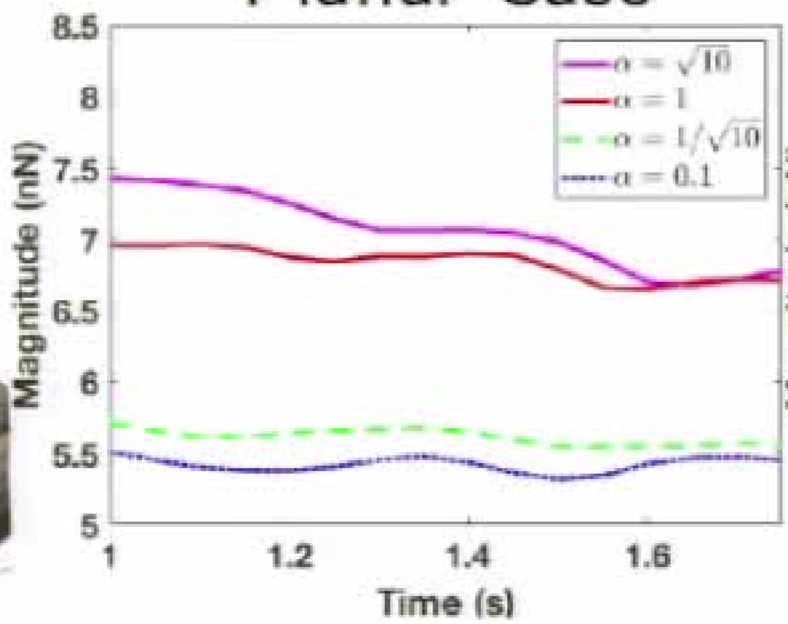
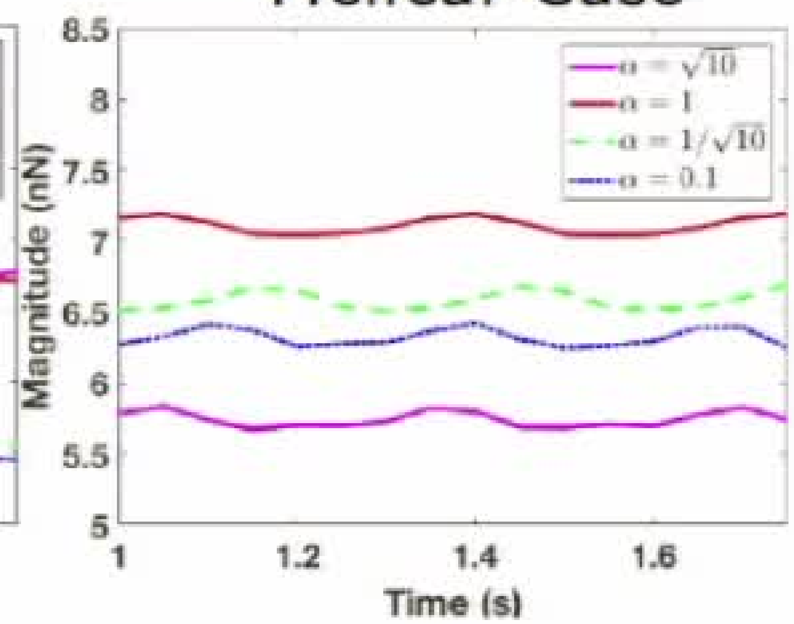
Surface Elements



Planar Case



Helical Case



Ho, Leiderman, and Olson. *In Review.*

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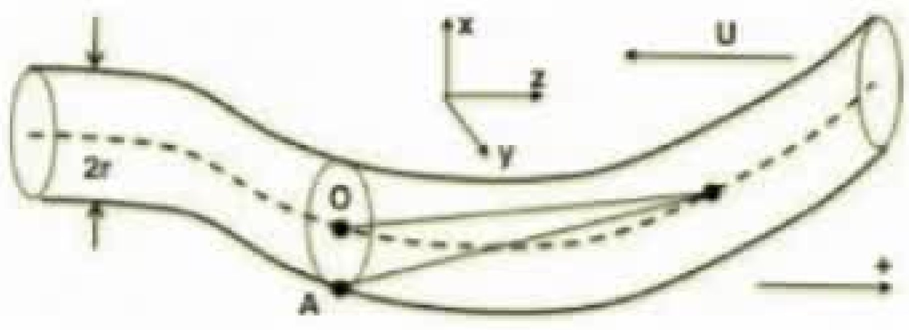

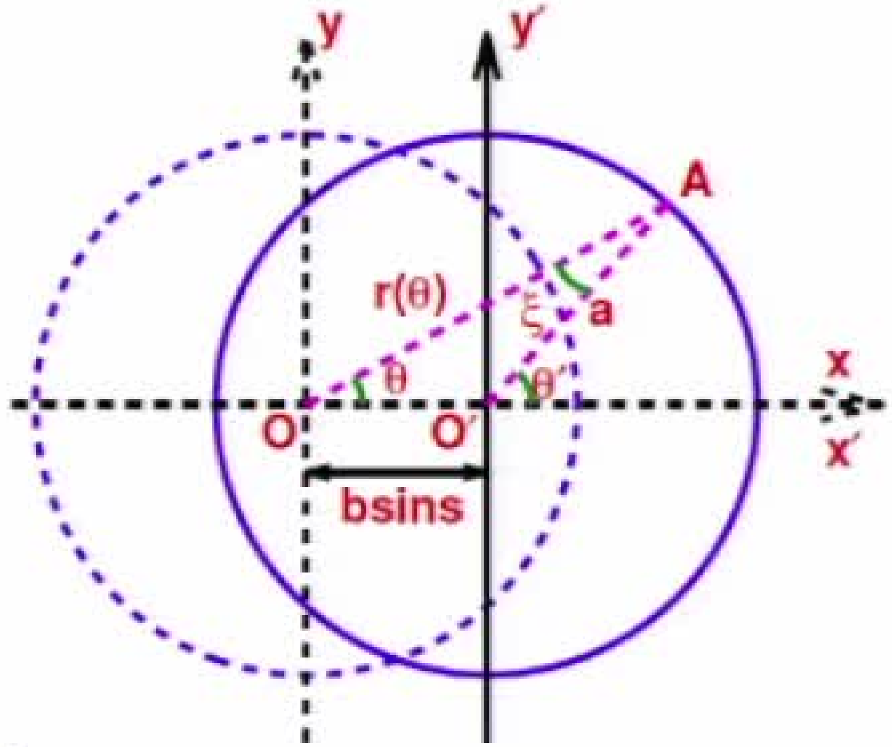

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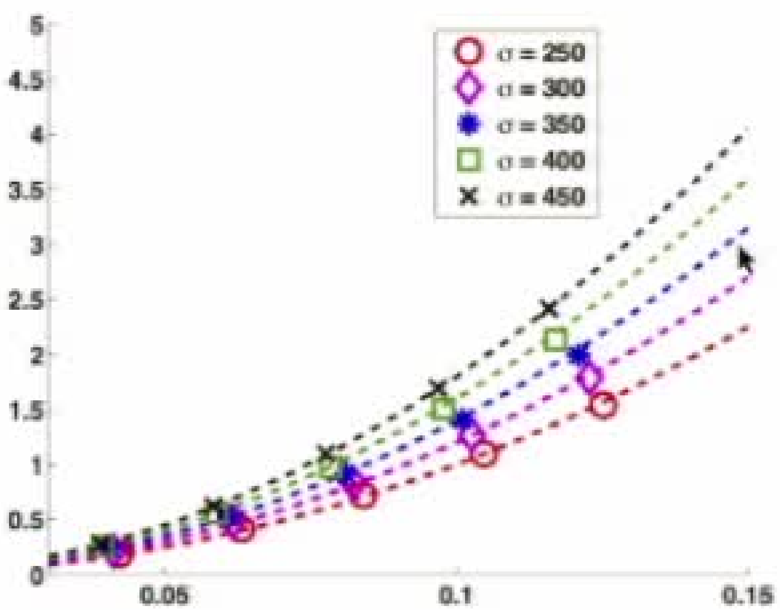
Ho, Leiderman, Olson. Phys Rev E (2016).

Swimming Speeds

Nondimensional swimming speed V/U:

$$\frac{V}{U} = \frac{1}{2}b^2k^2 \cdot \frac{(1-\xi^2)K_0(\zeta_1) - \xi^2 \log \xi}{(1-\xi^2)K_0(\zeta_1) - (2-\xi^2)\log \xi}$$

where $\xi = \sqrt{1 + (\alpha/k)^2}$ and $\zeta_1 = ka \ll 1$.



For $\alpha = 0.1$

Ho, Leiderman, and Olson. Phys Rev E (2016).

When $\alpha \to 0$:

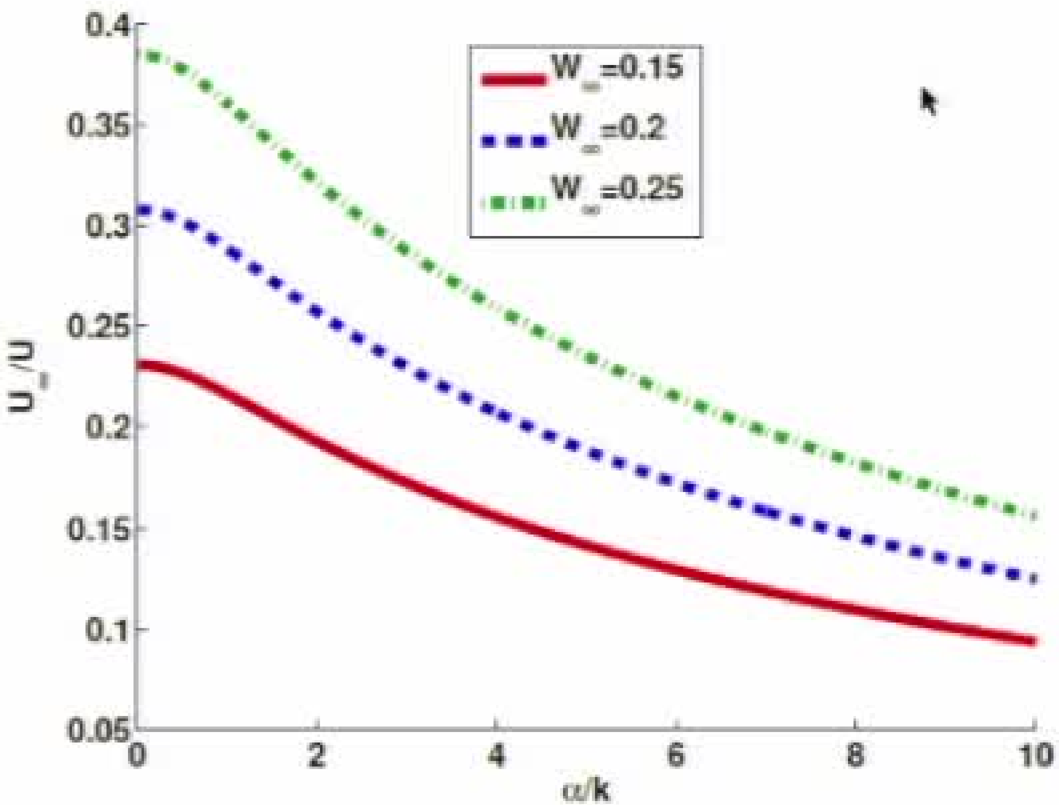
$$\frac{V}{U} = \frac{1}{2}b^2k^2 \cdot \frac{K_0(\zeta_1) - \frac{1}{2}}{K_0(\zeta_1) + \frac{1}{2}}$$

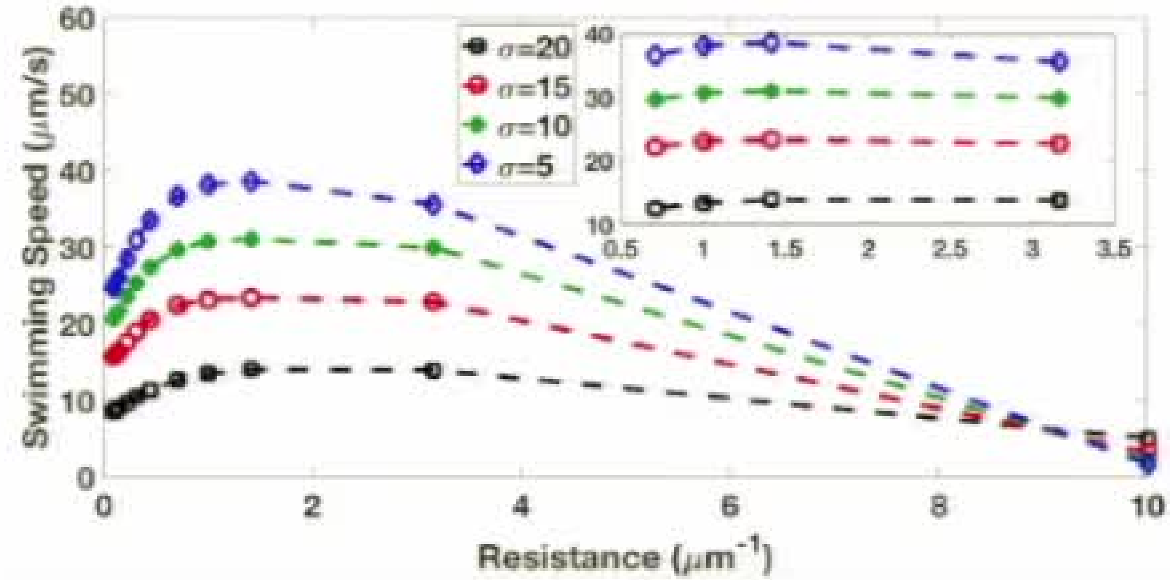
Swimming Speed & Work

- Asymptotics - work and swimming speed increase as α increases
- Numerical method - swimming speed is non-monotonic function of α
- Interpreting the results:

Rewrite swimming speed in terms of work $W_\infty = \overline{W}/\mu\pi U^2$

$$\frac{U_\infty}{U} = \frac{1}{2} W_\infty \left[K_0(\zeta_1) - \frac{1}{2}\left(\frac{k^2}{\alpha^2}+1\right)\log\left(1+\frac{\alpha^2}{k^2}\right)\right],$$

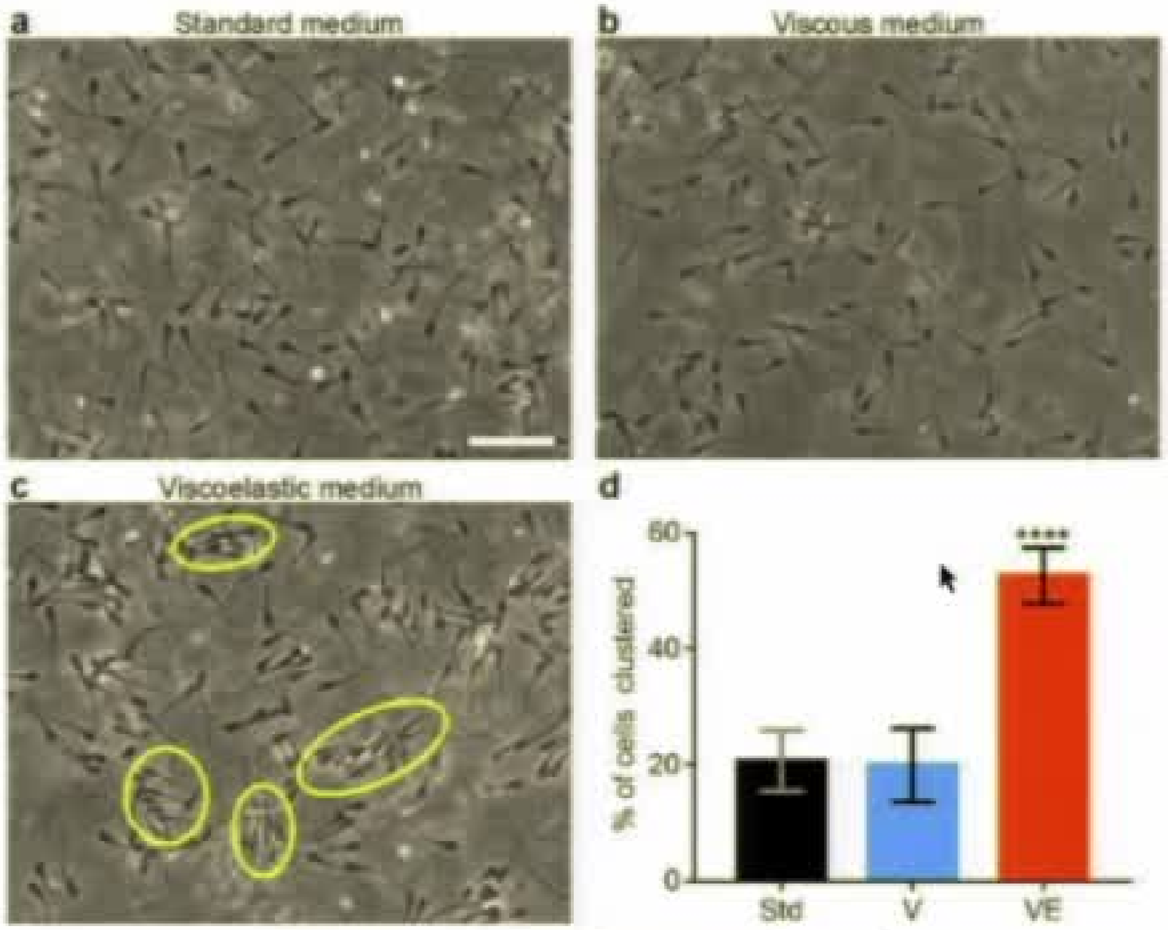




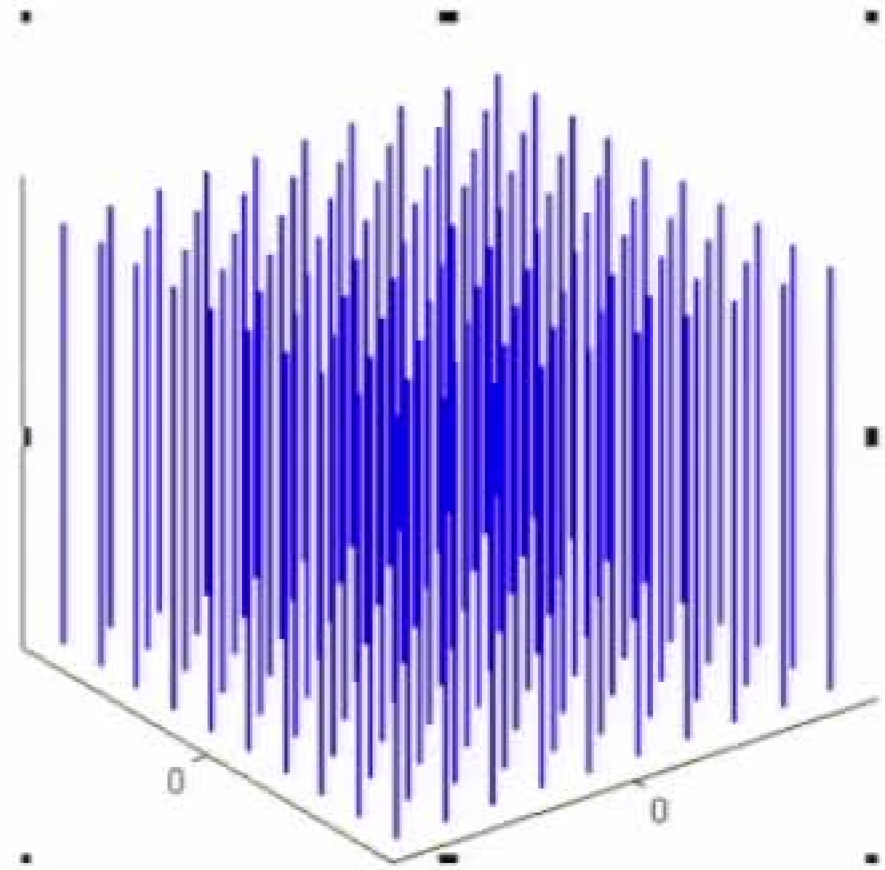
Ho, Leiderman, and Olson. Phys Rev E (2016).

Current & Future Work

Interactions of many swimmers in a Brinkman fluid



Tung et al. Sci Reports (2017).



Rostami and Olson. Fluids Struct (2016).

Acknowledgements

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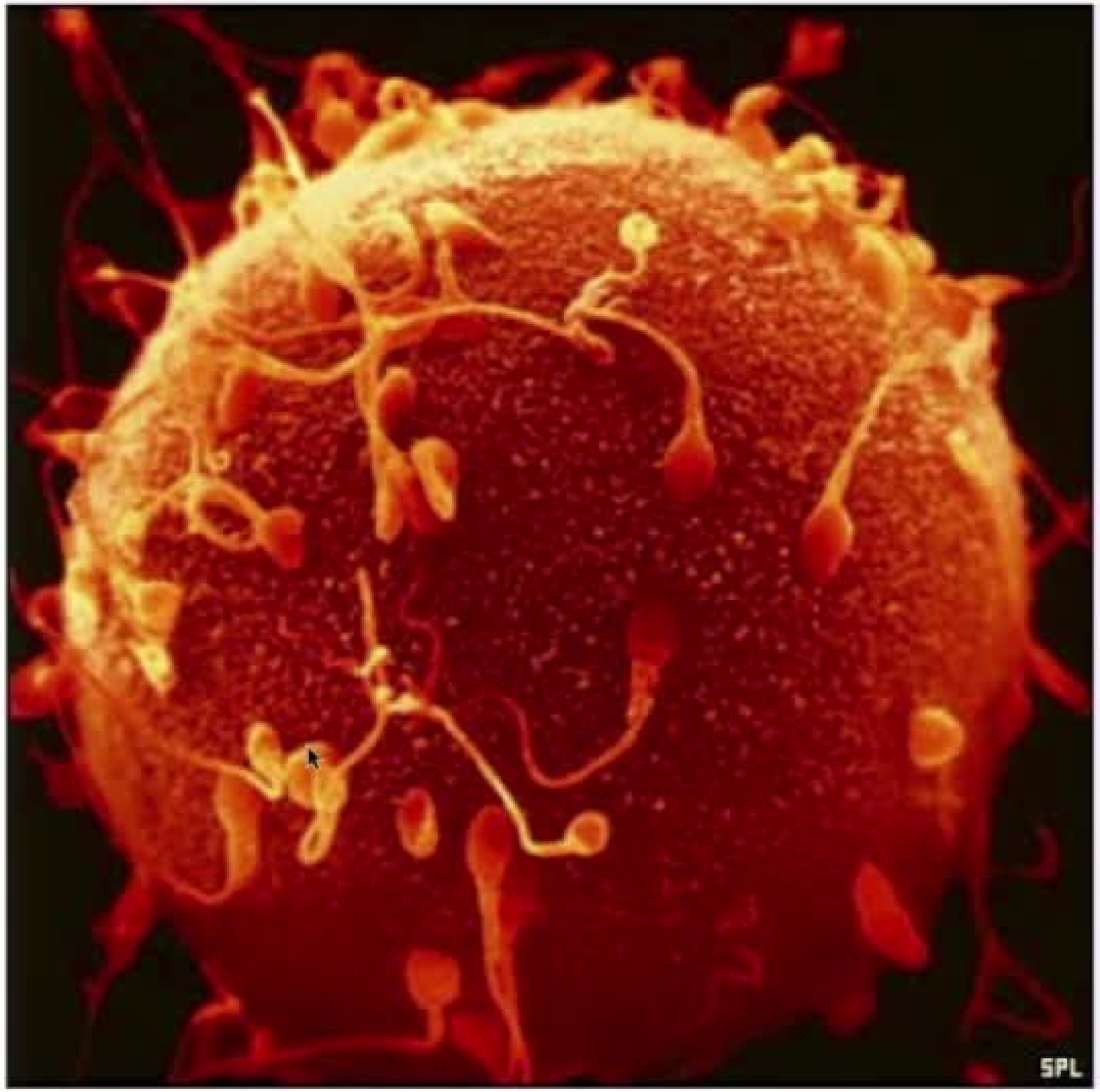
Questions?



http://timcourtois.files.wordpress.com/2010/11/sperm-and-egg.jpg

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