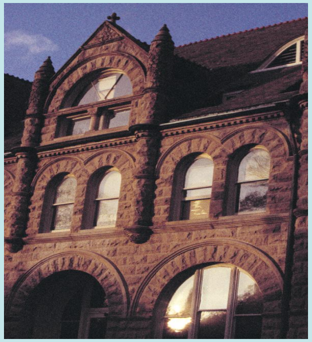


Biofluids of reproduction: oscillators, viscoelastic networks and sticky situations.

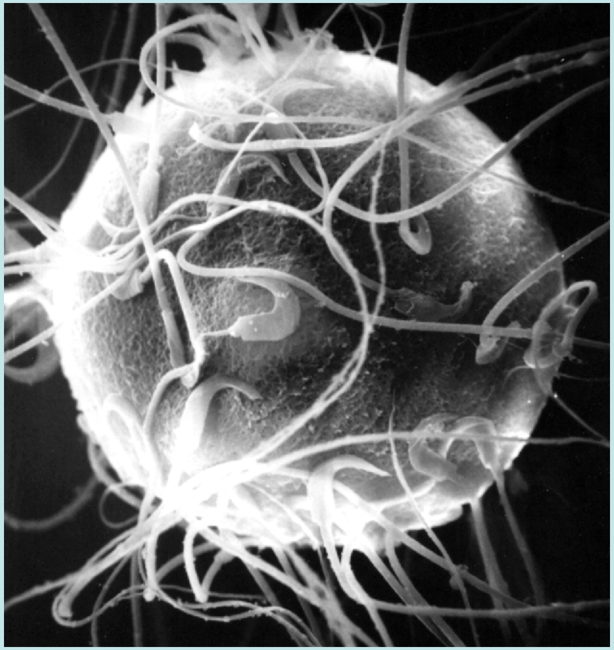
AWM-SIAM
July 11, 2016

Lisa J. Fauci
Tulane University, Math Dept.
New Orleans, Louisiana, USA

Collaborators:

Susan Suarez	Cornell University
Robert Dillon	Washington State Univ.
Sarah Olson	Worcester Polytechnic
Julie Simons	Cal State Maritime
Ricardo Cortez	Tulane University
Jacek Wrobel	Raytheon

Reproduction –
No better illustration of complex fluid-structure interactions



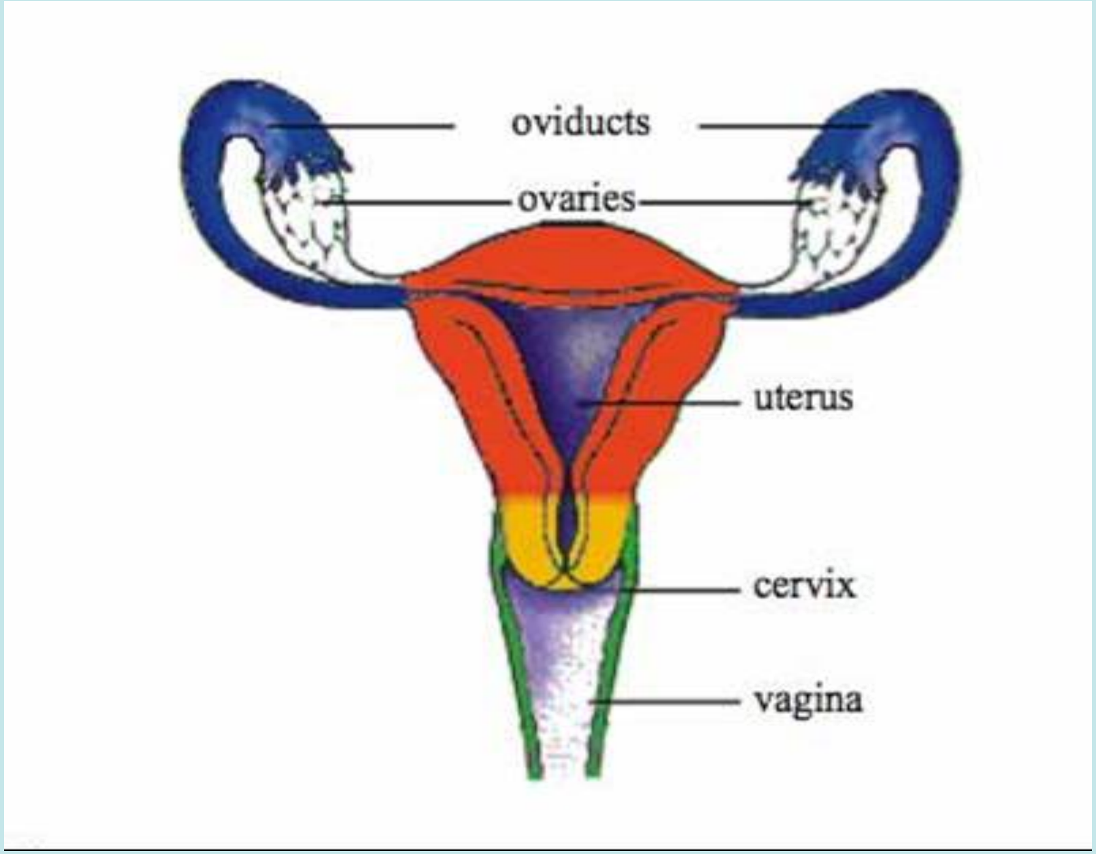
ZP –glycoprotein layer
surrounding oocyte

Fauci and Dillon,
Ann. Rev. Fluid Mech.,
Vol. 38, 2006

A scanning electron micrograph of hamster sperm bound to a zona pellucida.

courtesy of
P. Talbot, Cell Biol.
UC Riverside

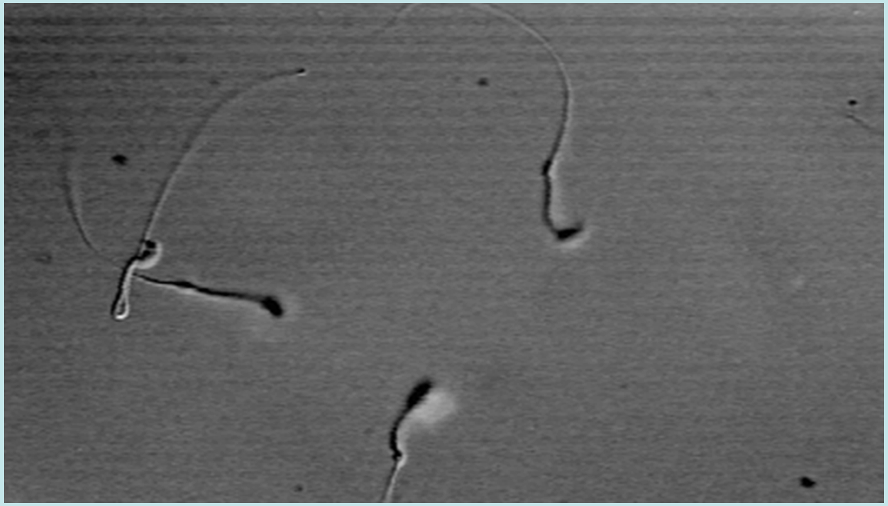
- Transport of sperm to site of fertilization
- Transport of oocyte cumulus complex (OCC) to oviduct
- Transport and implantation of embryo in uterus

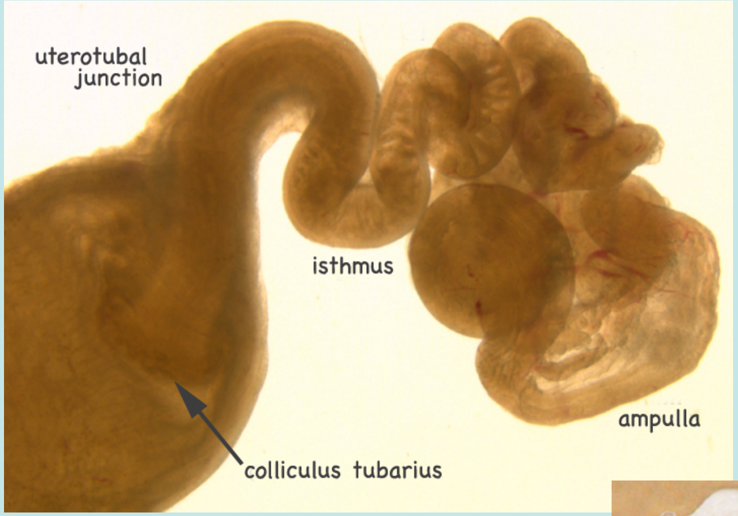


•Motile spermatozoa

•Muscular contractions

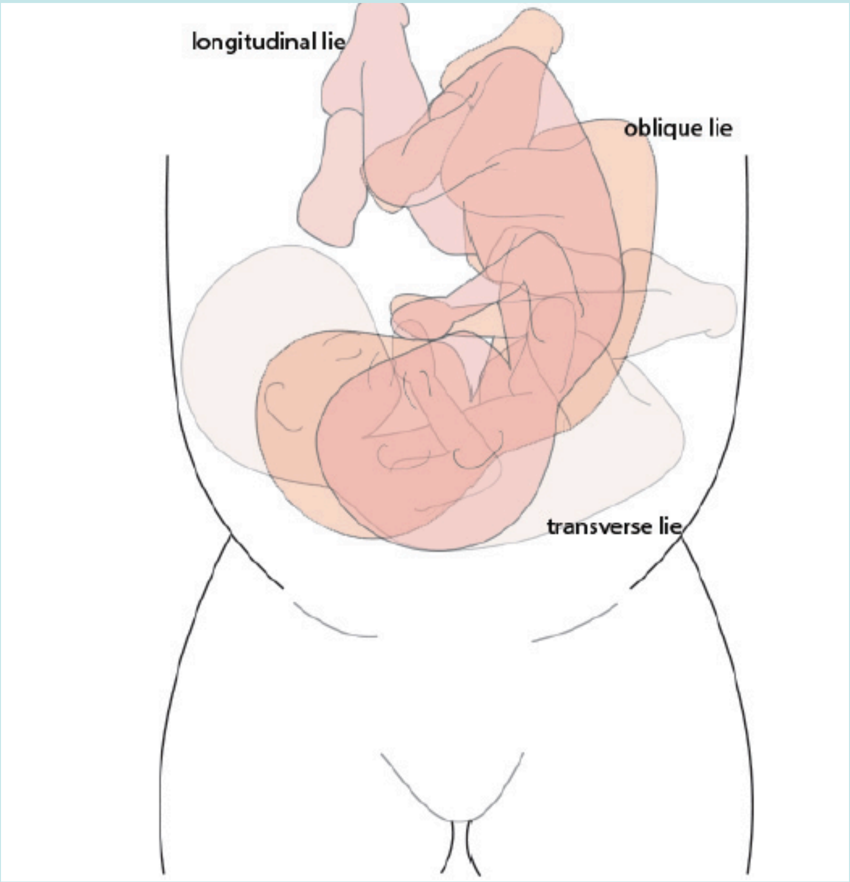
•Ciliary beating





Courtesy: Susan Suarez,
Cornell U.

Human birth: What forces are experienced by the fetus?
How does the force depend upon fetal lie (angle)?
How does the force depend upon fluid properties?
What are the fluid properties?



Megan Leftwich, GWU
Alexa Baumer, GWU
Roseanna Pealatere, Tulane

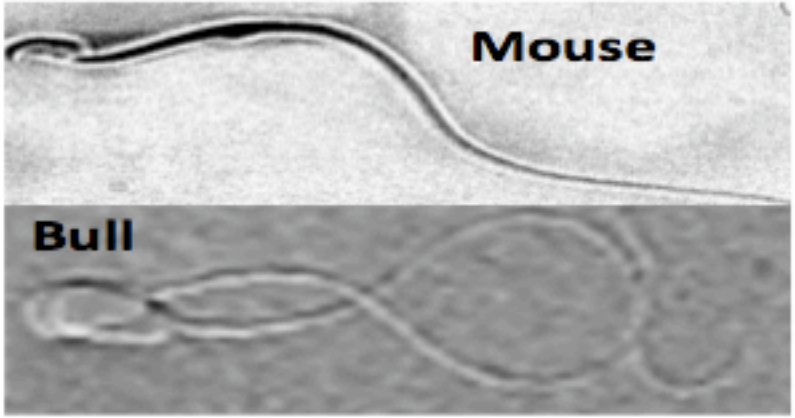
Today's tour:

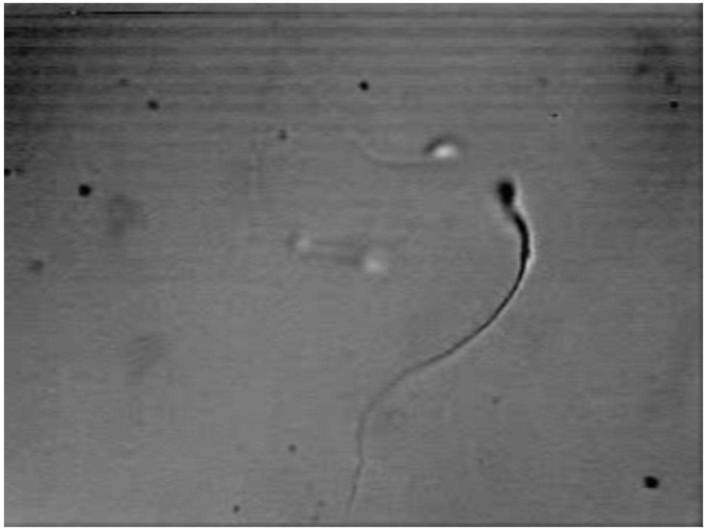
- **Sperm motility**/hyperactivation
- Viscoelastic networks
- Human birth

Types of Sperm Motility

Activated motility

- Symmetrical flagellar bending
- Linear trajectories
- Resting level of Ca^{2+}





Movie courtesy of S. Suarez

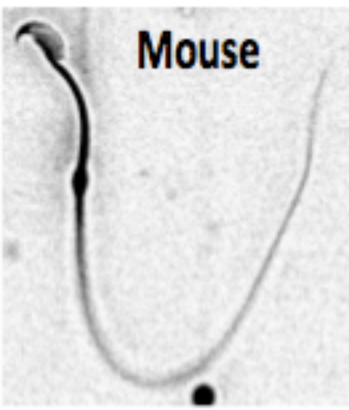
Marquez and Suarez. Different signaling pathways in bovine sperm regulate capacitation and hyperactivation, *Biol Reprod* 70 (2004) 1626–1633.

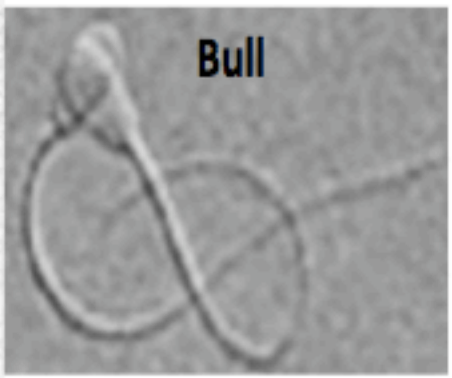
Chang and Suarez. Rethinking the relationship between hyperactivation and chemotaxis in mammalian sperm, *Biol Reprod* 83 (2010) 507–513.

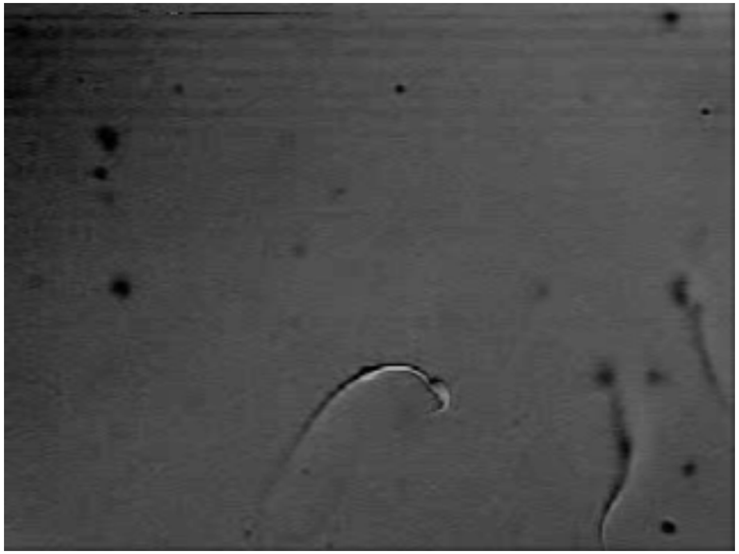
Types of Sperm Motility

Hyperactivated motility

- Highly asymmetrical flagellar bending
- Increased curvature, amplitude
- Increased Ca^{2+}







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Chang and Suarez. Rethinking the relationship between hyperactivation and chemotaxis in mammalian sperm, *Biol Reprod* 83 (2010) 507–513.

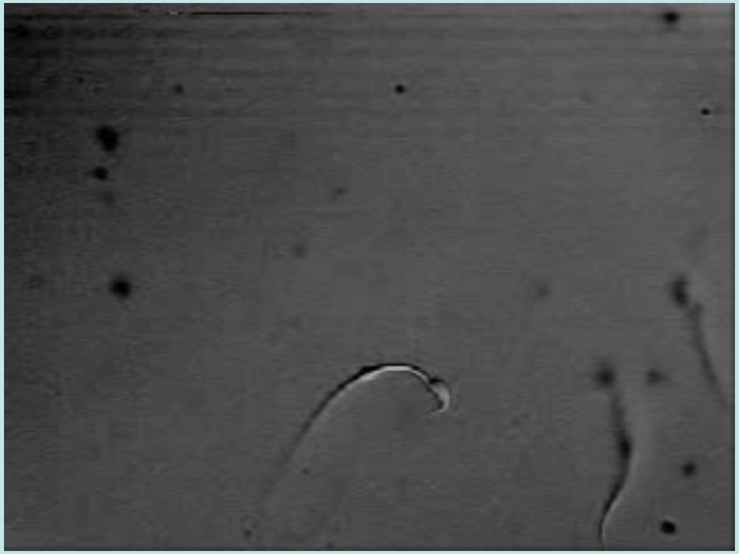
Computational fluid dynamics

What do we want to learn?

What are the complications?

What choices do we make?

- What are biochemical pathways that initiate hyperactivation?
- How do these biochemical signals change the internal force-generating mechanisms?
- What are the functional implications of a hyperactivated waveform?



What are the complications?

What are the complications?

- Moving interfaces!

What are the complications?

- Moving interfaces!
- Complicated geometries!

What are the complications?

- Moving interfaces!
- Complicated geometries!
- Many interfaces!

What are the complications?

- Moving interfaces!
- Complicated geometries!
- Many interfaces!
- Flexible, elastic, actuated interfaces!

What are the complications?

- Moving interfaces!
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- Many interfaces!
- Flexible, elastic, actuated interfaces!
- Non-Newtonian fluid!!

What are the complications?

- Moving interfaces!
- Complicated geometries!
- Many interfaces!
- Flexible, elastic, actuated interfaces!
- Non-Newtonian fluid!!
- Biochemical signaling!!

What are the choices?

- 2D versus 3D?

What are the choices?

- 2D versus 3D?
- Simpler domain geometries (a box)?

What are the choices?

- 2D versus 3D?
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- Start with one interface (cilium or sperm)?

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- Prescribe kinematics?

What are the choices?

- 2D versus 3D?
- Simpler domain geometries (a box)?
- Start with one interface (cilium or sperm)?
- Prescribe kinematics?
- Idealized fluid model ?

What are the choices?

- 2D versus 3D?
- Simpler domain geometries (a box)?
- Start with one interface (cilium or sperm)?
- Prescribe kinematics?
- Specify preferred curvature?
- Ignore biochemical signaling or include a simple model?

What are the choices?

- 2D versus 3D?
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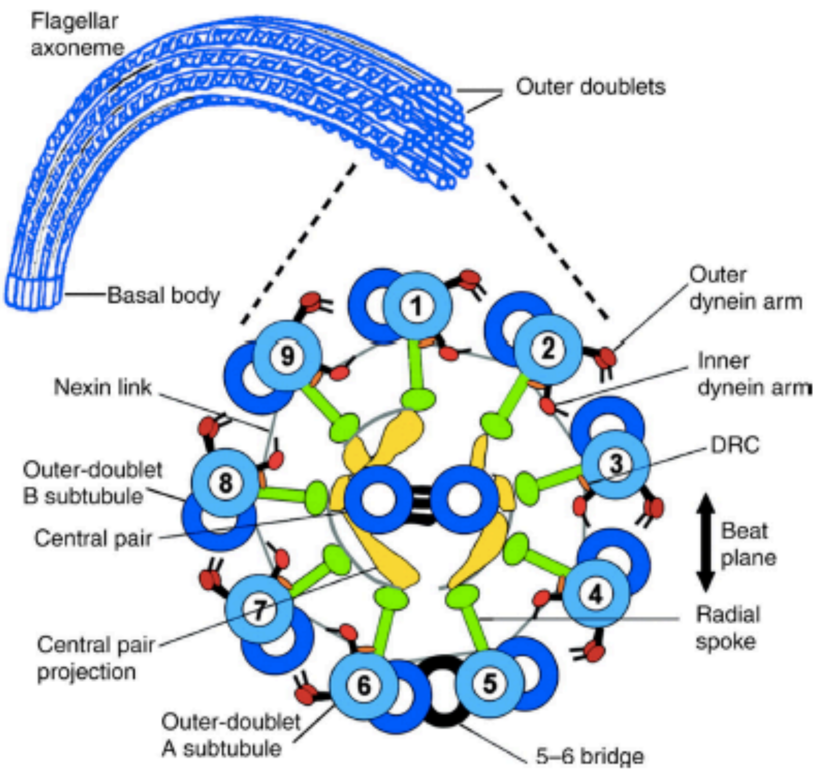
- Simple elastic model (Kirchoff rod?)

What are the choices?

- 2D versus 3D?
- Simpler domain geometries (a box)?
- Start with one interface (cilium or sperm)?
- Prescribe kinematics?
- Specify preferred curvature?
- Ignore biochemical signaling or include a simple model?
- Simple elastic model (Kirchoff rod?)
- Viscoelastic model?

Nearly Planar Swimming



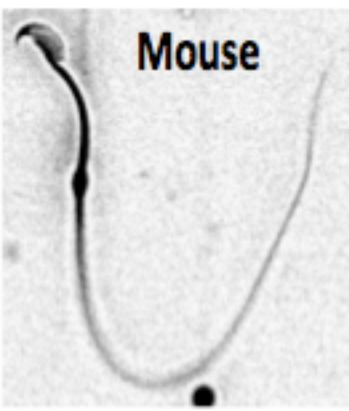
Lindemann C.B. and K.A. Lesich. **J. Cell Sci**, 2010.

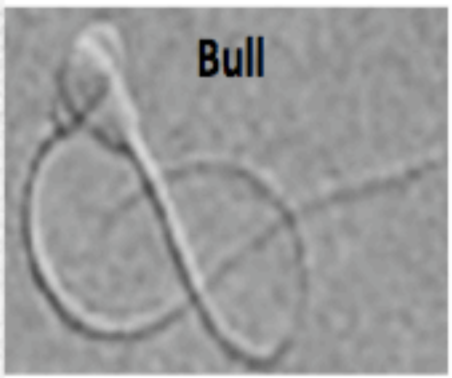
Kantsler, V. et al. **eLife**, 3, 2014.

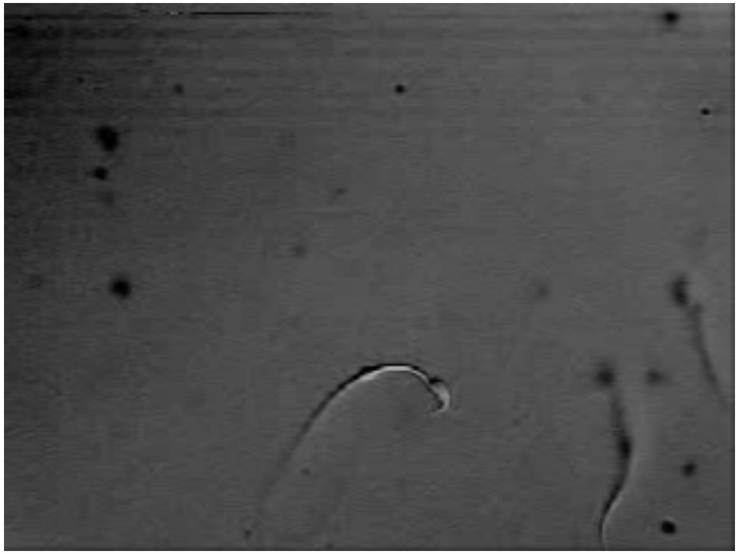
Types of Sperm Motility

Hyperactivated motility

- Highly asymmetrical flagellar bending
- Increased curvature, amplitude
- Increased Ca^{2+}







Movie courtesy of S. Suarez

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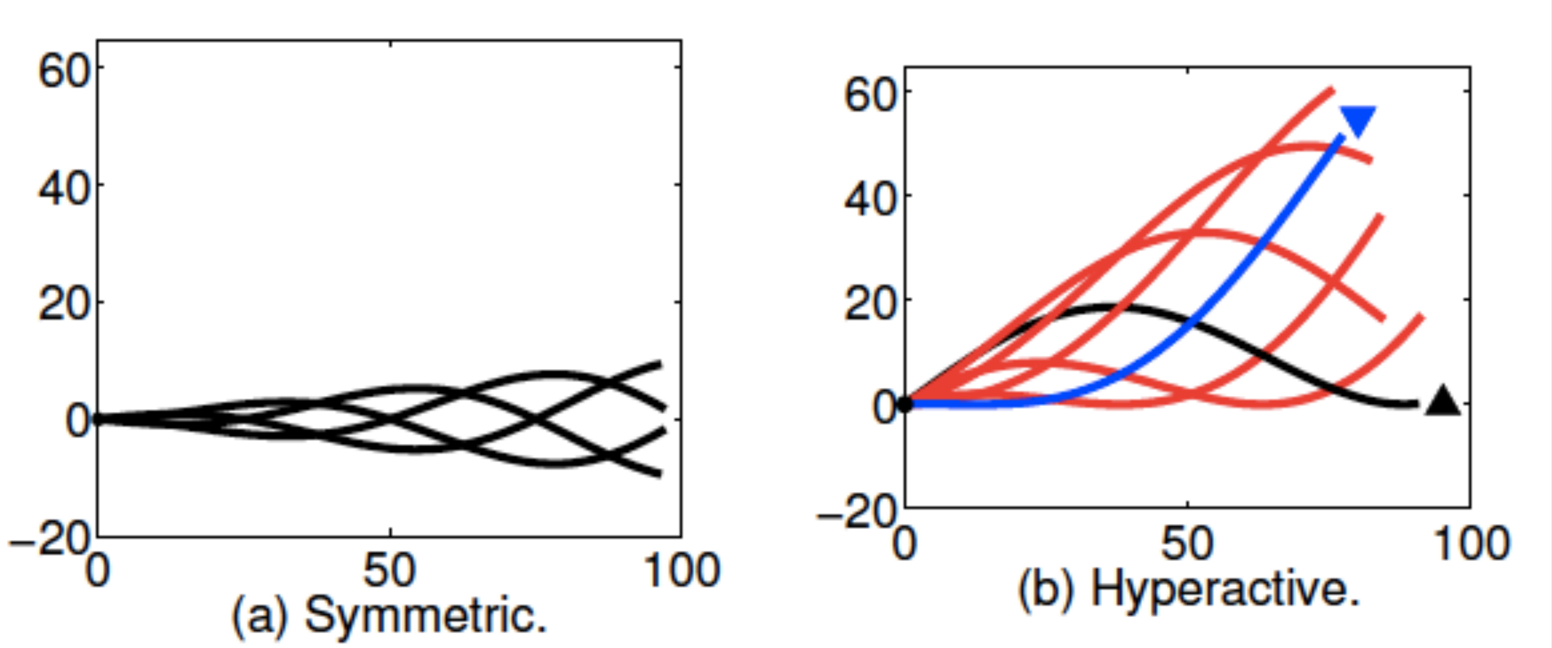
- Recent work by *Curtis, M. P. , Kirkman-Brown, J. C., Connolly, T. J. and E. A. Gaffney, 2012, J. Theor. Biol.*

showed that for wave of **given kinematics**, asymmetry could produce both tugging and thrusting forces at different wave phases.



(a) Symmetric.
(b) Hyperactive.

Forces

- The bending filament, $\mathbf{X}(s,t)$, is taken to be a generalized Euler elastica whose energy, E, is given by:

$$E = \int_\Gamma (\varepsilon_{tens} + \varepsilon_{bend})ds$$

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

- $\frac{\partial \Theta}{\partial s}$= shear angle, $\zeta(s,t)$= preferred curvature
- Energy function is non-negative and translation and rotation invariant
- Force per unit length, $\mathbf{g}$, is derived from the energy function:

$$\mathbf{g} = -\frac{d}{d\mathbf{X}} \left(\varepsilon_{tens} + \varepsilon_{bend} \right) .$$

L. Fauci, A. McDonald, Sperm motility in the presence of boundaries, *Bull Math Biol* 57 (1995) 679–699.

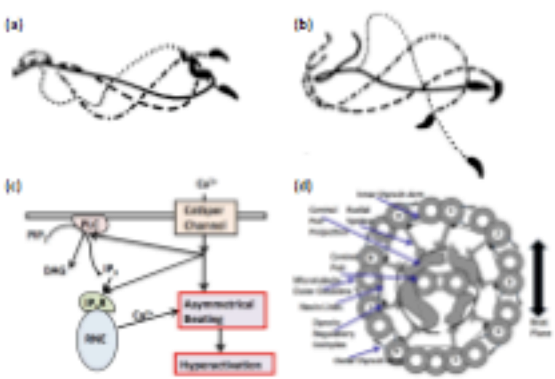
Calcium Dependent Curvature Model

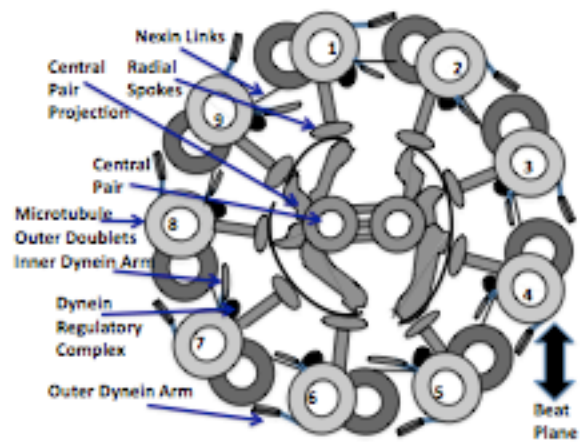
Preferred (signed) curvature function corresponding to a simple sine wave with $x(s,t) = s$ and $y(s,t) = b\sin(\kappa s - \omega t)$ for small amplitude b is:

$$\zeta(s,t) = -\kappa^2 b \sin(\kappa s - \omega t)$$

Dependence of local dynein force generation on calcium:

$$b(s,t) = V_A \frac{Ca(s,t)}{Ca(s,t) + k_A}, \qquad k_A = \begin{cases} k_{A,1} & -\kappa^2 \sin(\kappa s - \omega t) > 0 \\ k_{A,2} & -\kappa^2 \sin(\kappa s - \omega t) < 0 \end{cases}$$





Fluid coupled with ‘elastic structure’

Flow is governed by the incompressible Navier Stokes equations:

$$\rho\left[\frac{\partial \mathbf{u}}{\partial t} + \mathbf{u}\cdot\nabla\mathbf{u}\right] = -\nabla p + \mu\Delta\mathbf{u} + \sum_{\mathbf{k}} \mathbf{F}^{\mathbf{k}}(\mathbf{x},\mathbf{t})$$

$$\nabla\cdot\mathbf{u} = 0$$

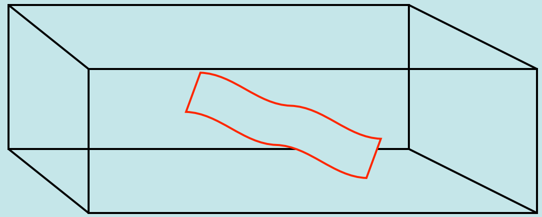
F^{k} is a ‘delta function’ layer of force exerted by the kth filament on the fluid.

$$\mathbf{F}^{\mathbf{k}}(\mathbf{x},t) = \int_S \mathbf{f}^{\mathbf{k}}(s,t)\delta(\mathbf{x}-\mathbf{X}^{\mathbf{k}}(s,t))ds$$

$$\frac{\partial \mathbf{X}^{\mathbf{k}}(s,t)}{\partial t} = \mathbf{u}(\mathbf{X}^{\mathbf{k}}(s,t),t) = \int_\Omega \mathbf{u}(\mathbf{x},t)\delta(\mathbf{x}-\mathbf{X}^{\mathbf{k}}(s,t))d\mathbf{x}$$

Peskin, ACTA Numerica, 2002

Immersed boundary framework



$X_k(t) \Rightarrow f_k(t)$

Grid-based

Transmit $f_k(t)$ to grid

Solve Navier - Stokes on grid

Interpolate grid velocity

Stokes flow

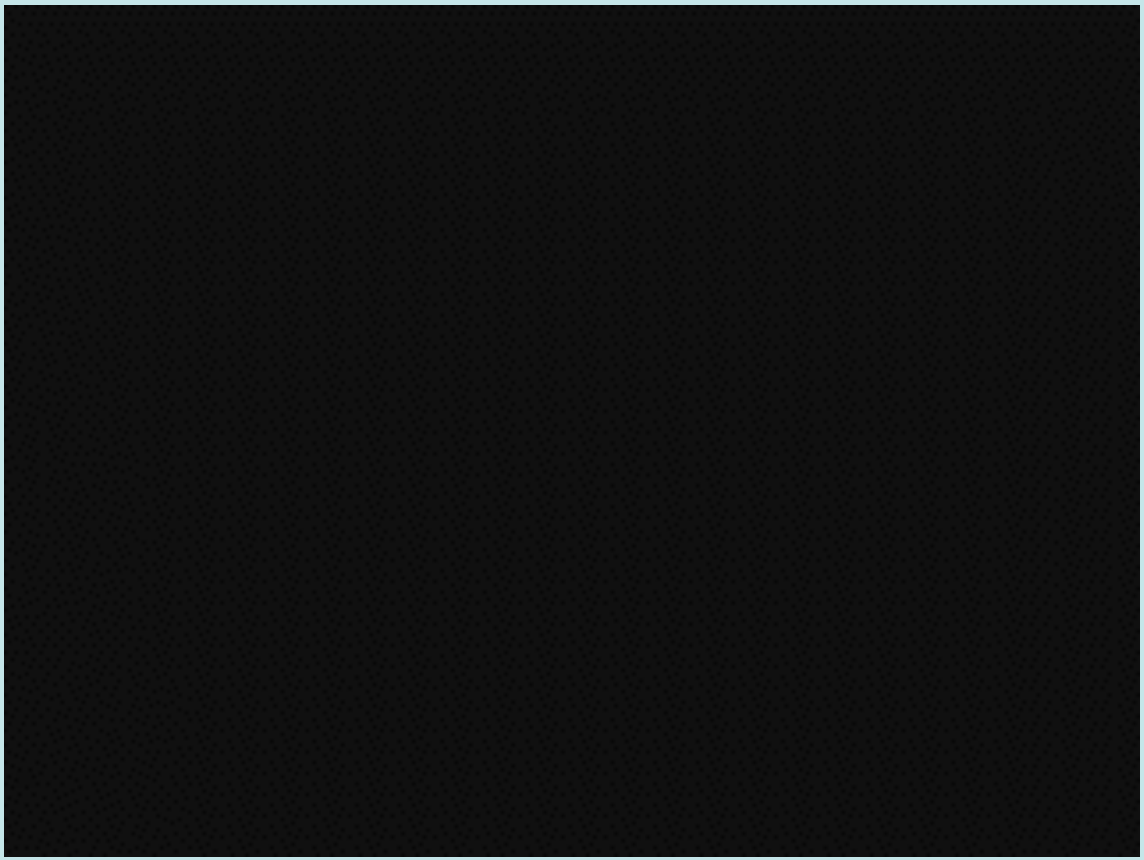
Direct sum formula

Grid-free

$U_k(t)$

$X_k(t+\Delta t) = X_k(t) + \Delta t\, U_k(t)$

2D sperm motility



LF and A. McDonald, 1994
Bull. Math. Biol.

Grid – free numerical method for zero Reynolds number

Steady Stokes equations:

$$\mu \Delta \mathbf{u} = \nabla p - \mathbf{F}$$

$$\nabla \cdot \mathbf{u} = 0$$

Method of regularized Stokeslets (R. Cortez, SIAM SISC 2001; Cortez, Fauci,Medovikov, Phys. Fluids, 2004)

Forces are spread over a small ball -- in the case x_k=0:

$$\mathbf{F}(\mathbf{x}) = \mathrm{f}_0 \ \phi_\epsilon(\mathbf{x}), \qquad \int \phi_\epsilon(\mathbf{x}) d\mathbf{x} = 1$$

For the choice:

$$\phi_\epsilon(\mathbf{x}) = \frac{15\epsilon^4}{8\pi(r^2+\epsilon^2)^{7/2}}.$$

the resulting velocity field is:

$$\mathbf{u}(\mathbf{x}) \;\; = \;\; \frac{1}{8\pi\mu}\left\{\mathrm{f}_0 \frac{2\epsilon^2 + r^2}{(r^2+\epsilon^2)^{3/2}} + \frac{(\mathrm{f}_0 \cdot \mathbf{x})\mathbf{x}}{(r^2+\epsilon^2)^{3/2}}\right\}$$

$$\mathbf{u}(\mathbf{x}) \quad = \quad \frac{1}{8\pi\mu}\left\{\mathbf{f}_0 \frac{2\epsilon^2 + r^2}{(r^2+\epsilon^2)^{3/2}} + \frac{(\mathbf{f}_0 \cdot \mathbf{x})\mathbf{x}}{(r^2+\epsilon^2)^{3/2}}\right\}$$

Note:

u(x) is defined everywhere

u(x) is an exact solution to the Stokes equations, and is incompressible

$$u_j(\mathbf{x_0}) = \frac{1}{8\pi\mu} \sum_{n=1}^{N} \sum_{i=1}^{3} S_{ij}(\mathbf{x_n}, \mathbf{x_0}) g_{n,i} \; A_n$$

If regularized forces are exerted at "N" points, the velocities at these points can be computed by superposition of Regularized Stokeslets

or

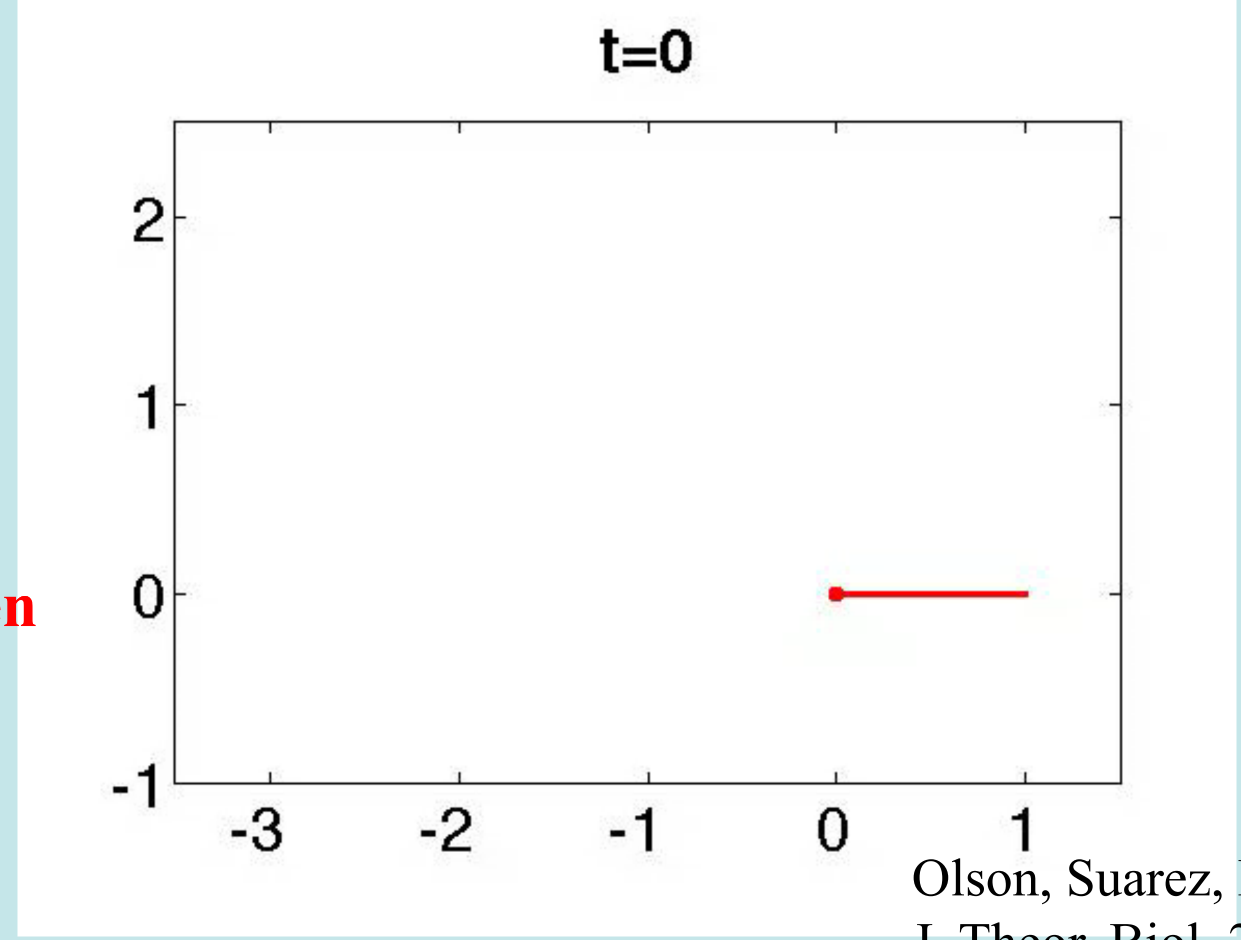
$$u = A\, g$$

Here A is a 3n by 3n matrix that depends upon the **geometry**.

Hyperactivated sperm motility

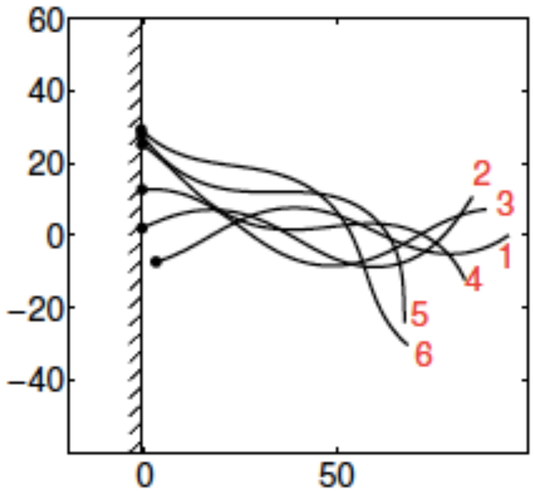
- 3D Stokes
- Planar beat
- *Preferred* kinematics *evolves* from calcium model

- **Symmetric**
- **Asymmetric**
- **Calcium driven**

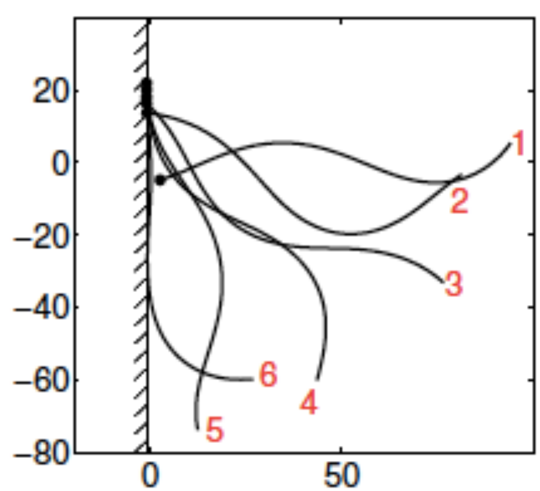


Olson, Suarez, Fauci,
J. Theor. Biol, 2011

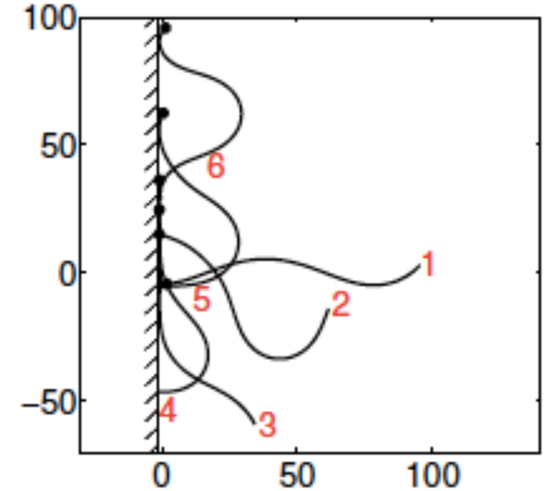
Planar wall



(a) Symmetric.

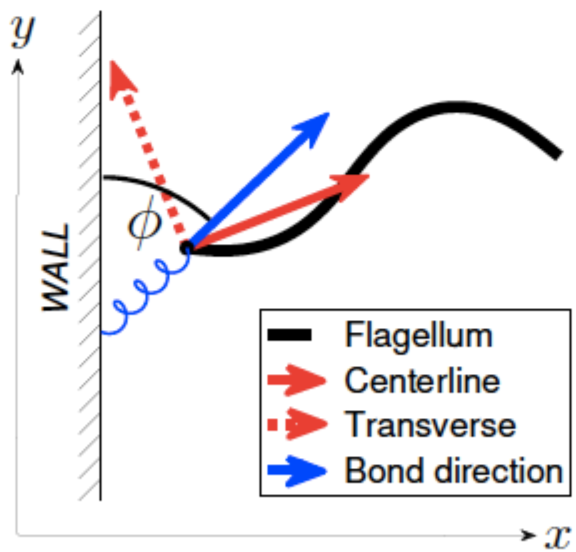


(b) Asymmetric.



(c) Ca^{2+}-dependent.

Bond Force



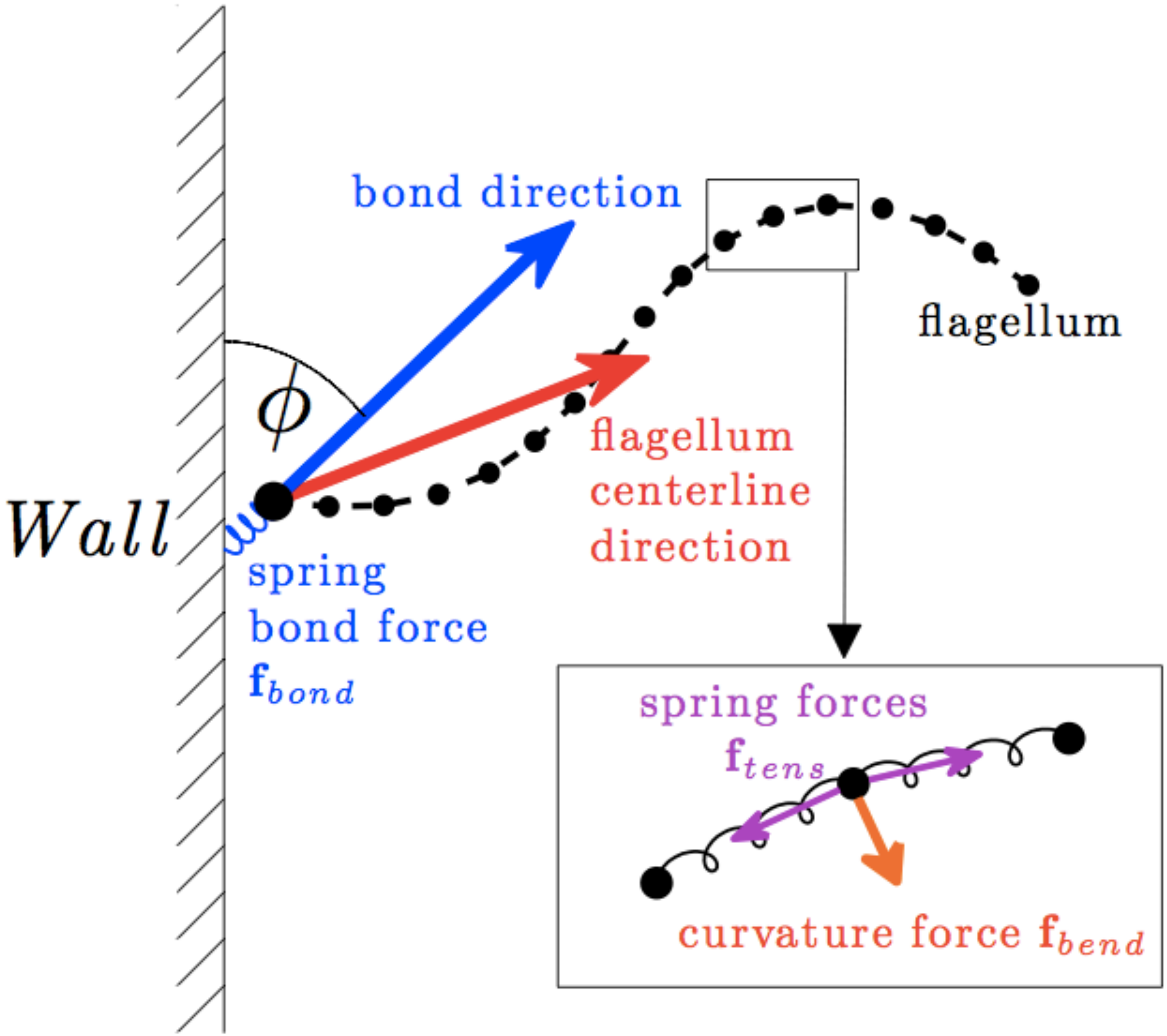
- **Bond formation**: when head comes within a capture radius L_c of the wall.
- **Spring bond force** for head of sperm when near surface:

$$f_{bond} = -k_b(L - L_*)$$

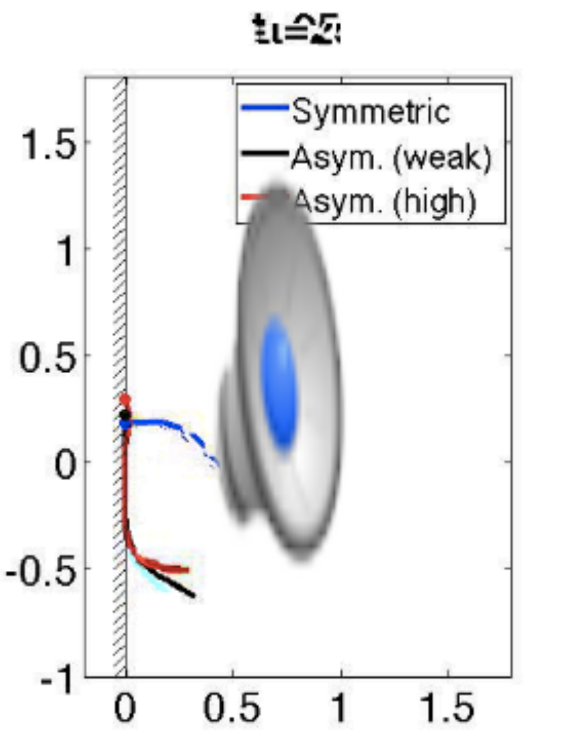
(k_b = ideal spring constant, L = spring length, L_* = resting length.)

- **Bond breaking**: when spring stretched beyond a breaking distance of

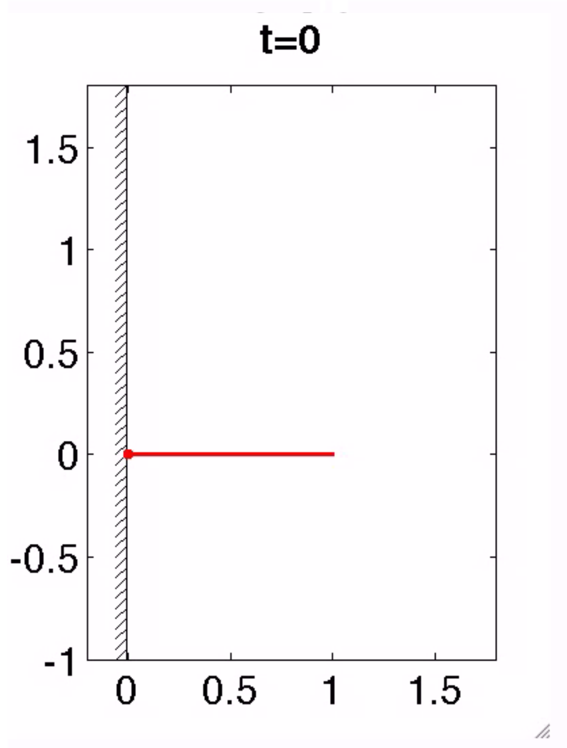
$$[(1-\alpha) + \alpha \sin(\phi)]L_b$$


bond direction
flagellum
ϕ
flagellum
centerline
direction
Wall
spring
bond force
$\mathbf{f}_{bond}$
spring forces
$\mathbf{f}_{tens}$
curvature force $\mathbf{f}_{bend}$

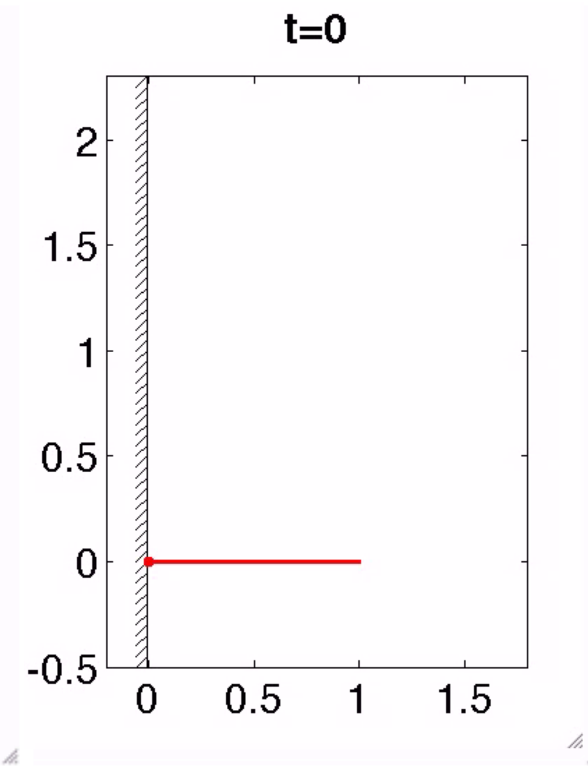
Swimming Near A Wall



No bond

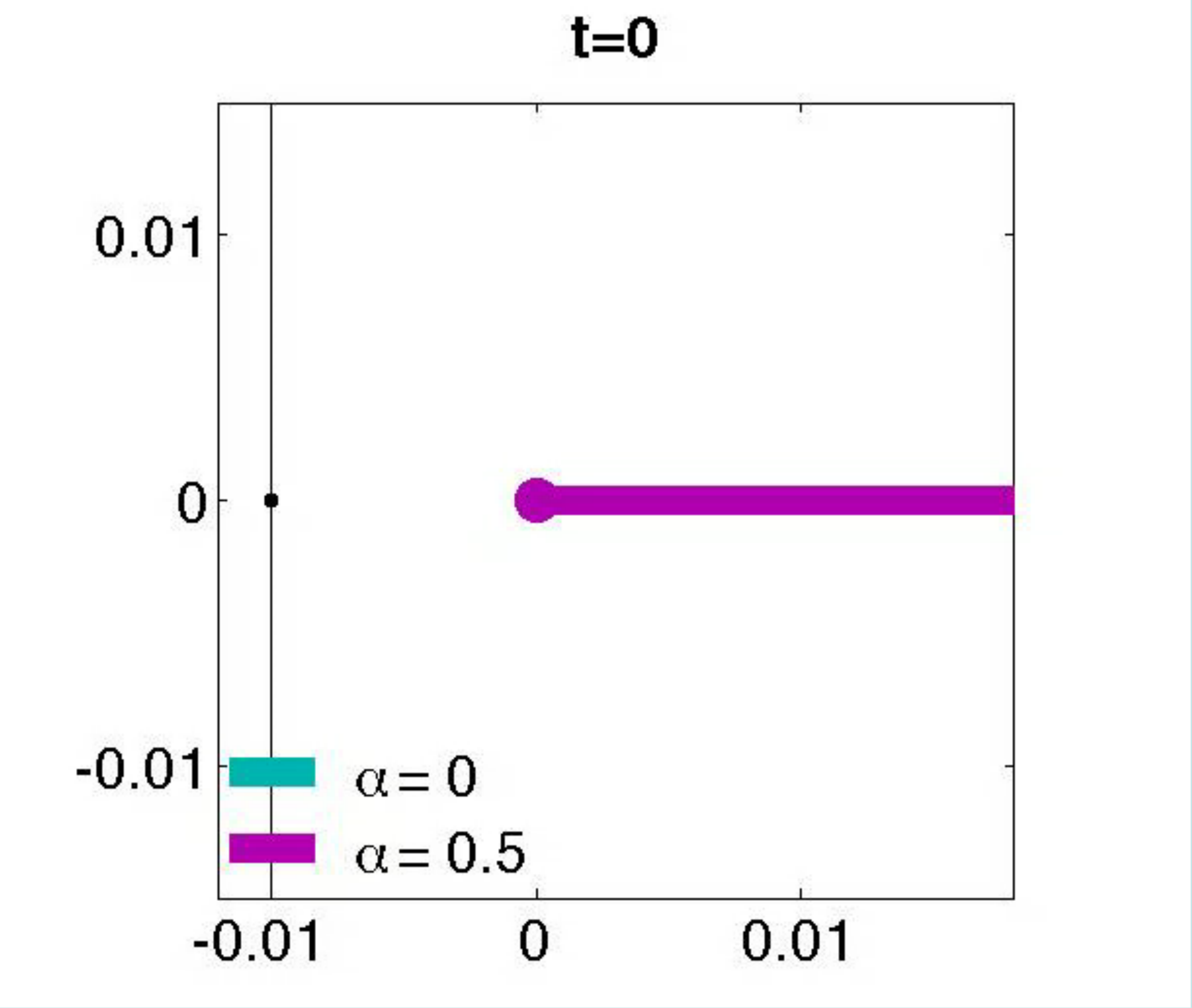


$\alpha = 0$



$\alpha = 0.5$

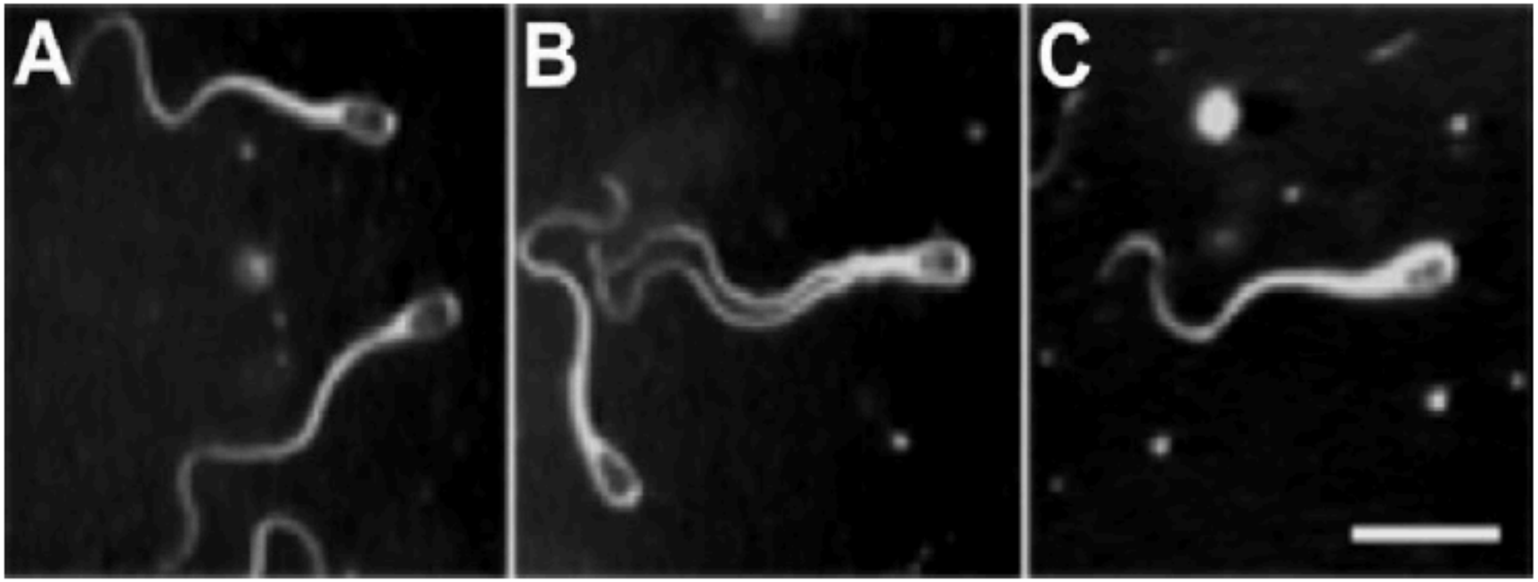
Simons, J., Olson, S.D., Cortez, R. and L. Fauci, **J. Theor. Biol.**, 2014.



t=0
0.01
0
-0.01
$\alpha = 0$
$\alpha = 0.5$
-0.01
0
0.01

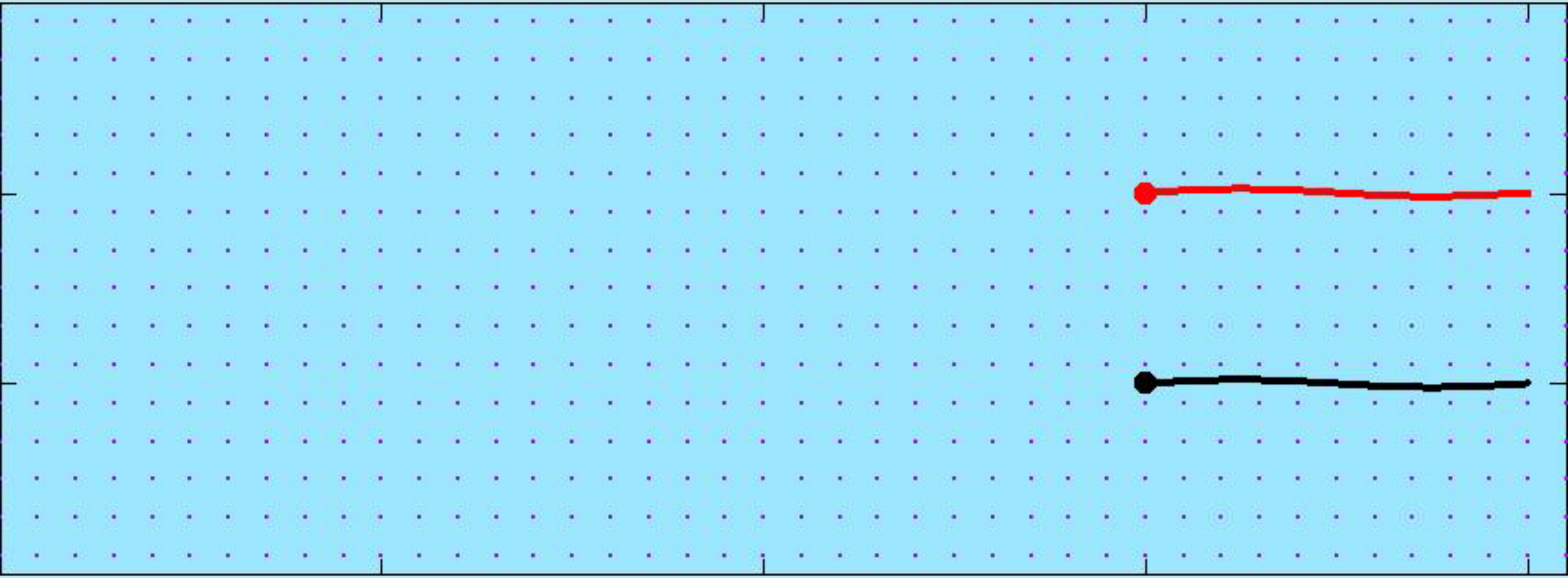
- The frequent binding and attaching of hyperactivated sperm as seen in Chang and Suarez 2012 relies upon both asymmetry and high-amplitude.
- Elastic bond behavior can actually enable sperm to move away from epithelium.
- Bonding mechanisms affect detachment dynamics.

Attracting Swimmers



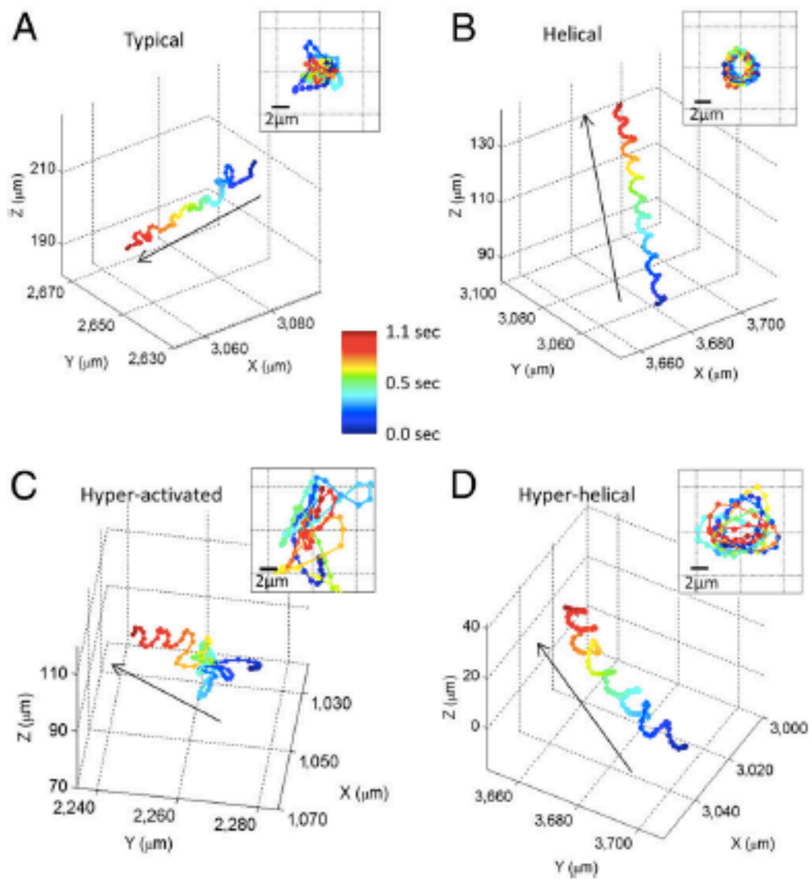
- Experimental attraction (bull, near surface): Woolley, D. et al., **J. Exp. Biol.**, 2009.
- Attraction in 2D fluid model: Yang, Y., Elgeti, J., G. Gompper, **Phys. Rev. E.**, 2008.
- Attraction in 3D fluid with bead-chain model: Llopis, I. et al., **Phys. Rev. E.**, 2013.

3D Stokes
Planar waveform
Preferred curvature



Olson, LF, *Phys. Fluids*, 2016
Simons, LF, Cortez, *J. Biomech.*, 2015

3D Trajectories



Su, T.-W., Xue, L., Ozcan, A., 2012. *High-throughput lensfree 3D tracking of human sperms reveals rare statistics of helical trajectories.* **PNAS**, 109 (40), 16018–16022.

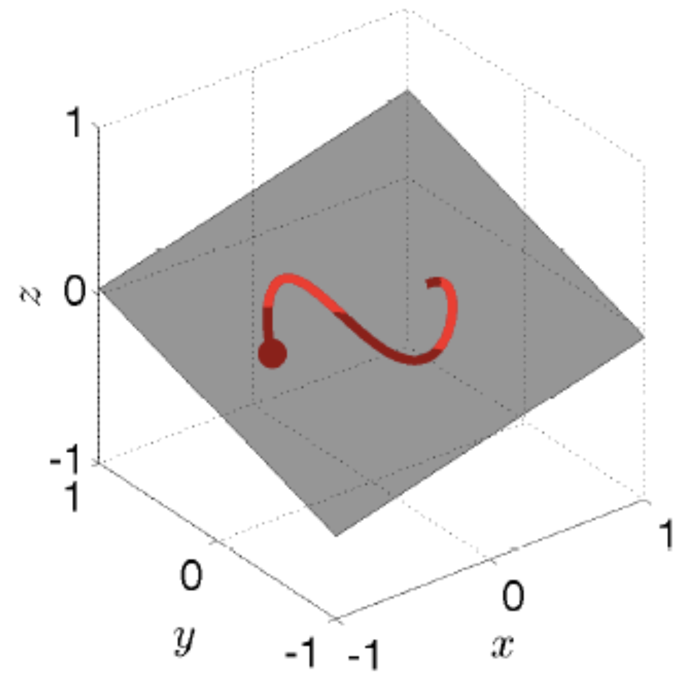
- Previous (planar) models cannot model the general interaction of 2 or more sperm!
- Can we develop a model that can incorporate 3D effects?
- How do sperm in populations affect each other's trajectories?
- Can helical/chiral trajectories arise from a planar motility behavior?

Three-Dimensional Model Extension

Concept: penalize out-of-plane components.

- Define the flagellum plane.
- Define a *new* energy to minimize these out-of-plane deviations:

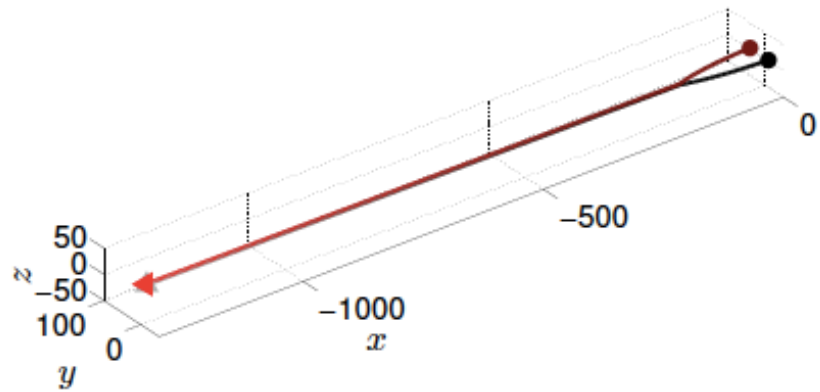
$$E_{pen} = \frac{1}{2} S_p \int_0^L \left[\frac{\partial \hat{\mathbf{X}}}{\partial s} \cdot \mathbf{e}_3 \right]^2 ds$$



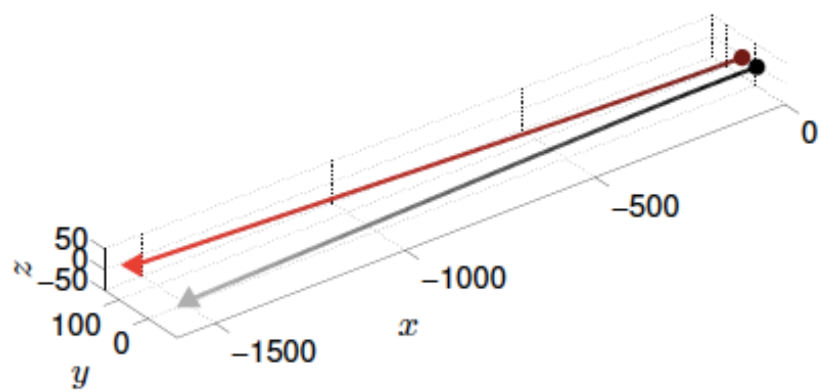
Simons, J., Fauci, L. and R. Cortez, **J. Biomechanics**, 2015.

Parallel planar swimmers

Trajectories



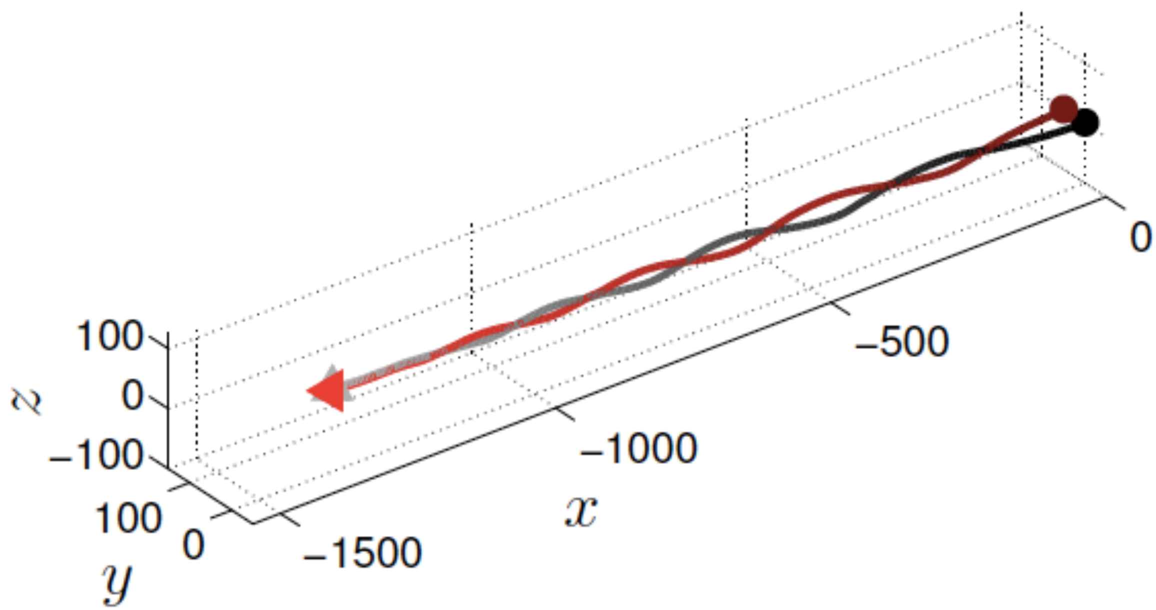
(a) Coplanar.



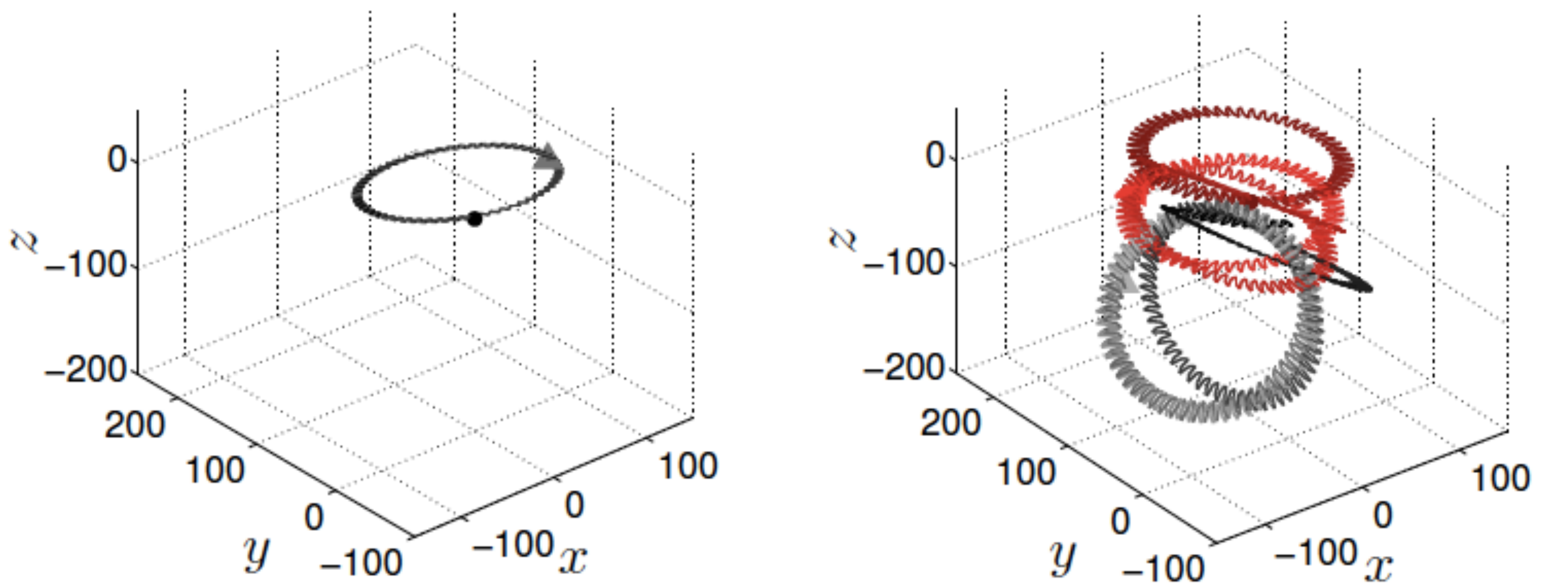
(b) Parallel initial flagellar planes.

Perturbed coplanar swimmers

Perturbed Coplanar Configurations



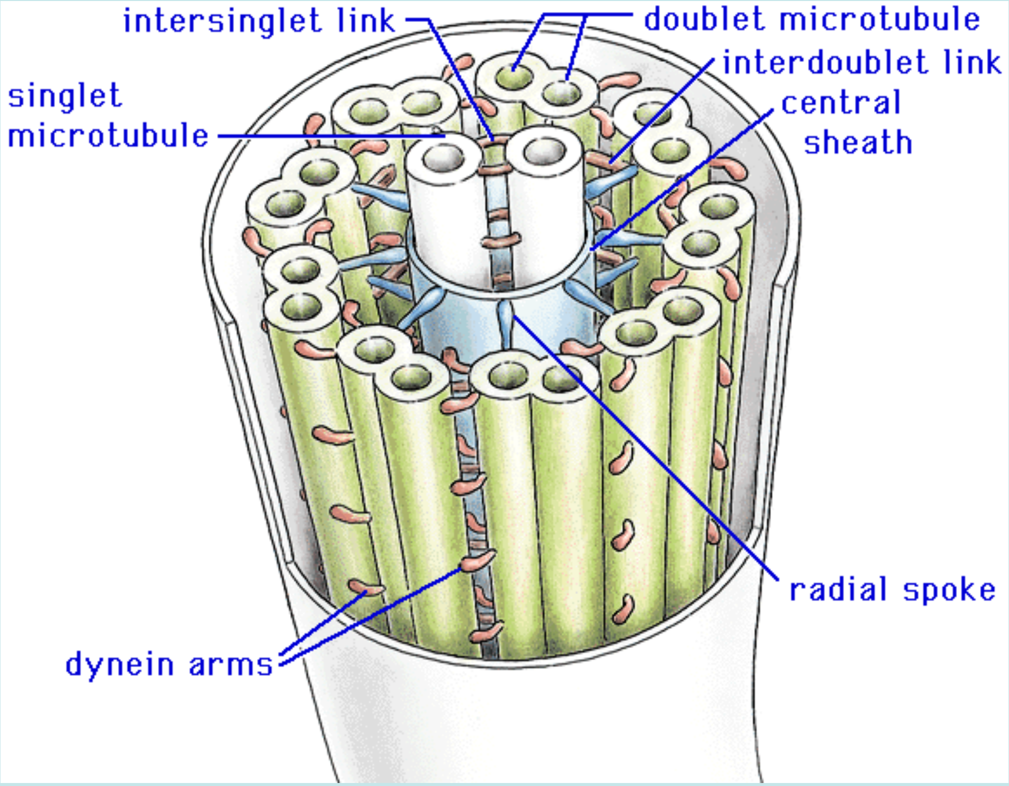
Asymmetric Trajectories

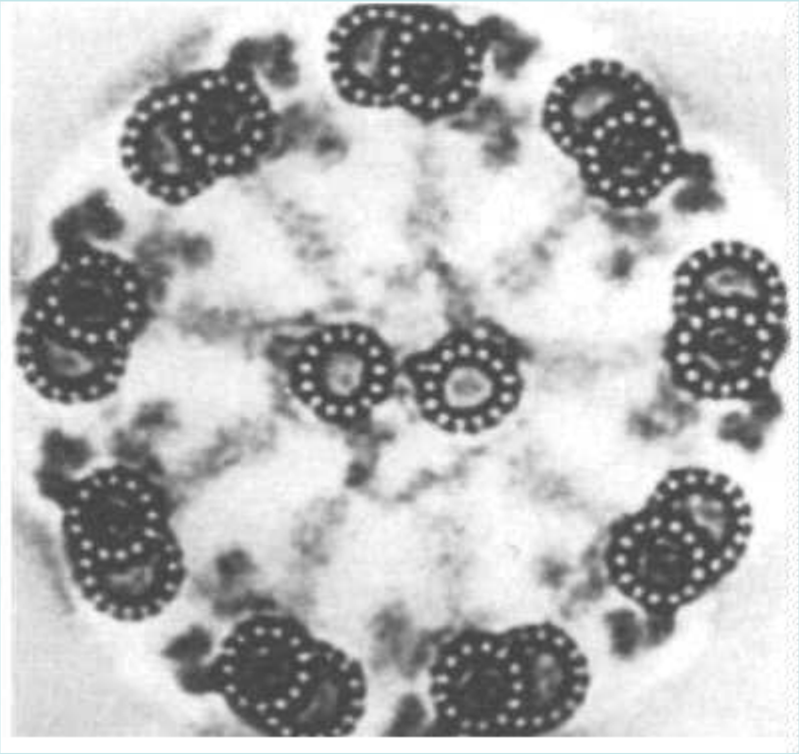


(a) Single sperm. (b) Two sperm.

- 3D trajectories can evolve from waveforms that are primarily planar.
- Intuition from 2D may be misleading for 3D behavior: coplanar cooperative swimming represents an *unstable* state (from a dynamical systems perspective).
- Complex environments may *enable* sperm to reach the egg more effectively (a fully 3D search).

Eucaryotic axoneme

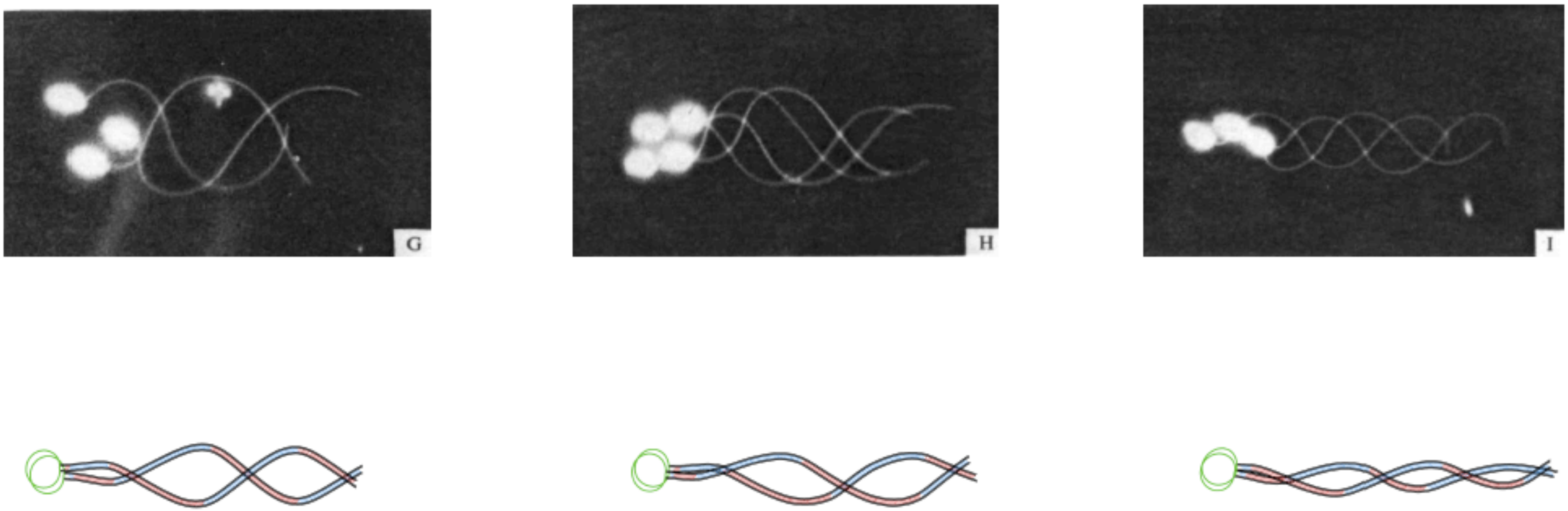




3D schematic

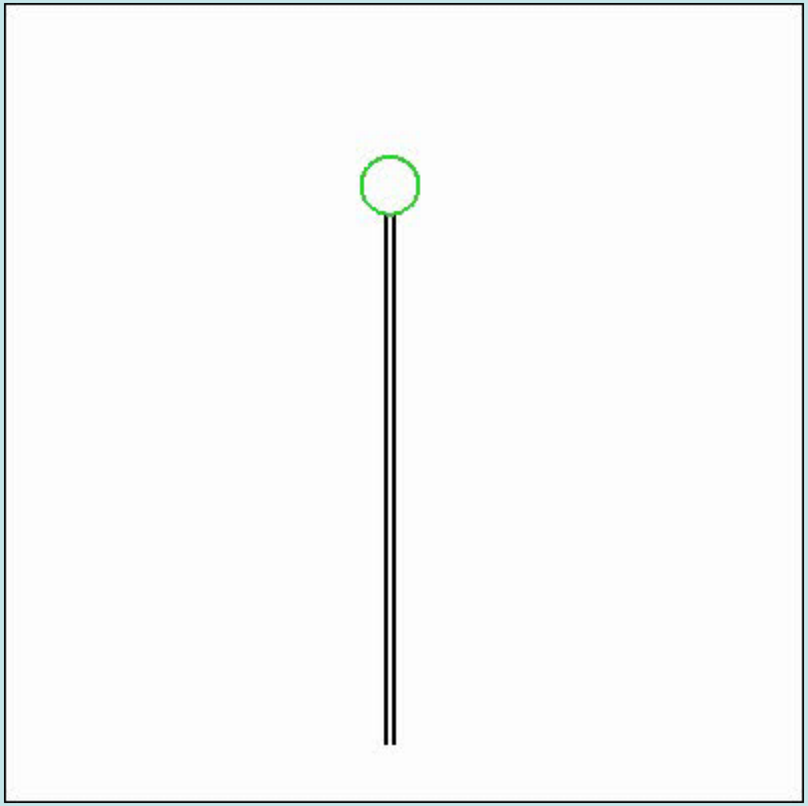
The precise nature of the spatial and temporal control mechanisms regulating various wavefoms of cilia and flagella is still unknown.

What are the internal mechanisms that cause flagella (or cilia) to beat?

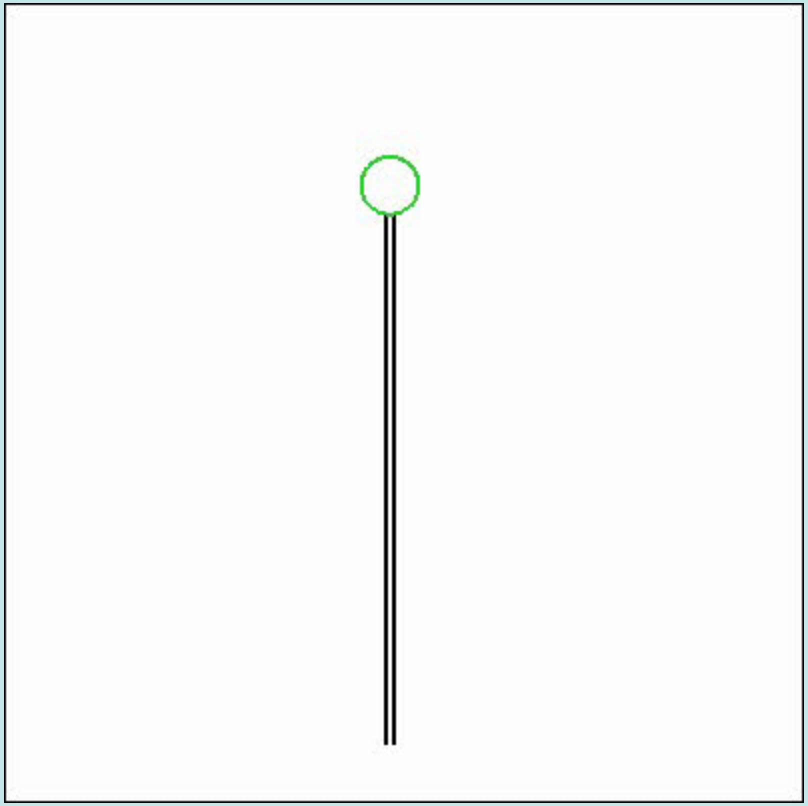


C. Brokaw, sea-urchin sperm swimming in fluids of increasing viscosity….1972

- 2D Navier-Stokes
- Individual dynein motors - activation curvature controlled



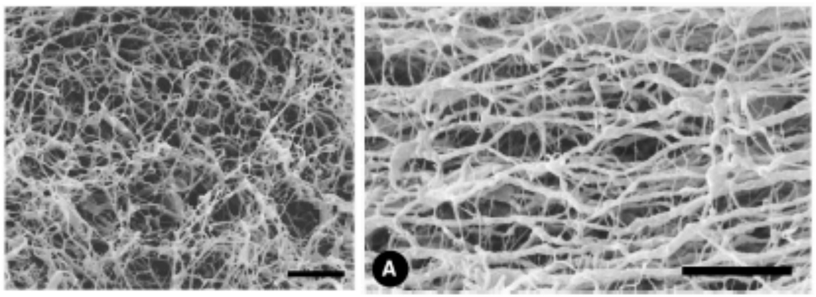
10 centipoise



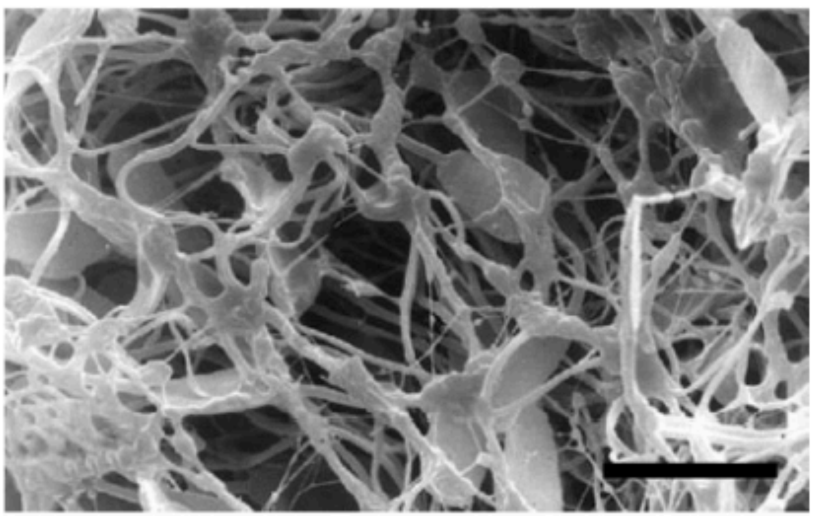
1 centipoise

Highly Heterogeneous, Viscoelastic Media

- Biological fluid is typically highly viscous.
- Biological fluid is composed of networks of branched polymers.
- Goal is to model viscoelastic behavior of medium.
- Swimming through a viscoelastic medium depends on its properties.
- Study of swimming in heterogeneous fluid.

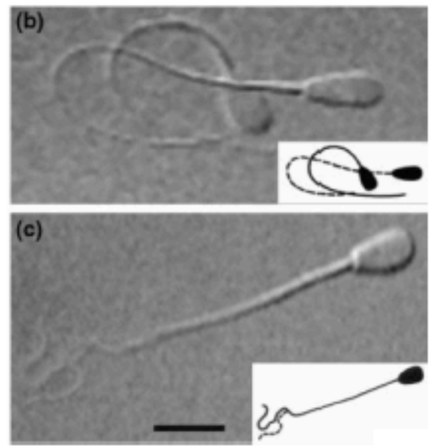


Rutlland et al. *J. Anat.* **201**, 2002

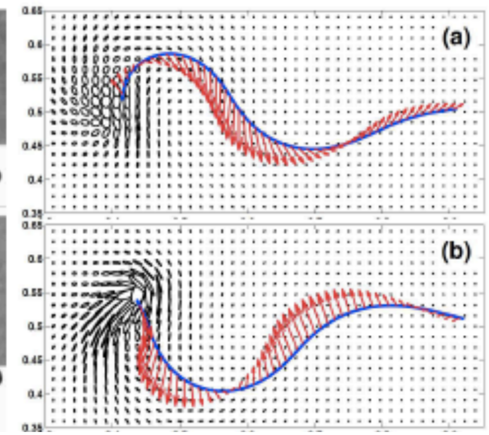


Rutlland et al. *Reprod. Dom. Anim.* **40**, 2005

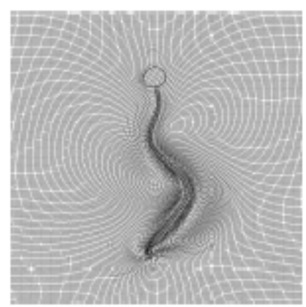
Gap size: 0.5 – 25μm
Swimmer's head: 5 – 10μm long, 3μm wide



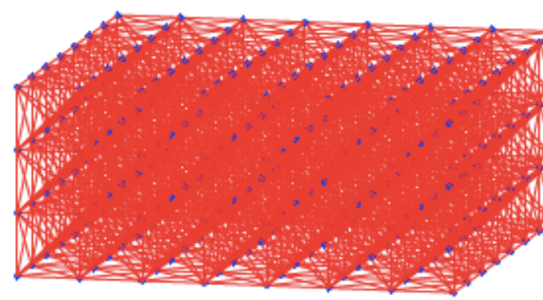
Ho, Suarez, *Reprod.* **122**, 2001



Teran, Fauci, Shelley, PRL **104** 2010



Dillon, Zhuo, Disc.Cont.Dyn.S **12**, 2011

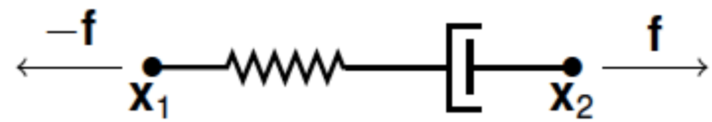


Wróbel et al. Phys.Fluids **24**, 2014

Simple Elements in Stokes Flow

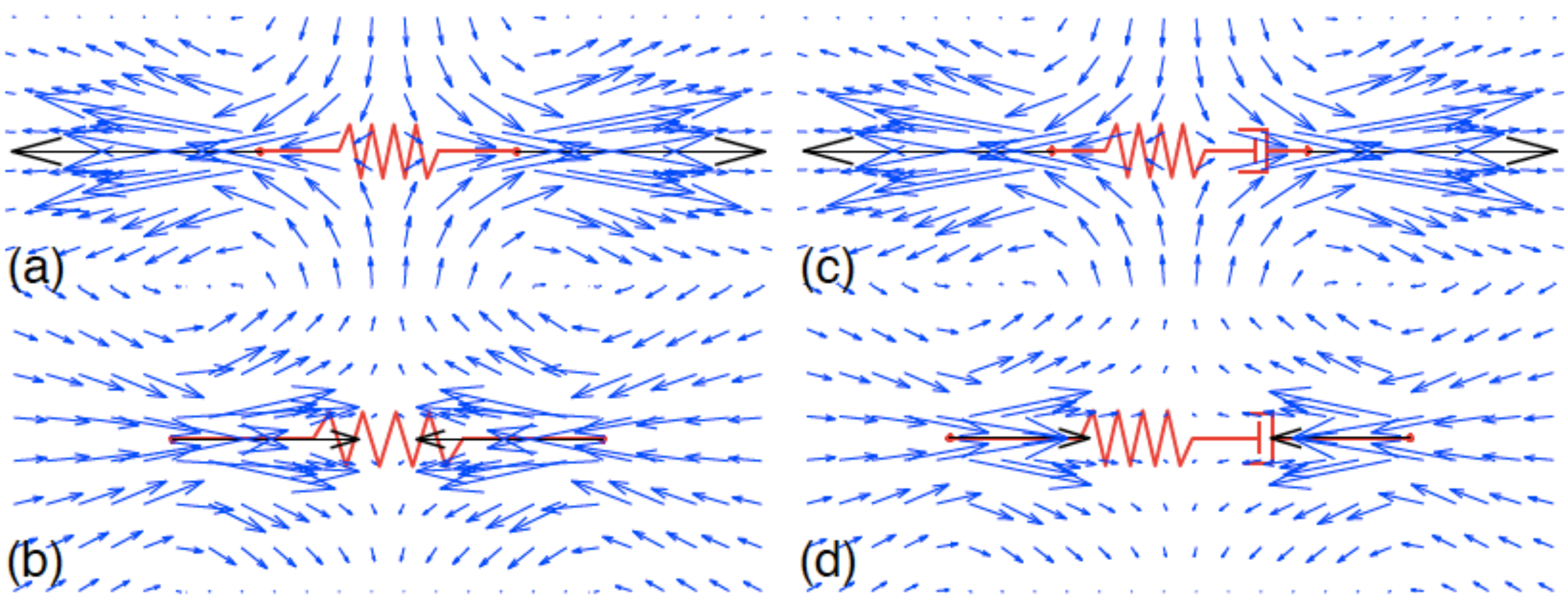
Stokes-Spring element

Stokes-Maxwell element



$$\mathbf{f}_s(\mathbf{x}_1) = -\mathbf{f}_s(\mathbf{x}_2) = E\left(\frac{\|\mathbf{x}_2 - \mathbf{x}_1\|}{\ell} - 1\right)\frac{\mathbf{x}_2 - \mathbf{x}_1}{\|\mathbf{x}_2 - \mathbf{x}_1\|}$$

$$\frac{d\ell(t)}{dt} = \frac{E\ell_0}{\eta}\left(\frac{\|\mathbf{x}_2 - \mathbf{x}_1\|}{\ell(t)} - 1\right)$$



Linear Viscoelasticity - Rheology

$\varepsilon(t) = \Delta L/L$ – strain – dimensionless deformation,
$\sigma(t) = \mathbf{f}/A$ – stress – force per area

Creep test – strain response to a step-stress:

$$\sigma(t) = \sigma_0(H(t - t_0) - H(t - t_1)) \longrightarrow \varepsilon(t)$$

Stress Relaxation test – stress response to a constant strain:

$$\varepsilon(t) = \varepsilon_0 H(t - t_0) \longrightarrow G(t) = \frac{\sigma(t)}{\varepsilon_0}$$

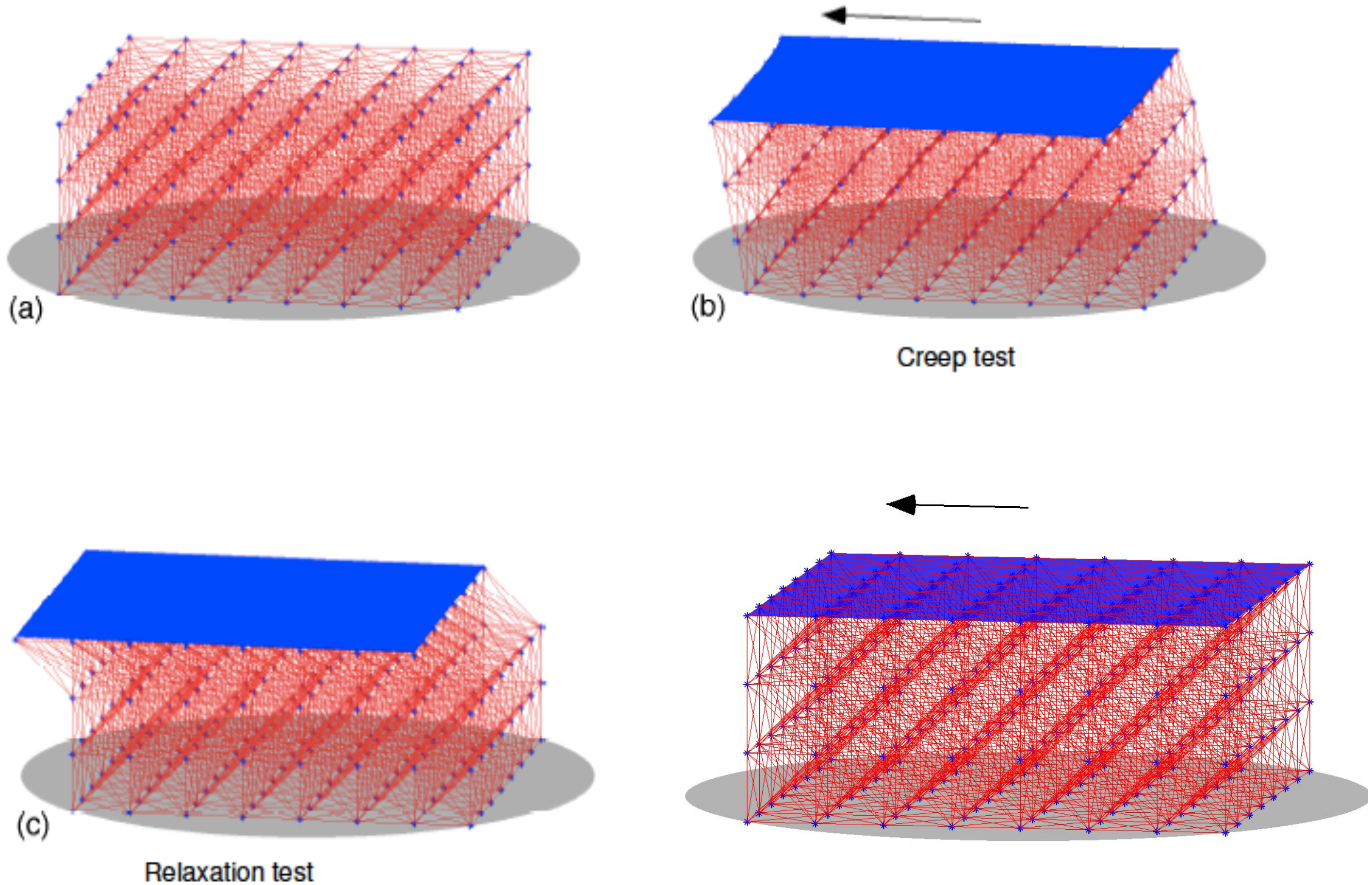
Small Amplitude Oscillatory Shear test – stress response to an oscillatory strain:

$$\varepsilon(t) = \varepsilon_0 \sin(\omega t) \quad \longrightarrow \quad \sigma(t) = \varepsilon_0 \left[G'(\omega) \sin(\omega t) + G''(\omega) \cos(\omega t) \right]$$

additionally

$$\eta' = \frac{G''(\omega)}{\omega} \quad \text{– dynamic viscosity,} \quad \eta'' = \frac{G'(\omega)}{\omega} \quad \text{– elastic viscosity}$$

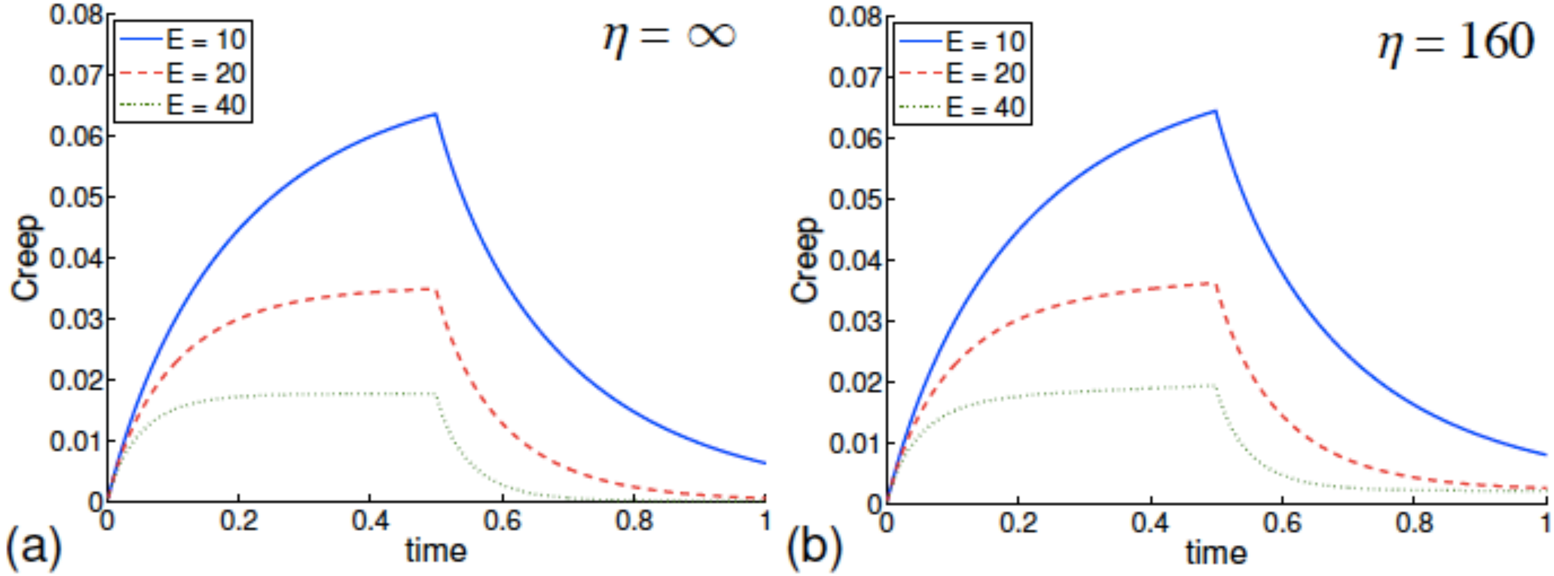
Structure in Stokes Fluid – Sliding Plate Rheometer

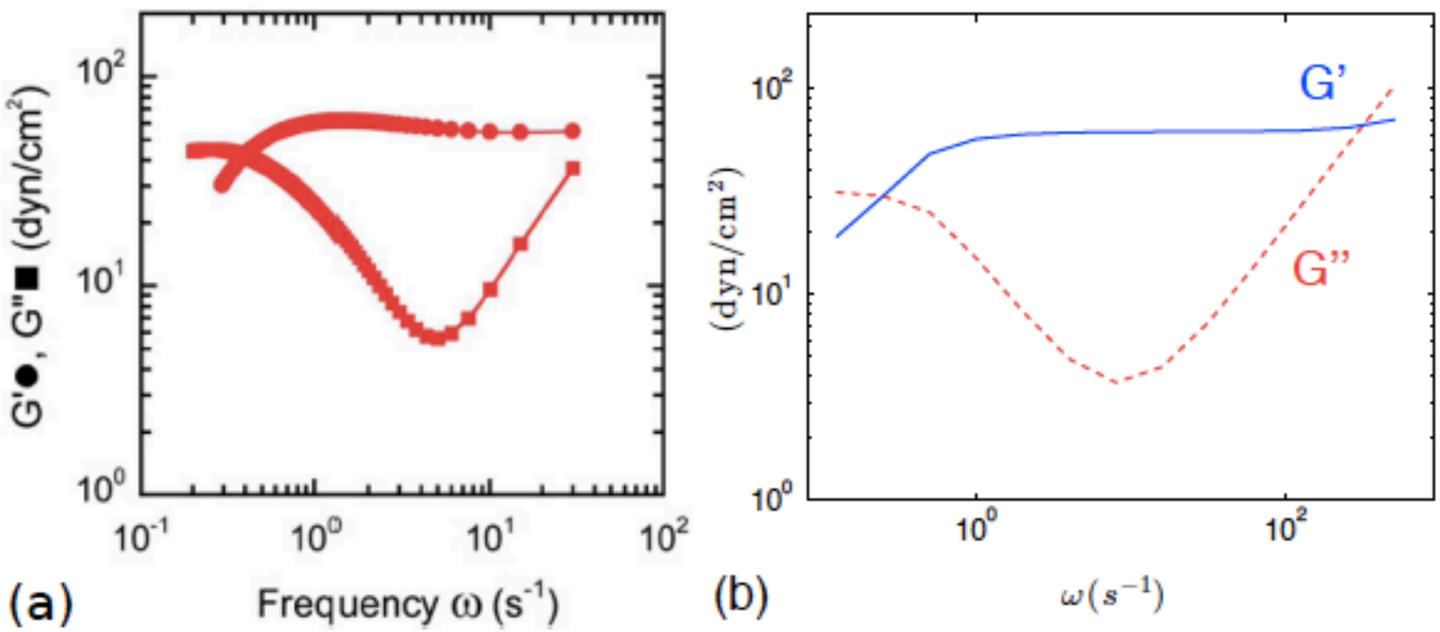


The total force at the node $\mathbf{x}_i$ is

$$\mathbf{f}_i = \sum_j \mathbf{f}_j^s = \sum_j \ell_{ij}^2(0) E_{ij} \left(\frac{||\mathbf{x}_j - \mathbf{x}_i||}{\ell_{ij}(t)} - 1 \right) \frac{\mathbf{x}_j - \mathbf{x}_i}{||\mathbf{x}_j - \mathbf{x}_i||},$$

where E_{ij} is a stiffness and $\ell_{ij}(t)$ is the resting length of the link between nodes $\mathbf{x}_i$ and $\mathbf{x}_j$.



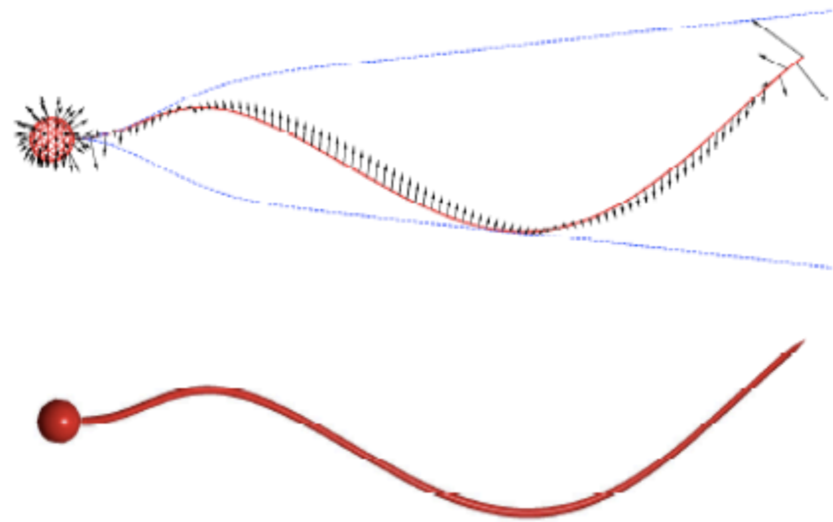


Wrobel, Cortez, Fauci; *Phys. Fluids*, 2014

Free Swimmer Model I – Prescribed Motion

Motility problem:

$$\mathbf{u}_d + \mathbf{U} + \Omega \times (\mathbf{x} - \mathbf{x}_c) = \frac{1}{\mu}\int_{\partial B} \mathbf{S}^{\epsilon}(\mathbf{x}, \mathbf{x}_0)\mathbf{f} dS$$



Free swimmer:

$$\mathbf{u}_d = \frac{1}{\mu}\int_{\partial B} \mathbf{S}^{\epsilon}(\mathbf{x}, \mathbf{x}_0)\mathbf{f} dS - \mathbf{U} - \Omega \times (\mathbf{x} - \mathbf{x}_c)$$

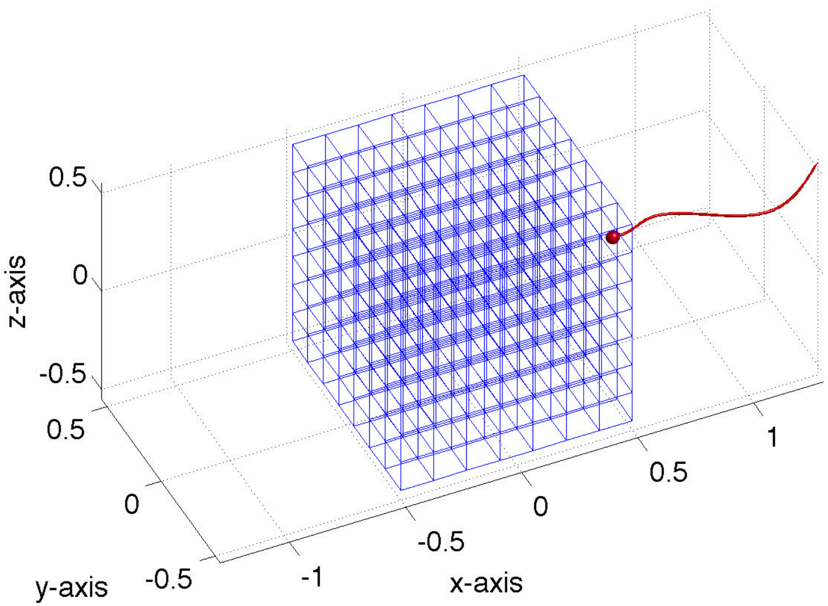
$$0 = \int_{\partial B} \mathbf{f} dS \qquad 0 = \int_{\partial B} (\mathbf{x} - \mathbf{x}_c) \times \mathbf{f} dS$$

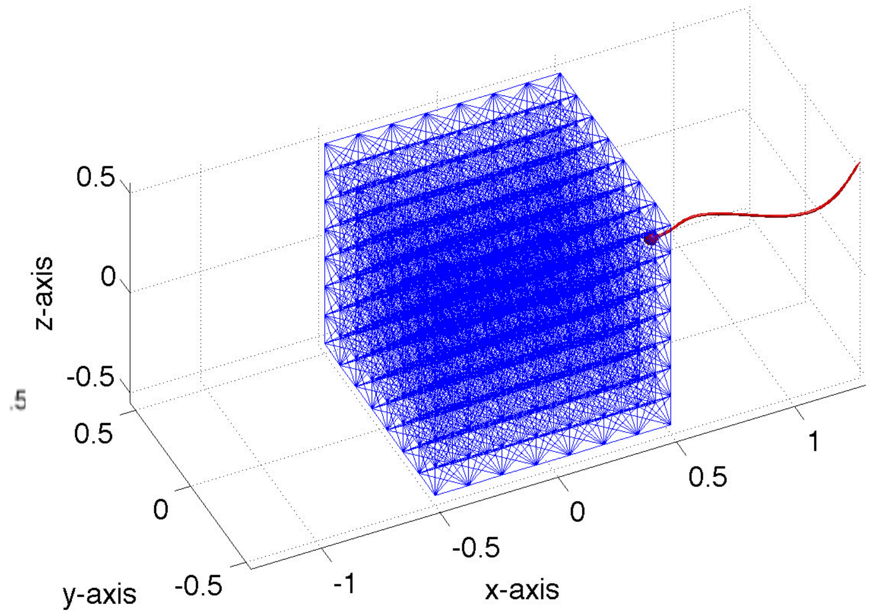
- Wave velocity boundary condition at tail points.
- Zero velocity (no-slip) boundary condition at head points.
- Head points updated using rotation and translational velocities, i.e.

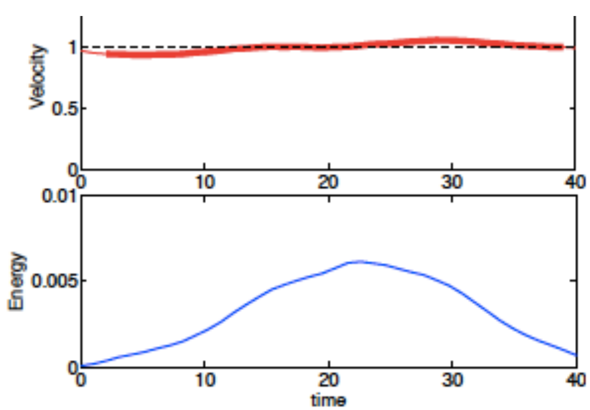
$$\frac{d\mathbf{x}}{dt} = \mathbf{U} + \Omega \times (\mathbf{x} - \mathbf{x}_c)$$

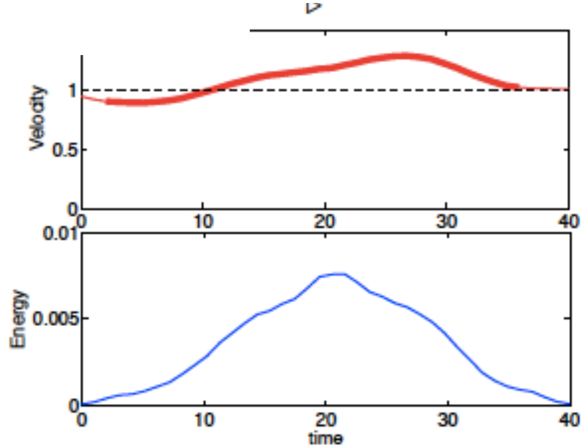
Swimming through Viscoelastic Structures

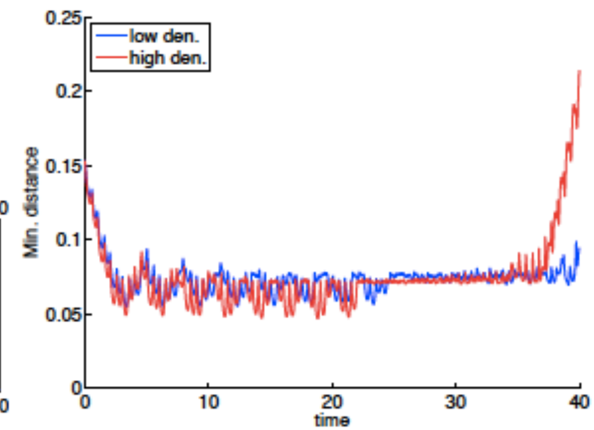
Wrobel, Lynch, Barrett, Fauci, Cortez, J. Fluid Mech. (2016)

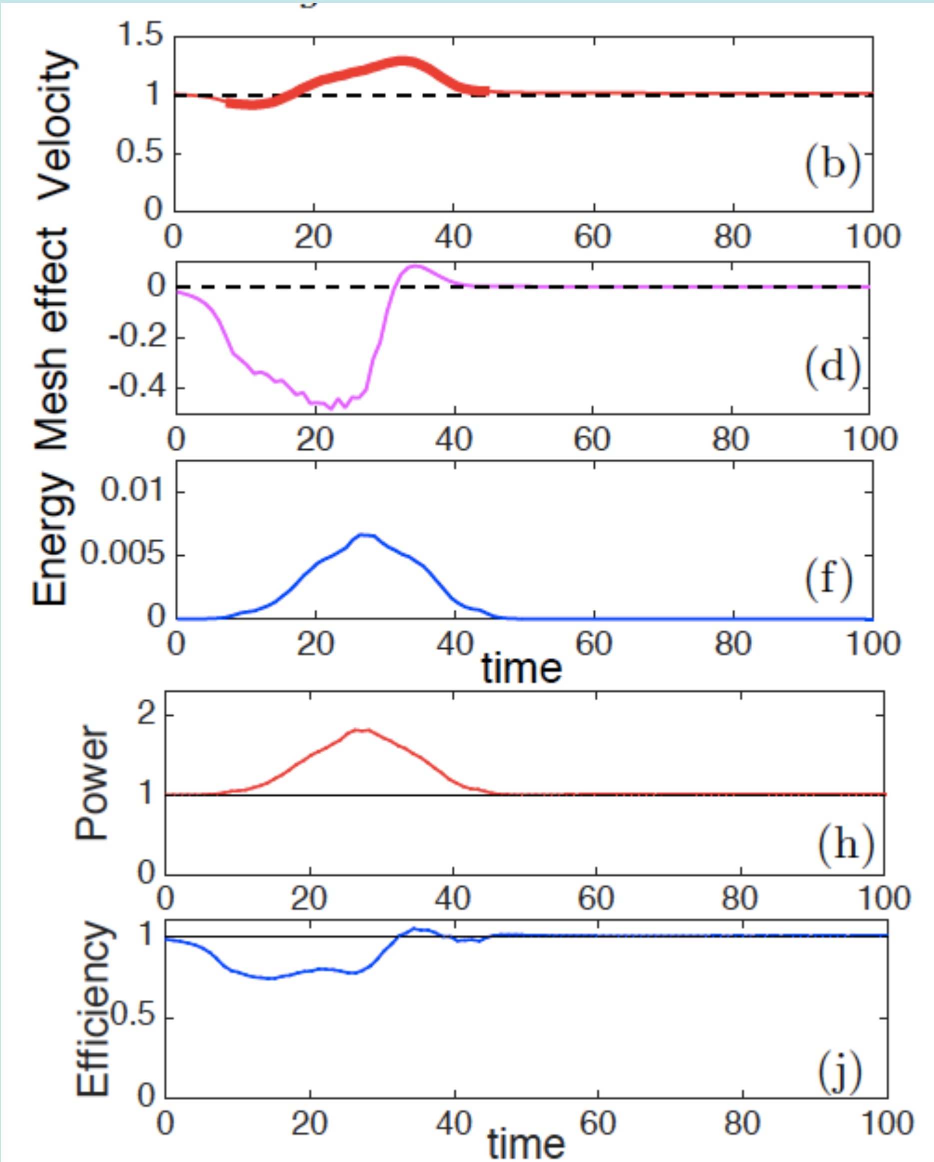




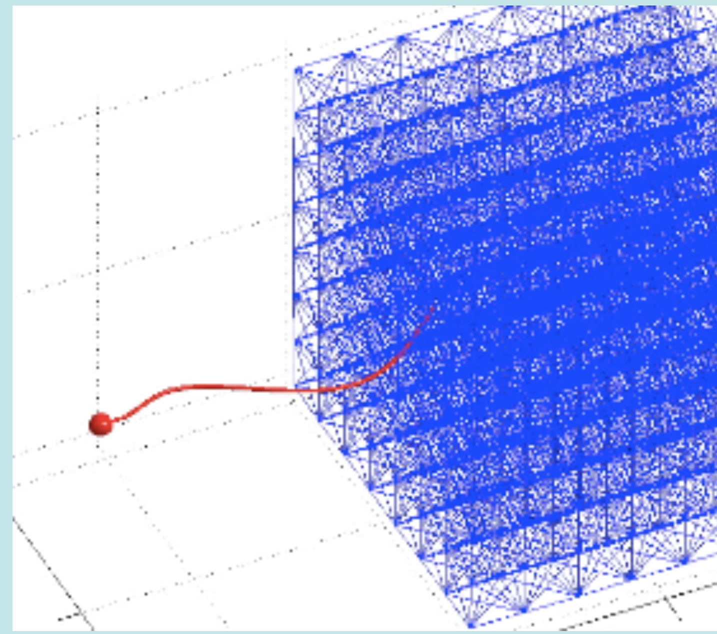






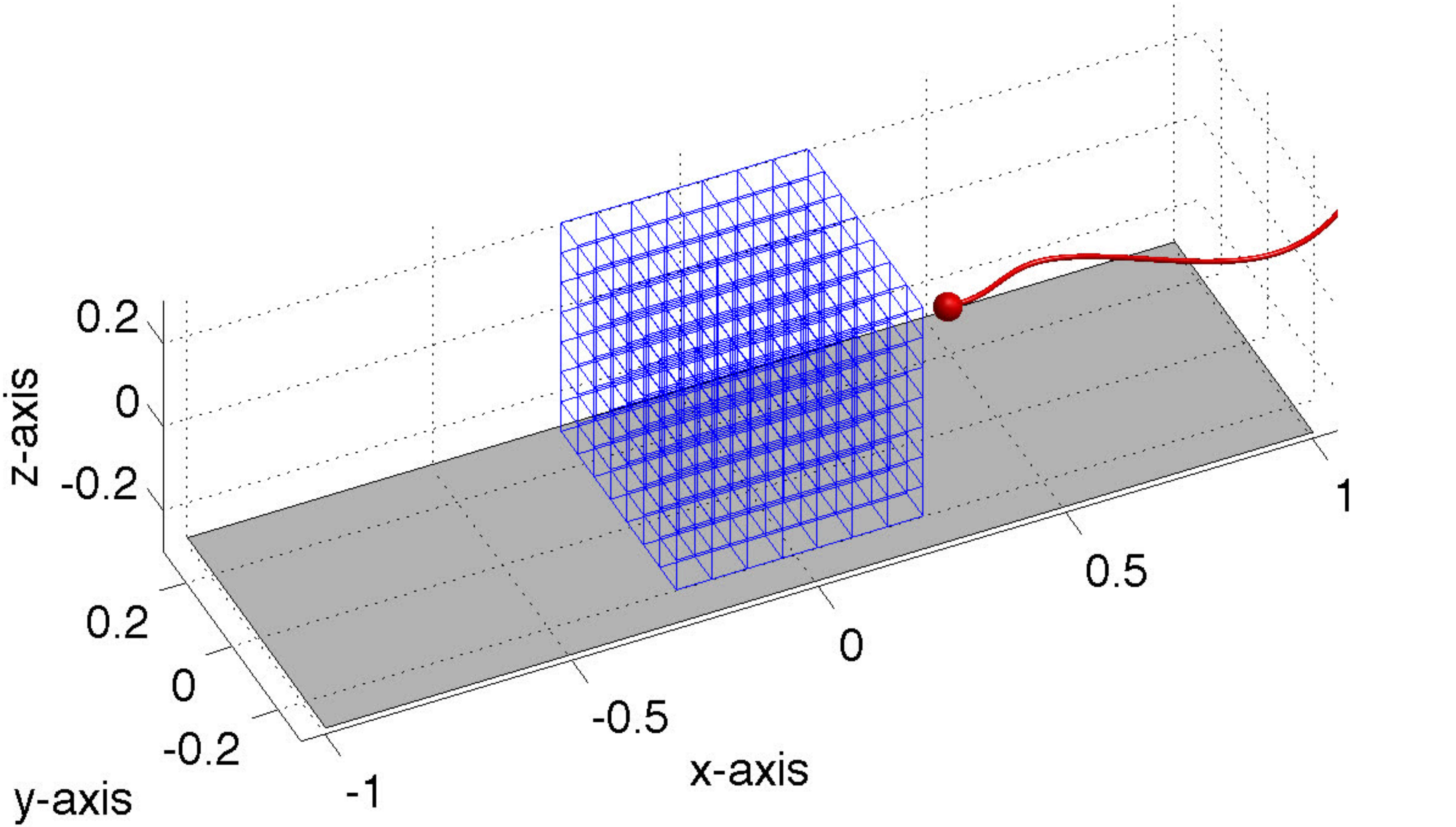


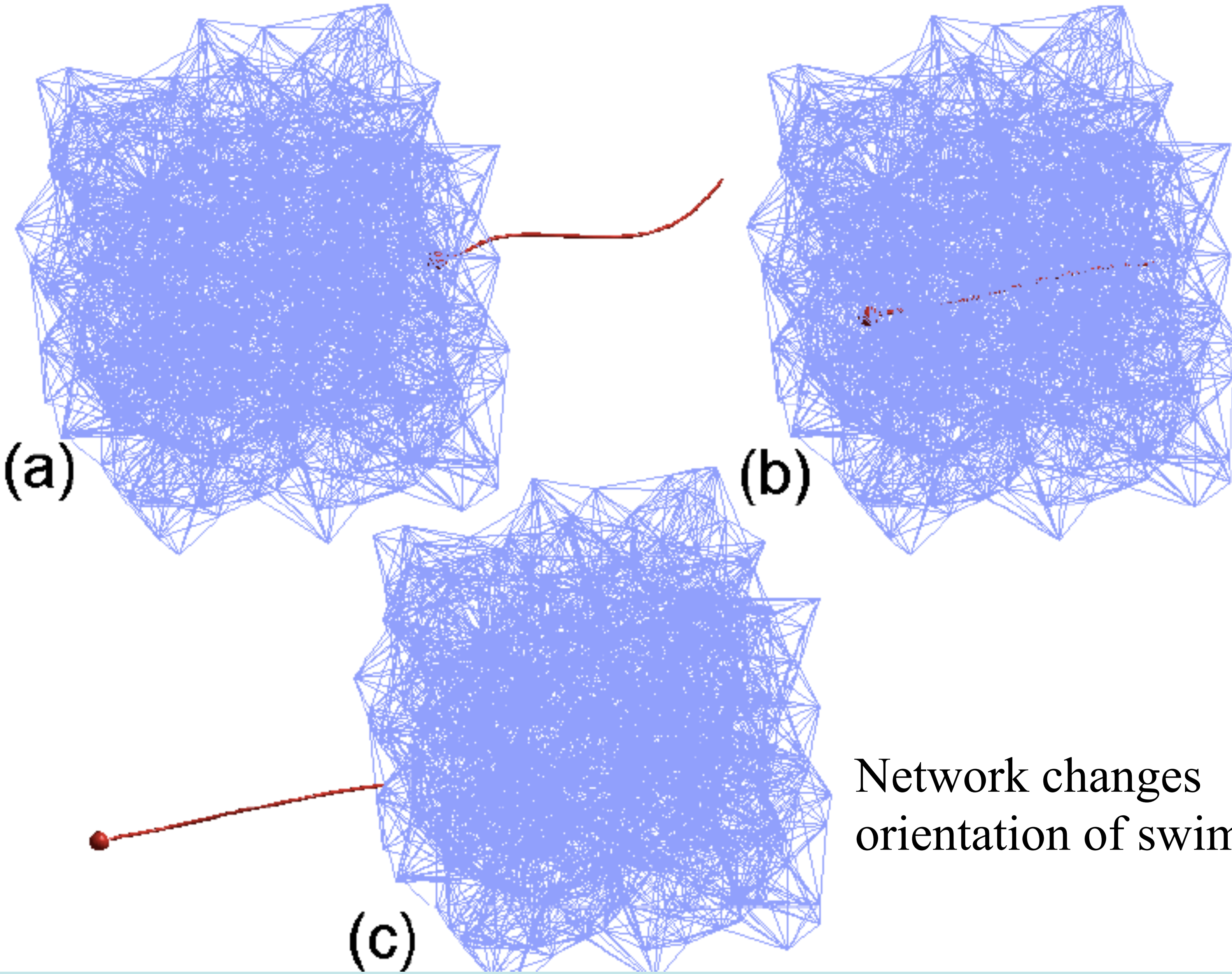
Swimmer gets a boost in velocity within network, but also requires more power to maintain specified waveform.



Wrobel, Lynch, Barrett, Fauci, Cortez, J. Fluid Mech. (2016)

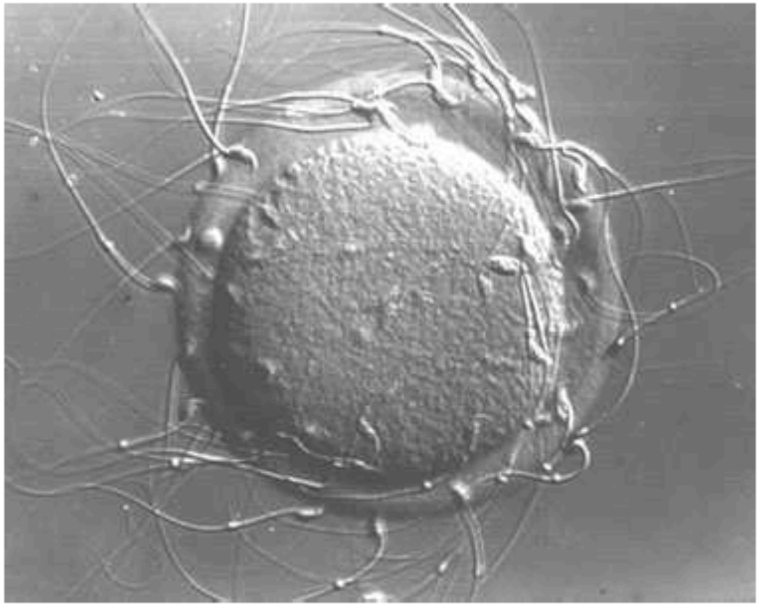
Network attached to wall.



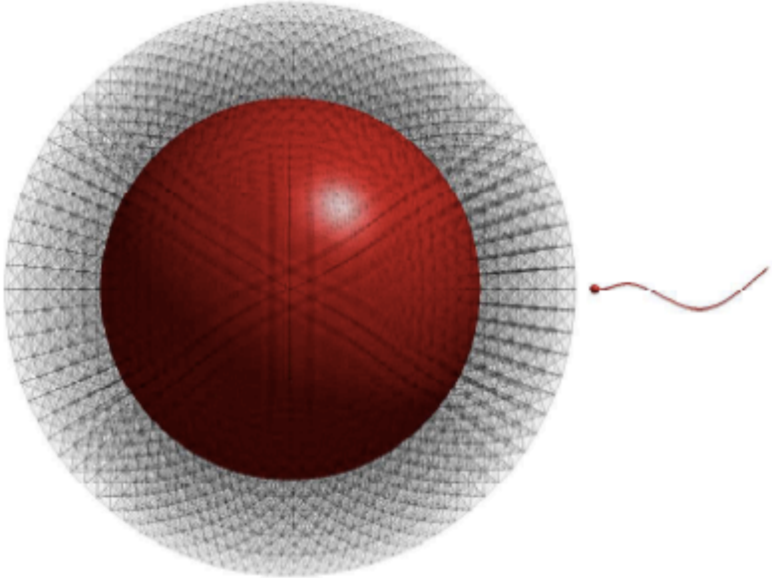


Network changes orientation of swimmer

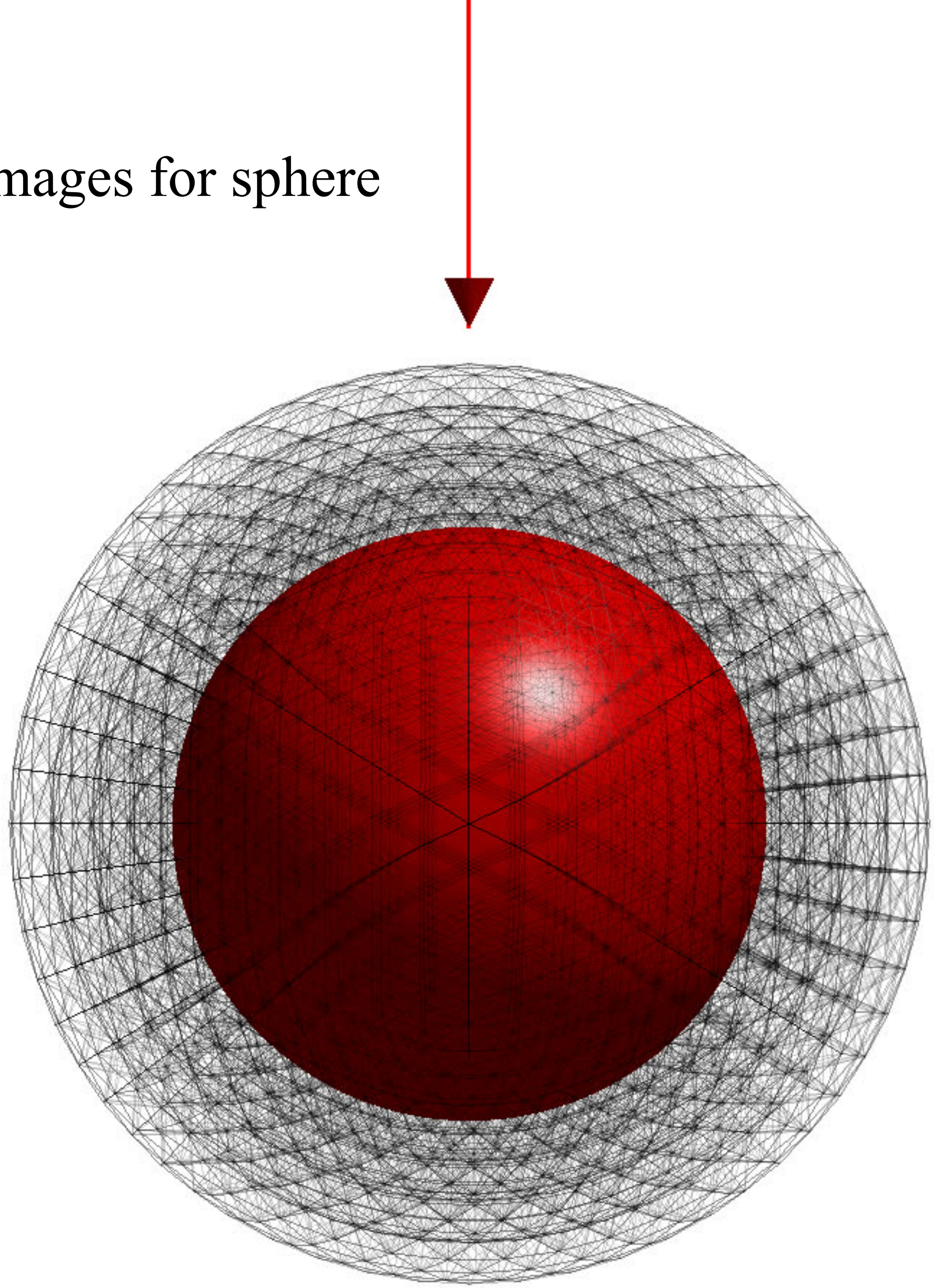
Ovum with its outer protective layer



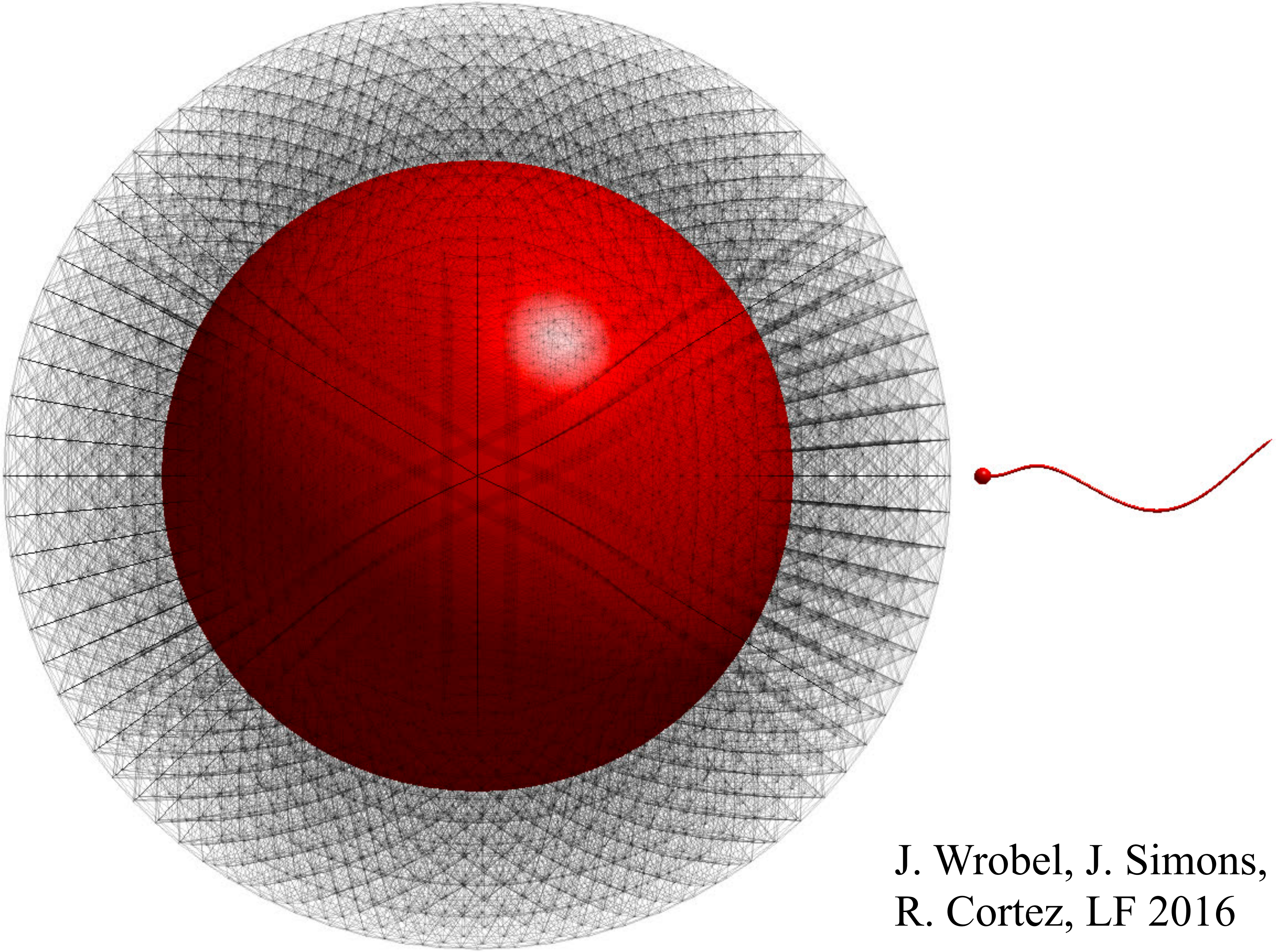
Wassarman, J. Biol. Chem. **283**, 2008



Regularized images for sphere



Wrobel, Cortez,
Varela, Fauci,
J. Comp. Phys. 2016



J. Wrobel, J. Simons,
R. Cortez, LF 2016

Motivation

Vaginal delivery is linked to

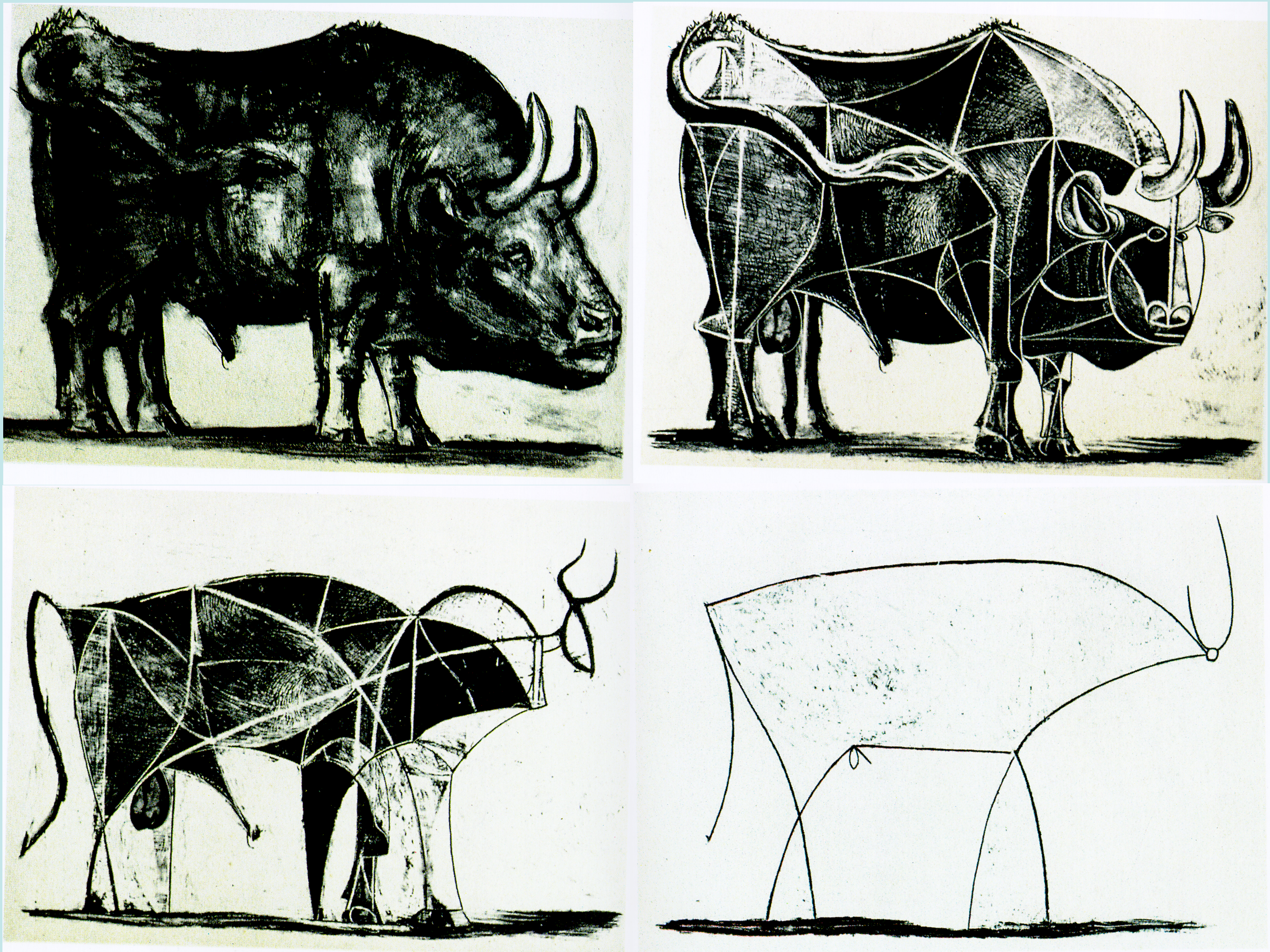
- shorter post-birth hospital stays
- lower likelihood of intensive care stays
- lower mortality rates [1]

Fluid mechanics greatly informs the total mechanics of birth.

- vernix caseosa
- amniotic fluid

[1] C. S. Buhimschi, I. A. Buhimschi (2006). *Advantages of vaginal delivery*, Clinical obstetrics and gynecology.
Fig. 1: "HumanNewborn" by Ernest F - Own work. Licensed under CC BY-SA 3.0 via Commons - https://commons.wikimedia.org/wiki/File:HumanNewborn.JPG#/media/File:HumanNewborn.JPG
Fig. 2: "Postpartum baby2" by Tom Adriaenssen - http://www.flickr.com/photos/inferis/110652572/. Licensed under CC BY-SA 2.0 via Commons - https://commons.wikimedia.org/wiki/File:Postpartum_baby2.jpg#/media/File:Postpartum_baby2.jpg

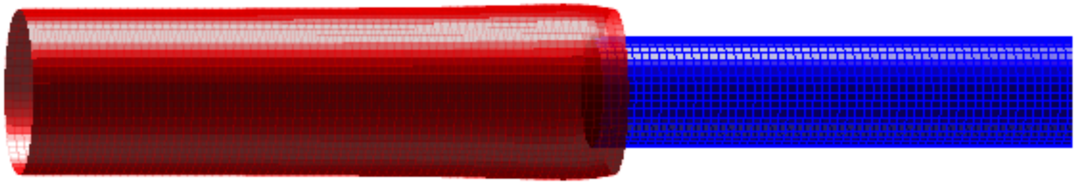
Abstraction - Picasso



Chris Johnson, U. Utah

Baby: rigid cylinder
Uterus: flexible tube

Leftwich lab, GWU



Elastic Tube

- Tube modeled by network of Hookean springs.
- Force at $\mathbf{x}_l$ due to spring from $\mathbf{x}_m$:
  $\mathbf{f}(\mathbf{x}_l) = \tau \left(\frac{\|\mathbf{x}_m - \mathbf{x}_l\|}{\Delta_{lm}} - 1 \right) \frac{(\mathbf{x}_m - \mathbf{x}_l)}{\|\mathbf{x}_m - \mathbf{x}_l\|}$
- τ chosen to match elastic properties to physical experiment.

Rigid Inner Rod

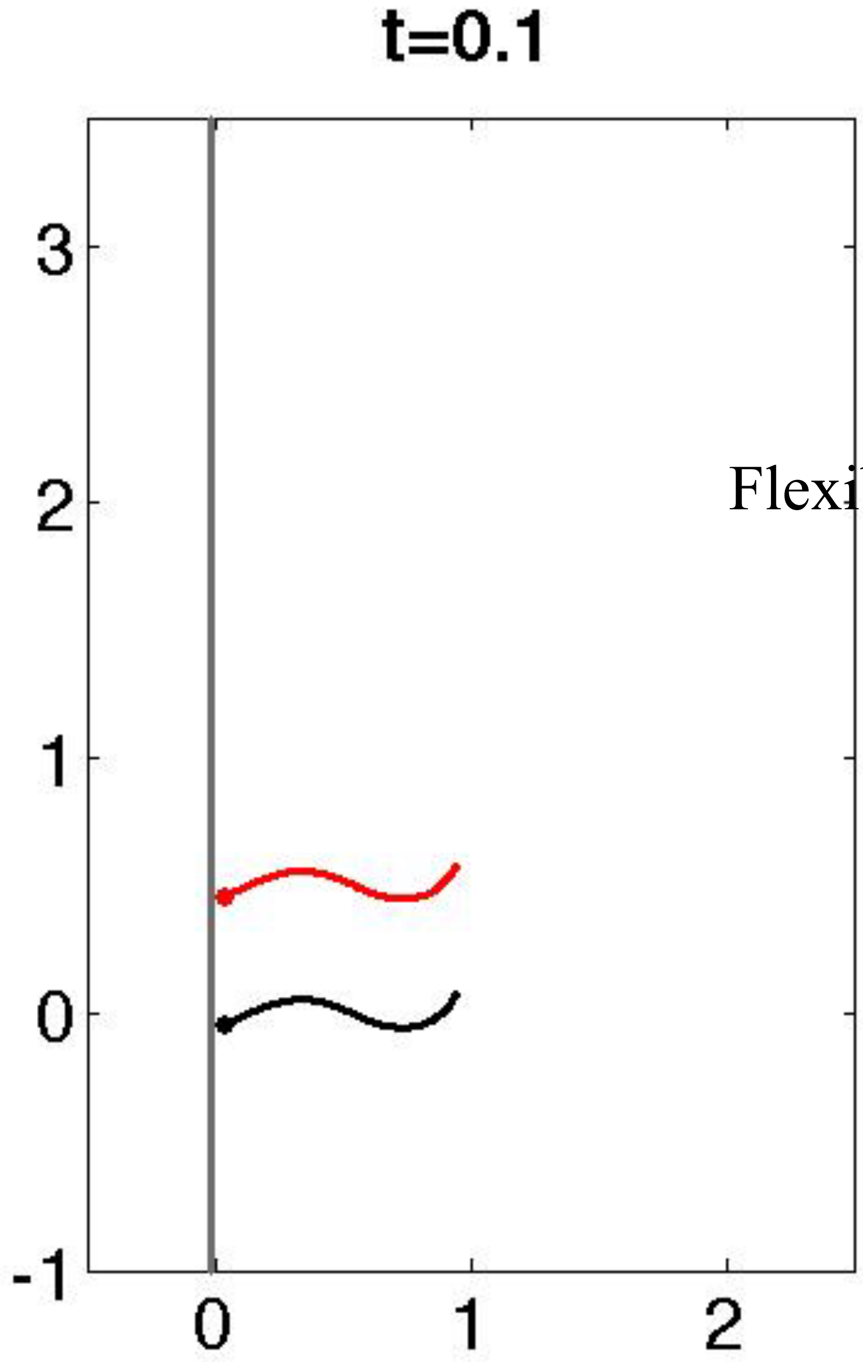
- A constant velocity $\mathbf{u}$ is specified in the z-direction.

R. Pealatere, Tulane

Can we characterize tube buckling?

Nevermind the baby… this is interesting elasto/ hydrodynamics…

Thank you so much!!!!!!!!!



Flexible wall!!