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/

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Motility

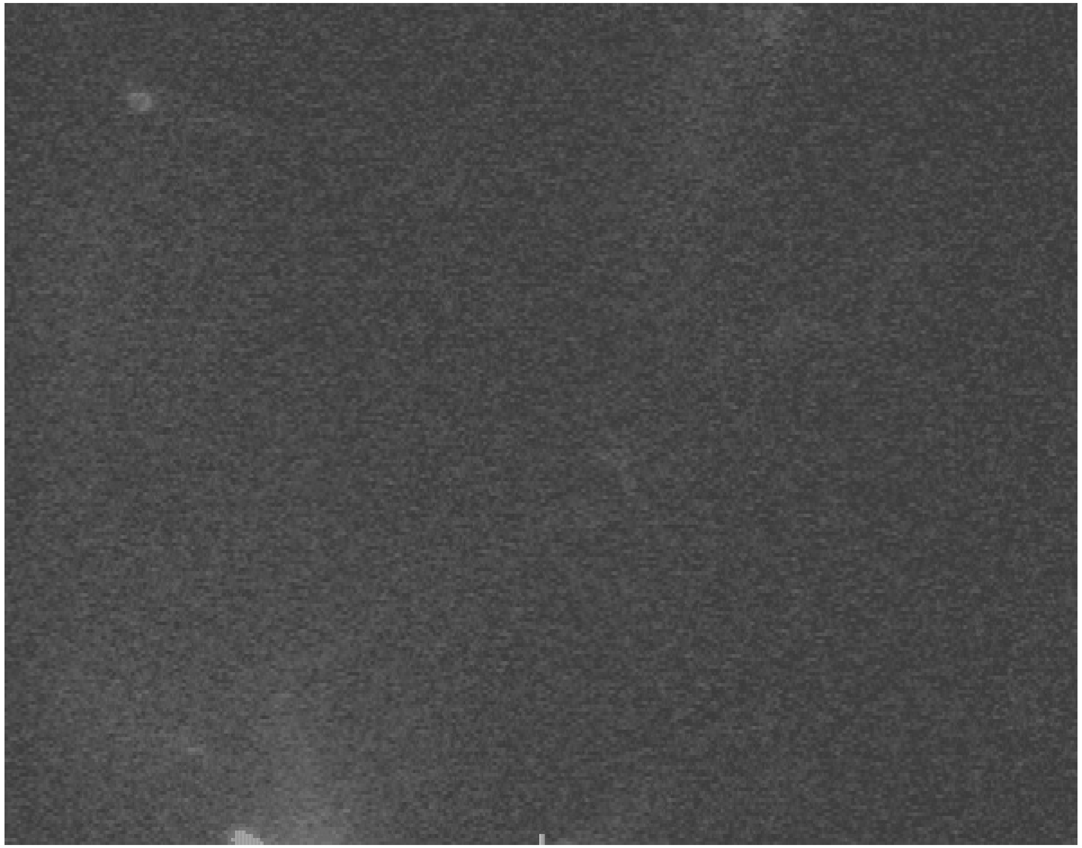
Motility is the capability of exhibiting directed, purposeful movement.

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)

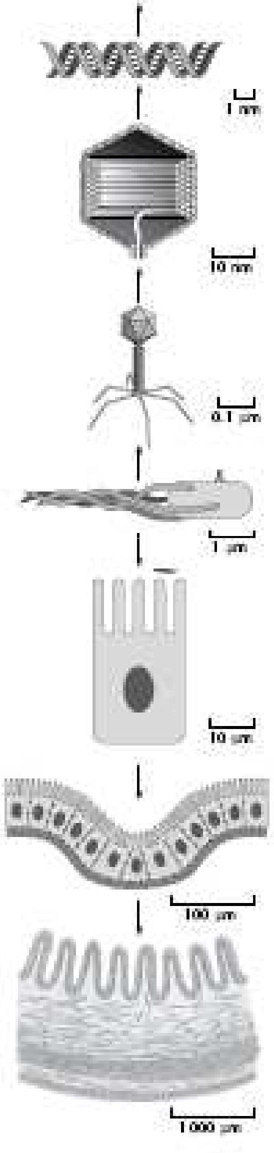
We are currently unable to obtain self-propulsion at microscopic scales artificially

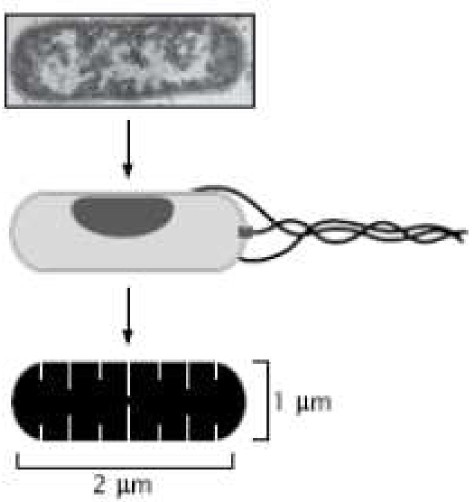
Maybe we can learn from Nature ?
(bio-mimetic or bio-inspired design)

Using Nature as a template is sometimes naive
(airplanes don’t flap their wings)

PeregrinFalconTrim.flv

Microscopic bio-swimmers: bacteria and cells





Escherichia Coli (E. Coli)

Euglenoids

Two movies of metaboly in Eutreptiella sp.

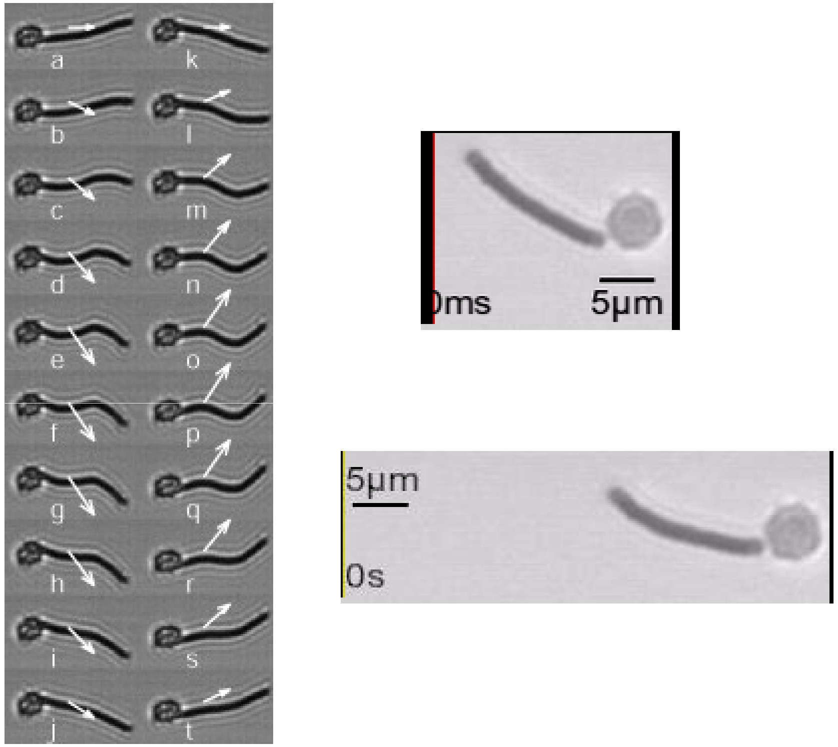
Eutrep2.mov

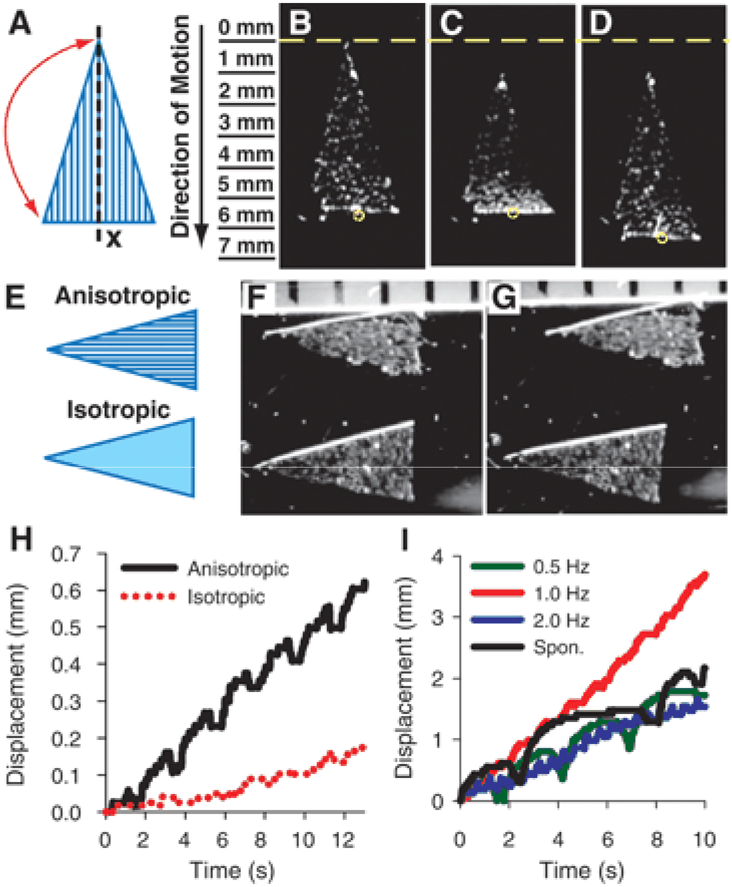
Ccmp389a.mov

One movie of swimming in Anisonema sp.

Aniso2.mov

Man made micro-swimmers: micro-robots





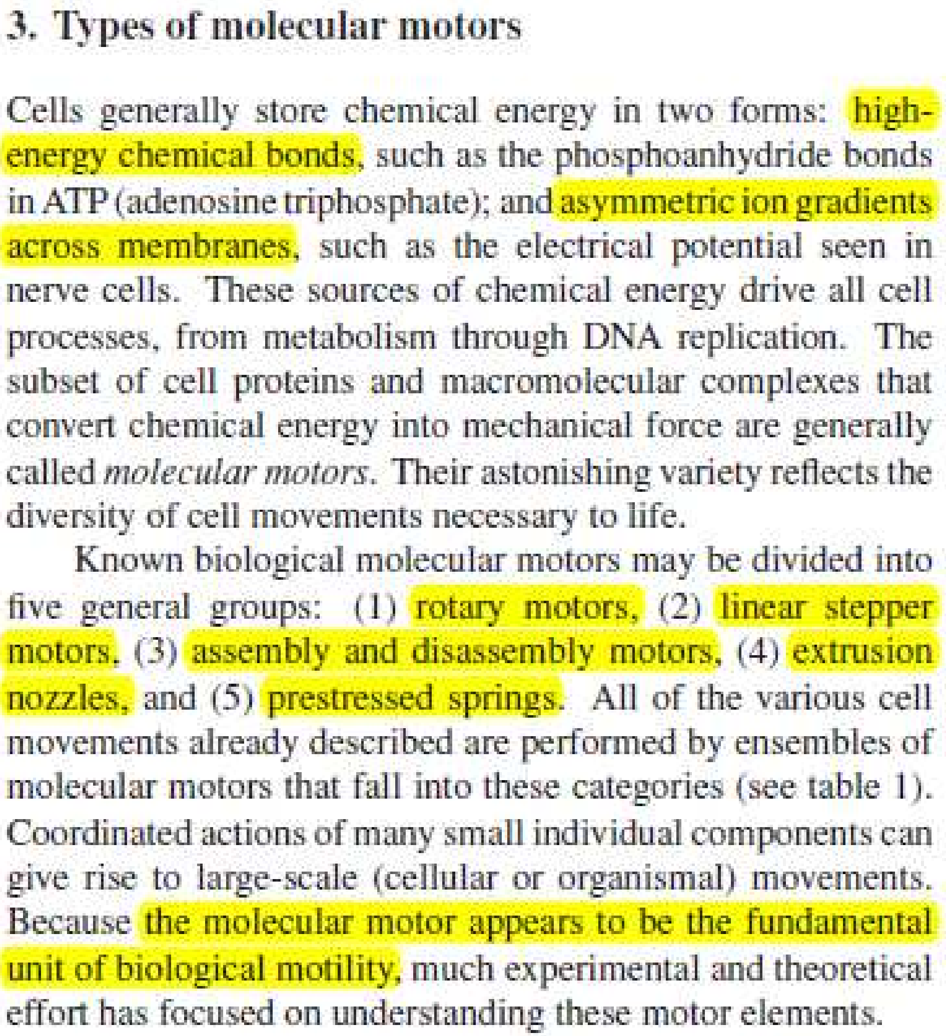
red blood cell + flexible magnetic filament

polymer film + muscle cells

H. Stone et al., Nature (2005)

G. Whitesides et al., Science (2007)

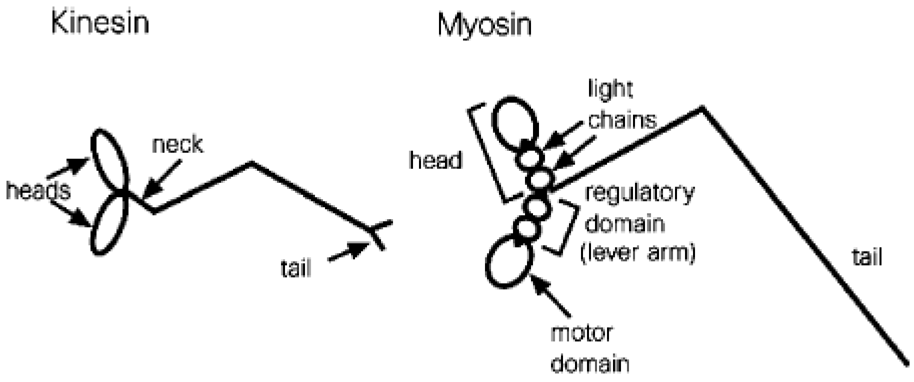
Molecular motors



3. Types of molecular motors

Cells generally store chemical energy in two forms: high-energy chemical bonds, such as the phosphoanhydride 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

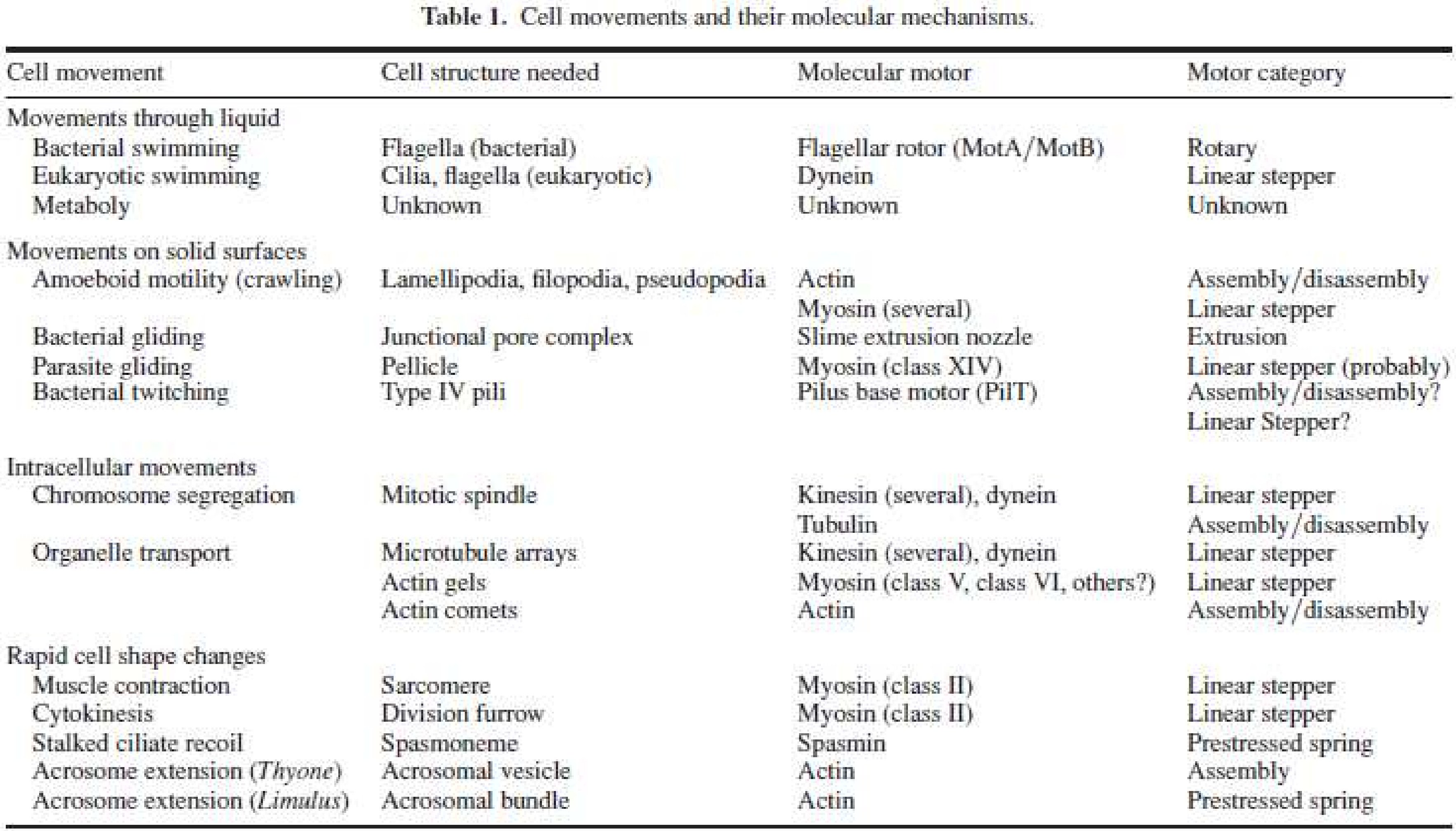
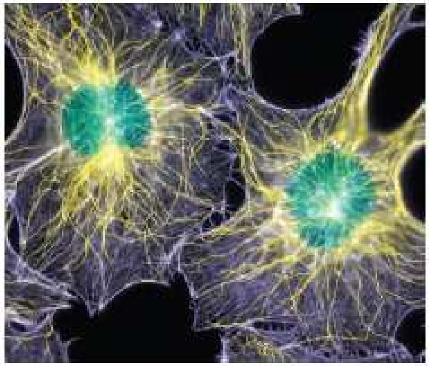
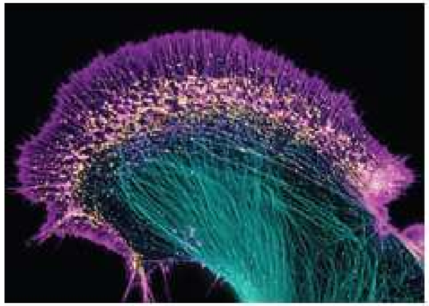


Table 1. Cell movements and their molecular mechanisms.

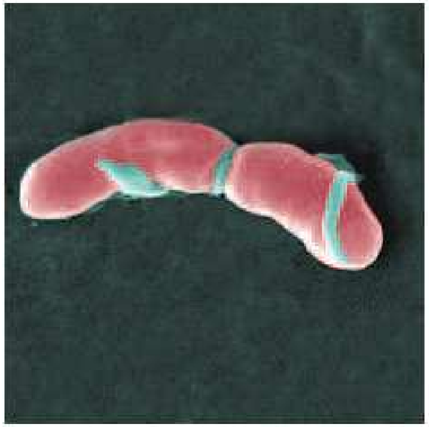
Cell movement	Cell structure needed	Molecular motor	Motor category
Movements through liquid			
Bacterial swimming	Flagella (bacterial)	Flagellar rotor (MotA/MotB)	Rotary
Eukaryotic swimming	Cilia, flagella (eukaryotic)	Dynein	Linear stepper
Metaboly	Unknown	Unknown	Unknown
Movements on solid surfaces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

Actin-based motility


fibroblasts

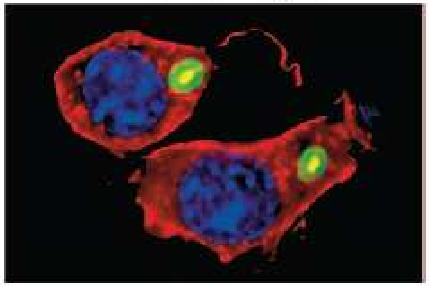

neuronal growth cones

Neuron1.flv

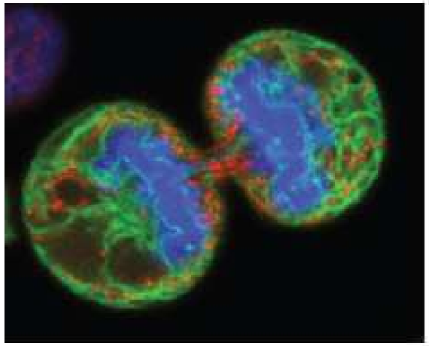

listeria

Listeria monocytogenes.mp4

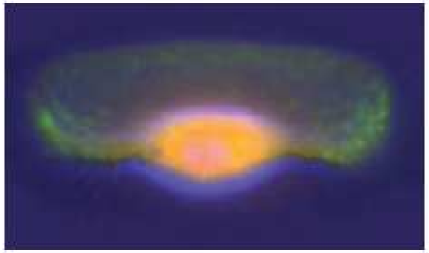
macrophages



cancer cells



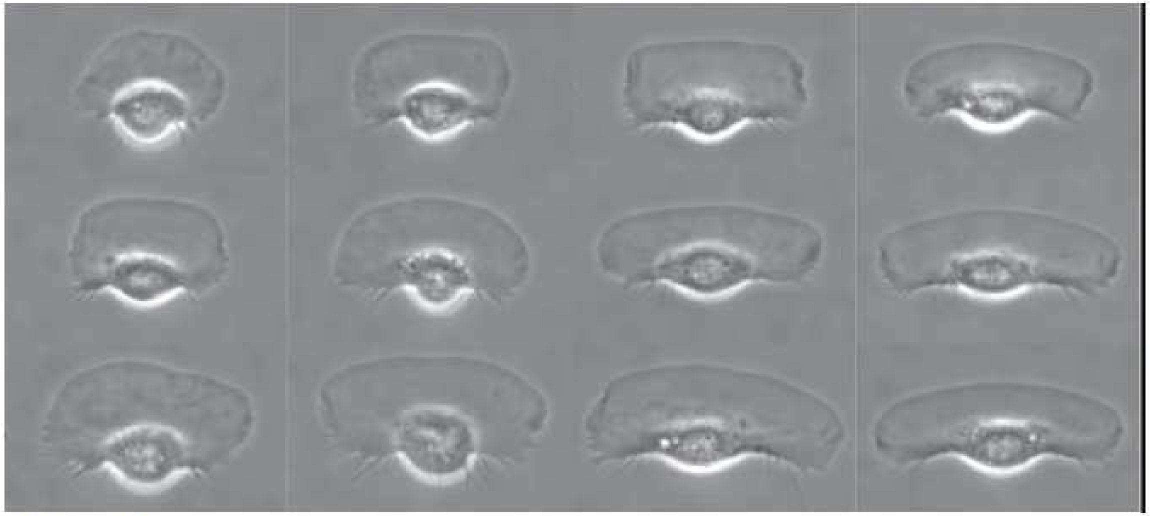
keratocytes



cellix.imba.oeaw.ac.at fileadmin conferences Videotour_.mov

Actin polymerization at the leading edge drives motility of crawling cells*

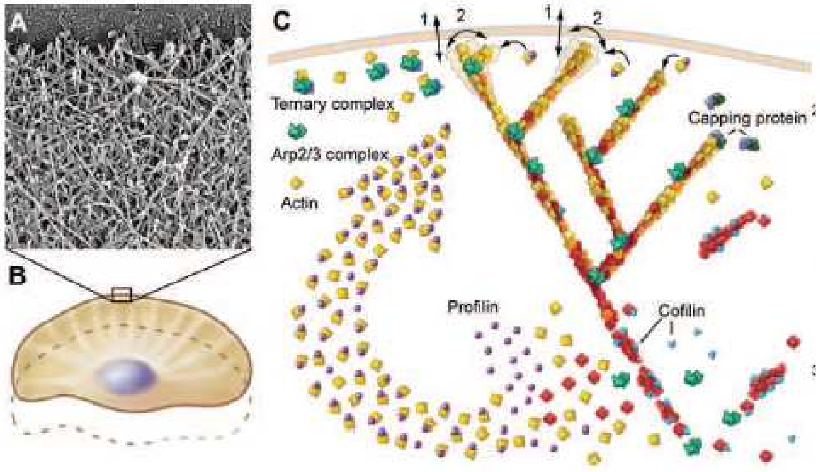
(* metastatic tumor cells, immune system response ...)



K. Keren et al. (2008)

FishKeratocytes2.mov

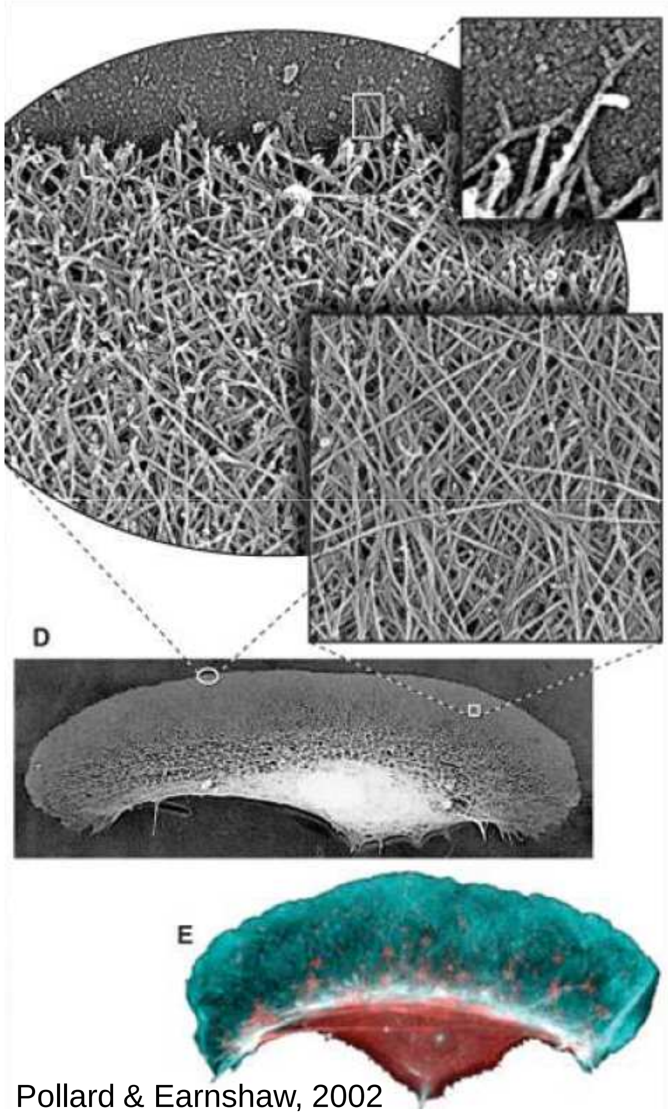
Protrusion



T. D. Pollard and J. Berro (2009)

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

Long range order: where from?



Pollard & Earnshaw, 2002

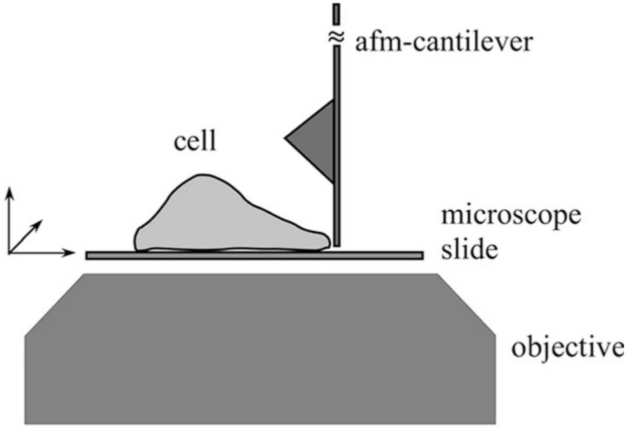
Long range order at the μm scale of the cell
(the front is flat)

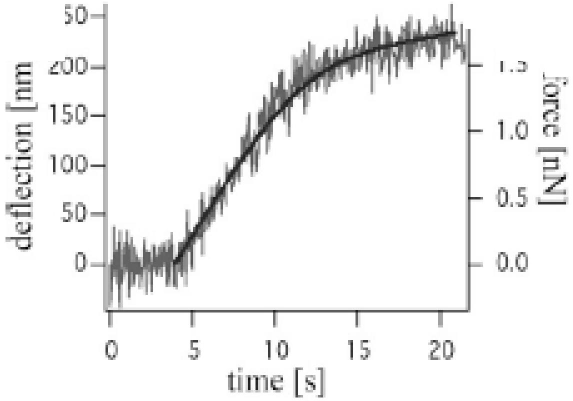
emerging from uncoordinated growth at the nm scale of the individual filaments.

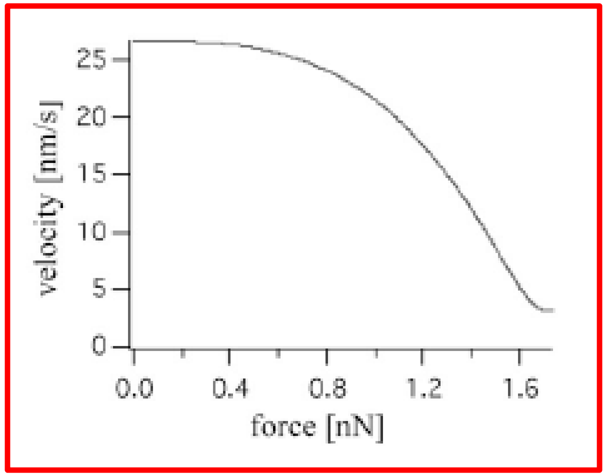
Hypothesis:
self-organized growth is orchestrated by long range **mechanical interactions** mediated by the membrane.

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

Gathering of facts: 1. F vs V relation



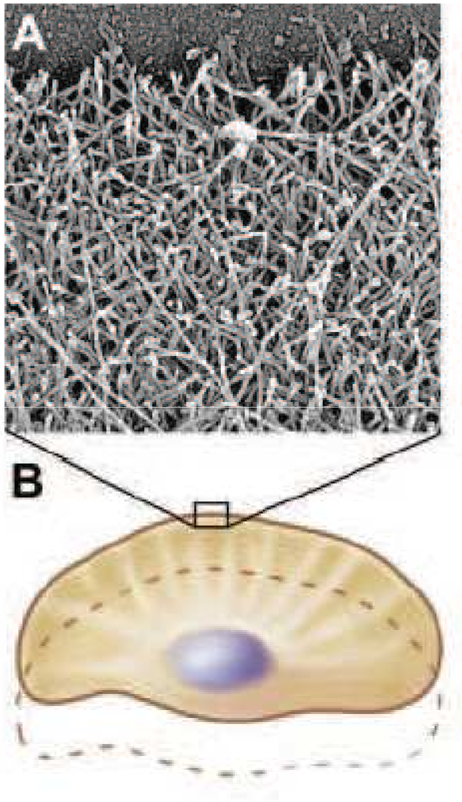


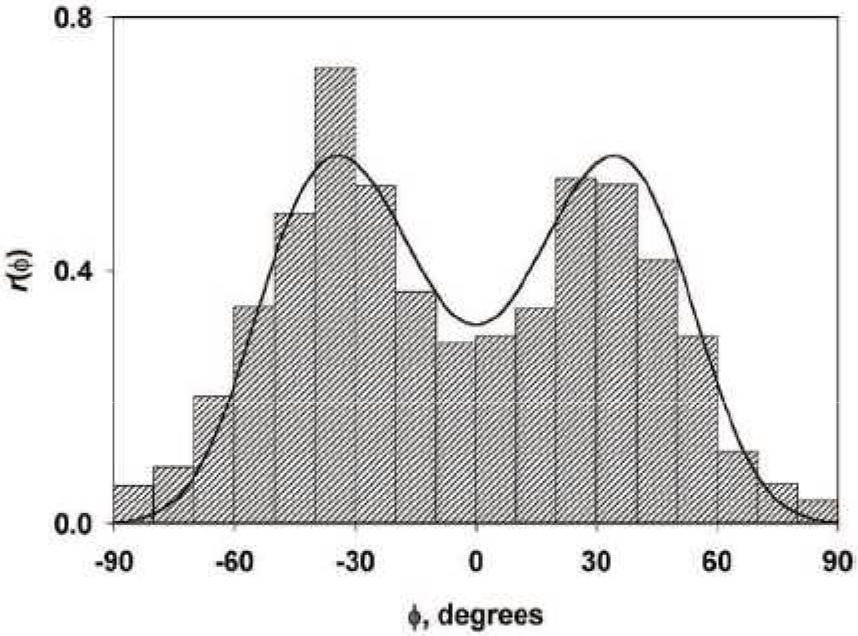


Trout keratocytes, M. Prass et al., J. Cell Biol. (2006)

Growth velocity rather insensitive to opposing force, up to a stall force.

Fact 2. Filament orientation

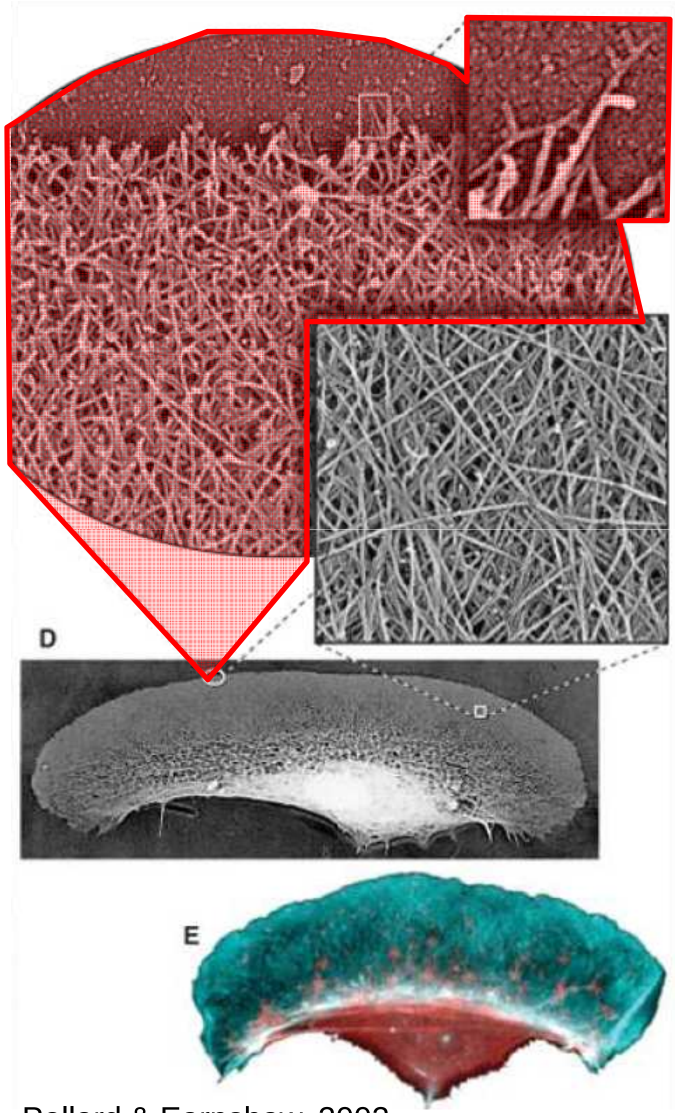




Maly and Borisy (2001)

Actin filaments symmetrically oriented with respect to the protrusion direction.

A mechanical model for the active layer at the leading edge (2d horizontal slice)

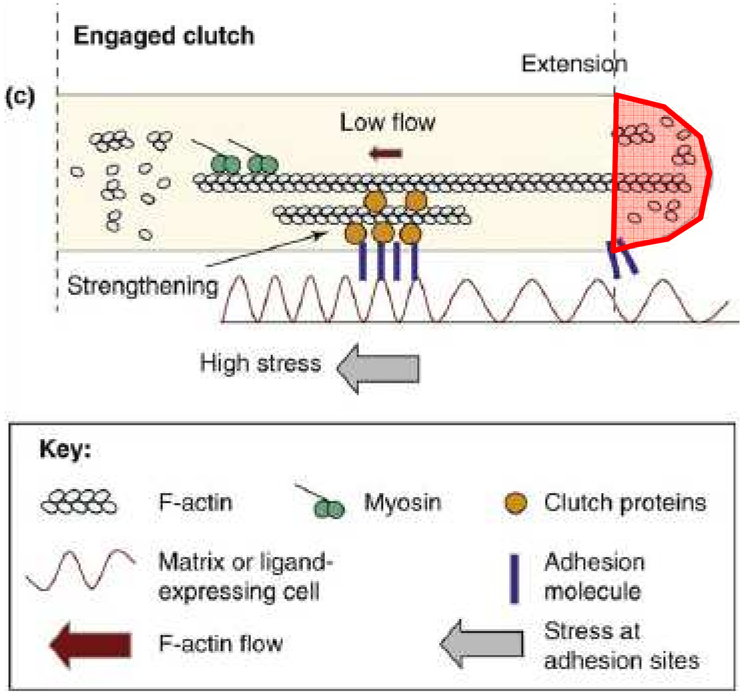


Pollard & Earnshaw, 2002

An “active” layer of growing actin network between

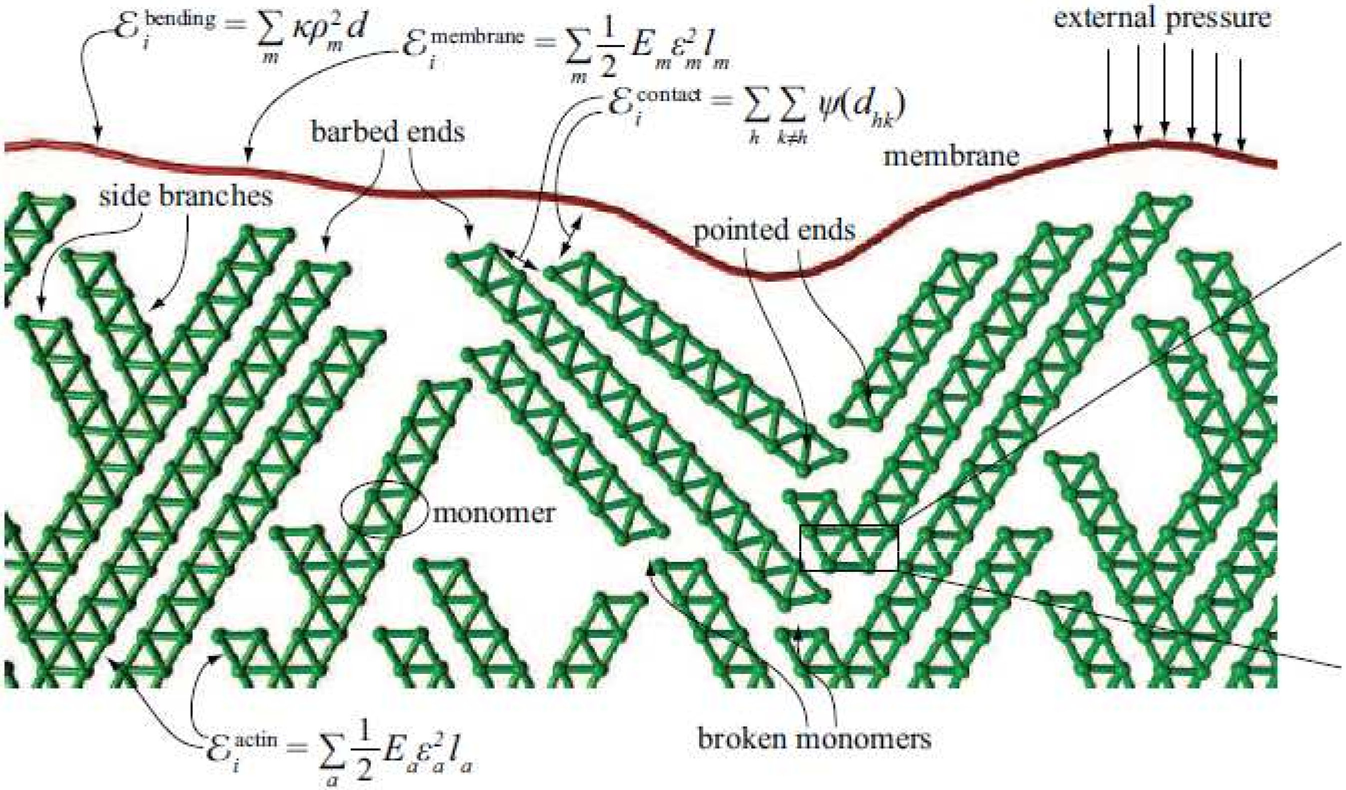
the plasma membrane (above)

and the previously grown, immobilized network (entanglements, crosslinks, and adhesion to substrate mediated by moleular clutches, below)



Molecular clutch, Giannone et al., 2009

The model. 1: growth and branching events



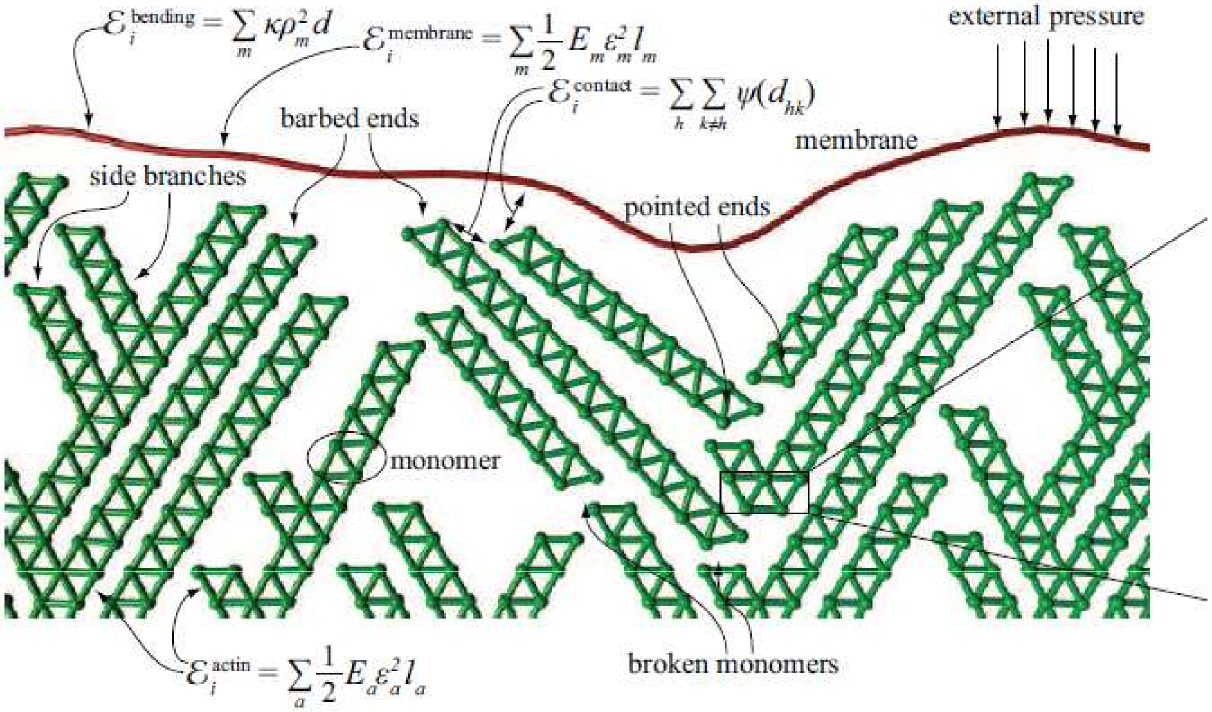
Starting from a set of fixed "seeds", at each time step *i* a random filament grows at its barbed end, and a branch originates at a random location with probability *Pb.* (growth and branching)

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



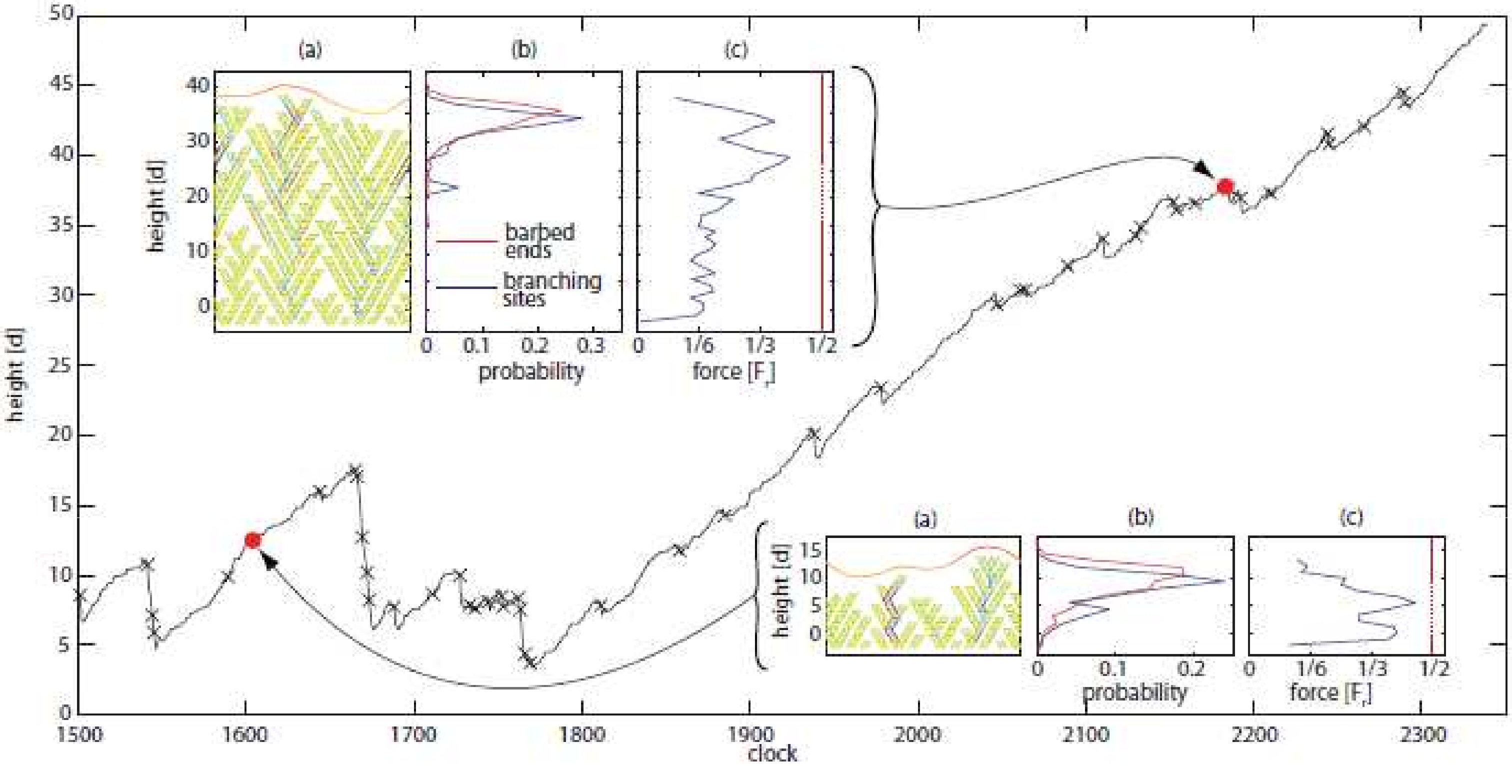
Stresses are computed by minimizing total elastic energy at each growth step

$$\mathscr{E}_i^{\text{actin}} = \sum_a \frac{1}{2} E_a \varepsilon_a^2 l_a, \quad \mathscr{E}_i^{\text{membrane}} = \sum_m \frac{1}{2} E_m \varepsilon_m^2 l_m, \quad \mathscr{E}_i^{\text{bending}} = \sum_m \kappa \rho_m^2 d, \quad \mathscr{E}_i^{\text{contact}} = \sum_h \sum_{k \neq h} \psi(d_{hk}).$$

$$\mathscr{E}_i = \mathscr{E}_i^{\text{actin}} + \mathscr{E}_i^{\text{membrane}} + \mathscr{E}_i^{\text{bending}} + \mathscr{E}_i^{\text{contact}} - \mathscr{L}_i^{\text{ext}}, \quad \{u^{eq}\}_i = \underset{\{u\}_i}{\operatorname{argmin}} \mathscr{E}_i(\{u\}_i).$$

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



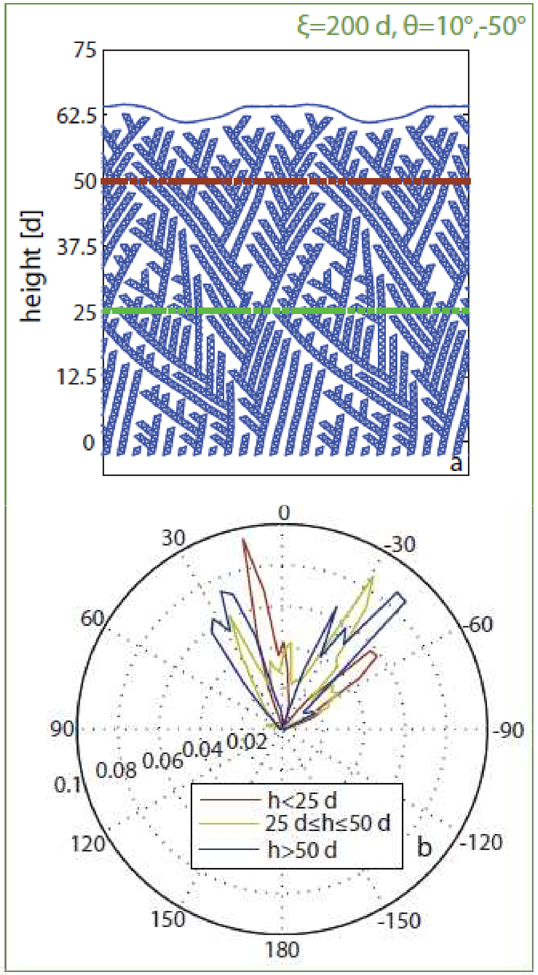
ActinMovie.mov

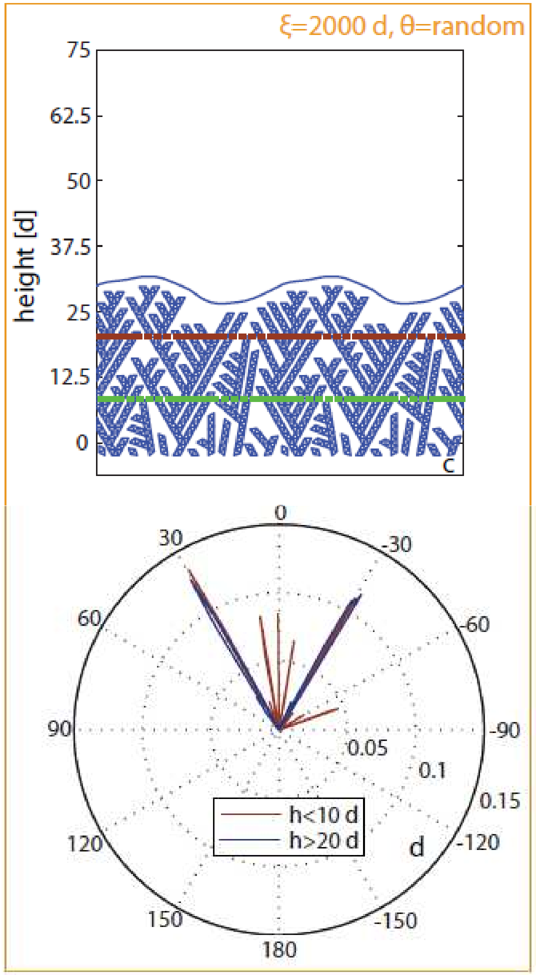
Growth periods alternate with retractions (avalanches of local rupture events).

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 ?)

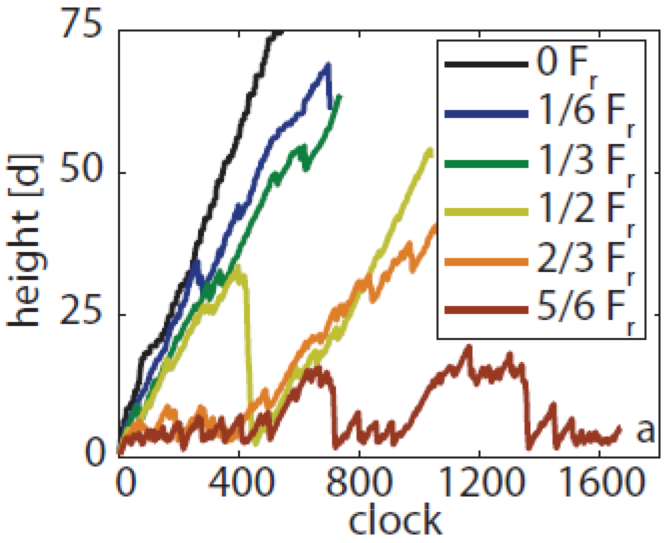


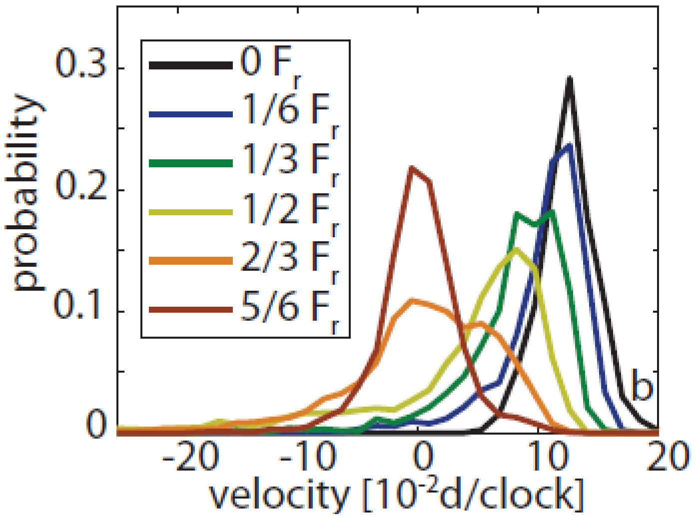


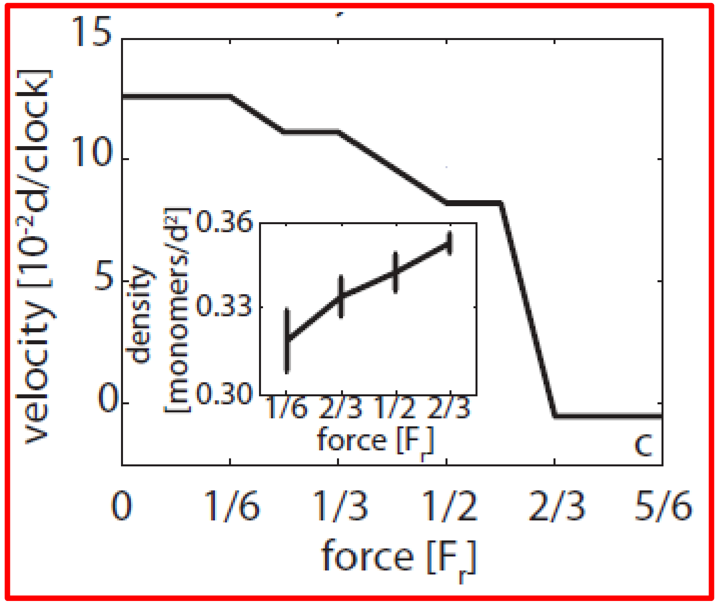
Flexible filaments: large deformations
(elastic deflections compensate misalignment)

Stiff filaments: selection
(cleavage of misoriented filaments)

Force vs growth Velocity



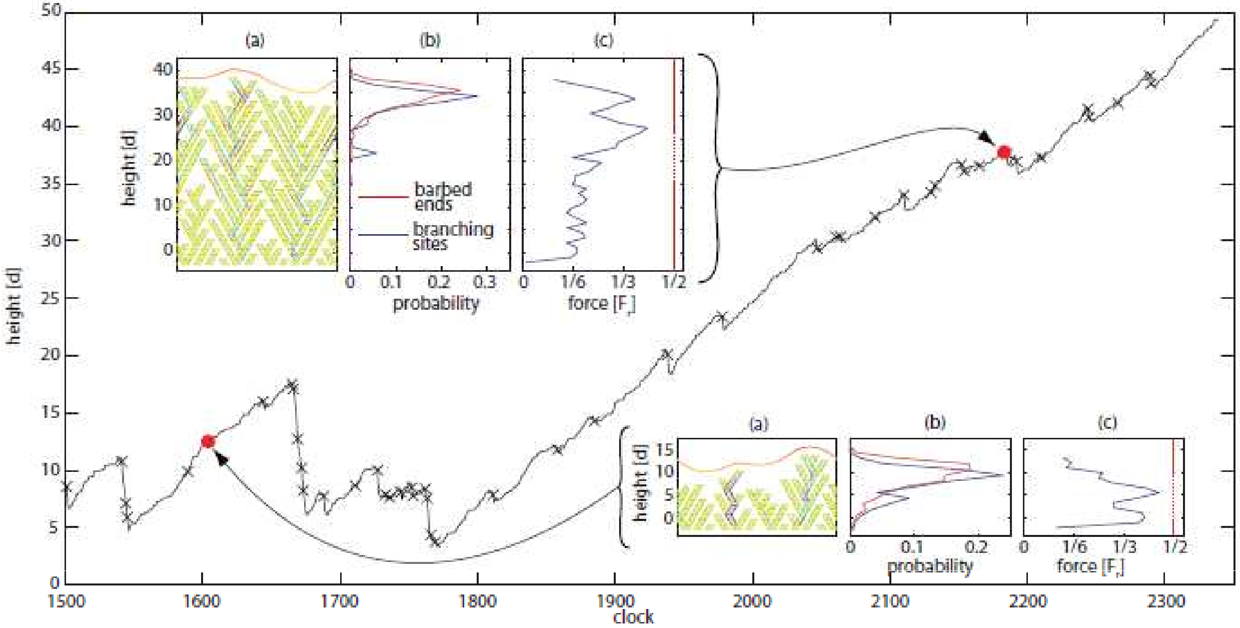




Growth velocity depends only weakly on the opposing force, up to stall force when growth becomes impossible

Growth against higher values
of opposing force requires higher density of actin monomers

Mechanical self-organization: summary



L. Cardamone et al.: Proceedings of the National Academy of Sciences, **108**: 13978–13983 (2011)

- 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

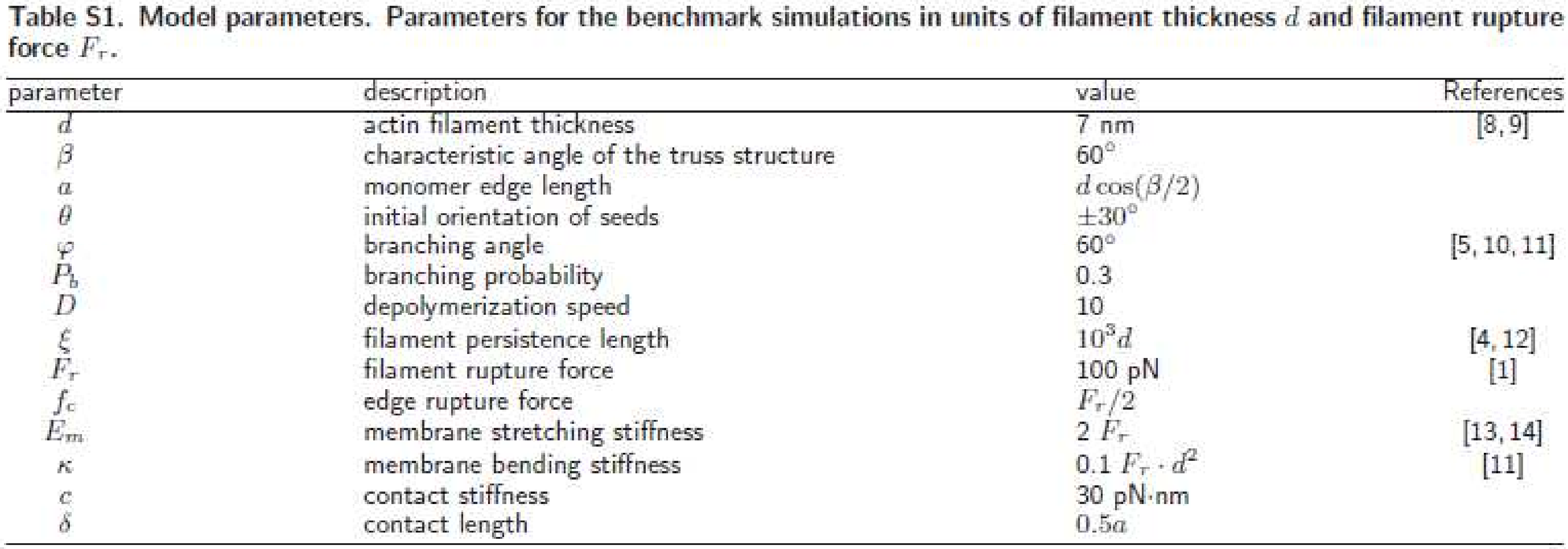


Table S1. Model parameters. Parameters for the benchmark simulations in units of filament thickness d and filament rupture force F_r.

parameter	description	value	References
d	actin filament thickness	7 nm	[8, 9]
β	characteristic angle of the truss structure	60°	
a	monomer edge length	$d\cos(\beta/2)$	
θ	initial orientation of seeds	$\pm 30^\circ$	
φ	branching angle	60°	[5, 10, 11]
P_b	branching probability	0.3	
D	depolymerization speed	10	
ξ	filament persistence length	$10^3 d$	[4, 12]
F_r	filament rupture force	100 pN	[1]
f_c	edge rupture force	$F_r/2$	
E_m	membrane stretching stiffness	$2\ F_r$	[13, 14]
κ	membrane bending stiffness	$0.1\ F_r \cdot d^2$	[11]
c	contact stiffness	30 pN·nm	
δ	contact length	$0.5a$	

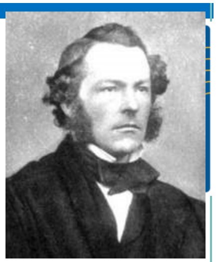
$d = 7$ nm

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



$$\rho\left(\frac{\partial v}{\partial t} + (v\cdot\nabla)v\right) = -\nabla p + \eta\Delta v$$
$$\mathrm{div}\ v = 0$$

Navier-Stokes

Non-dimensionalization

$$x_* = \frac{x}{L}\ ,\ t_* = \frac{t}{T}\ ,\ p_* = \frac{p}{V\eta}\ ,\ u_* = \frac{\mathrm{v}}{V}$$

$$\left[\begin{array}{l} \boxed{\sigma Re\frac{\partial u_*}{\partial t_*} + Re(u_*\cdot\nabla_*)u_*} - \Delta_* u_* + \nabla_* p_* = 0, \\ \mathrm{div}_* u_* = 0 \end{array}\right.$$

$$\boxed{\mathrm{Re} = \frac{VL\rho}{\eta}} \ \text{and}\ \ \sigma = \frac{\mathrm{L}}{\mathrm{VT}}$$

$$-\eta\Delta v + \nabla p = 0$$
$$\mathrm{div}\ v = 0$$

Stokes

All inertial effects neglected, formal limit.

Reynolds Number (Re)

$$\mathrm{Re} = \frac{VL\rho}{\eta}$$

Velocity (typical order of magnitude)	V
Diameter (typical length scale)	L
Mass density of the fluid	ρ
Viscosity of the fluid	η

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

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

Orders of magnitude for swimmers:

Men, tuna, sharks:	$L=1m$, $V=1\text{-}10\ ms^{-1}$	$Re=10^6\text{-}10^7$
Bacteria:	$L=1x10^{-6}m$, $V=1\text{-}10x10^{-6}\ ms^{-1}$	$Re=10^{-6}\text{-}10^{-5}$

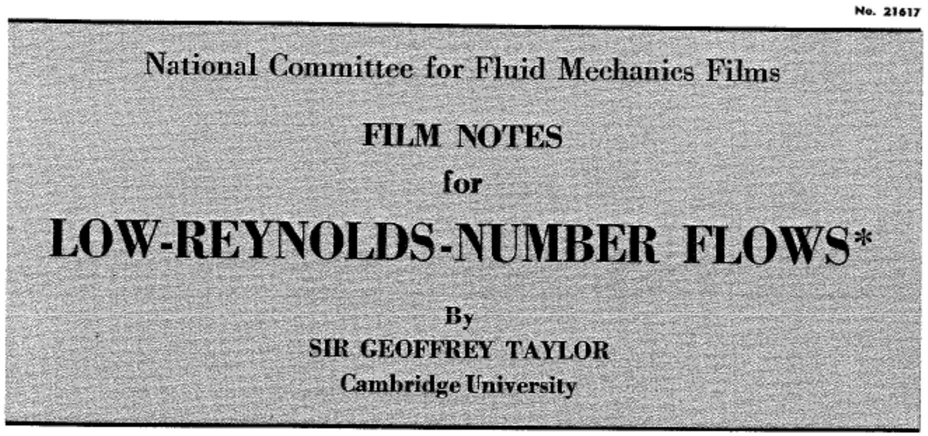
G.I Taylor and low Re flows

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



No. 21617

National Committee for Fluid Mechanics Films

FILM NOTES
for
LOW-REYNOLDS-NUMBER FLOWS*

By
SIR GEOFFREY TAYLOR
Cambridge University

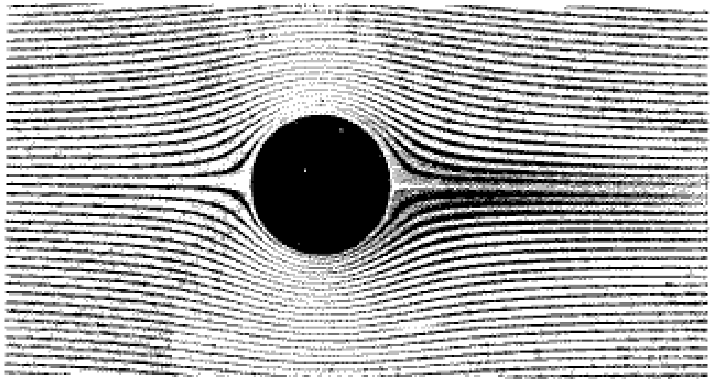
Modern classical physics through the work of G.I. Taylor:

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

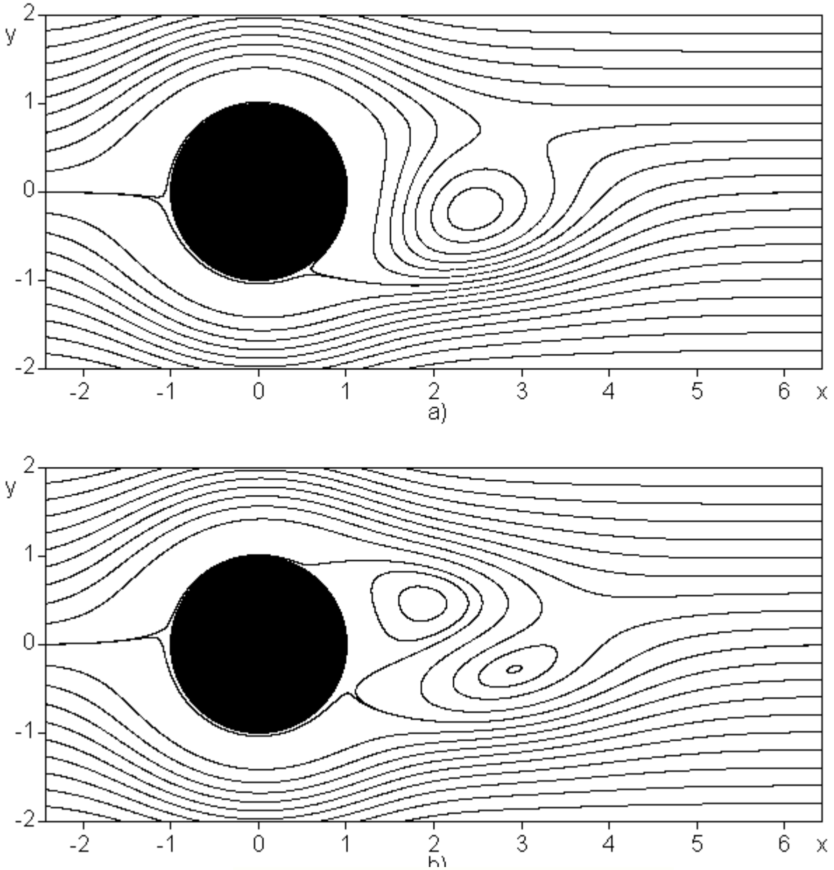
http://www.deas.harvard.edu/brenner/taylor/physic_today/taylor.htm

Flow past a sphere (Stokes formula)

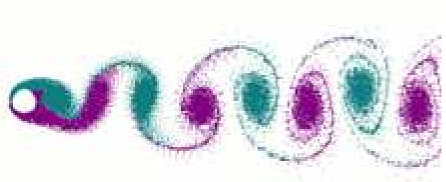
Re = 0



Re > 250



Drag = 6 π μ R V (Stokes, 1851)

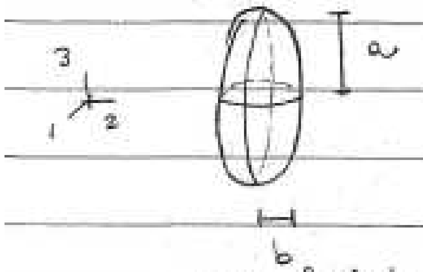


Resistance matrix for ellipsoidal shapes

The resistance matrix K shares the symmetries of Ω: if Ω is symmetric, then the e-vectors of K are along the axes of symmetry

sphere $$K = 6\pi L\mu\, I = 6\pi L\mu \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

prolate ellipsoid of revolution



$a>b$, finite b

$$K = 6\pi b\mu \begin{bmatrix} \xi_b & 0 & 0 \\ 0 & \xi_b & 0 \\ 0 & 0 & \xi_a \end{bmatrix},$$

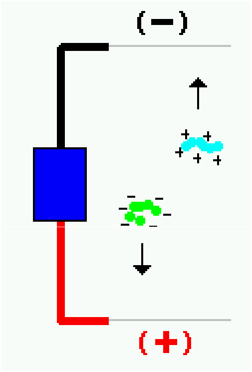
$\frac{a}{b}=1 \qquad a\to\infty$

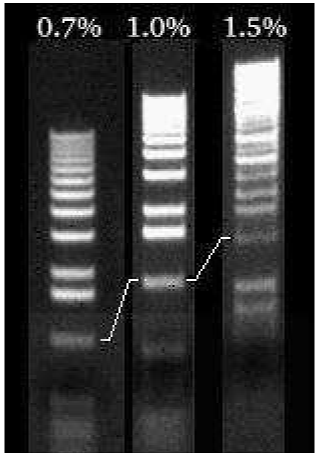
$\downarrow$

$\xi_b \in (1, +\infty)$

$\frac{\xi_a}{\xi_b} \in (1, 1/2)$

Gel electrophoresis of DNA and RNA

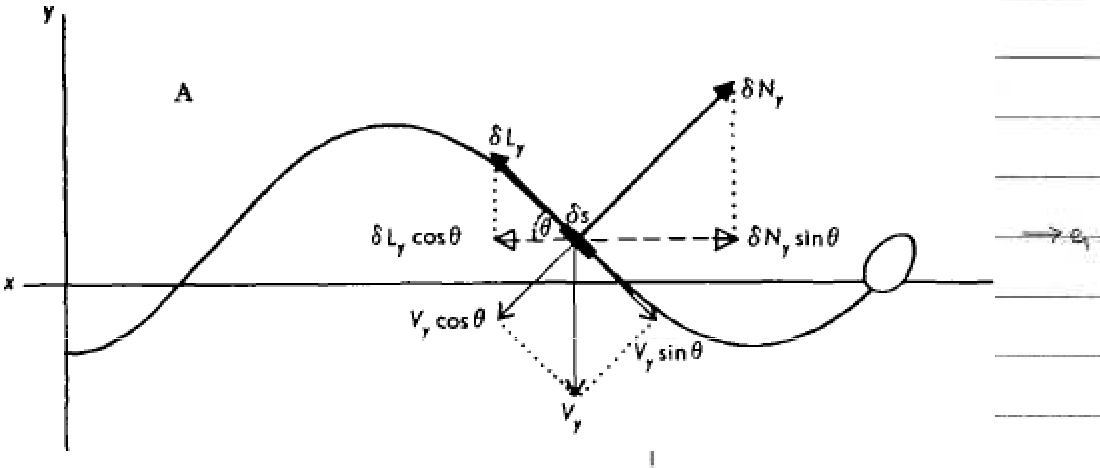




Viscous drag on a filament

Apply result that $\frac{\xi_a}{\xi_b} \to \frac{1}{2}$ if $\frac{a}{b} \to \infty$ to the case of finite a and b → 0

∞-ly thin cylinder, $\xi^{\parallel} = \frac{1}{2}\xi^{\perp} < \xi^{\perp}$, falling at 45° from axis



Since $\xi^{\parallel} < \xi^{\perp}$, F has a net positive component along e

If motion along the vertical is prescribed, get a propulsive component along e_1

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

Then

$$\xi^{\parallel} V^{\parallel} = \xi^{\perp} V^{\perp} \Rightarrow V_{\parallel} = \underbrace{\frac{\xi^{\perp}}{\xi^{\parallel}}}_{>1} V^{\perp} > V^{\perp}$$

and the object will slide laterally towards e_1

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)

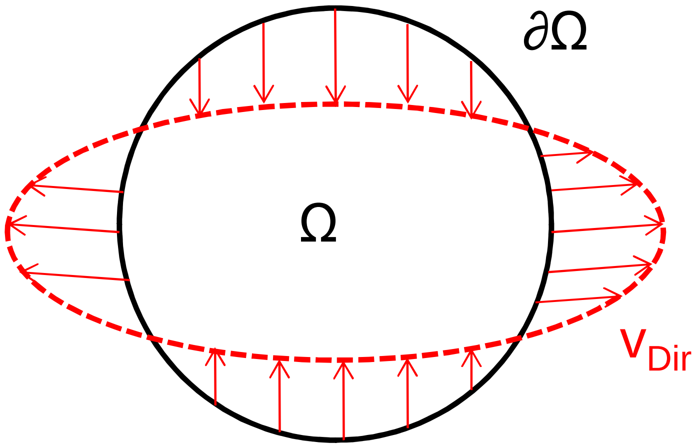
2.

How does the swimmer move in repsonse 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 Ω by its shape changes:



$$
\begin{aligned}
-\eta\Delta u + \nabla p = 0 \quad & \text{on } \mathbb{R}^3 \setminus \Omega, \\
\operatorname{div}(u) = 0 \quad & \text{on } \mathbb{R}^3 \setminus \Omega,
\end{aligned}
$$

$u = v_{Dir}$ on ∂Ω

$$u \to 0 \quad \text{at infinity.}$$

$\sigma n = DN_{\Omega}[v_{Dir}]$ viscous “reactive” force p.u. area on ∂Ω

Equation of motion = Self-propulsion

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

Equations of motion:

$$m\ (x_c)_{,tt} = F_{tot}$$

$$0 = F_{tot}$$ neglecting swimmer’s inertia

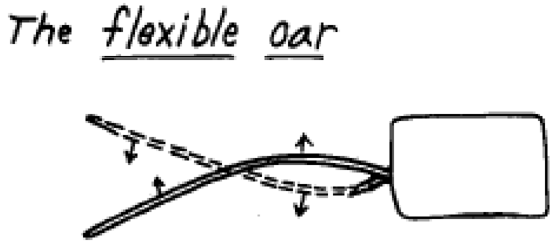
$$0 = F_{ext} + F_{visc}$$

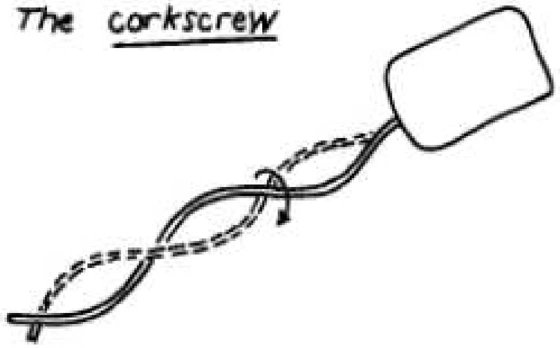
$$0 = F_{visc}$$ self-propulsion

Similarly, total viscous torque = 0 .

Life at low Reynolds numbers

GITaylorSwimmers.mpeg





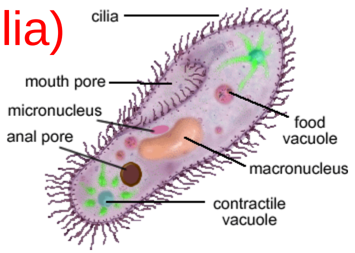
in a flow regime obeying Stokes equations, a scallop cannot advance through the reciprocal motion of its valves

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

(eukariotic flagella)

(cilia)



H. Berg, 1973

(bacterial flagella)

Lecture 5: the 3-sphere swimmer

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

- F. Alouges, ADS, A. Lefebvre: Optimal strokes of low Reynolds number swimmers: an example. Journal of Nonlinear Science **18**, 277-302 (2008).
- F. Alouges, ADS, A. Lefebvre: Biological fluid dynamics. Springer Encyclopedia of Complexity and Systems Science (2009).
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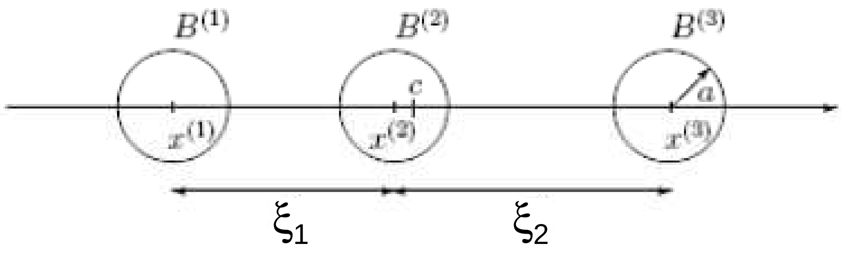
- F. Alouges, ADS, L. Heltai: Numerical strategies for stroke optimization at low Re numbers. M3AS **21**, 361-397 (2011).

Mathematical swimming in a nutshell



$$\xi_1 = x^{(2)} - x^{(1)}$$
$$\xi_2 = x^{(3)} - x^{(2)}$$

shape

$$c = \tfrac{1}{3}\sum_{i=1}^{3} x^{(i)}$$

position

Swimming is .....

$\xi_1(t)$, $\xi_2(t)$ periodic of period T

executing cyclic shape changes

producing

$$\Delta c = \int_0^T \dot{c}\,dt \neq 0$$

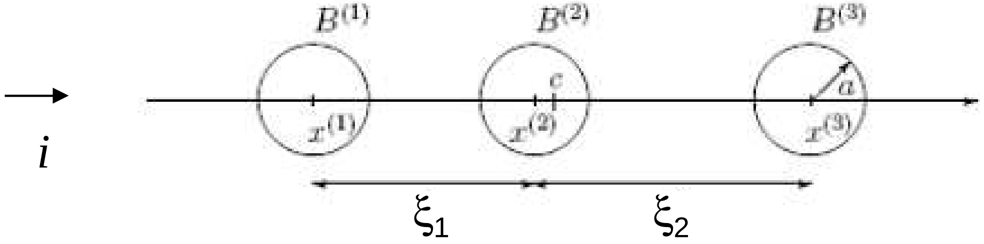
net positional change after one period

under

$f^{(1)} + f^{(2)} + f^{(3)} = 0$

no external force (self-propulsion)

Positional change from shape change (axisym.)



v_{Dir} Dirichlet data on $\partial\Omega$

$DN_\xi[v_{Dir}] = \sigma\, n$ surface force on $\partial\Omega$

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

$$= \varphi_1(\xi,\cancel{c})\,\dot{\xi}_1 + \varphi_2(\xi,\cancel{c})\,\dot{\xi}_2 + \underset{\neq 0}{\underline{\varphi_3(\xi,\cancel{c})}}\,\dot{c}$$

by transl. inv.

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

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

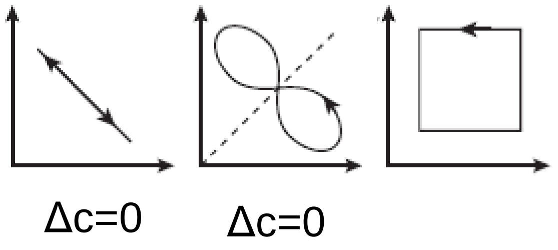
nonlinear dep. on ξ !

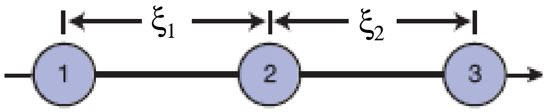
$$V_i(\xi) = -\varphi_i(\xi)/\varphi_{n+1}(\xi)$$

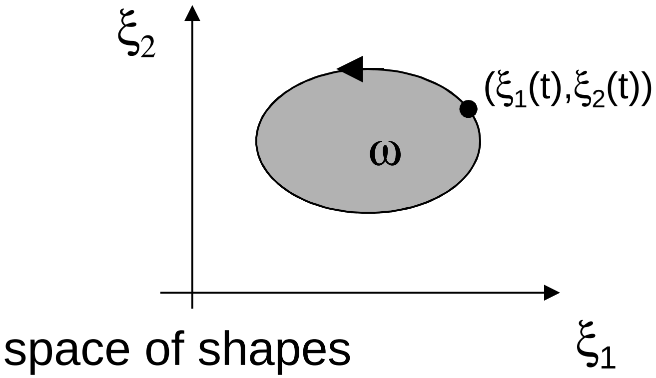
Swimming with one formula

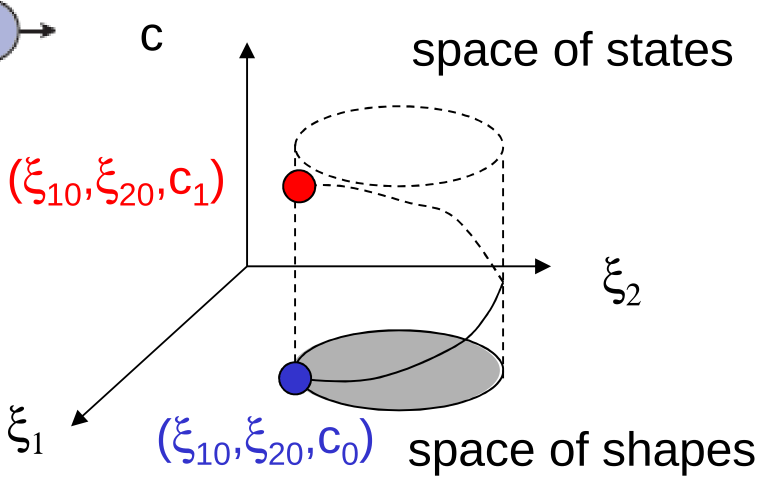
$$\Delta c = \int_0^T \dot{c}\, dt = \int_0^T \left(V_1 \frac{d\xi_1}{dt} + V_2 \frac{d\xi_2}{dt}\right) dt = \int_\omega \operatorname{curl} V \, d\xi_1 d\xi_2$$

(notice that it's entirely geometric!)









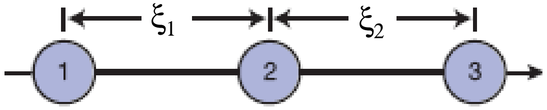
Swimming rests on the differential form $V_1 d\xi_1 + V_2 d\xi_2$ not being exact

$V(\xi)$ 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



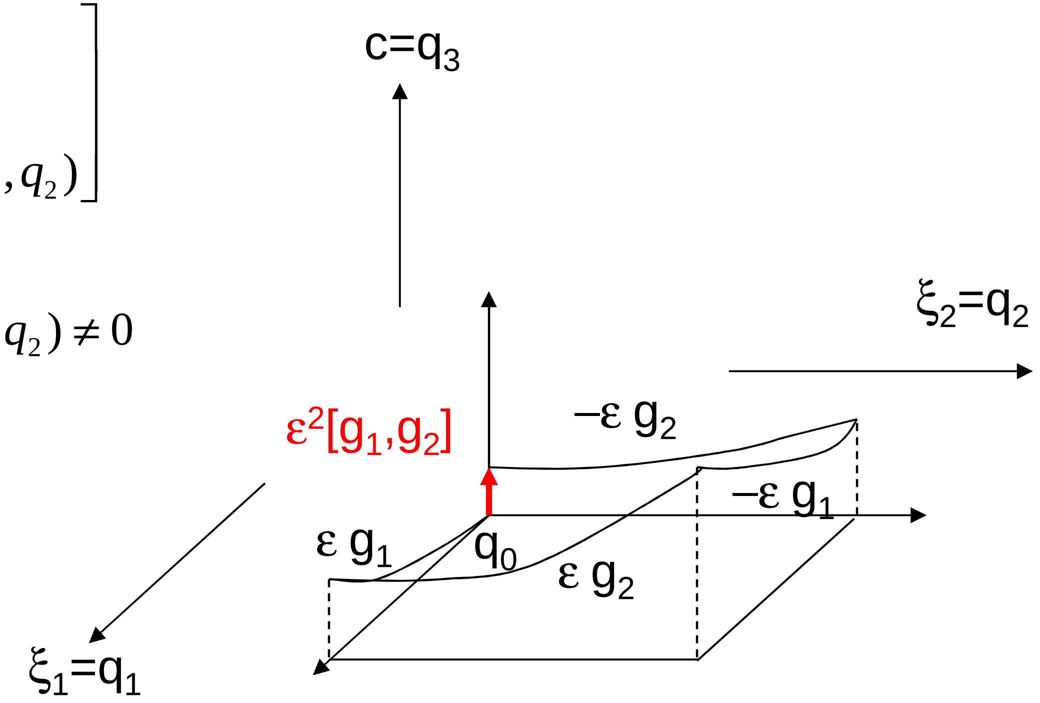
$$\begin{aligned}\dot{\xi}_1 &= u_1\\ \dot{\xi}_2 &= u_2\\ \dot{c} &= V_1(\xi)\,u_1 + V_2(\xi)\,u_2\end{aligned}$$

$$\dot{q} = \frac{d}{dt}\begin{bmatrix} q_1 := \xi_1 \\ q_2 := \xi_2 \\ q_3 := c \end{bmatrix} = \begin{bmatrix} 1 \\ 0 \\ V_1(q_1,q_2) \end{bmatrix} u_1 + \begin{bmatrix} 0 \\ 1 \\ V_2(q_1,q_2) \end{bmatrix} u_2 = \sum_{i=1}^{2} g_i(q)u_i$$

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

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

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



Swimming at max efficiency (geodesic strokes)

(strokes of max Lighthill efficiency)

Rescale to unit time interval. Minimize expended power

$$\int_0^1 \int_\Omega \sigma \, \mathrm{n} \bullet \mathrm{v} \, dt = \int_0^1 \int_{\partial\Omega} DN_\xi [\mathrm{v}_{\mathrm{Dir}}] \cdot \mathrm{v}_{\mathrm{Dir}} \, dA dt = \int_0^1 G(\xi) \dot{\xi} \cdot \dot{\xi} \, dt$$

stroke “length”

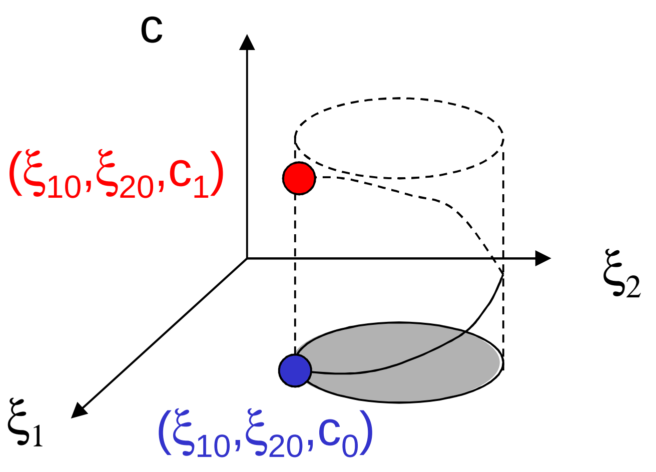
at given

$$\Delta c = \int_0^1 V(\xi) \cdot \dot{\xi} = \int_\omega \mathrm{curl}\, V(\xi) \, d\xi$$

enclosed area

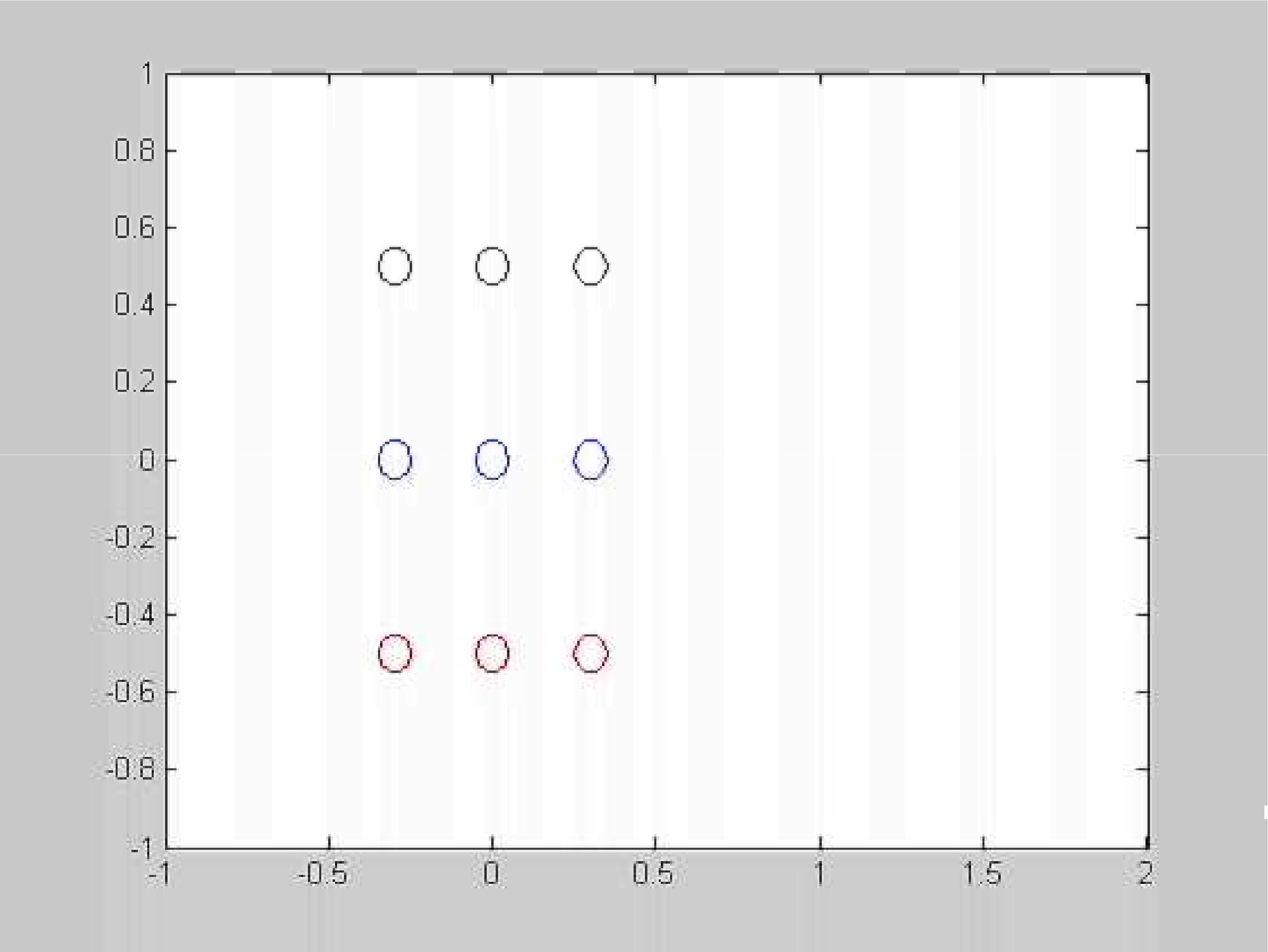
Euler-Lagrange eqn.

$$-\frac{d}{dt}(G\dot{\xi}) + \frac{1}{2} \begin{pmatrix} \partial_1 G\dot{\xi} \cdot \dot{\xi} \\ \partial_2 G\dot{\xi} \cdot \dot{\xi} \end{pmatrix} + \lambda \, \mathrm{curl} V(\xi) \, \dot{\xi}^{\perp} = 0$$



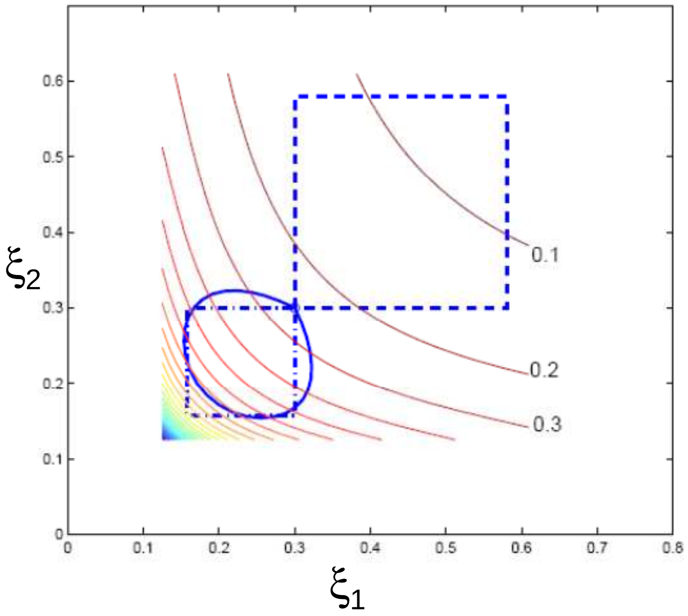
Optimal paths are sub-riemannian geodesics.
Optimal strokes exist.
They can be computed numerically.

Three sphere swimmers: a race

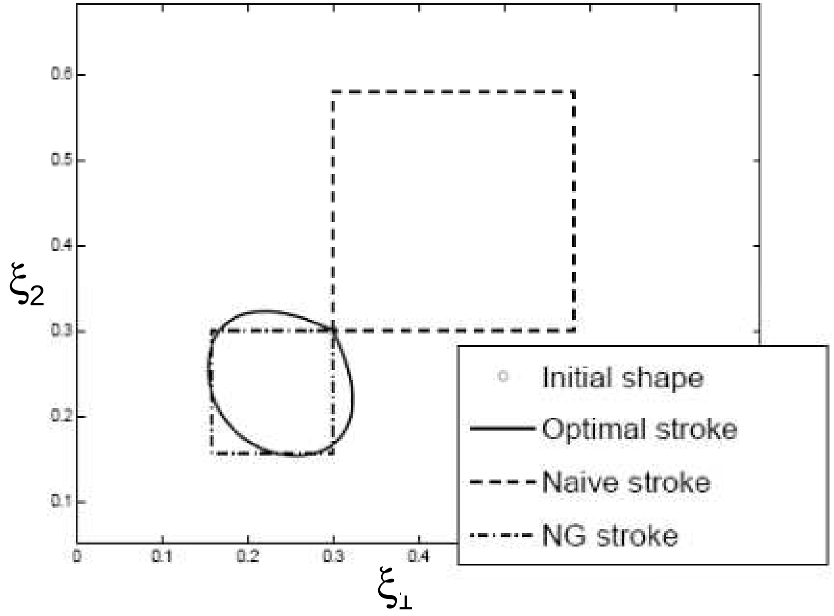


race

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 ?

Eutrep2.mov

Metaboly of Eutreptiella sp.

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

Lecture 6: the infinite-dimensional case

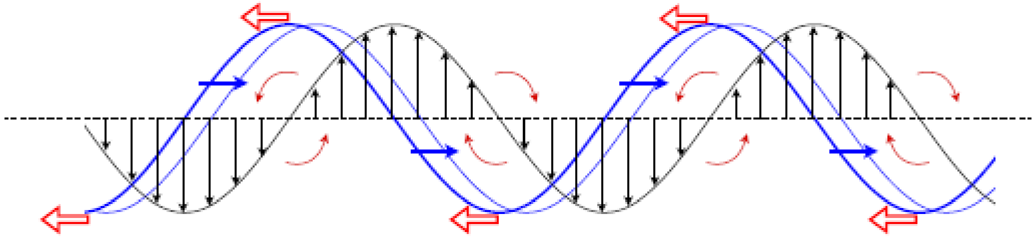
G.I. Taylor:
Analysis of the swimming of microscopic organisms,
Proc. Roy. Soc. A **209**, 447- 461 (1951).

G. Gray and G.J. Hancock:
The propulsion of sea-urchin spermatozoa,
J. Exp. Biol. **32**, 802- 814 (1955).

G. Dal Maso, ADS, M. Morandotti: An existence and uniqueness result for the self-propelled motion of micro-swimmers, SIAM J. Math Analysis **43**, 1345-1368 (2011).

Taylor's swimming sheet

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



Wave vector: $k\,\mathbf{e}_x$

Wave speed: ω / 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.

Solving the outer Stokes problem:

$$\mathbf{U} = -\frac{1}{2}\omega \mathbf{k} b^2.$$

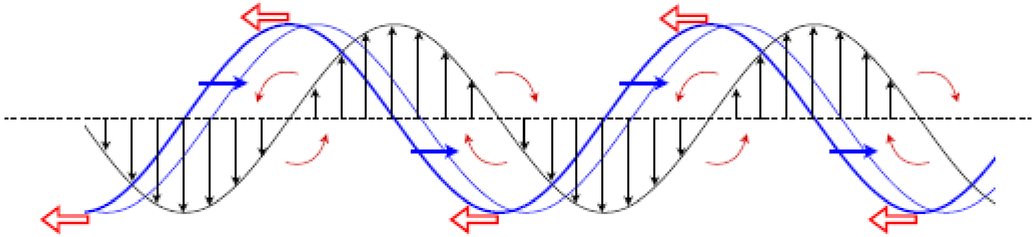
Wave travels to the right

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

Longitudinal (stretching) wave:
sheet moves to the right
(see Ezio's talk on Monday)

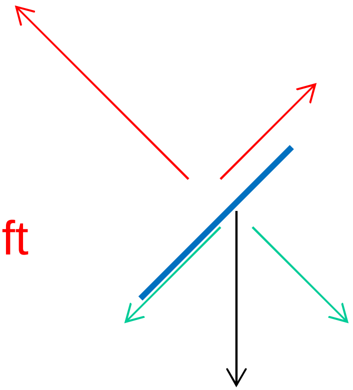
Swimming direction from drag anisotropy (heuristics)

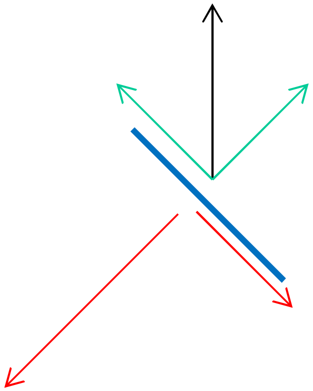
$$h = b\sin(kx - \omega t),$$



Since $\xi_{\perp} > \xi_{||}$

net force towards left



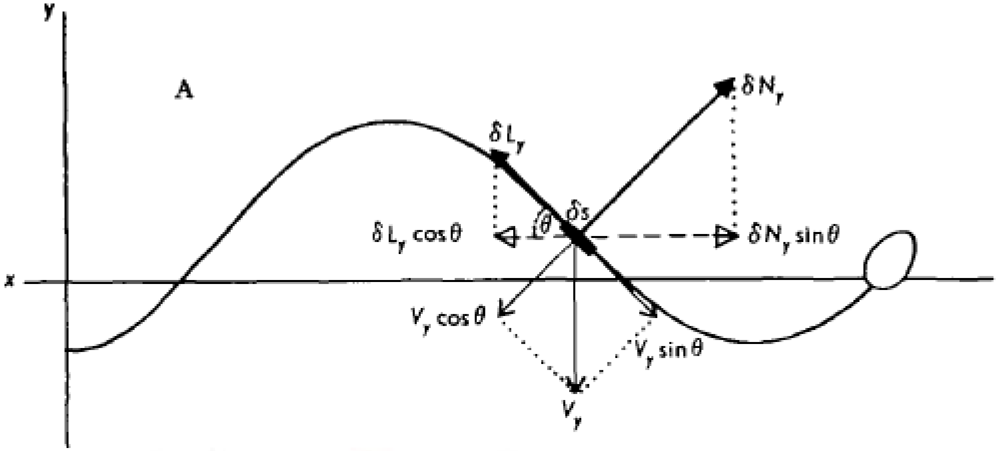


Wave travels to the right

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

If the sheet is blocked:
the sheet pumps fluid towards right

Gray-Hancock beating flagellum



$$h(x,t) = b\sin(kx - \omega t).$$

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

$$\mathbf{f} = -\xi_{\|}\mathbf{u}_{\|} - \xi_{\perp}\mathbf{u}_{\perp},$$

Eq. of motion:

$$\mathbf{F}_{head} + \int \mathbf{f} = \mathbf{0}$$

Solve for the unknown swimming velocity:

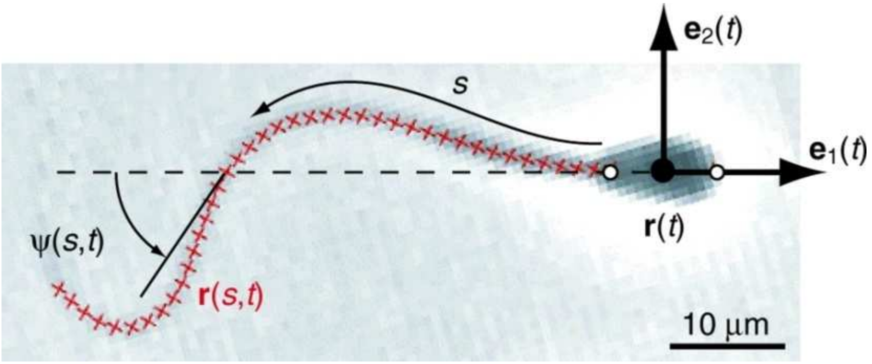
$$U = \frac{(\xi_{\perp} - \xi_{\|})\int_0^L \dot{h}h'\,\mathrm{d}x}{\xi_{\|}L + \xi_0 a}.$$

Average over one period of oscillation:

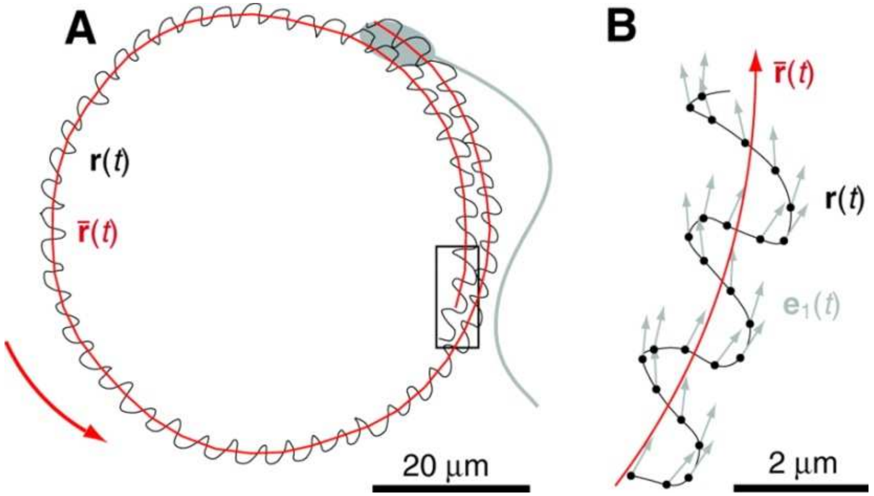
$$\langle U \rangle = -\frac{\xi_{\perp} - \xi_{\|}}{2\xi_{\|}}\frac{\omega k b^2}{1 + (\xi_0 a)/(\xi_{\|}L)}.$$

Remark: get back Taylor’s formula with $L >> a$ (head radius) and $\xi_{\perp} = 2\,\xi_{\|}$ (??)

Resistive force theory works surprisingly well



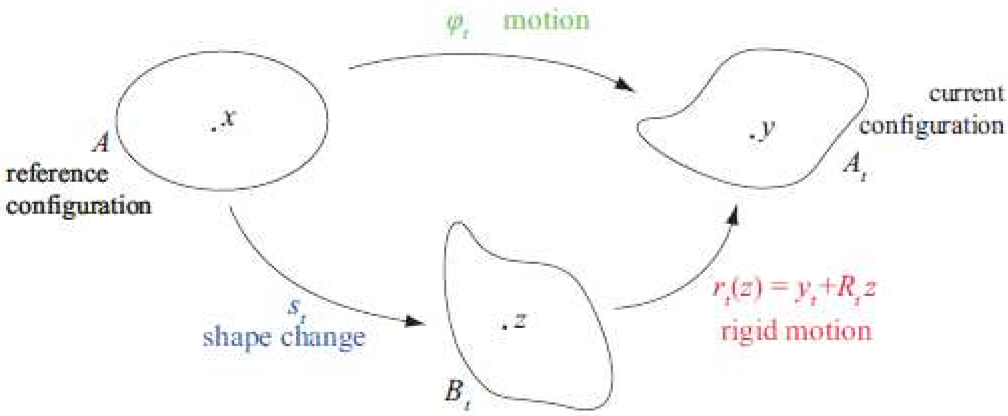
$$\xi_\perp = 1.8\,\xi_{||}$$



BullSpermCell.mov

B.M. Friedrich et al., High precision tracking of sperm swimming fine structure provides strong test of resistive force theory. J. Exp. Biol. 213, 1226-1234 (2010).

Generic swimming blob



$$\varphi_t = \underbrace{r_t}_{\text{unknowns}} \circ \underbrace{s_t}_{\text{data}}$$

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

$$\begin{bmatrix} F_t^{\mathrm{visc}} \\ M_t^{\mathrm{visc}} \end{bmatrix} = -\begin{bmatrix} K_t & C_t^{\top} \\ C_t & J_t \end{bmatrix} \begin{bmatrix} R_t^{\top} & 0 \\ 0 & R_t^{\top} \end{bmatrix} \begin{bmatrix} \dot{y}_t \\ \omega_t \end{bmatrix} + \begin{bmatrix} F_t^{\mathrm{shape}} \\ M_t^{\mathrm{shape}} \end{bmatrix}$$

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

Velocity at points of swimmer:

$$V_t^{\mathrm{rigid}}[\dot{y}_t\,, \omega_t] + V_t^{\mathrm{shape}}[\dot{s}_t \circ s_t^{-1}],$$

Polar Decompostition

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

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)

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