Continuum mechanics and thermodynamics of living matter

Jocelyn Étienne and Pierre Recho
LIPHY, CNRS – Univ Grenoble Alpes

E.D. Physique
Univ Grenoble Alpes
2025

Overview of the course

I. Today, room A120 – Introduction: active stresses in living systems. Discussion of length scales. Define the scope of the course: give a framework that is thermodynamically sound on how to include these active stresses in mechanical models (but not on their origin) and provide examples of the complex behaviours that can result. Thermodynamics of molecular motors. *(Jocelyn Etienne)*

II. Thu 13/2, room **A103** – Fundamental balance laws: kinematics - mass balance - force balance - energy balance - entropy production *(Pierre Recho)*

III. Thu 20/2, room A120 – Thermodynamics: Entropy production, close-to-equilibrium dynamics, Onsager approach. Dynamical equations / limiting behaviours *(Pierre Recho)*

IV. Thu 27/2, room A120 – Microstructure: Derivation of a constitutive equation from the dynamics of the microstructure. *(Jocelyn Etienne)*

(no course on 6/3 – university break)

V. Thu 13/3, room A120 – Motility: initiation of self-propulsion by interaction with a substrate. *(Pierre Recho)*

VI. Thu 20/3, room **A119** – Complements and conclusions. *(either or both)*

This course: an introduction

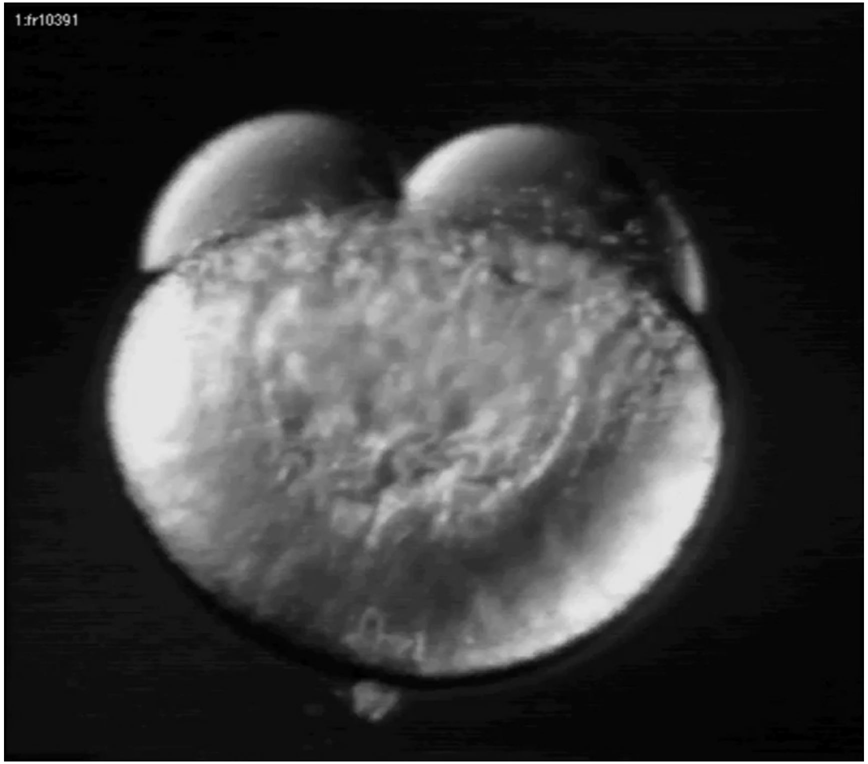
1) Some morphogenetic transformations
2) Morphoelasticity
3) Spatial structure
4) Cellularised tissue
5) Biopolymer networks
6) Molecular motors

In a large part based on Erlich et al, *Interface Focus*, 2022.

1. Some morphogenetic transformations

Seemingly Forever Timelapse
21.4K subscribers

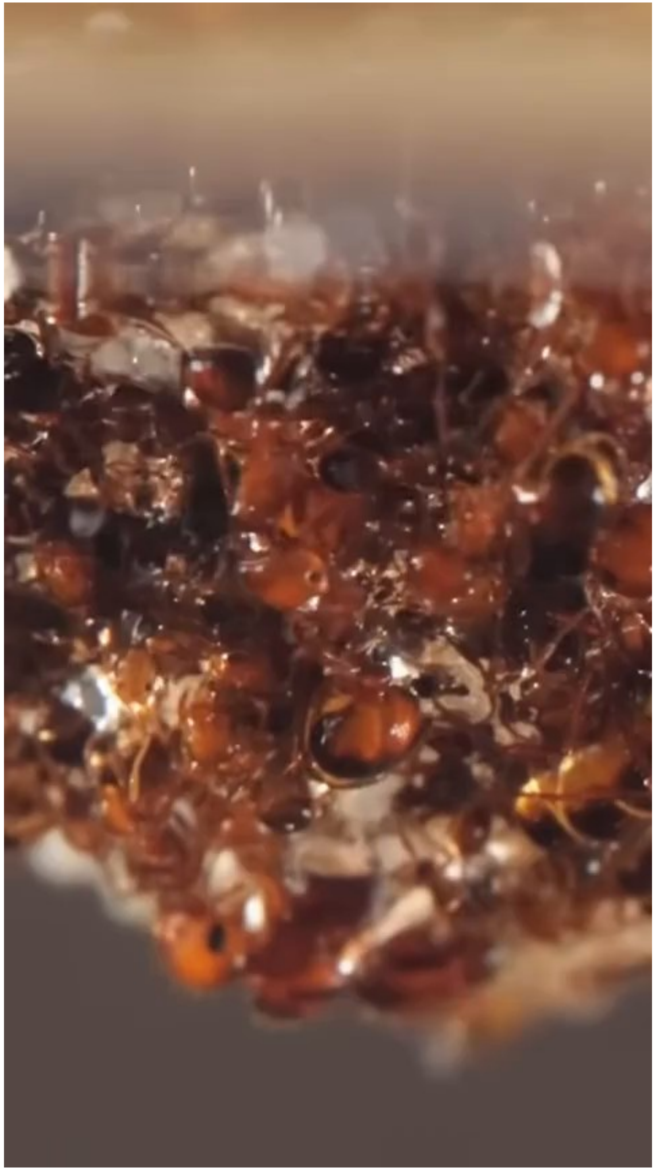
Living matter undergoes morphogenetic transformations

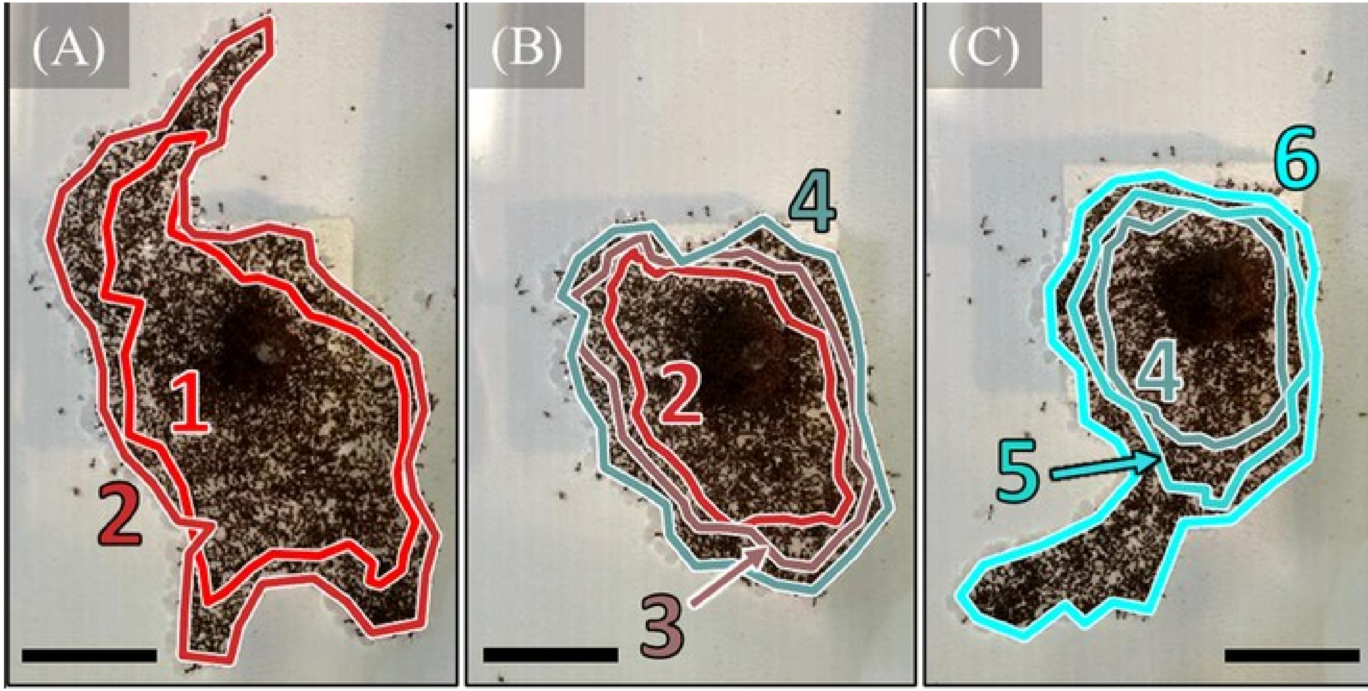


Zebrafish development

The Company of Biologists

4.68K subscribers

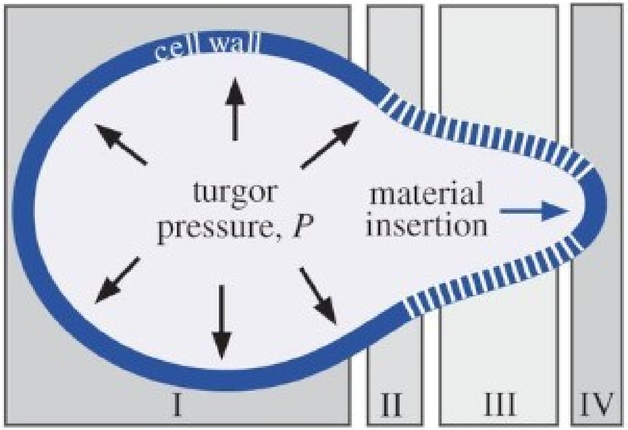




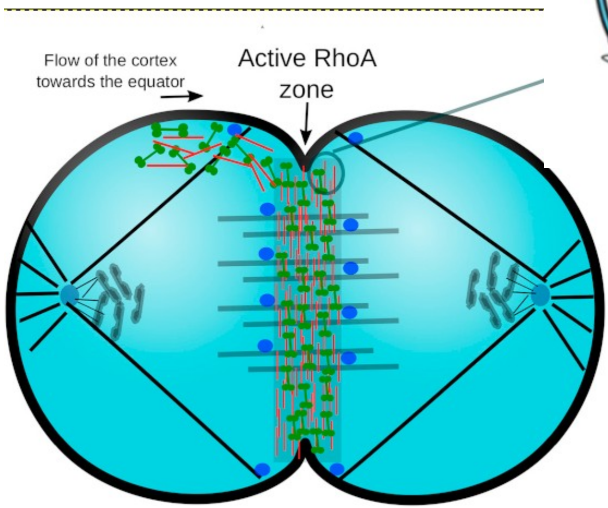
Fire-ants raft

Wagner and Vernerey,
PLOS Comput Biol, 2022

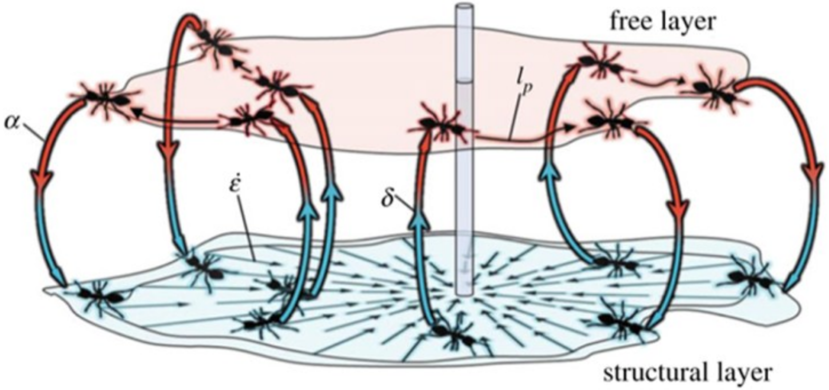
Many microscopic mechanisms, can there be some common mechanics?



Yeast (& plants) tip-growth
Goldenbogen et al, *Open Biol*, 2016



Animal cell division
Schwayer et al, *Dev Cell* 2016



Fire-ants raft
Wagner and Vernerey,
PLOS Comput Biol, 2022

2. Morphoelasticity

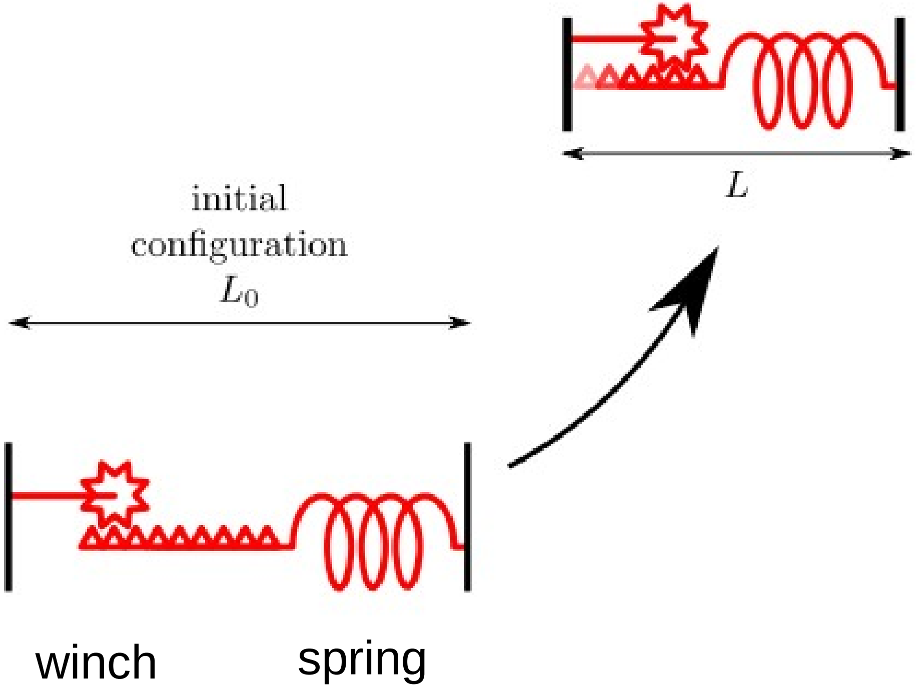
Epstein M. 2012 *The elements of continuum biomechanics*. Chichester, UK: John Wiley & Sons Ltd.

Lubarda VA. 2004 Constitutive theories based on the multiplicative decomposition of deformation gradient: thermoelasticity, elastoplasticity, and biomechanics. *Appl. Mech. Rev.* **57**, 95–108. (doi:10.1115/1.1591000)

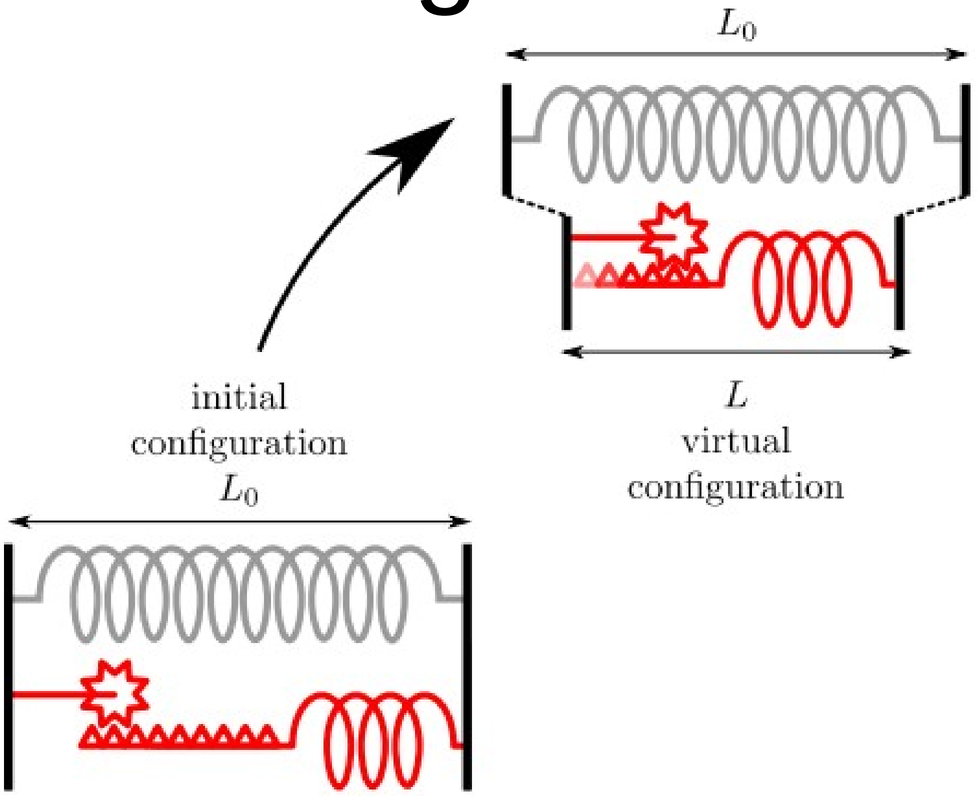
Rodriguez EK, Hoger A, McCulloch AD. 1994 Stress-dependent finite growth in soft elastic tissues. *J. Biomech.* **27**, 455–467. (doi:10.1016/0021-9290(94)90021-3)

Goriely A. 2017 *The mathematics and mechanics of biological growth*, vol. 45. New York, NY: Springer.

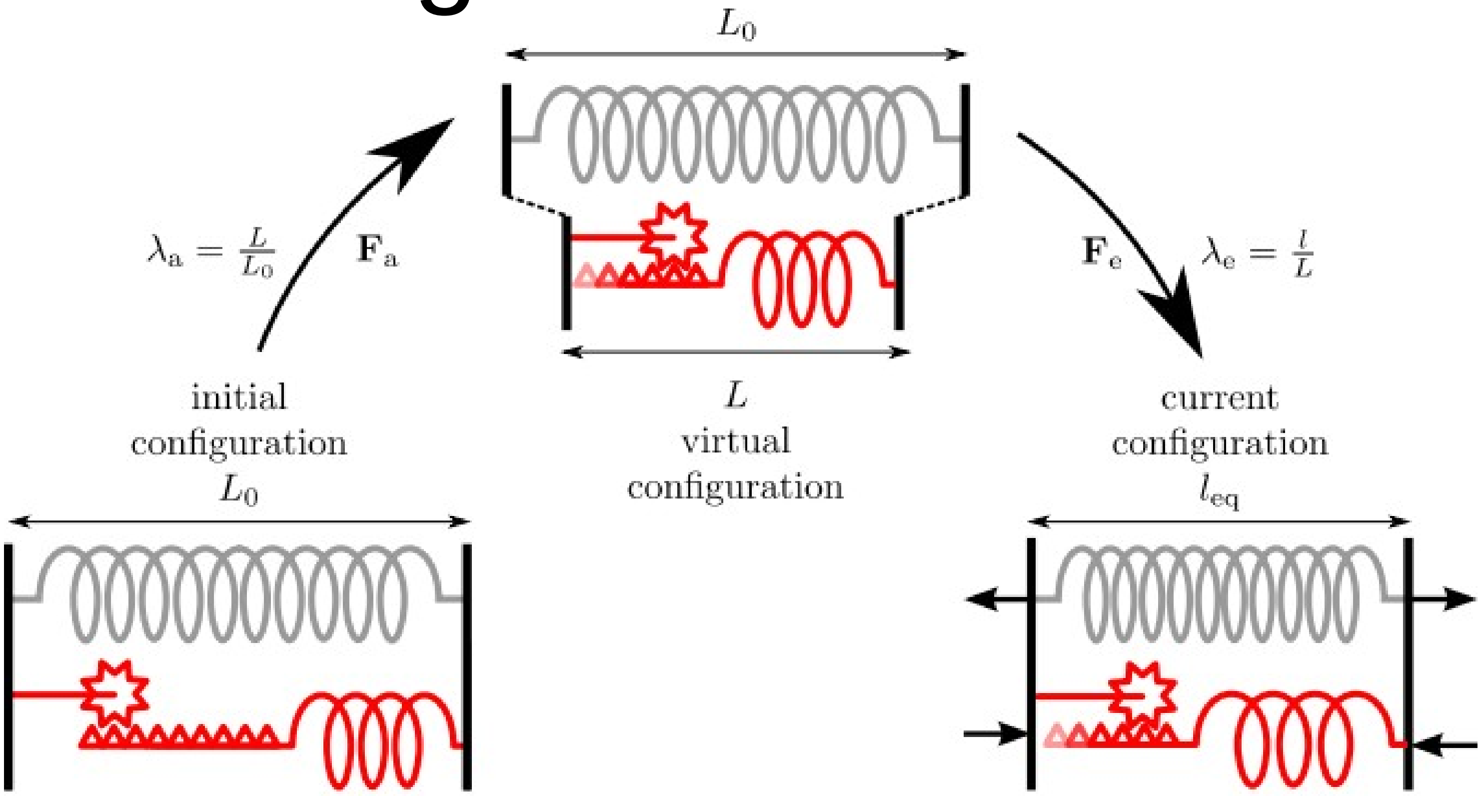
Anelastic growth and contraction



Anelastic growth and contraction

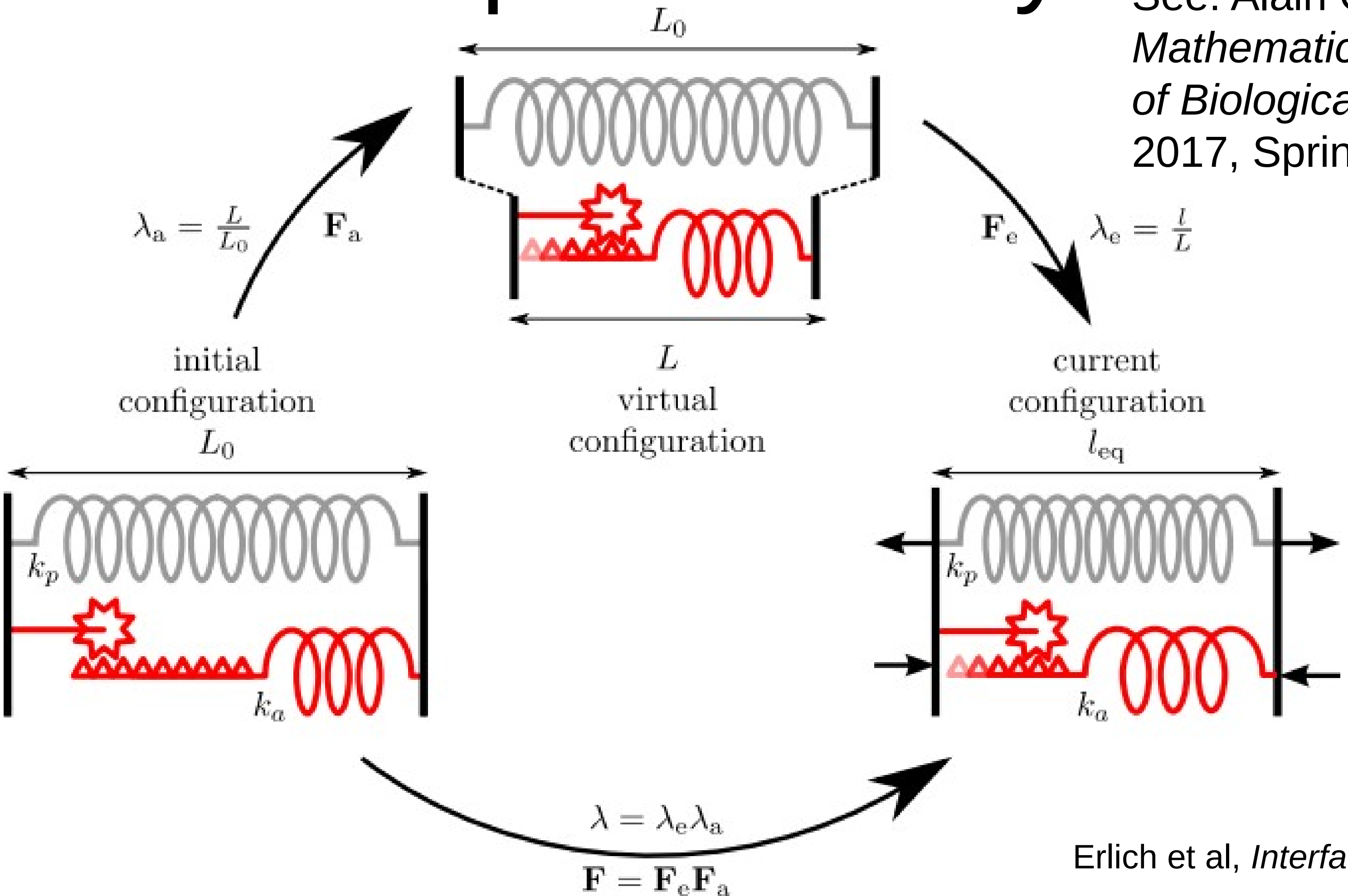


Anelastic growth and contraction



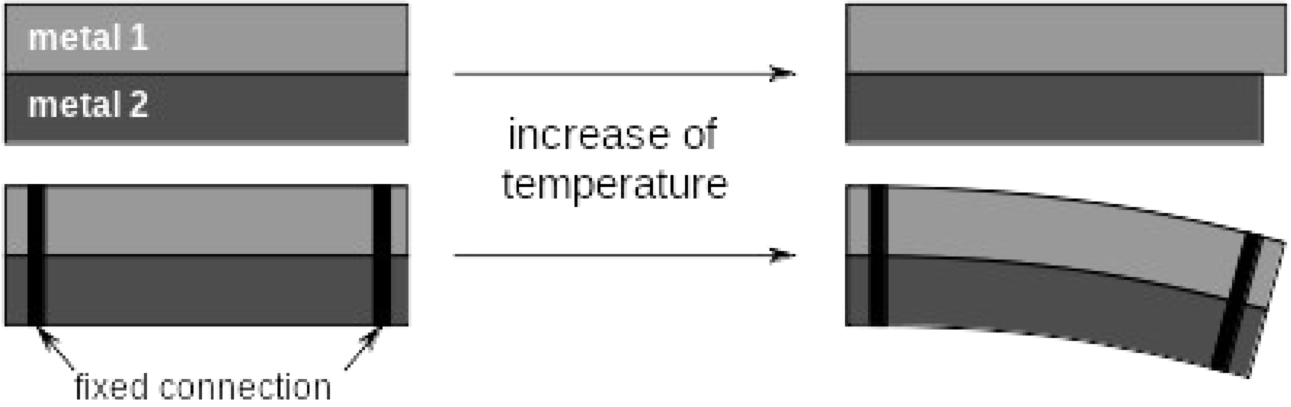
Morphoelasticity

See: Alain Goriely, *The Mathematics & Mechanics of Biological Growth*, 2017, Springer.

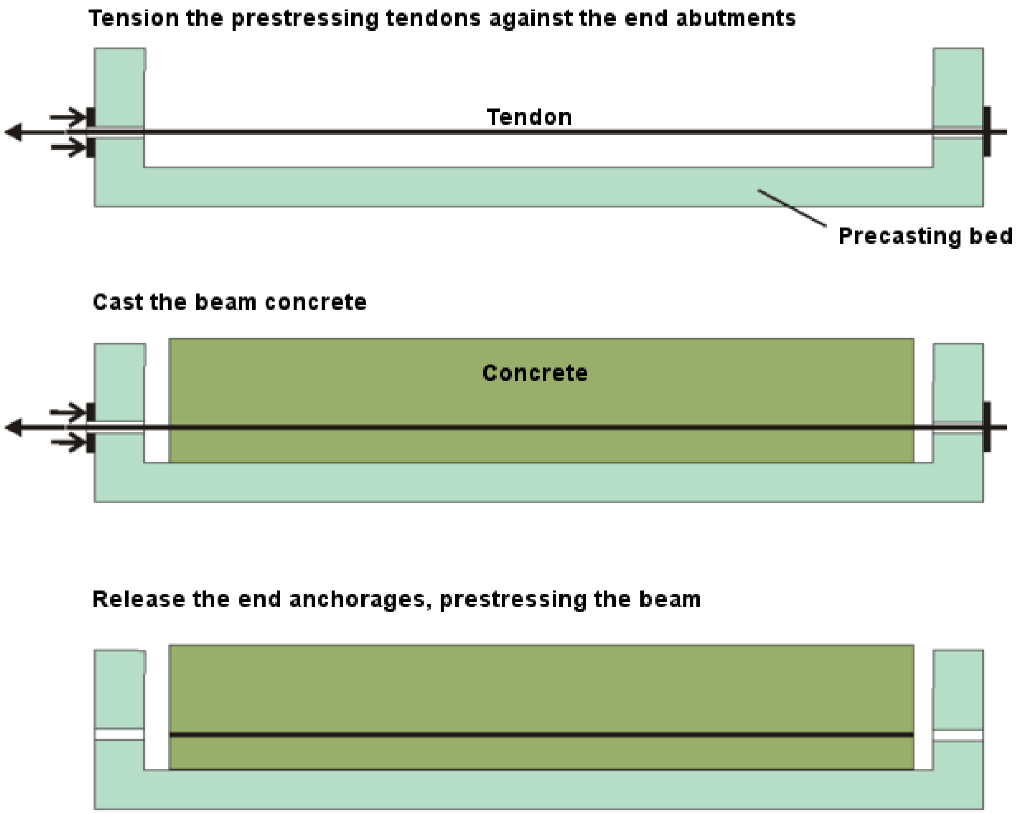


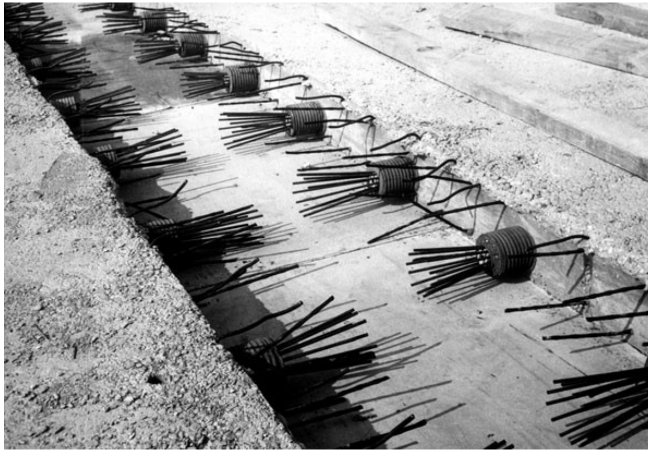
Erlich et al, *Interface Focus*, 2022

Morphoelasticity in inert materials



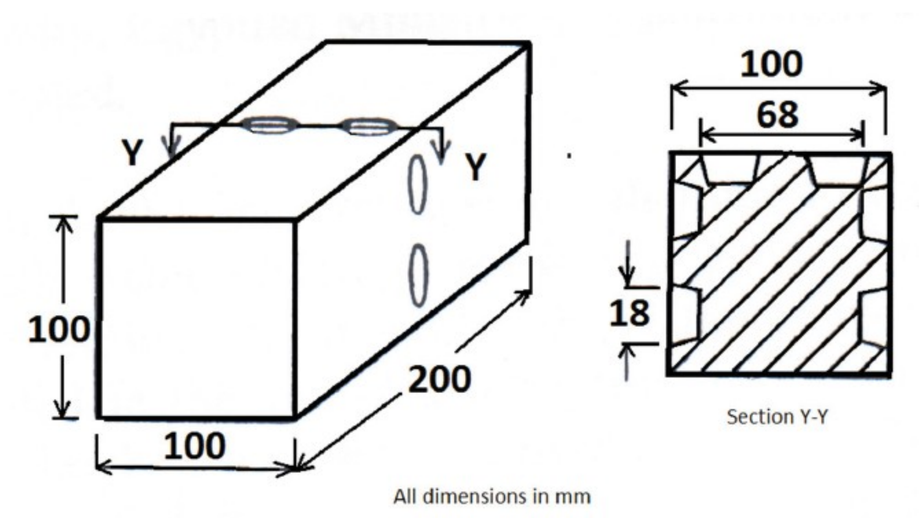
Prestress in inert materials





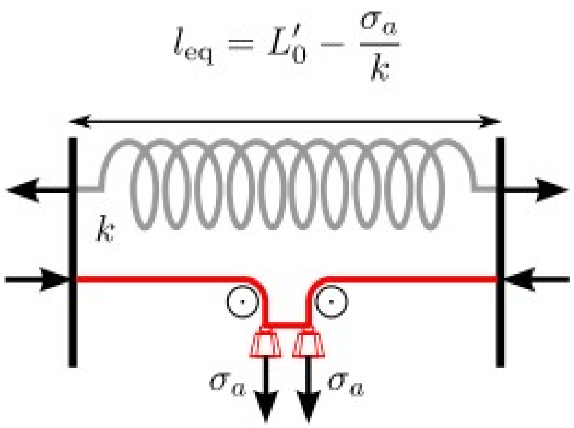
Association Eugène Freyssinet

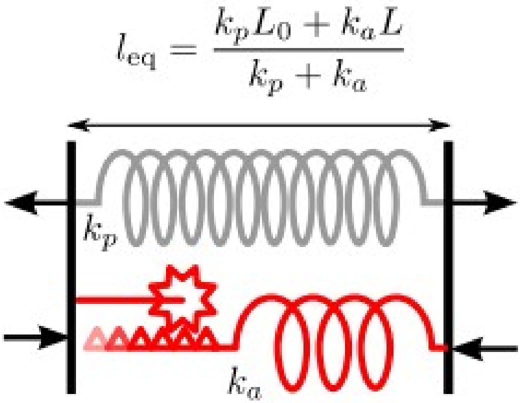
Prestress in inert materials



B. M. El-Sehily, *Procedia Structural Integrity 2* (2016) 2921–2928

Prestrain or prestress?

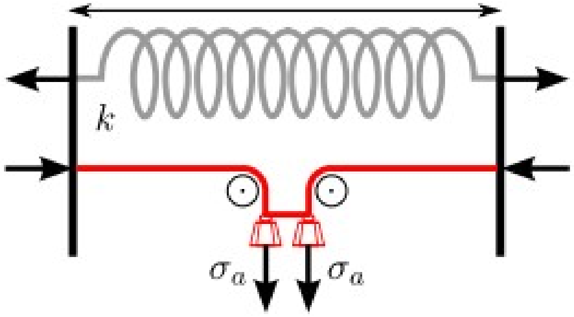


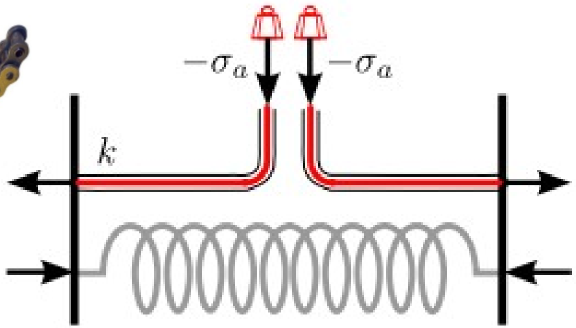


Erlich et al, *Interface Focus* 2022

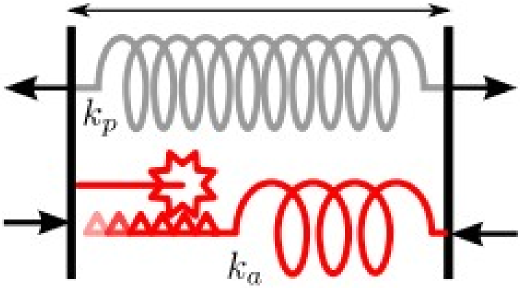
Prestrain or prestress? Winch or potential?

$$l_{\text{eq}} = L_0' - \frac{\sigma_a}{k}$$



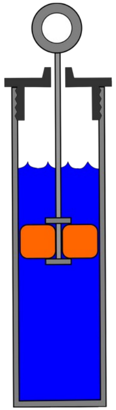


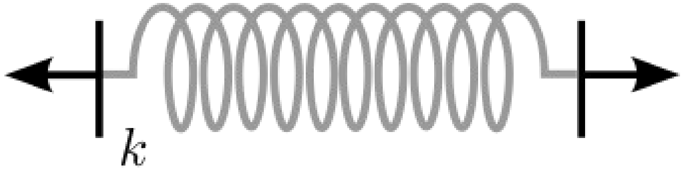
$$l_{\text{eq}} = \frac{k_p L_0 + k_a L}{k_p + k_a}$$

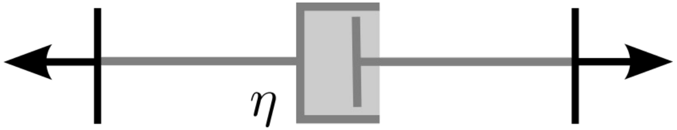


Erlich et al, *Interface Focus* 2022

A word about springs and dashpots



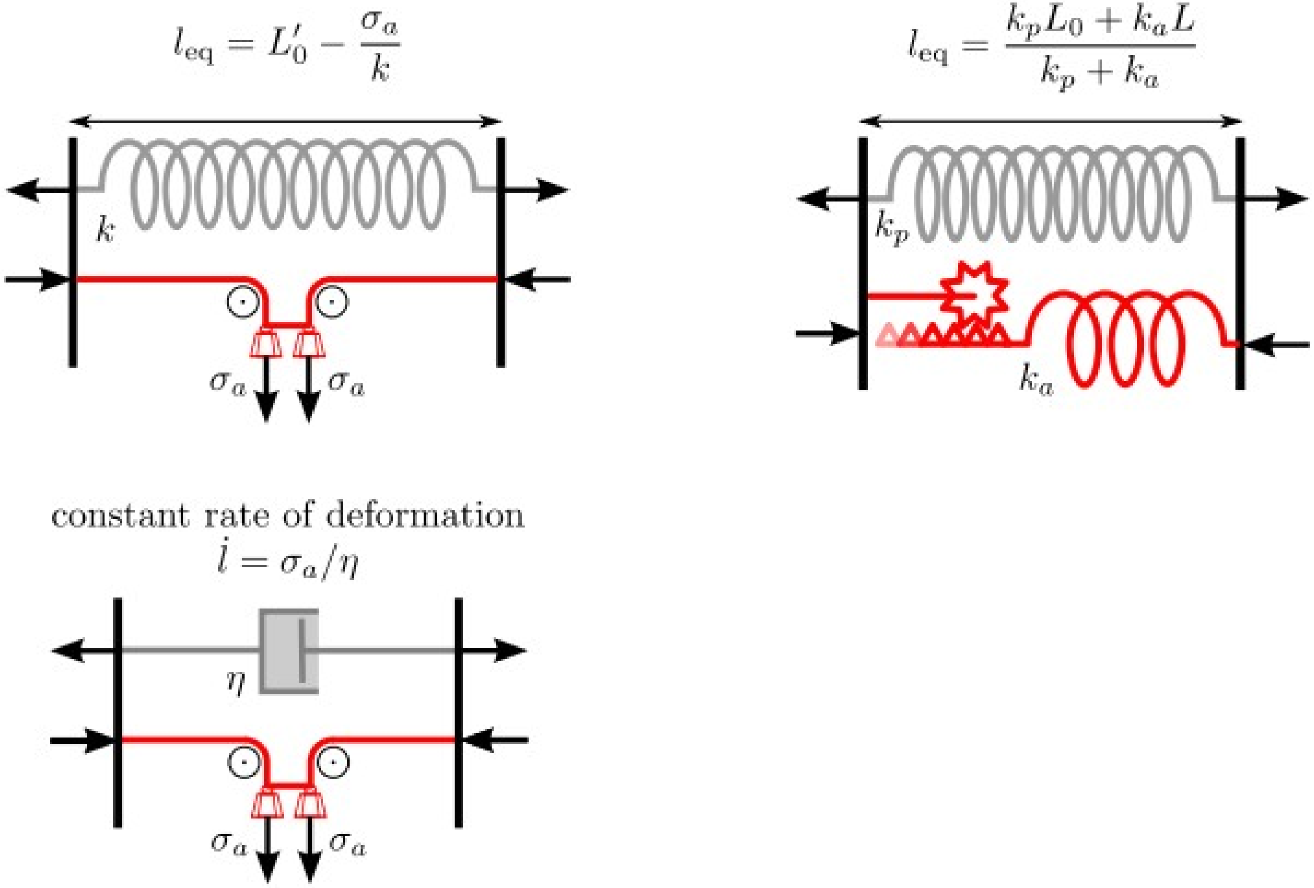




$$F = k(l - L_0)$$
$$\text{“}\Leftrightarrow\text{”}$$
$$\sigma = E\varepsilon = \eta\partial_x u$$

$$F = \eta\dot{l}$$
$$\text{“}\Leftrightarrow\text{”}$$
$$\sigma = \eta\dot{\varepsilon} = \eta\partial_x\dot{u}$$

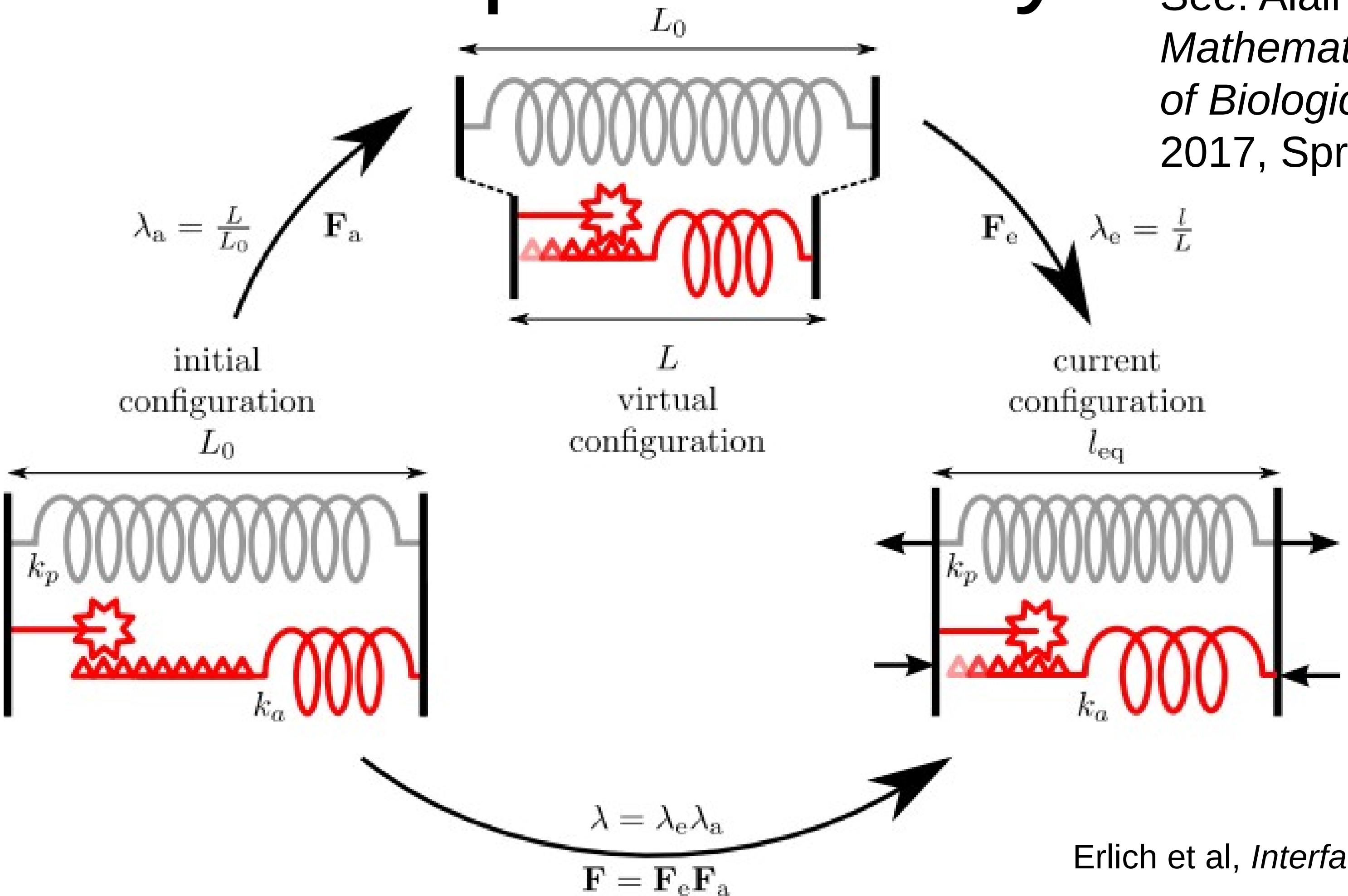
Prestrain or prestress? Anelastic or potential?



Erlich et al, *Interface Focus* 2022

Morphoelasticity

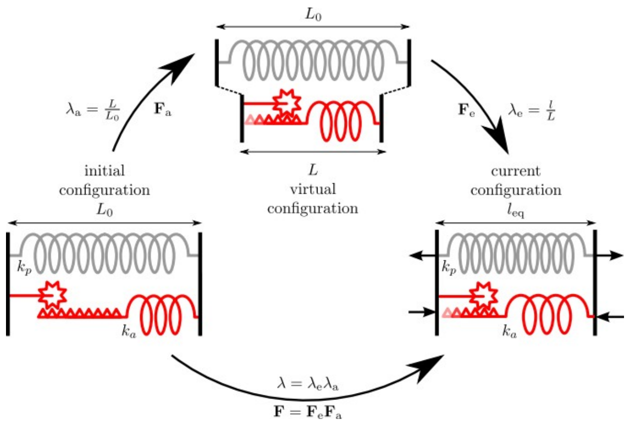
See: Alain Goriely, *The Mathematics, Mechanics of Biological Growth*, 2017, Springer.



Erlich et al, *Interface Focus*, 2022

3. Spatial structure and prestressed materials

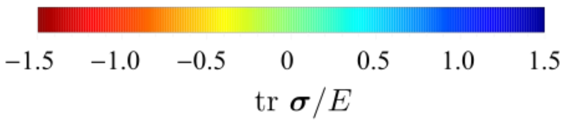
Erlich et al, *How dynamic prestress governs the shape of living systems, from the subcellular to tissue scale*, 2022, *Interface Focus.*, 12(6):058101



Space

differential
prestrain

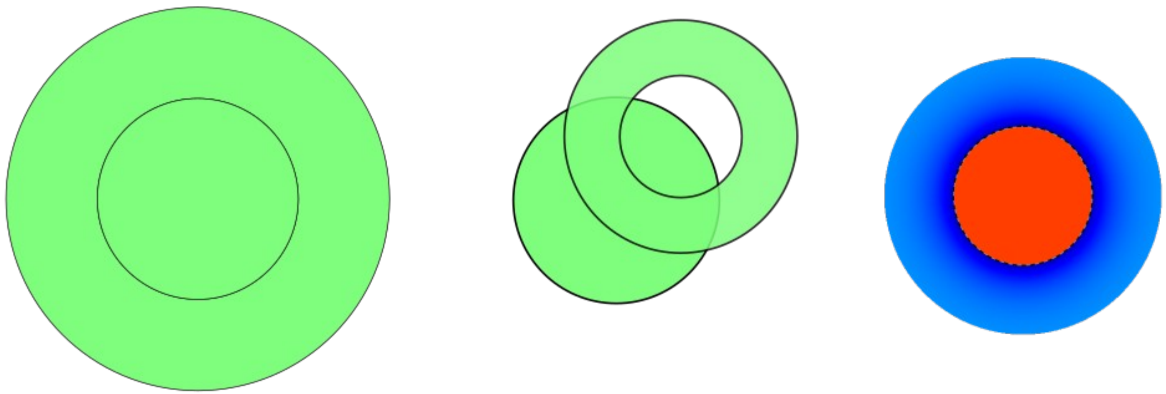
$$\mathbf{F}_a^{\mathrm{in}} \neq \mathbf{F}_a^{\mathrm{out}}$$

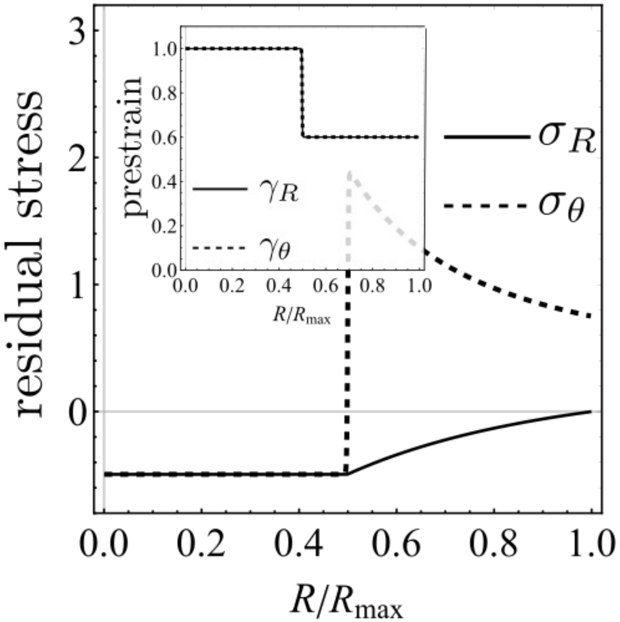


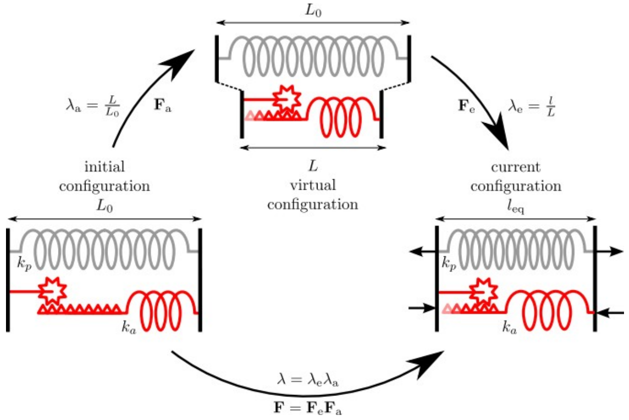
initial configuration

virtual configuration

current configuration



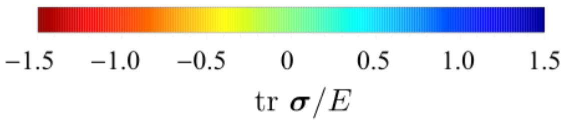




Space

heterogeneous prestrain

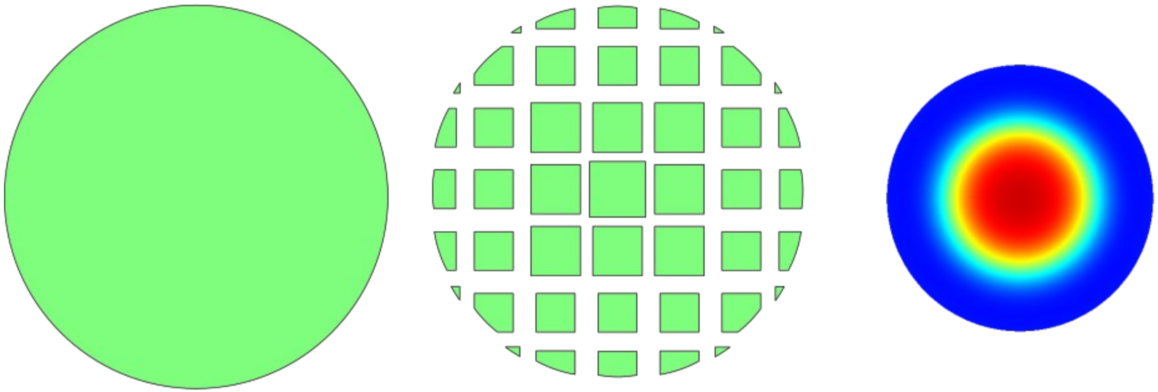
$$\mathbf{F}_a(\mathbf{r}) \neq \mathbf{F}_a(\mathbf{r} + \Delta\mathbf{r})$$

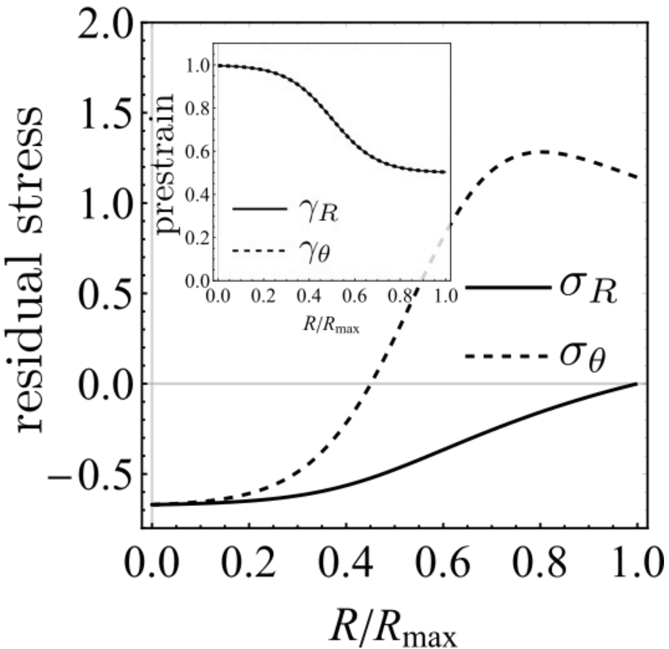


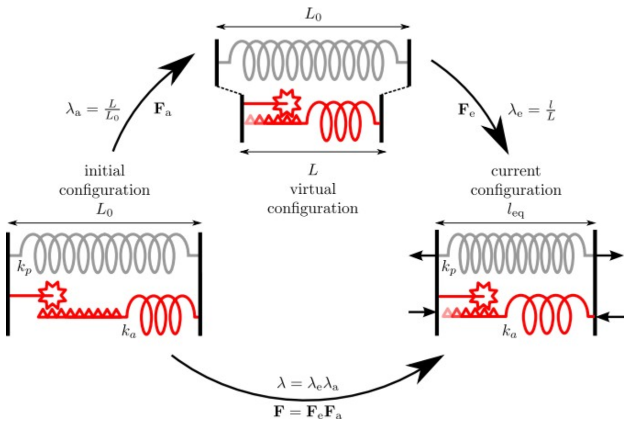
initial configuration

virtual configuration

current configuration







Space

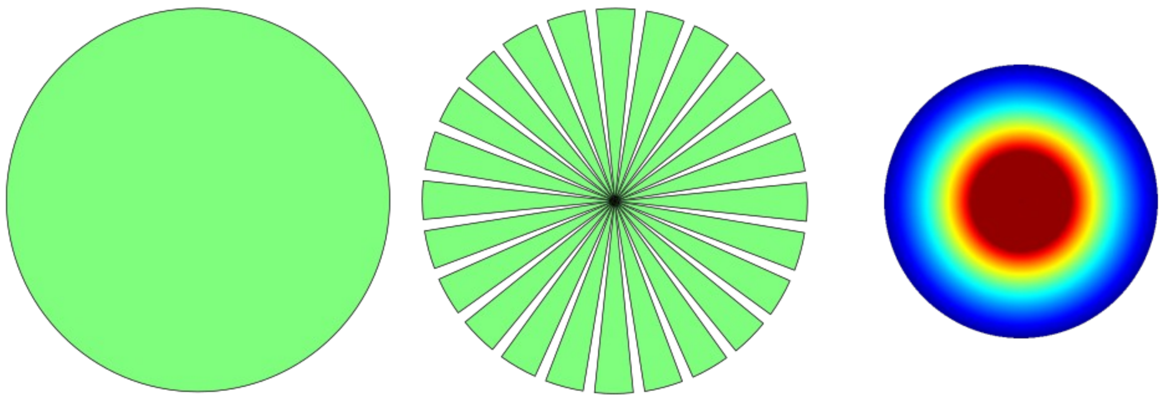
anisotropic prestrain

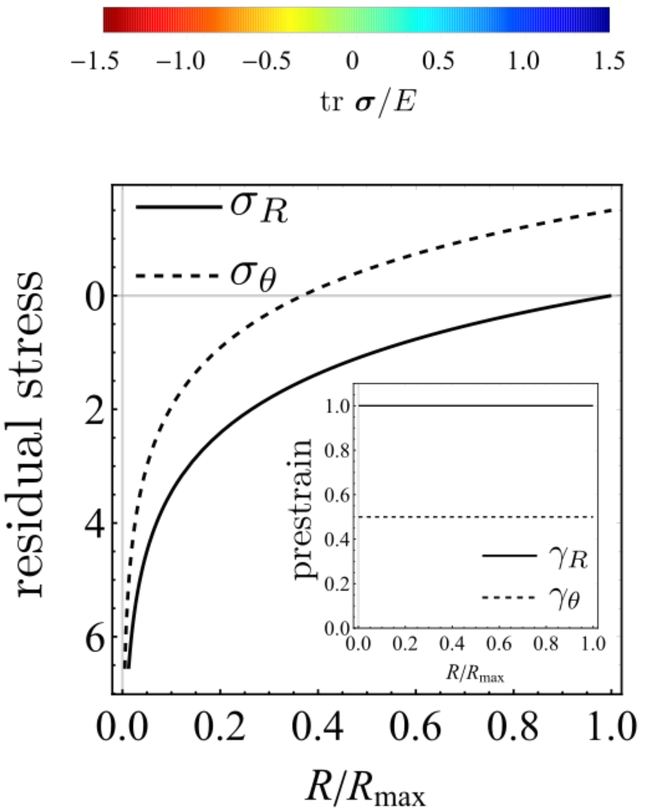
$$\mathbf{e}_r \mathbf{F}_a \mathbf{e}_r \neq \mathbf{e}_\theta \mathbf{F}_a \mathbf{e}_\theta$$

initial configuration

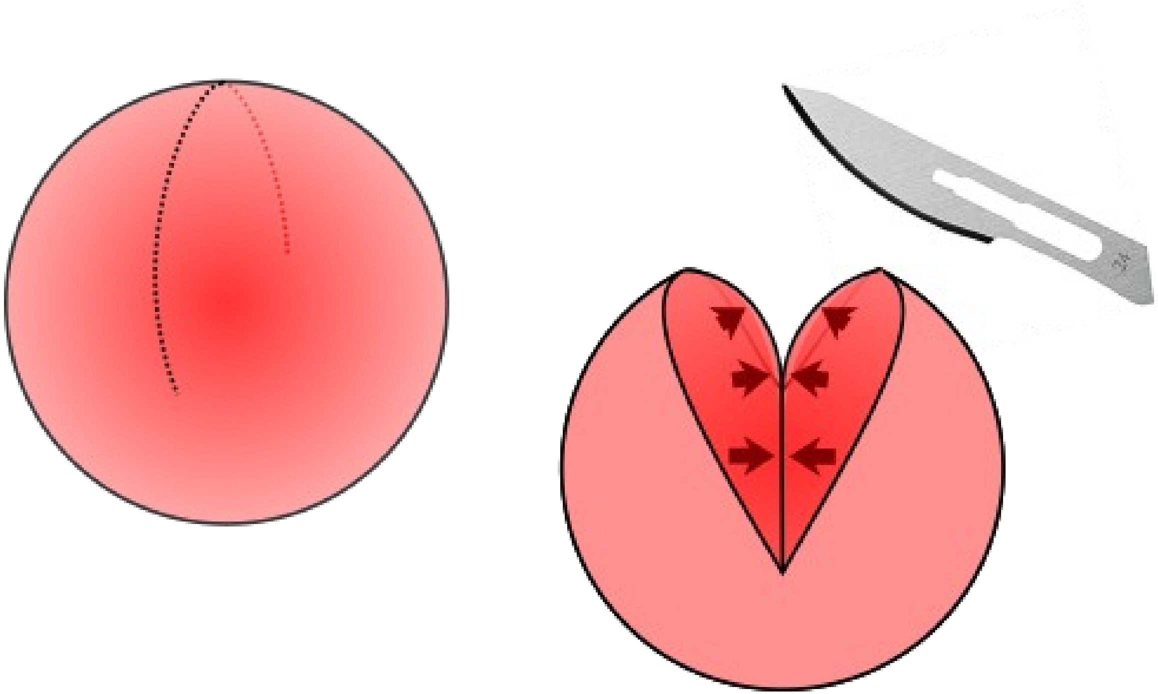
virtual configuration

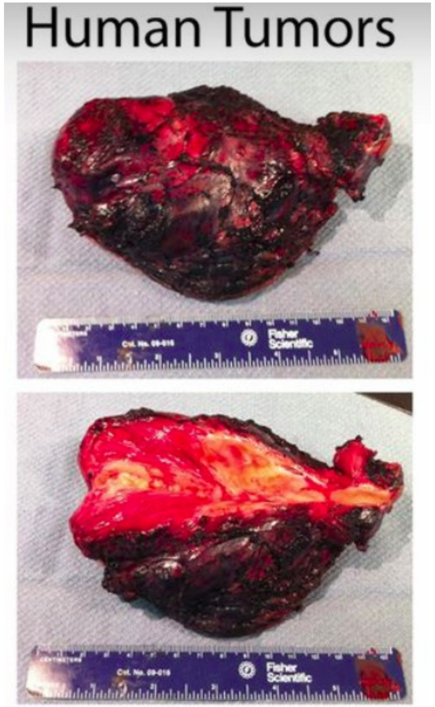
current configuration





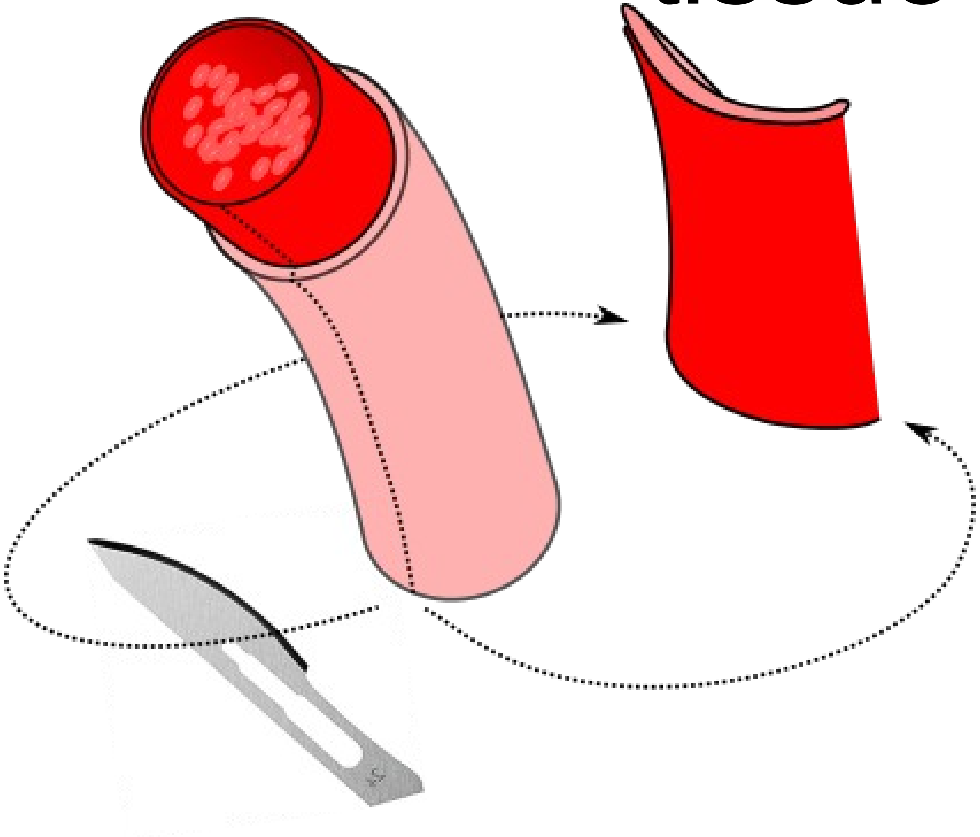
Evidence of residual stress in living tissue

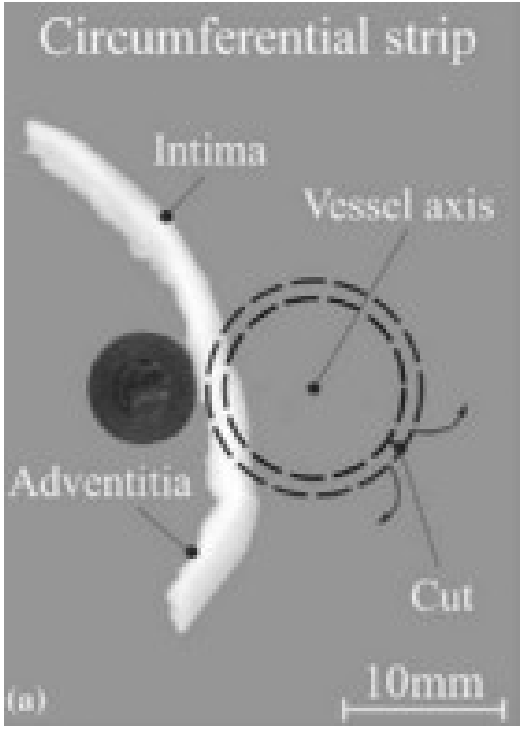




Stylianopoulos T *et al.* 2012 Causes, consequences, and remedies for growth-induced solid stress in murine and human tumors. *Proc. Natl Acad. Sci. USA* **109**, 15 101–15 108. (doi:10.1073/pnas.1213353109)

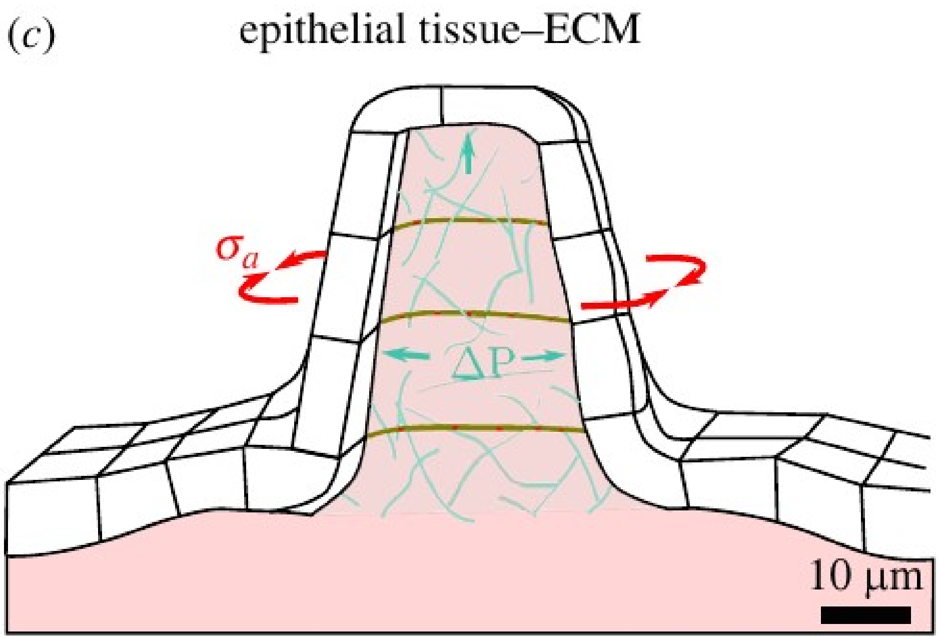
Evidence of residual stress in living tissue



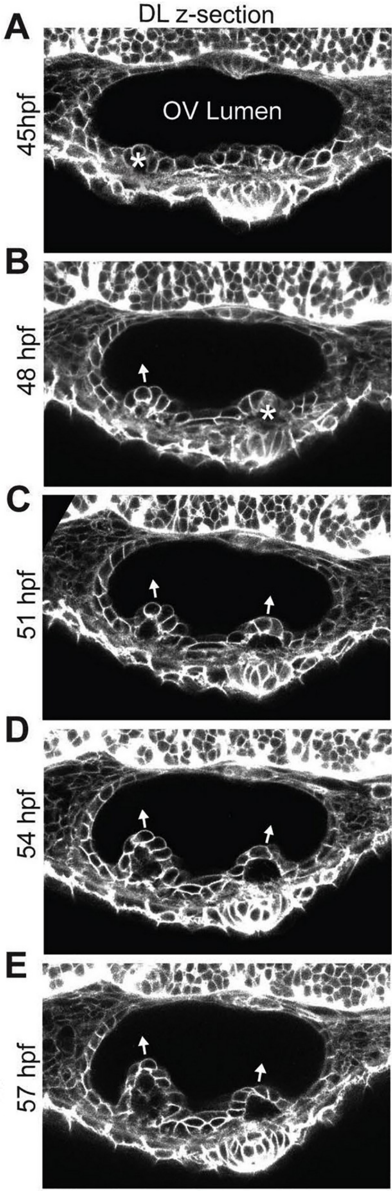


Holzapfel et al, *Ann. Biomed. Engng.*, 2007

Swelling of the ECM



Munjal A, Hannezo E, Tsai TY-C, Mitchison TJ, Megason SG. 2021 Extracellular hyaluronate pressure shaped by cellular tethers drives tissue morphogenesis. *Cell* **184**, 6313–6325. (doi:10.1016/j.cell.2021.11.025)



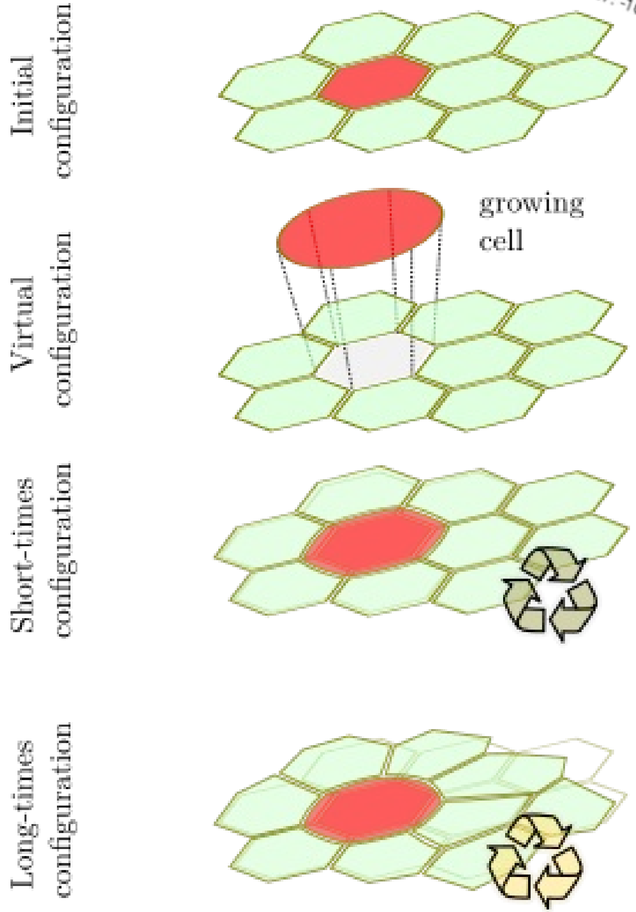
4. Prestress in cellularised tissue

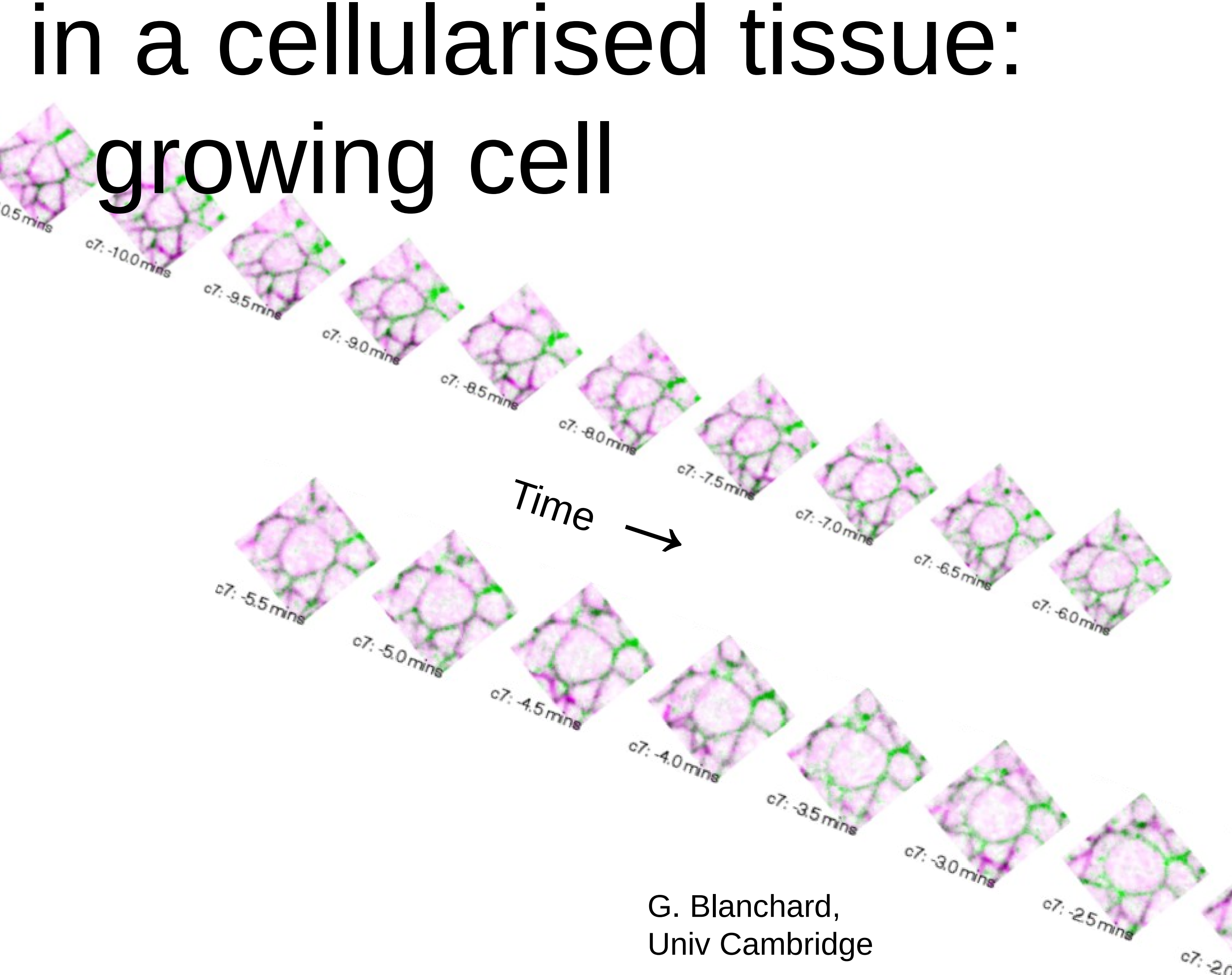
Irvine, E. Wieschaus, *Cell intercalation during* Drosophila *germband extension and its regulation by pair-rule segmentation genes,* 1994, Devel., 120(4):827--841

Blanchard et al, *Tissue tectonics: morphogenetic strain rates, cell shape change and intercalation,* 2009, *Nature Methods,* 6():458--464

Ranft et al, *Fluidization of tissues by cell division and apoptosis,* 2010, *Proc. Natl. Acad. Sci. USA,* 107(49):20863--20868

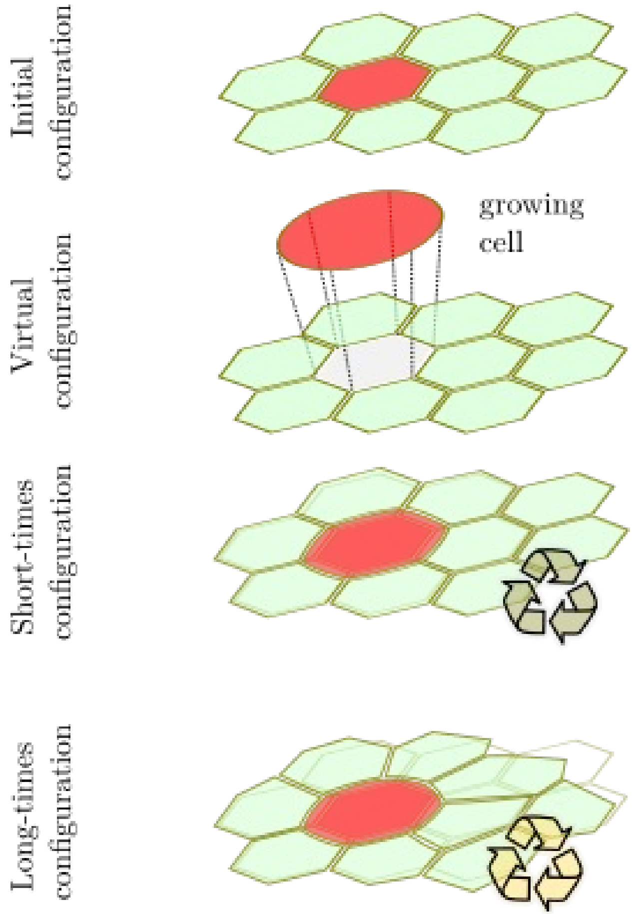
Growth in a cellularised tissue: growing cell

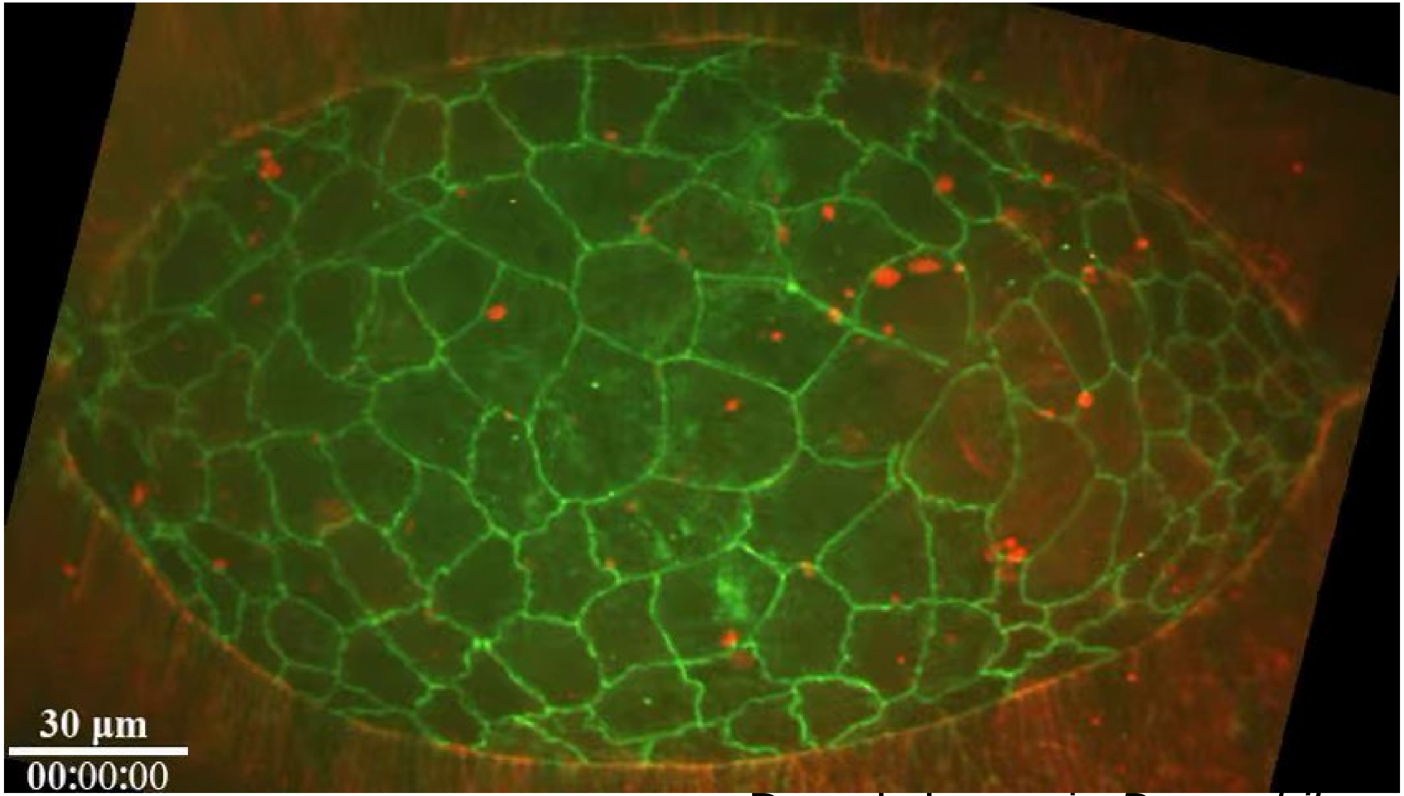




G. Blanchard,
Univ Cambridge

Growth/contraction in an epithelium

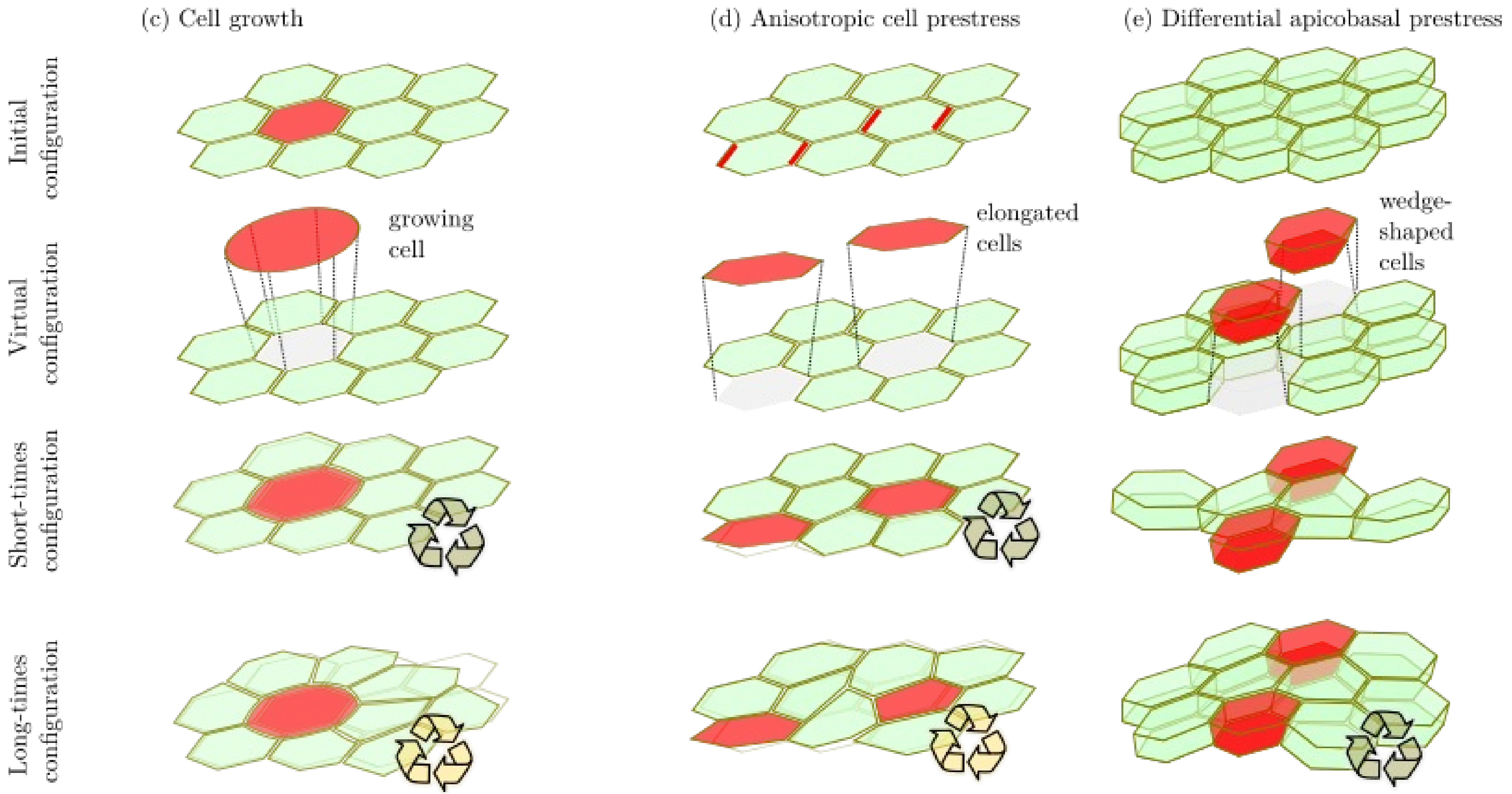




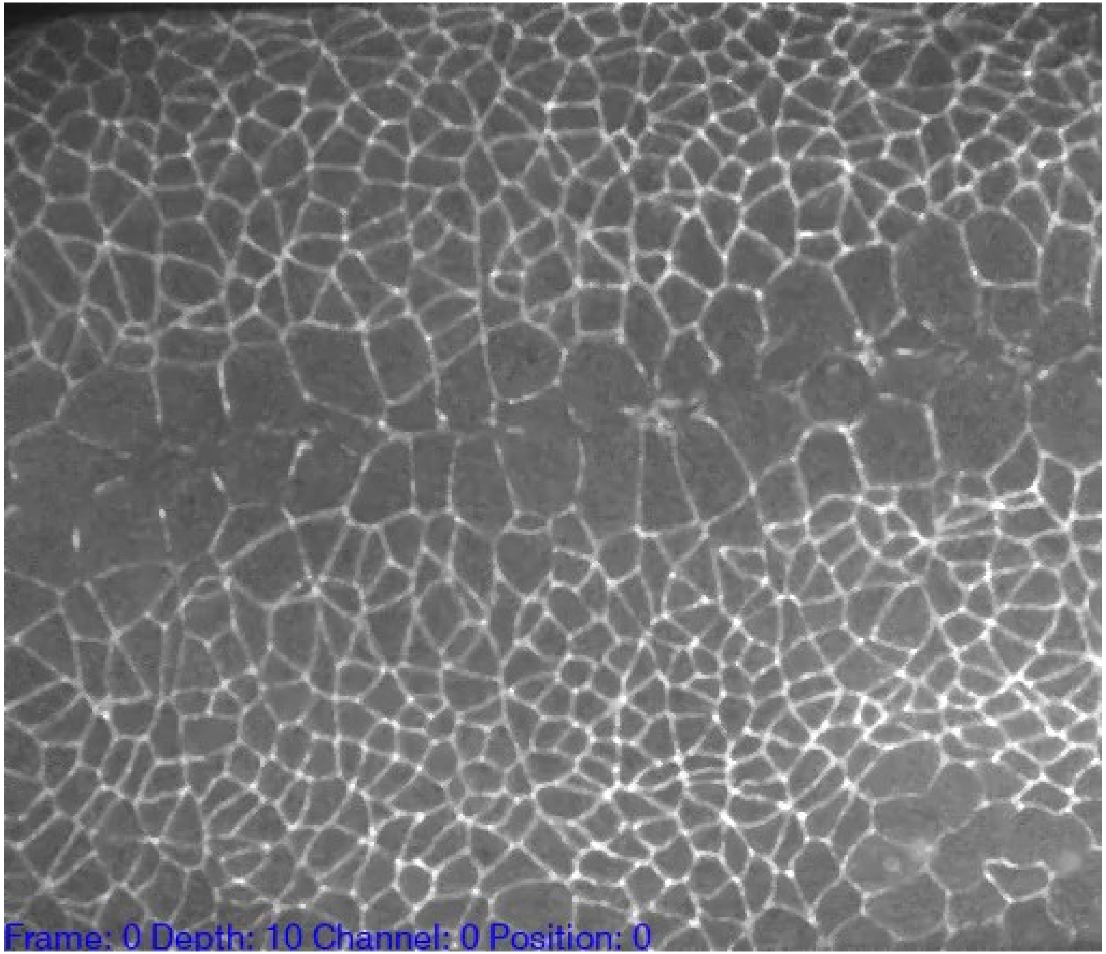
Dorsal closure in *Drosophila*

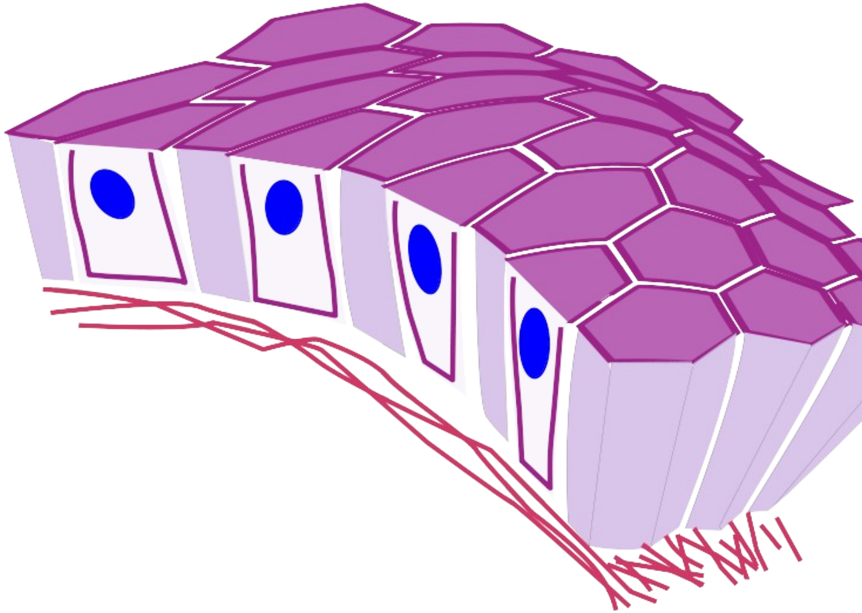
Lu et al, *Biophys J* 2015

Growth/contraction in cellularised tissue



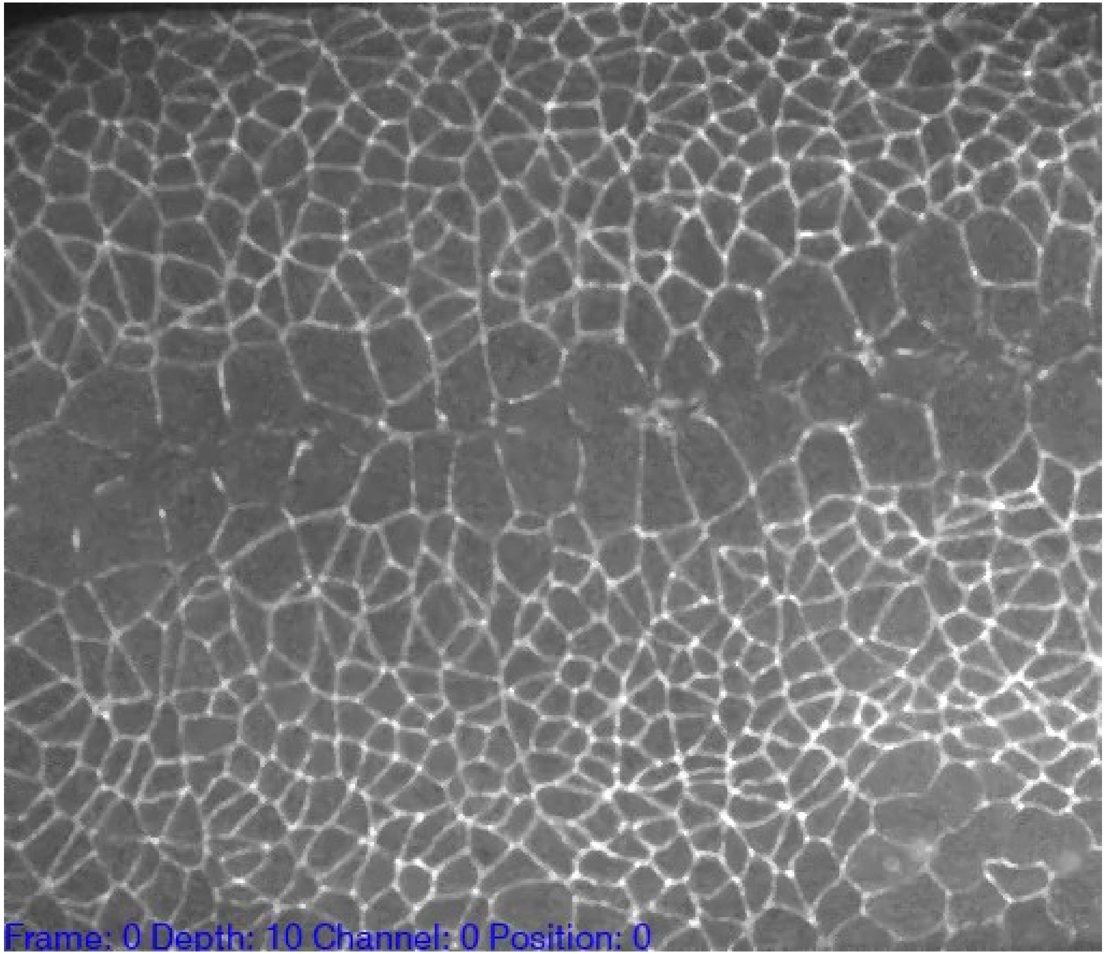
Epithelial morphogenesis



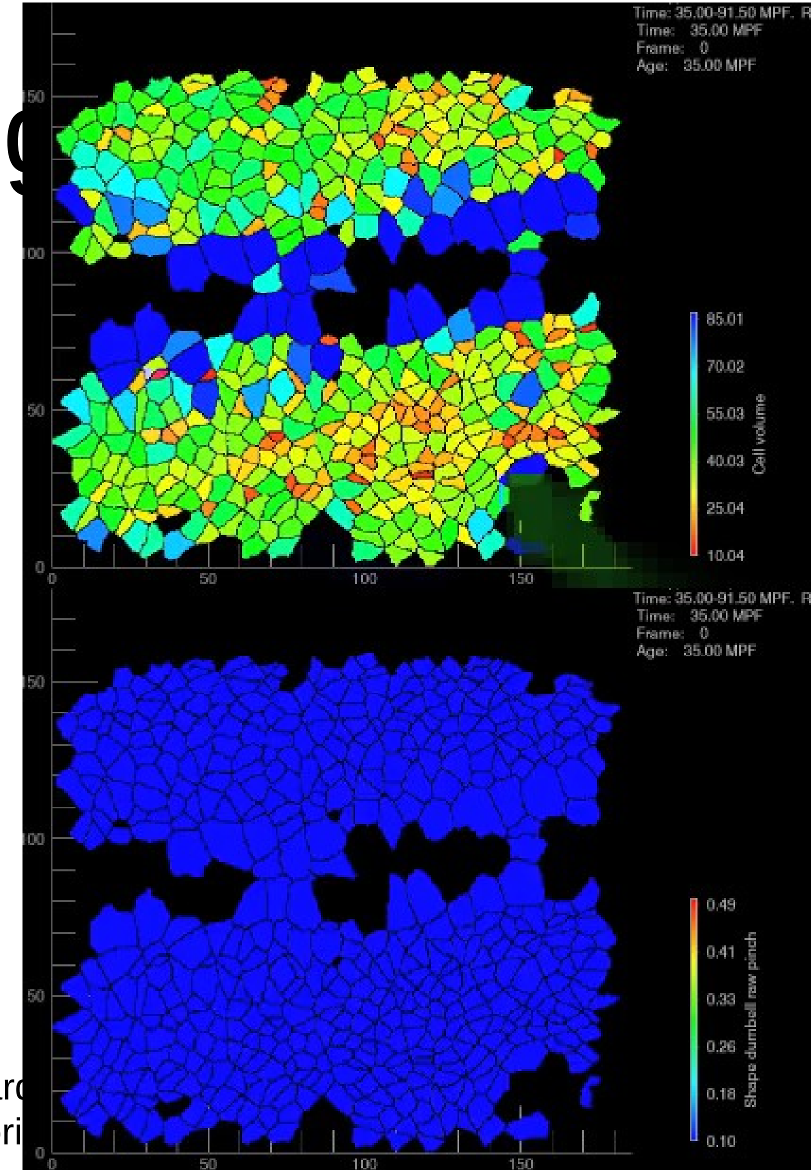


G. Blanchard,
Univ Cambridge

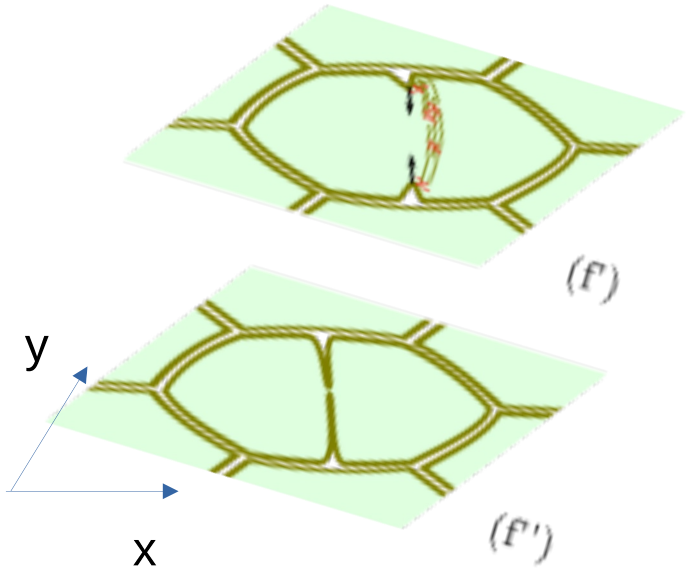
Epithelial morphog

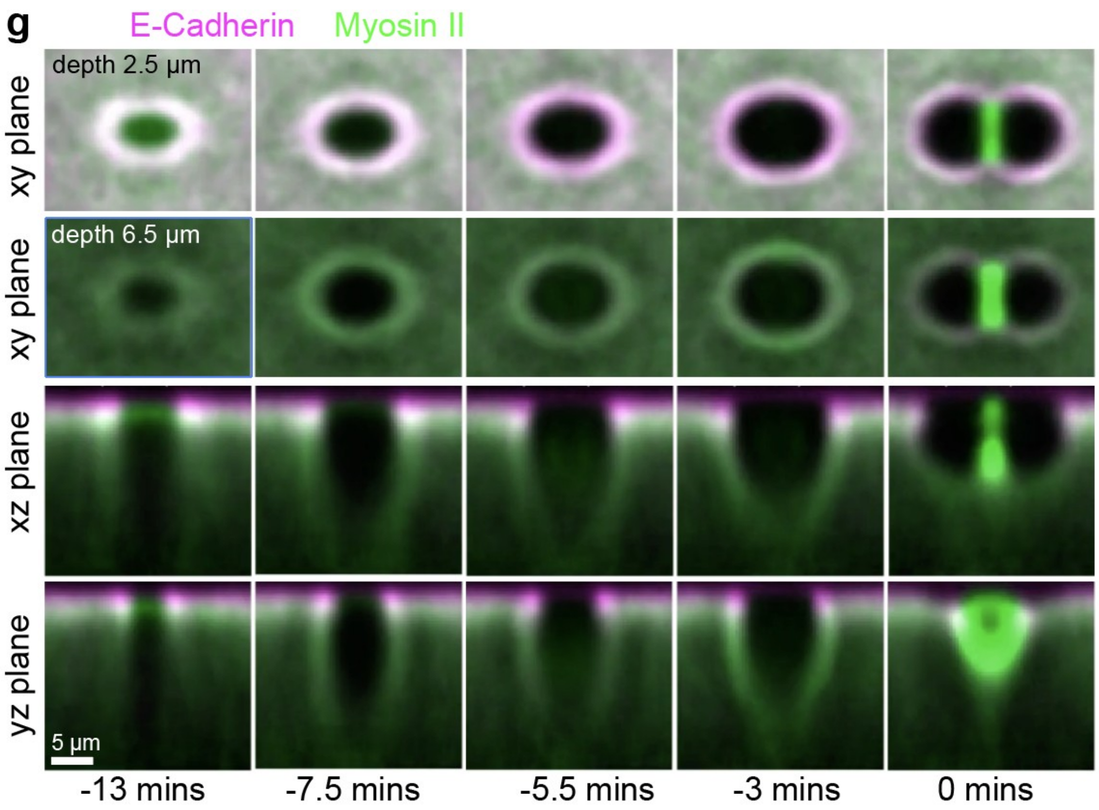


G. Blanchard
Univ Cambri



Cytokinesis in epithelia





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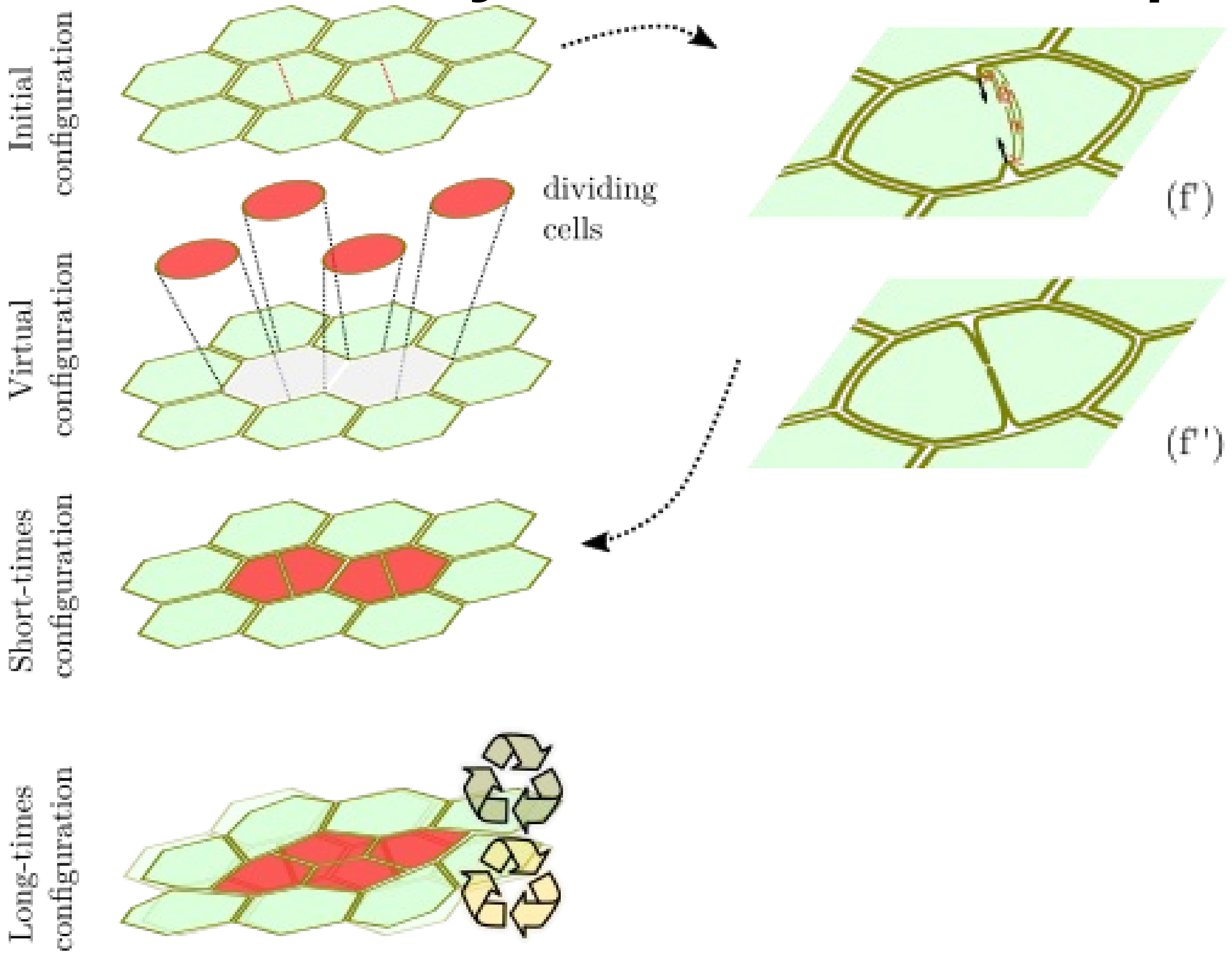
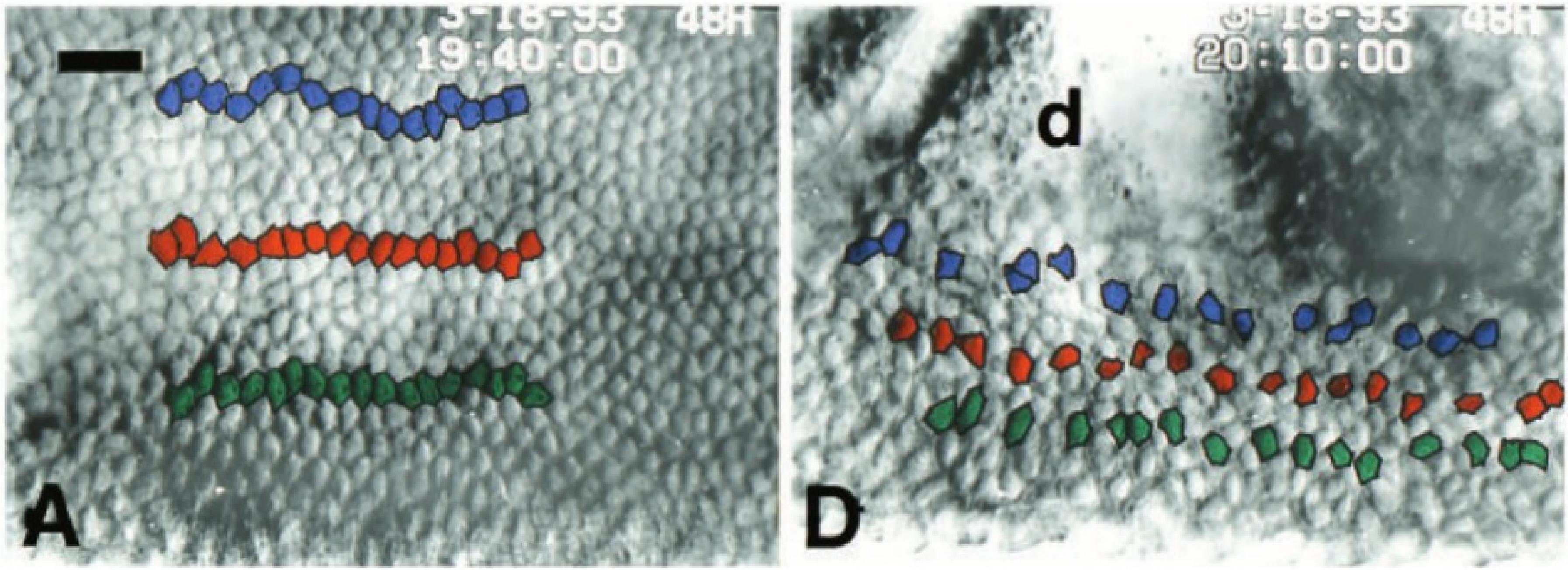
Cytokinesis in epithelia



Active cell intercalation

(a.k.a. neighbour exchange, T1 transition)

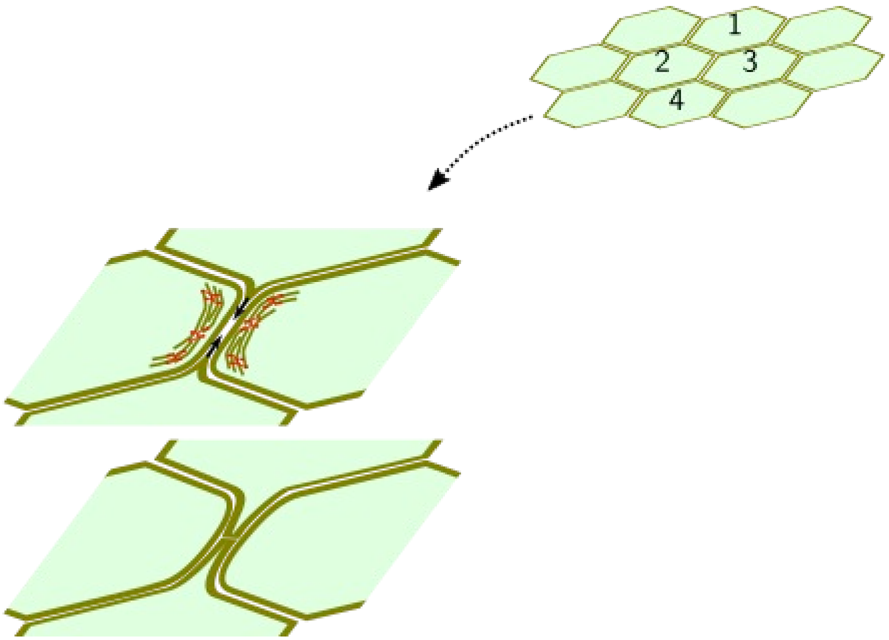


Axis extension in *Drosophila*

Irvine & Wieschaus, *Devel.* 1994

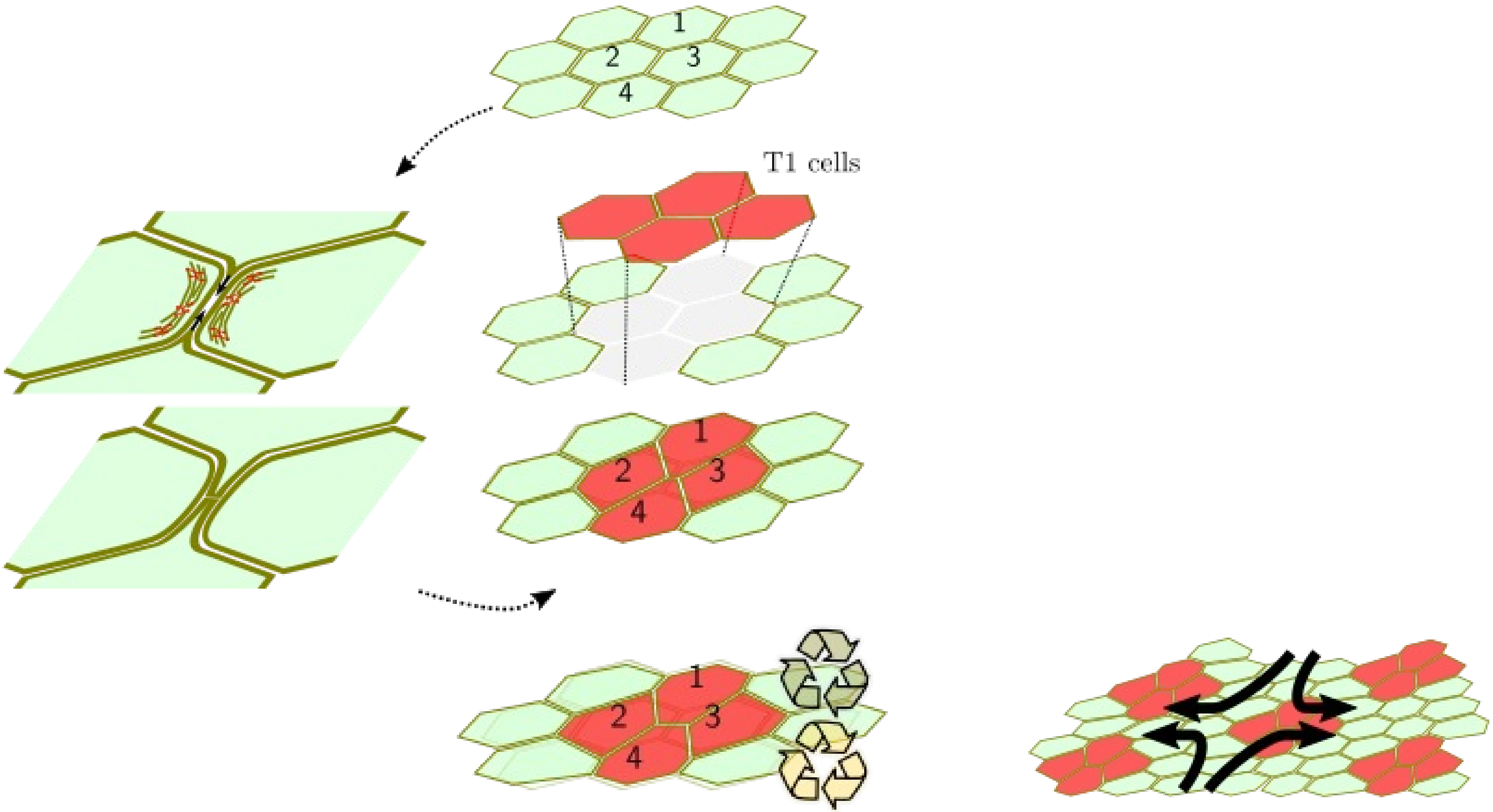
Active cell intercalation

(a.k.a. neighbour exchange, T1 transition)

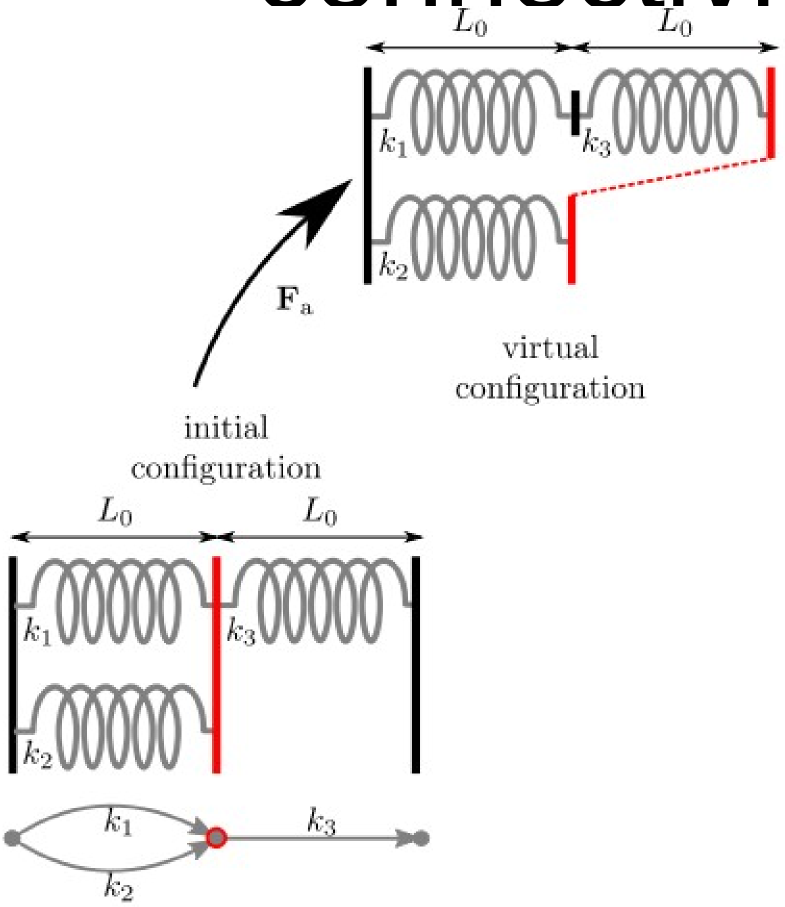


Active cell intercalation

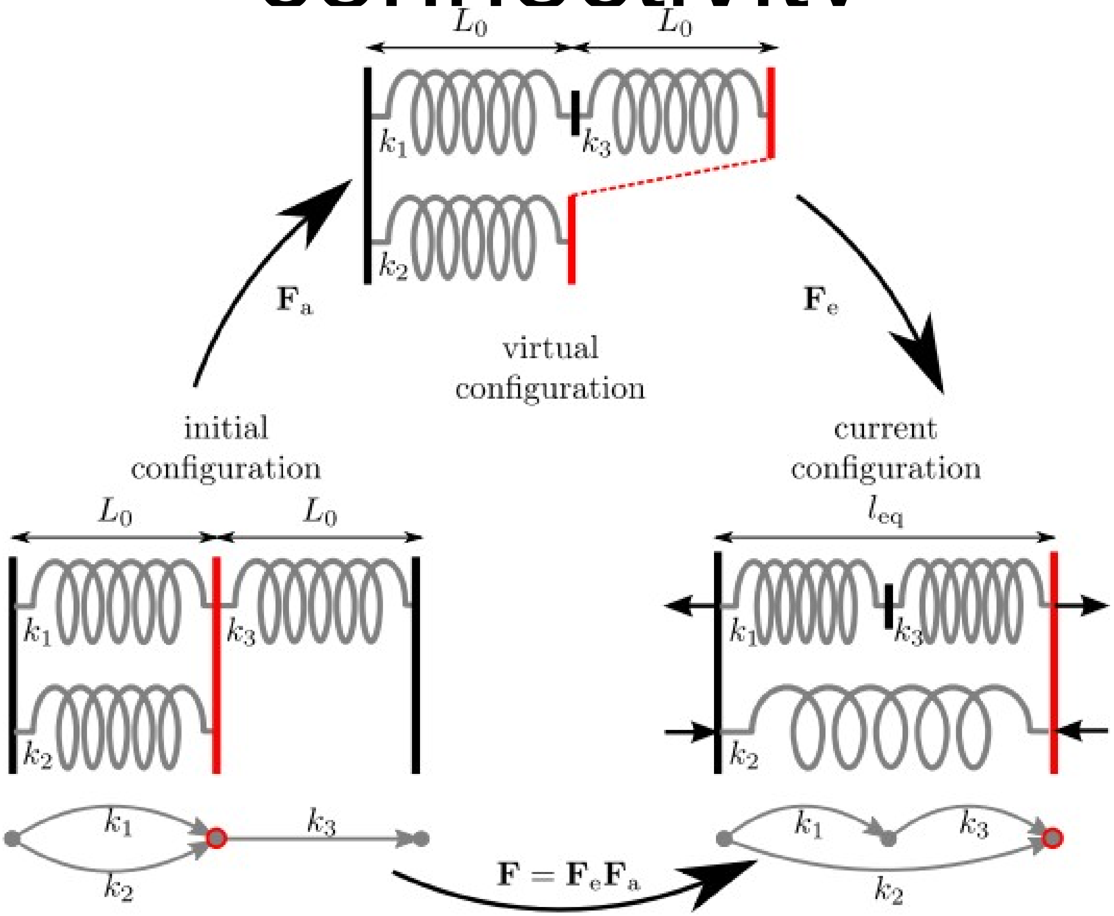
(a.k.a. neighbour exchange, T1 transition)



Topological prestress and change of connectivity



Topological prestress and change of connectivity



5. *Active stress in biopolymer networks*

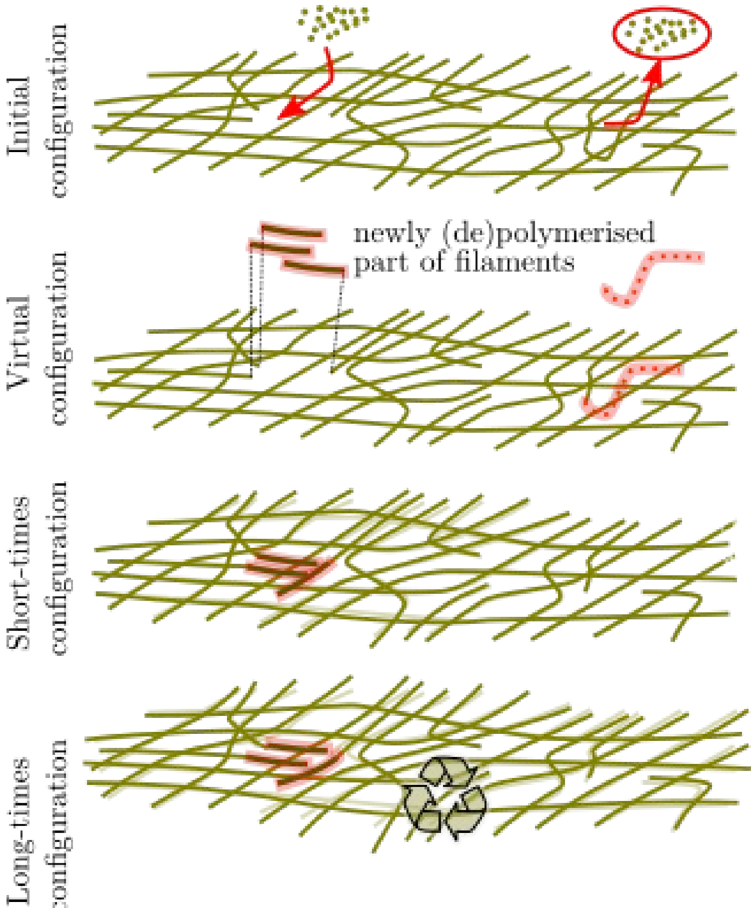
Verkhovsky, Svitkina, Borisy, *Self-polarization and directional motility of cytoplasm,* 1999, *Curr. Biol.,* 9(1):11--20

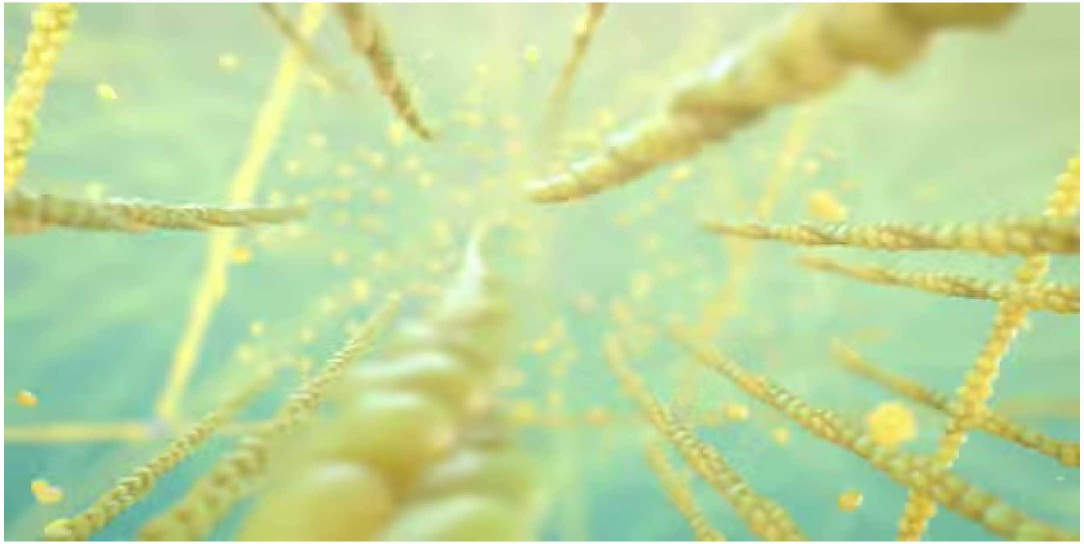
Pollard, Blanchoin, Mullins, *Molecular mechanisms controlling actin filament dynamics in nonmuscle cells,* 2000, *Annu. Rev. Biophys. Biomol. Struct.,* 29:545--576

Julicher et al, *Active Behavior of the Cytoskeleton,* 2007, *Phys. Rep.,* 449:3--28

Marchetti et al, *Hydrodynamics of soft active matter,* 2013, *Rev. Mod. Phys.,* 85(3):1143--1189

Growth prestress in a biopolymer meshwork: actin polymerisation





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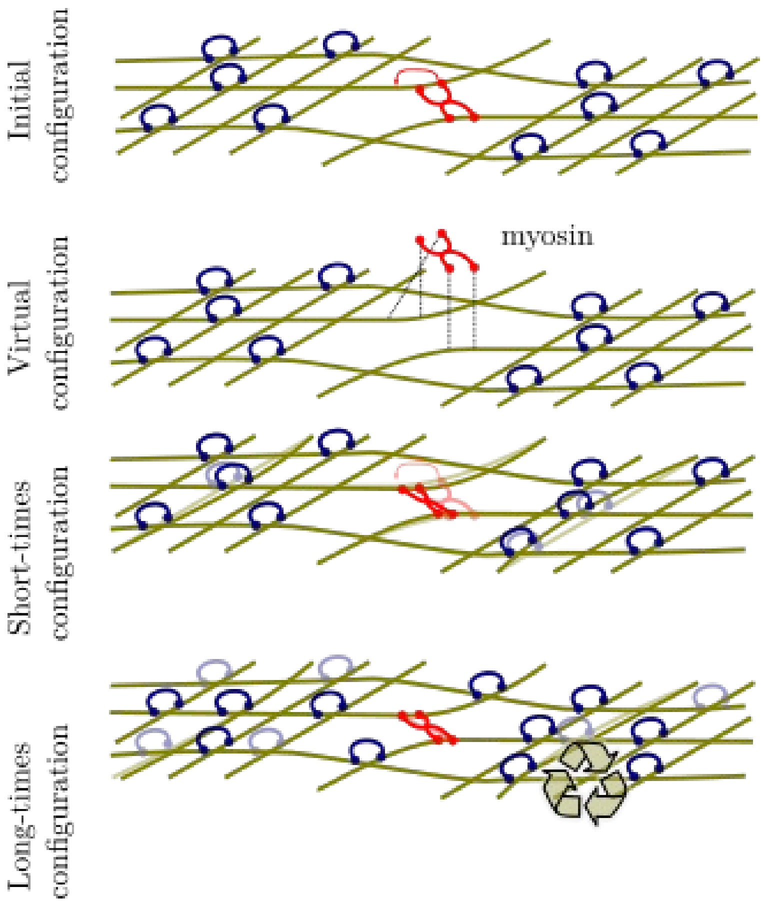
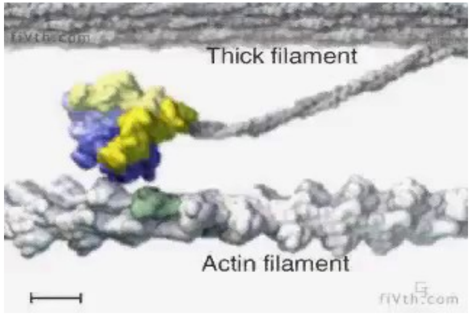
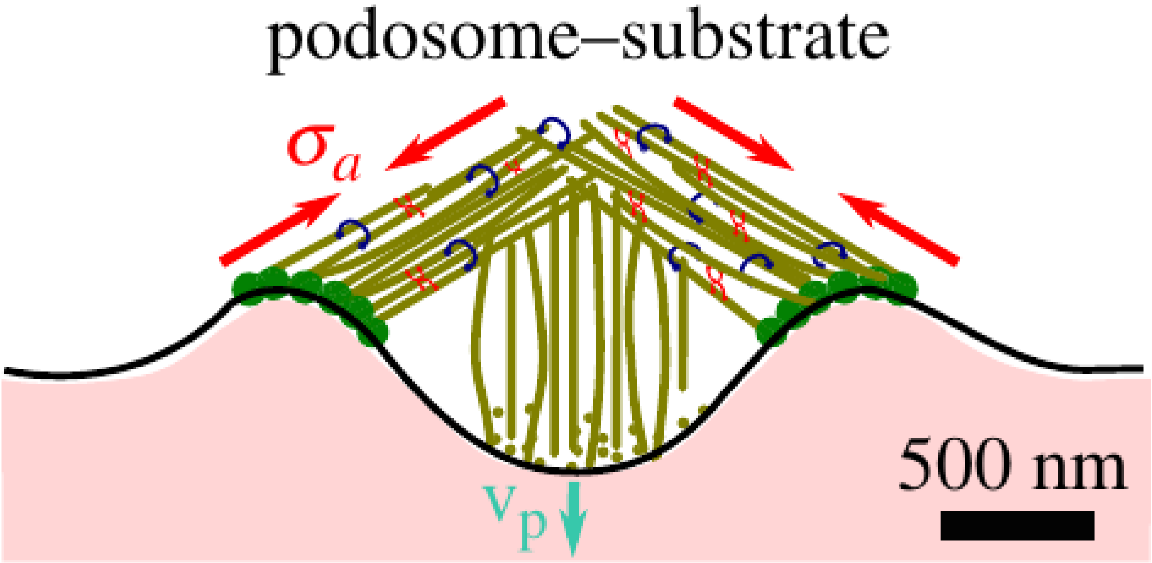
Contraction in a biopolymer meshwork: actin polymerisation

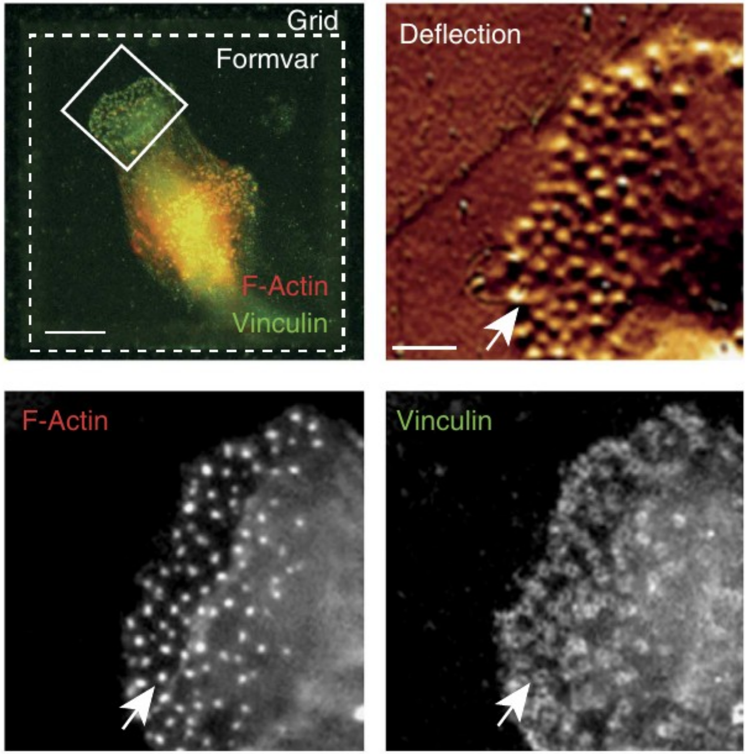




Vale and Miligan, *Science* 2000

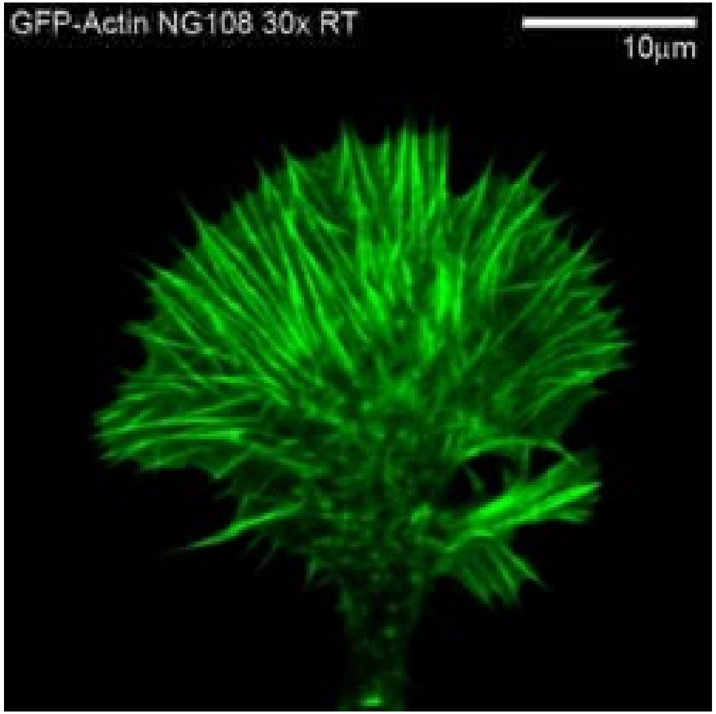
Example: podosomes

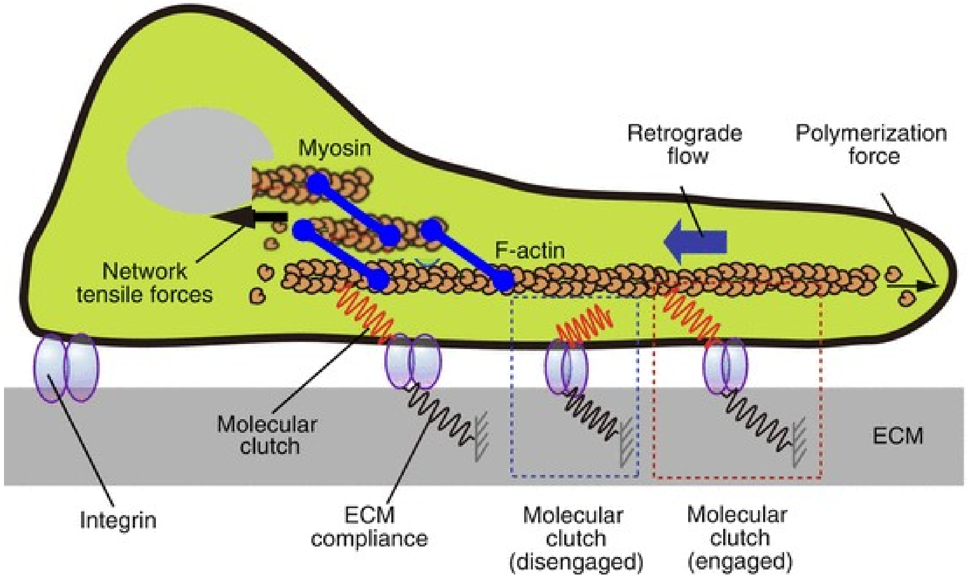




Labernadie A *et al.* 2014 Protrusion force microscopy reveals oscillatory force generation and mechanosensing activity of human macrophage podosomes. *Nat. Commun.* **5**, 1–10. (doi:Publisher:

Actomyosin protrusion and contraction





Cell migration
Mitchison & Cramer, *Cell* 1996
Schematic adapted from Okeyo et al, Springer, 2014

Neuron growth cone
Betz et al, *PRL* 2006

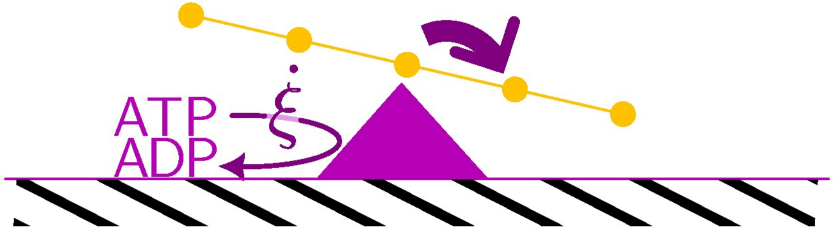
6. Molecular motors

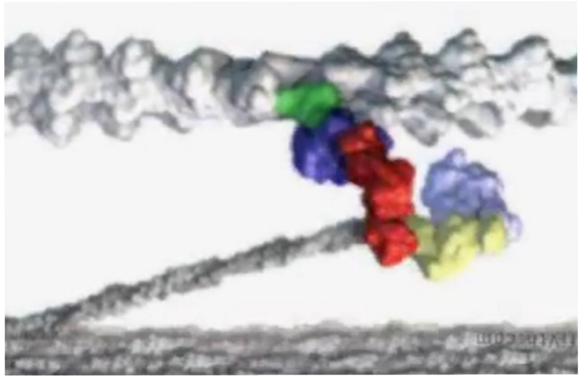
Jülicher, Ajdari and Prost, Modeling molecular motors,
Rev. Mod. Phys., 1997, 69(4):1269–1282

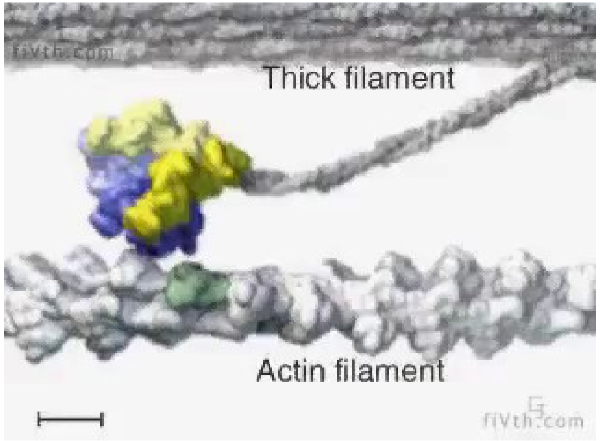
Lau, Lacoste and Mallick, *Phys. Rev. Lett.* 99, 2007

Bameta, Padinhateeri and Inamdar, *J. Stat. Mech.*, 2013

Thermodynamics of molecular motors

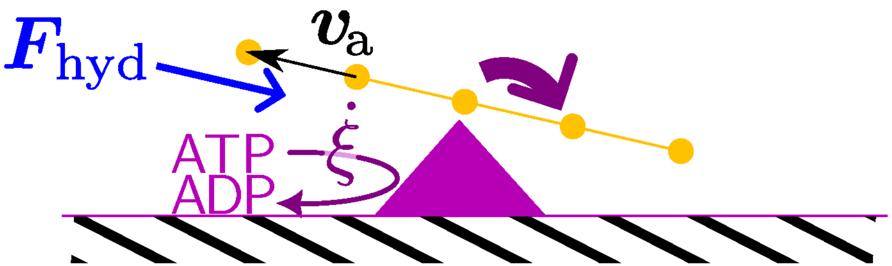


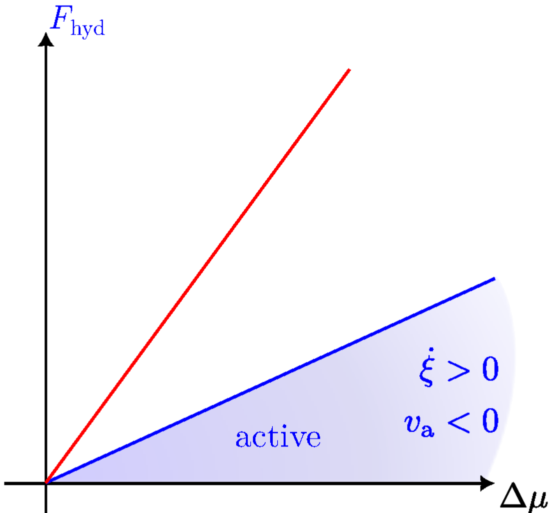




Vale and Miligan, *Science* 2000

Thermodynamics of molecular motors

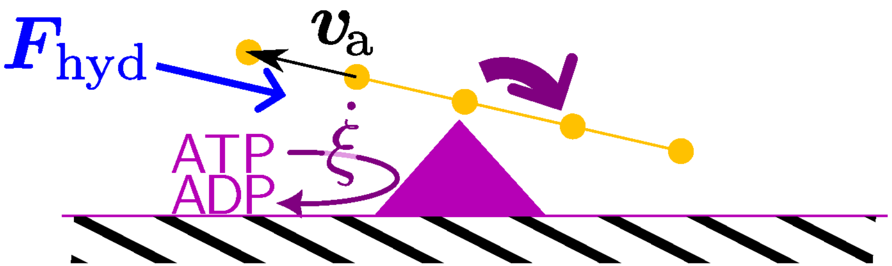


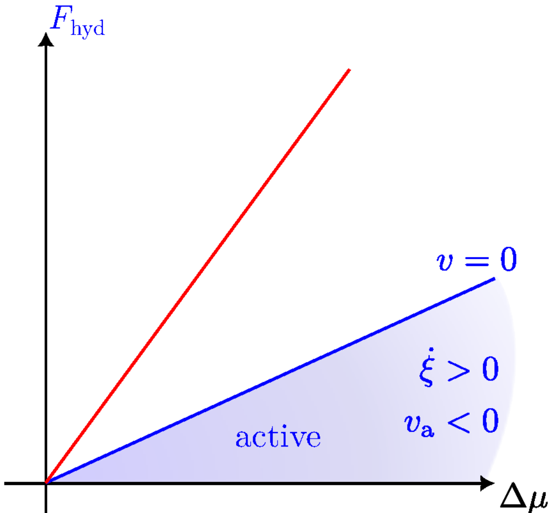


Dissipation rate:

$$\mathcal{D}_{\mathrm{m}} = F_{\mathrm{hyd}} v_{\mathrm{a}} + \dot{\xi}\Delta\mu \geq 0$$

Thermodynamics of molecular motors



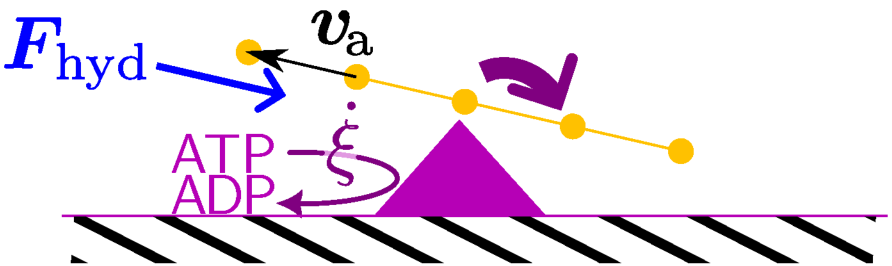


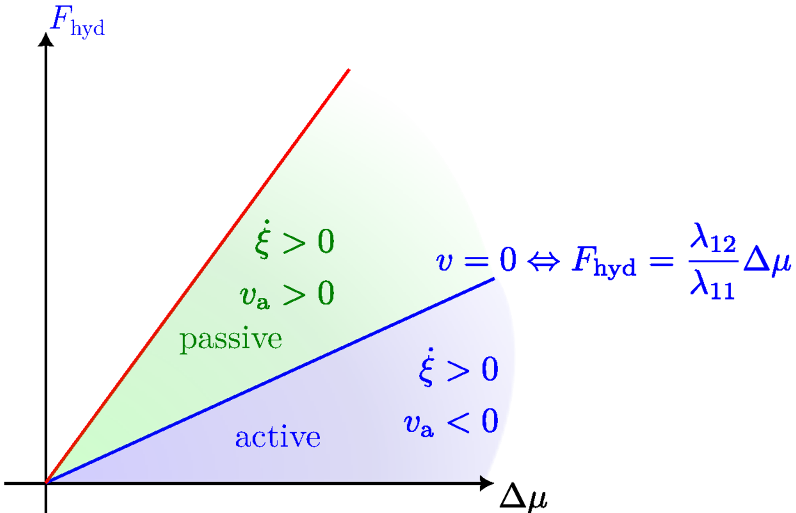
Dissipation rate:

$$\mathcal{D}_{\mathrm{m}} = \underbrace{F_{\mathrm{hyd}} v_{\mathrm{a}}}_{\substack{<\,0 \text{ when} \\ \text{work is performed}}} + \dot{\xi}\Delta\mu \geq 0$$

Jülicher, Ajdari and Prost, Modeling molecular motors,
Rev. Mod. Phys., 1997, 69(4):1269–1282

Thermodynamics of molecular motors





Dissipation rate:

$$\mathcal{D}_{\mathrm{m}} = \underbrace{F_{\mathrm{hyd}} v_{\mathrm{a}}}_{\substack{<0 \text{ when} \\ \text{work is performed}}} + \dot{\xi}\Delta\mu \geq 0$$

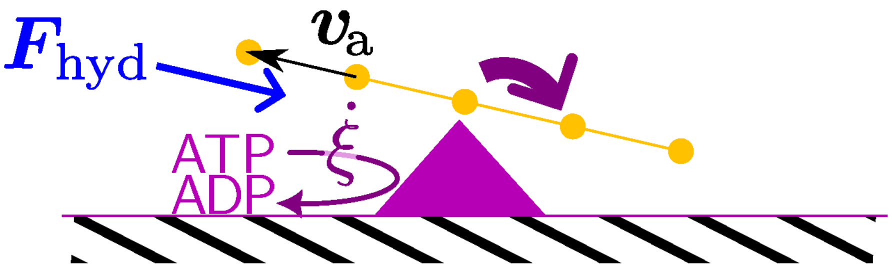
Onsager near equilibrium expansion:

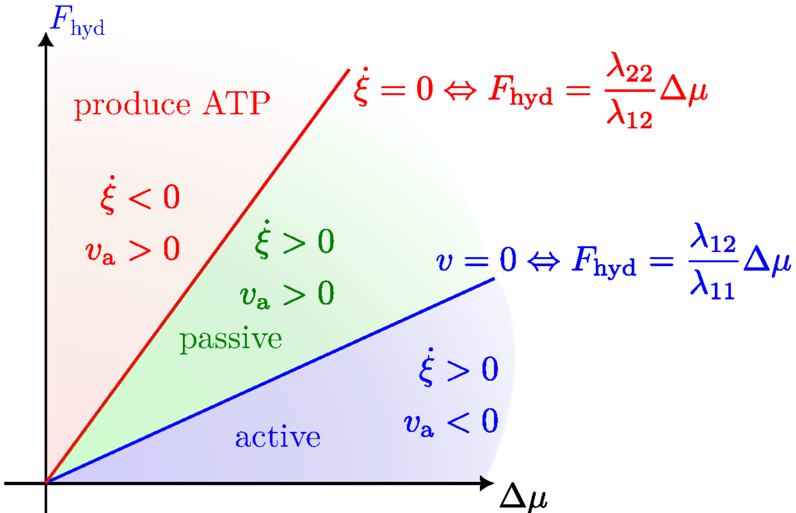
$$\begin{aligned} v_{\mathrm{a}} &= \lambda_{11} F_{\mathrm{hyd}} - \lambda_{12}\Delta\mu \\ \dot{\xi} &= -\lambda_{12} F_{\mathrm{hyd}} + \lambda_{22}\Delta\mu \end{aligned}$$

with $\lambda_{11}\lambda_{22} - (\lambda_{12})^2 \geq 0$.

Jülicher, Ajdari and Prost, Modeling molecular motors, Rev. Mod. Phys., 1997, 69(4):1269–1282

Thermodynamics of molecular motors





Dissipation rate:

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Lau, Lacoste and Mallick, 2007
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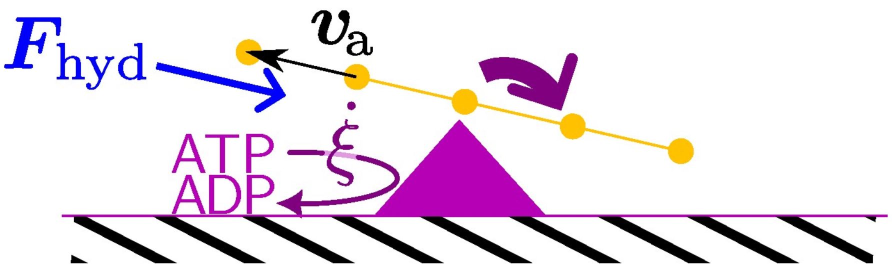
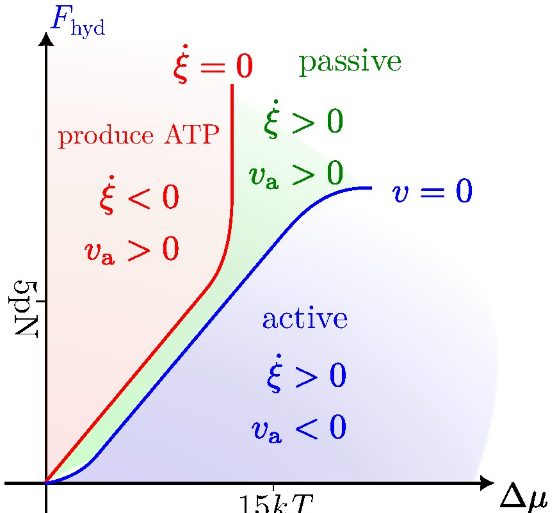
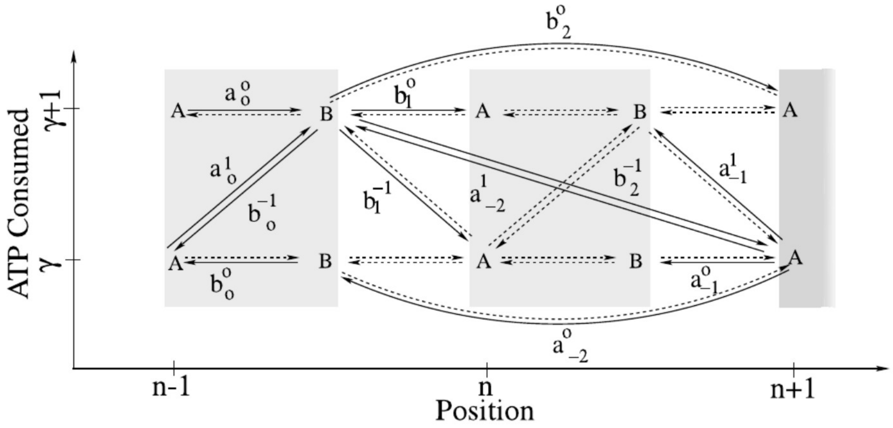
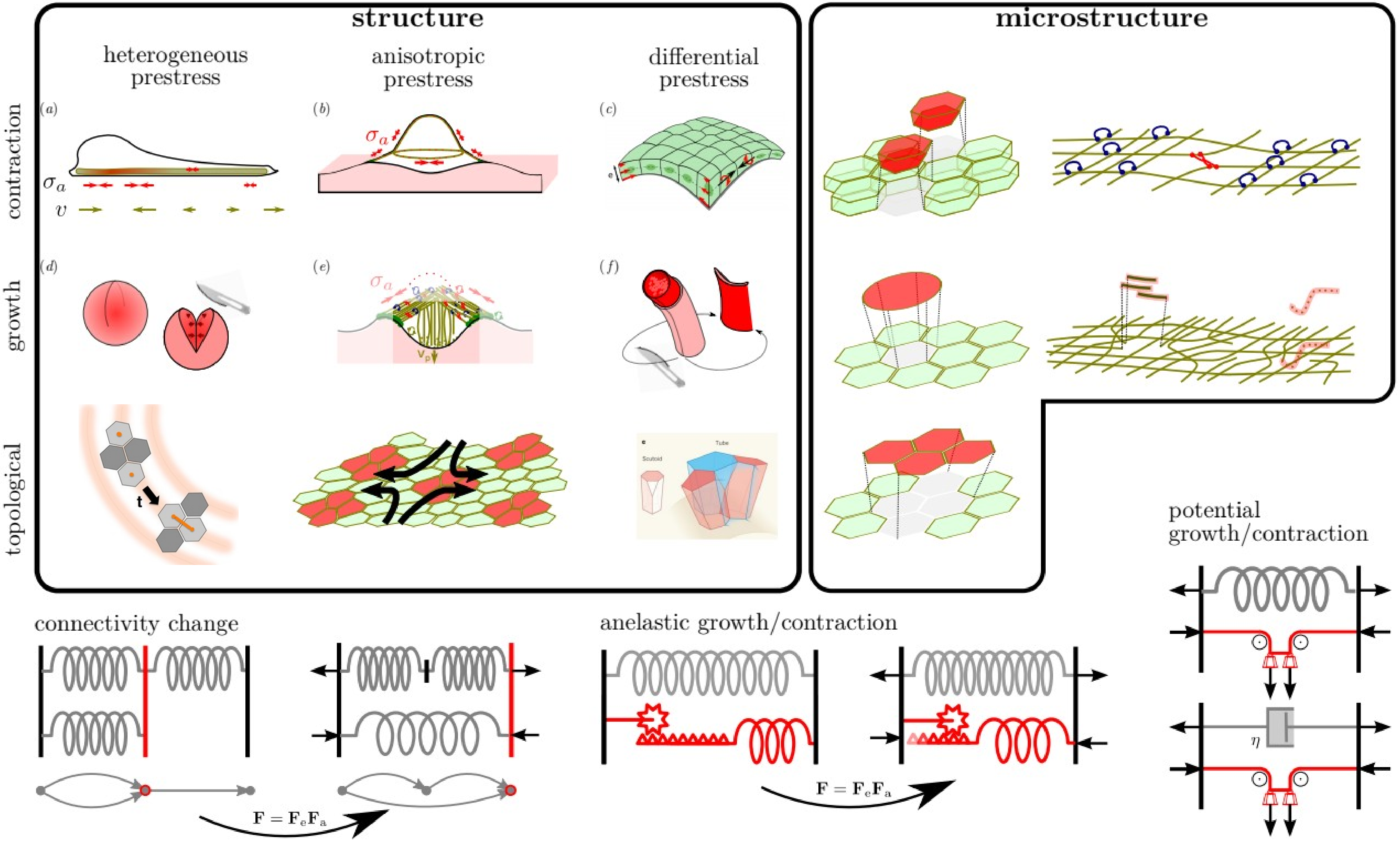
Thermodynamics of molecular motors

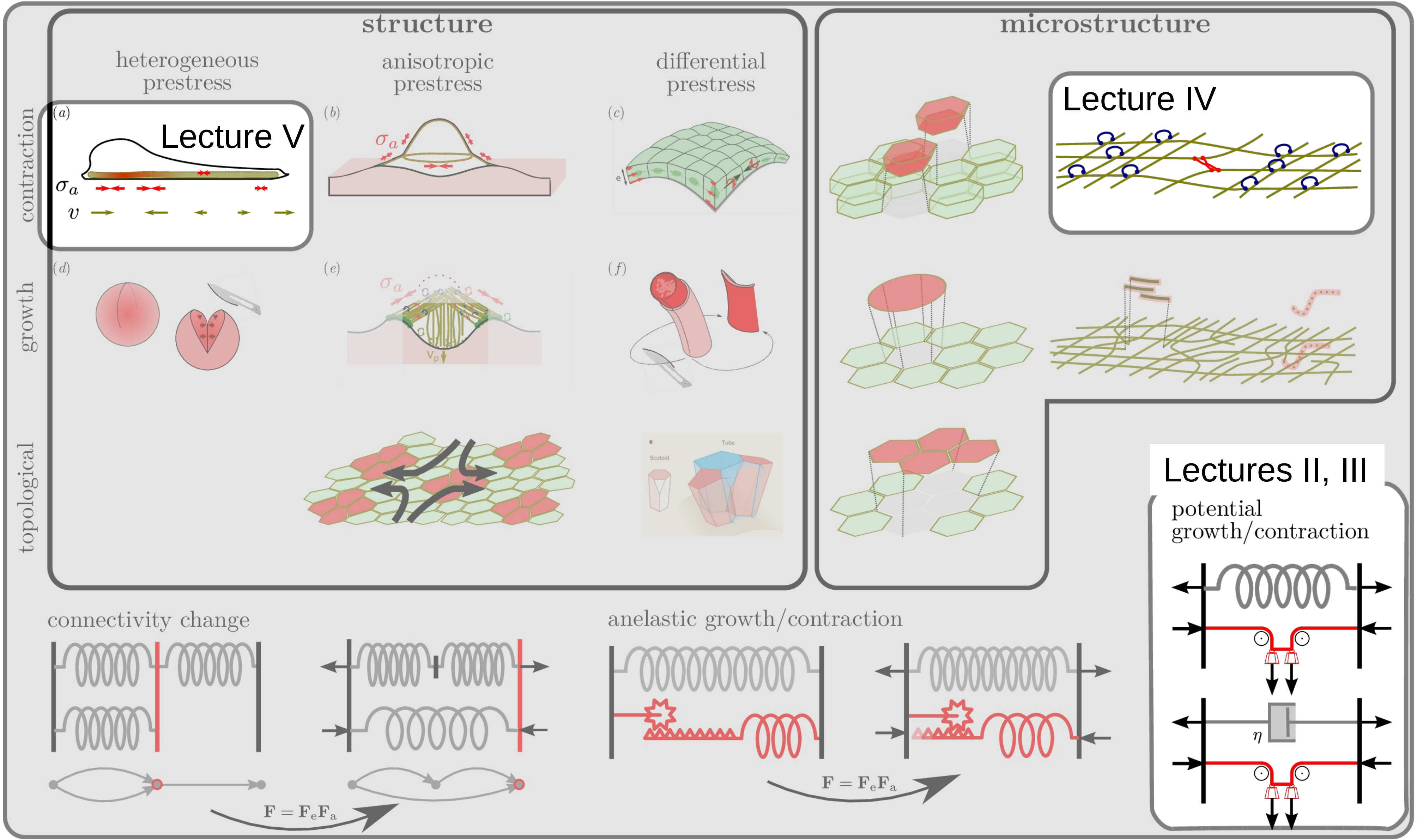






Summary and programme


structure
microstructure
heterogeneous prestress
anisotropic prestress
differential prestress
contraction
growth
topological
(a)
(b)
(c)
(d)
(e)
(f)
σ_a
v
v_p
t
Tube
Scutoid
potential growth/contraction
η
connectivity change
anelastic growth/contraction
$\mathbf{F} = \mathbf{F}_e\mathbf{F}_a$
$\mathbf{F} = \mathbf{F}_e\mathbf{F}_a$


structure
microstructure
heterogeneous prestress
anisotropic prestress
differential prestress
contraction
growth
topological
(a)
Lecture V
σ_a
v
(b)
σ_a
(c)
(d)
(e)
σ_a
(f)
Scutoid
Tube
Lecture IV
Lectures II, III
potential growth/contraction
η
connectivity change
$\mathbf{F} = \mathbf{F}_e\mathbf{F}_a$
anelastic growth/contraction
$\mathbf{F} = \mathbf{F}_e\mathbf{F}_a$