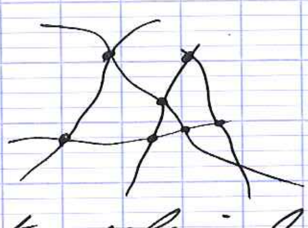
Entropic elasticity of a semiflexible filament



Networks of semiflexible filaments, e.g., actin filaments, are the mechanical scaffold that confer the cell with some of its most important mechanical characteristics. As the network gets deformed, forces are exerted on individual sections of the filaments btw two crosslinks. Their response to longitudinal forces is dom. by a spring-like elasticity coming from the straightening out of their transverse fluctuations, as we see here. We look for the force-extension relat° of that nonlinear spring.

I) Energy of a filament

The filament is almost inextensible but bends under thermal fluctuations. Thus its total arclength S is fixed but its end-to-end length L fluctuates.

The position of point s on the filament is given by
$$\vec{r}(s) = z(s)\cdot\hat{z} + \underbrace{\vec{r}_\perp(s)}_{\text{transverse displ.} = x(s)\hat{x} + y(s)\hat{y}}$$
$$\vec{r}_\perp(0) = \vec{r}_\perp(S) = 0$$

The molecular bonds in the filament like to keep it straight. Thus its energy density is a f^n of its local

curvature c with a minimum at $c=0$. To harmonic order:

$$\underbrace{E_b}_{\text{"bending"}} = \underbrace{\frac{k_B T l_p}{2}}_{\text{a coefficient}} \int_0^S c^2(s)\, ds$$

where l_p is the typical distance over which the filament bends in the absence of an external force: its persistence length.

Since for a curve $\vec{t} = \partial_s \vec{r}$ and $c\vec{n} = \partial_s \vec{t}$ we have

$$E_b = \frac{k_B T l_p}{2} \int_0^S \left(\partial_s^2 \vec{r}\right)^2 ds$$

The tension contributes $E_t = -F \cdot L = -F \int_0^S dz \cancel{= -F\int_0^S \frac{ds}{\sqrt{1+(\partial_z \vec{r}_\perp)^2}}}$

$$= -F \int_0^S ds \sqrt{1-(\partial_s \vec{r}_\perp)^2}$$

To lowest order in the ~~slope~~ slope

$$E = E_b + E_t \simeq \int_0^S \left[\frac{k_B T l_p}{2}\left(\partial_z^2 \vec{r}_\perp\right)^2 + \frac{F}{2}\left(\partial_z \vec{r}_\perp\right)^2\right] dz + ct$$

II) Force-extension relation

We let $\vec{r}_\perp(s) = \sum_{n=1}^{+\infty} \vec{\rho}_n \sin\left(\frac{n\pi z}{S}\right)$ w/ $\vec{\rho}_n = \tilde{x}_n \cdot \hat{x} + \tilde{y}_n \cdot \hat{y}$

Then

$$E = \frac{S}{2} \cdot \sum_{n=1}^{+\infty} \left[\frac{k_B T l_p}{2}\left(\frac{n\pi}{S}\right)^4 + \frac{F}{2}\left(\frac{n\pi}{S}\right)^2\right] \vec{\rho}_n^{\,2}$$

$$= \sum_{n=1}^{+\infty} \left\{ \left[\frac{k_B T l_p}{2}\frac{(n\pi)^4}{S^3} + \frac{F}{2}\frac{(n\pi)^2}{S}\right]\tilde{x}_n^2 + \left[\frac{k_B T l_p}{2}\frac{(n\pi)^4}{S^3} + \frac{F}{2}\frac{(n\pi)^2}{S}\right]\tilde{y}_n^2 \right\}$$

Equipartition implies that each harmonic d° of freedom has avg energy $\frac{k_B T}{2}$:

$$\left(\frac{k_B T l_p}{2}\frac{(n\pi)^4}{S^3} + \frac{F}{2}\frac{(n\pi)^2}{2}\right)\frac{1}{2}\langle \tilde{x}_n^2 \rangle = \frac{k_B T}{2}$$

Thus

$$\langle \tilde{x}_n^2 \rangle = \langle \tilde{y}_n^2 \rangle = \frac{2S^3}{\pi^4 \ell_p} \cdot \frac{1}{n^4 + \varphi n^2} \quad w/\ \varphi = \frac{F \cdot S^2}{\pi^2 k_B T \ell_p}$$

And the length of the filament is

$$\langle L \rangle \underset{\substack{\text{small}\\ \text{slope}}}{\simeq} S - \left\langle \frac{1}{2} \int_0^S (\partial_z \vec{r}_\perp)^2 \, dz \right\rangle$$

$$= S - \frac{S}{4} \sum_{n=1}^{+\infty} \left(\frac{n\pi}{S}\right)^2 \cdot \left(\langle \tilde{x}_n^2 \rangle + \langle \tilde{y}_n^2 \rangle \right)$$

$$= S - \frac{S^2}{\pi^2 \ell_p} \sum_{n=1}^{+\infty} \frac{n^2}{n^4 + \varphi n^2}$$

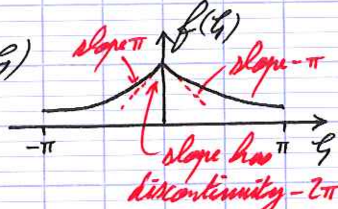
$$= S - \frac{S^2}{\pi^2 \ell_p} \sum_{n=1}^{+\infty} \frac{1}{n^2 + \varphi}$$

$$\langle L \rangle = S - \frac{S^2}{\ell_p} \, \frac{(\pi\sqrt{\varphi}) \cdot \coth(\pi\sqrt{\varphi}) - 1}{2\pi^2 \varphi}$$

<u>Proof of the last equality:</u>

Let $f(\xi) = \sum_{n=-\infty}^{+\infty} \frac{e^{in\xi}}{n^2+\varphi}$; then $\sum_{n=1}^{+\infty} \frac{1}{n^2+\varphi} = \frac{1}{2}\left(f(0) - \frac{1}{\varphi}\right)$

and f is even and 2π-periodic:



$$-f''(\xi) + \varphi f(\xi) = \sum_{n=-\infty}^{+\infty} e^{in\xi} = 2\pi\delta(\xi)$$

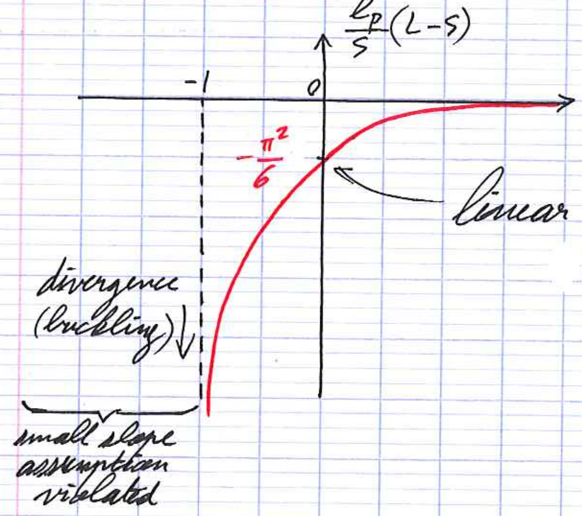
$$\Longleftrightarrow f'' - \varphi f = -2\pi\,\delta(\xi)$$

Thus on $]0,\pi]$ $f(\xi) = A e^{\sqrt{\varphi}\cdot\xi} + B e^{-\sqrt{\varphi}\cdot\xi}$

with $f'(0) = -\pi$ and $f'(\pi) = 0$ yielding

$B = A e^{2\pi\sqrt{\varphi}}$ and $A = \frac{\pi}{\sqrt{\varphi}} \cdot \frac{1}{e^{2\pi\sqrt{\varphi}} - 1} \Rightarrow f(0) = A + B = \frac{\pi}{\sqrt{\varphi}} \coth(\pi\sqrt{\varphi})$.

III) Discussion



$\varphi = \frac{F}{F_b}$ with buckling force $F_b = \frac{\pi^2 k_B T \ell_p}{S^2}$

linear response:

$$F \sim \underbrace{\frac{90\, k_B T \ell_p^2}{S^4}}_{=\alpha} \delta L$$

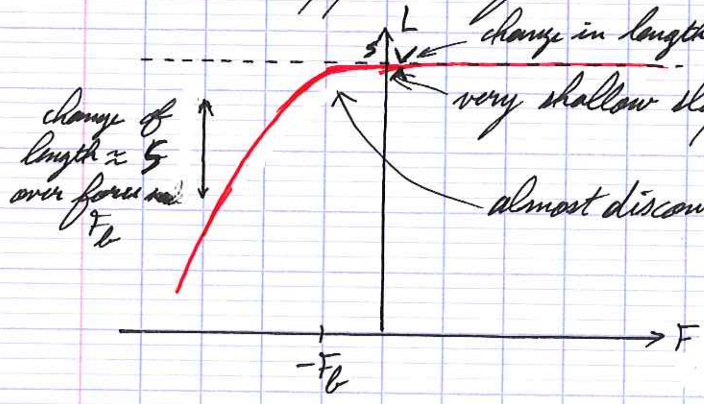
stiffness; remember $\propto \frac{k_B T \ell_p^2}{S^4}$ (prefactor fairly large but dependent on $B(s)$)

For actin $\ell_p \simeq 10\,\mu m$, and $S = 400\,nm$ is typical. Then $F_b = 2.5\,pN$. Molecular motors exert a fract of pN to several dozen pN if combined together. For $F = 1\,pN$, what is the displacement?

Or $\frac{\delta L}{F} = \frac{1}{\alpha} = 0.7\,nm/pN$ imperceptible

$\rightarrow$ Dchanges to 28 nm/pN for $S = 1\,\mu m$ because fourth power of S.

What happens beyond buckling?



change in length $\simeq \frac{S^2}{\ell_p}$ over force scale F_b

very shallow slope

almost discontinuous: goes from slope

$$\frac{\delta L}{F} \simeq \frac{S^2/\ell_p}{F_b} \simeq 5\,nm/pN$$

(forgetting prefactors)

to

$$\frac{\delta L}{F} \simeq \frac{S}{F_b} \simeq 150\,nm/pN$$

(for $S = 400\,nm$)

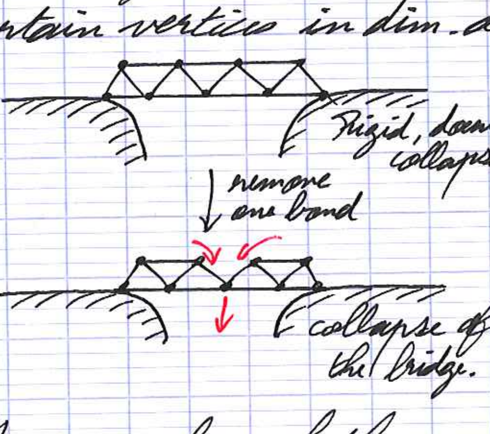
The filament undergoes a spectacular apparent softening upon buckling: go from pulling fluctuations out to bending the filament.

Chapter II: from filament to gel: effective medium theory

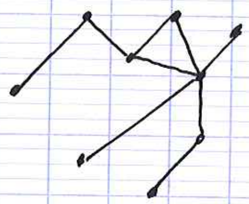
While we now have an idea of the tensile strength of a single bond in cytoskeletal networks, the relationship between this quantity and the overall modulus of the gel is not completely obvious in a random network; here we will discuss ~~[illegible]~~ the most basic version of a widely used mean-field method to answer this question. We will see that the modulus of the gel strongly depends on the connectivity of the network, leading to a paradox for crosslinked filament gels.

I) Maxwell's constraint-counting argument

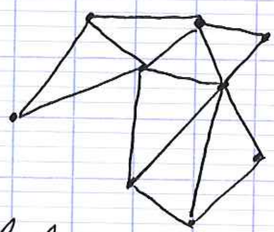
Consider an arbitrary mechanical frame made of stiff springs connected at certain vertices in dim. d. Is it rigid? One can think of this in the frame of a bridge btw the two sides of a gorge:



More generally, if I grab two points in a large frame I can ask whether I will be free to move them w/ respect to the other without compressing any spring:



Low connectivity: the answer is yes.



High connectivity: no.

What is the critical connectivity? The simplest argument consists in counting constraints in a frame with n_s springs and n_v vertices.
We define

N_f : # of degrees of freedom
N_c : # of constraints imposed by stiff springs

If $N_c > N_f$ the frame will be rigid* and

$$N_f = d \cdot n_v$$
$$N_c = n_s$$

* neglecting trivial global rotations and translations in the $N \to \infty$ limit.

~~Thus~~ Defining $\langle z \rangle$ as the average connectivity of the vertices each vertex is associated with $\frac{\langle z \rangle}{2}$ springs and

$$\frac{\langle z \rangle}{2} n_v = \quad n_s$$

Thus rigidity $\Leftrightarrow N_c > N_f$

$$\Leftrightarrow \frac{\langle z \rangle}{2} n_v > d\, n_v$$
$$\Leftrightarrow \langle z \rangle > \quad 2d$$

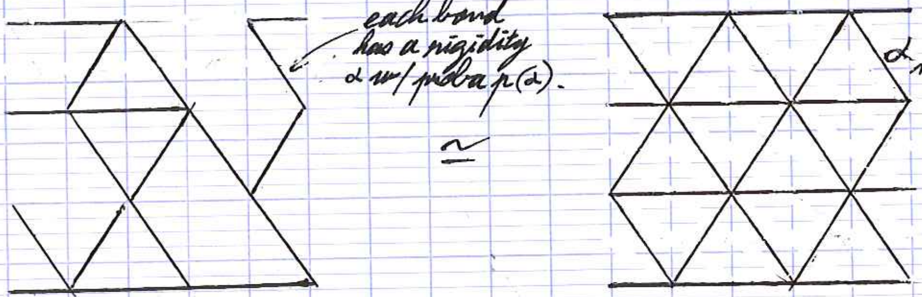
Thus the critical connectivity in $d=2$ is 4, and in $d=3$ it is 6. Note that this rigidity percolation threshold is distinct from and higher than the ordinary connectivity percolation threshold.

II) Effective medium theory for a simple network

After Feng & Thorpe, Phys. Rev. B 31, 276 (1985)

Beyond the simple constraint counting argument, can we predict what the modulus of the gel will be for a given average coordination?

Here we present a mean-field methods that yields quantitatively excellent results for simple central-force spring networks and is widely used even beyond that simple situation. It consists in approximating a randomly depleted network w/ a regular one:



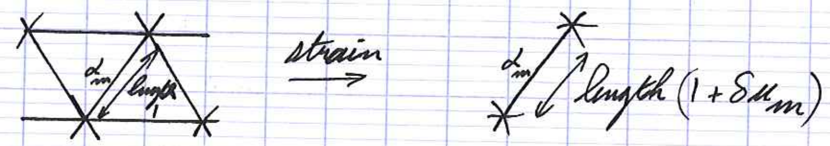
where α_m has to be determined self-consistently; this is our task in this section.

Note:
In practice we will consider $p(\alpha)$ such that
$\alpha = 1$ w/ proba p
$\alpha = 0$ w/ proba $1-p$

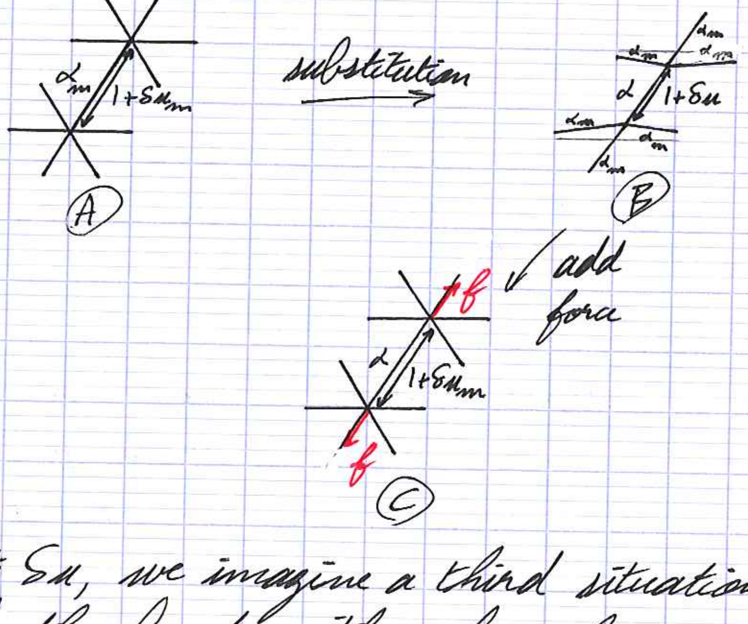
corresponding to a random bond depletion scheme.

1°) Formulating the self-consistency condition

Starting from the equivalent regular network, we exert a strain δu_m; since all bonds in the network are equivalent, all extend by an amount δu_m:



Starting from the strained state, we imagine replacing one of the bonds by a random bond of rigidity α (and rest length 1) drawn from the distribution $p(\alpha)$. If the bond is stiffer than α_m, the distance btw its two vertices will shrink, and vice-versa. Our self-consistency condition consists in demanding that the bond neither shrink nor extend on average:

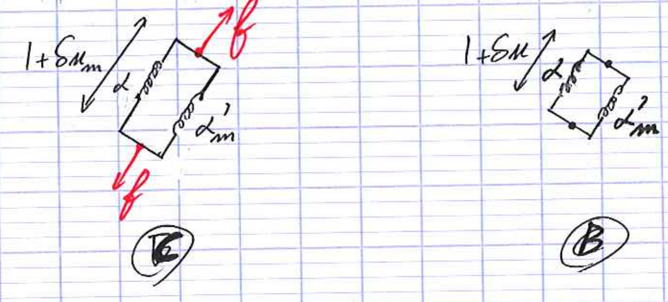


To compute δu, we imagine a third situation where we pull the bond with a force f so as to restore it to the length $(1+\delta u_m)$. Clearly

$$f + \alpha\,\delta u_m = \alpha_m\,\delta u_m$$

as seen from the fact that the sum of the bond tension + external force must be the same in (A) and in (C).

We now compare situations (B) and (C). The distance btw the two nodes of interest is given by the balance of forces between the bond of interest, the external force and the rest of the network. To linear order, the force exerted by the rest of the network is related to the displacement through an effective spring constant α_m':



Clearly $f = (\delta u_m - \delta u) \cdot (\alpha + \alpha_m')$.

Equating our two expressions for f we get

$$(\alpha + \alpha_m')(\delta u_m - \delta u) = (\alpha_m - \alpha)\,\delta u_m$$

$$\Longleftrightarrow \quad \delta u_m - \delta u = \frac{\alpha_m - \alpha}{\alpha_m' + \alpha}\,\delta u_m$$

and thus formulate our self-consistency condition:

$$\underline{\delta u_m = \langle \delta u \rangle}$$

$$\Longleftrightarrow \quad \left\langle \frac{\alpha_m - \alpha}{\alpha_m' + \alpha} \right\rangle = \int p(\alpha)\,\frac{\alpha_m - \alpha}{\alpha_m' + \alpha}\,d\alpha = 0,$$

which we must solve over the variable α_m to conclude.

~~2°) Elasticity of the surrounding network~~

~~Our self-consistent equation can only be tackled once we relate α_m' to α_m, which we do here.~~

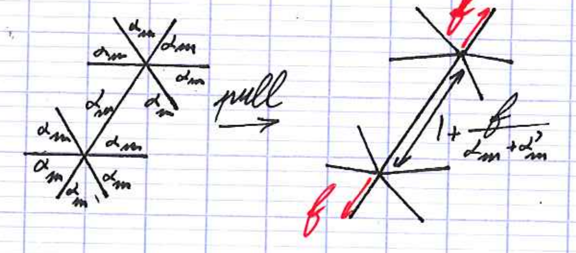
~~Consider the response of the network to an arbitrary set of forces $\vec{F}_i$ exerted on each node i; at equilibrium the forces are related to the displacements $\vec{u}_i$ through~~

$$\cancel{\vec{F}_i = -\frac{\partial V}{\partial \vec{u}_i},}$$

~~with $V = \frac{\alpha_m}{2} \sum_{\langle ij \rangle} \left[(\vec{u}_i - \vec{u}_j) \cdot \hat{r}_{ij} \right]^2$; here $\hat{r}_{ij}$ is the unit vector associated w/ bond $\langle ij \rangle$ and the sum is over nearest neighbors. As a result:~~

2°) Elasticity of the surrounding medium

Our self-consistent condition can only be tackled once we relate α_m' to α_m. Considering a pure α_m network and pulling two neighboring bonds apart, the effective spring ct relating force to displacement there will be $\alpha_m + \alpha_m'$.



Clearly that spring constant is linear in α_m, as all bonds have rigidity α_m. We denote by a^* the geometrical prefactor such that

$$\alpha_m + \alpha_m' = \frac{\alpha_m}{a^*}$$

and $a^* \in]0,1[$ (the whole network is more rigid than a single spring. a^* can be obtained from a direct calculation on the network, but here we use a

shortcut: For our specific proba. distribution

$$\mu(\alpha) = p\,\delta(\alpha-1) + (1-p)\,\delta(\alpha)$$

we have

$$\left\langle \frac{\alpha_m-\alpha}{\alpha_m'+\alpha} \right\rangle = \left\langle \frac{\alpha_m-\alpha}{\alpha_m\left(\frac{1}{a^*}-1\right)+\alpha} \right\rangle$$

$$= p\,\frac{\alpha_m-1}{\alpha_m\left(\frac{1}{a^*}-1\right)+1} + (1-p)\cdot\frac{\alpha_m}{\alpha_m\left(\frac{1}{a^*}-1\right)}$$

which vanishes iff

$$0 = p(\alpha_m-1)\cdot\cancel{\alpha_m}\left(\frac{1}{a^*}-1\right) + (1-p)\cancel{\alpha_m}\left[\alpha_m\left(\frac{1}{a^*}-1\right)+1\right]$$

$$\Leftrightarrow\quad 0 = p(\alpha_m-1)\cdot(1-a^*) + (1-p)\left[\alpha_m(1-a^*)+a^*\right]$$

$$\Leftrightarrow\quad 0 = \alpha_m\left[p(1-a^*) + (1-p)(1-a^*)\right] - p(1-a^*) + (1-p)a^*$$

$$\Leftrightarrow\quad \underline{\alpha_m = \frac{p-a^*}{1-a^*}}$$

Thus the effective spring constant vanishes at $p = p_c = a^*$. Recalling the Maxwell argument, we deduce that $p = a^*$ is the situation where the average connectivity is equal to $2d$. Denoting as z_{max} the connectivity of the fully connected network, we have

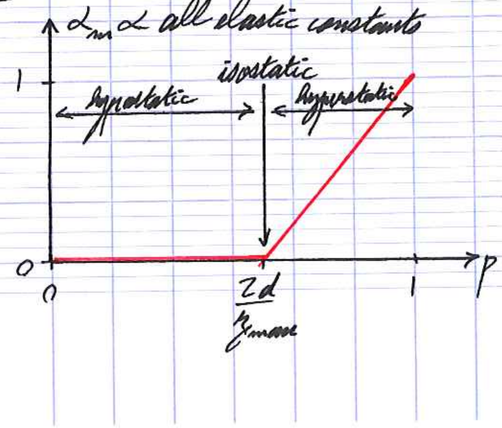
$$\langle z\rangle = p\cdot z_{max}$$

Thus

$$p_c\cdot z_{max} = 2d$$

$$\Rightarrow\quad p_c = a^* = \frac{2d}{z_{max}}$$

which is confirmed by direct calculation.

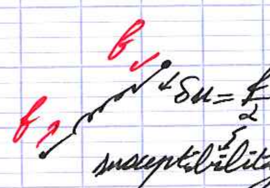


Chapter III
Elasticity: soft modes, bending and nonaffinity

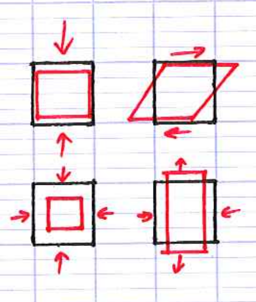
Chapter II taught us that a depleted disordered spring network is analogous to a full network of weaker springs; here we first look at how these full networks respond to large-scale stress and deformat°. Another point made in chapter II is that depleted spring networks should have no rigidity at all if the coordination of their vertices is less than $z = 6$ in dimension $d = 3$. Crosslinked actin networks typically have $z = 4$ at points where two filaments are crosslinked, and they have a substantial elastic response ($E \sim 10\,\text{Pa}$ to $1\,\text{kPa}$). Where does it come from?

I) A crash course in elasticity theory

Applying a small force on a spring induces a small displacement proportional to the force. We want to use this idea in solid pieces of material.



Instead of applying a force, we will apply a force per unit surface: a pressure/stress σ. We immediately run into a complication: there are many ways to exert a given σ to a cube, each inducing a ≠ type of displacement and potentially involving a ≠ susceptibility.



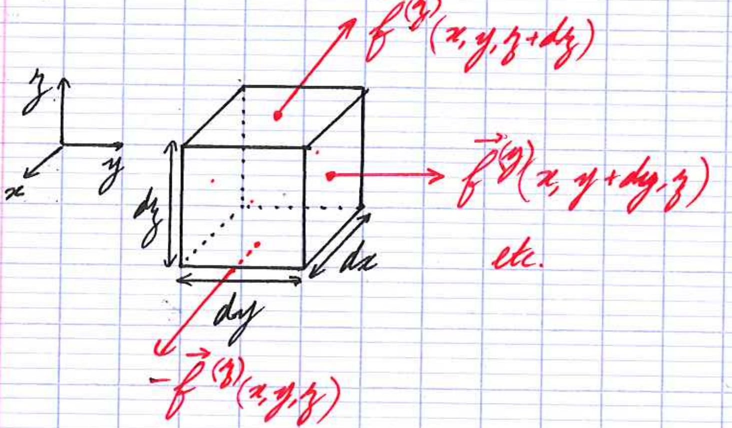
see also introductory paragraphs of Landau & Lifshitz, Theo. of elasticity

1°) Stress and strain

We introduce two qties generalizing "forces" and "displacements" to an elastic material.

Stress

Cut out a cubic piece of the material. What are the forces exerted on it by the rest of the material?



Chaque force a plusieurs composantes : $f^{(j)}_i$, et on définit donc le tenseur

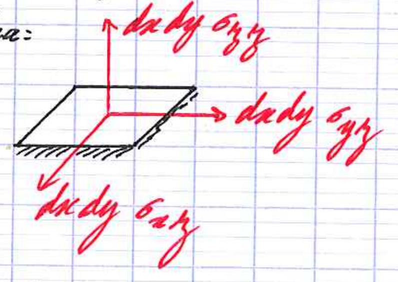
$$\sigma_{ij}(\vec{r}) = \frac{f^{(j)}_i(x,y,z)}{\prod_{k\neq j} dx_k}$$

Ex :

$$\vec{f}^{(z)} = dx\, dy\, \left(\sigma_{xz}\cdot\hat{x} + \sigma_{yz}\cdot\hat{y} + \sigma_{zz}\,\hat{z}\right)$$

units of a force per unit surface (≡ stress)

Top surface:

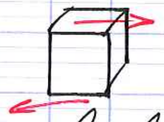


Examples

$\sigma_{zz} = \sigma_0$, others $= 0$

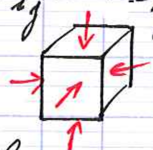
uniaxial stretching

$\sigma_{xz} = \sigma_0$



simple shear

$\sigma_{ij} = -P\,\delta_{ij}$



uniform compression (P = pressure)

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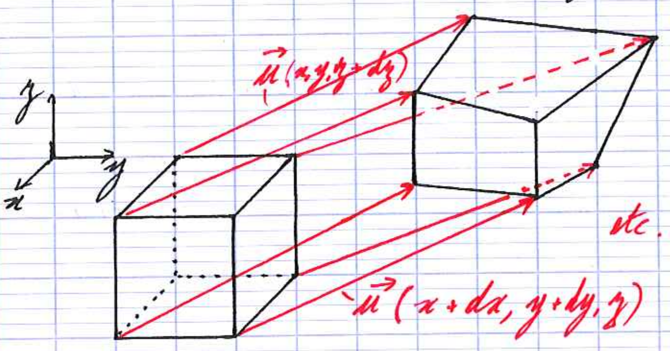
Strain

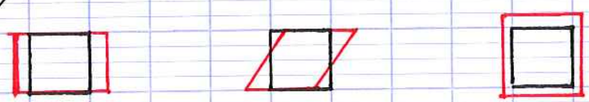
Let's look at how a cube deforms. Let $\vec{u}(x, y, z)$ be the displacement vector field.



A homogeneous displacem^t does not distort the material & does not elicit elastic stresses
$\Rightarrow$ only gradients matter.

$$\gamma_{ij} = \frac{1}{2}\left(\partial_i u_j + \partial_j u_i\right)$$

Examples in 2d



$\gamma = \begin{pmatrix} \gamma_0 & 0 \\ 0 & 0 \end{pmatrix}$ $\quad$ $\gamma = \begin{pmatrix} 0 & \gamma_0 \\ \gamma_0 & 0 \end{pmatrix}$ $\quad$ $\gamma = \begin{pmatrix} \gamma_0 & 0 \\ 0 & \gamma_0 \end{pmatrix}$

Note
$V_0 + \delta V = \det(1+\gamma) \cdot V_0$

(do this after 3°) actually)

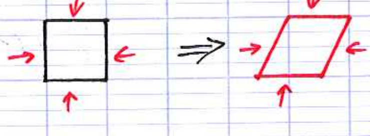
2°) Linear elasticity

As in Hooke's law small strains imply a linear relationship btw σ_{ij} and γ_{ij}. In its most general form:

$$\sigma_{ij} = K_{ijkl}\, \gamma_{kl}$$

K_{ijkl}: constant 4th-order tensor.

For an isotropic, achiral material K_{ijkl} is considerably constrained by symmetry. For instance one cannot get



as this clearly violates mirror symmetry.

In the end, K_{ijkl} has only 2 indpt components:

* $$\sigma_{ij} = 2\mu\,\gamma_{ij} + \lambda\,\gamma_{kk}\,\delta_{ij}$$

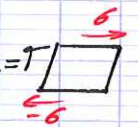
with μ, λ the Lamé parameters of the material.

Two other equivalent representations are common, where the elastic parameters have more intuitive interpretations:

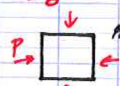
* $$\sigma_{ij} = K\,\gamma_{kk}\,\delta_{ij} + 2\mu\left(\gamma_{ij} - \frac{1}{d}\gamma_{kk}\,\delta_{ij}\right)$$

d dimension of space
μ shear modulus (same as above)
$K = \lambda + \frac{2\mu}{3}$ bulk modulus.

$\partial_y u_x = \tau$



$\sigma_{xy} = \mu\tau$



rel. change of volume $\frac{\delta V}{V_0}$

$\partial_x u_x = \partial_y u_y = \frac{\delta L_x}{L_x} = \text{etc} =$

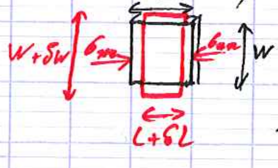
$\sigma_{ij} = -P\,\delta_{ij}$

then $P = -K\cdot\frac{\delta V}{V_0}$

* $$\sigma_{ij} = \frac{E}{1+\nu}\left(\gamma_{ij} + \frac{\sigma}{1-2\sigma}\gamma_{kk}\,\delta_{ik}\right)$$

E Young's modulus (in Pa)
ν Poisson ratio (dimensionless)

Useful for uniaxial compression:



in 2d
$$\begin{cases} \sigma_{xx} = E\cdot W^{\overset{=d-1}{2}}\cdot\delta L \\ \frac{\delta W}{W} = \nu\cdot\frac{\delta L}{L} \\ \text{so } \frac{\delta V}{V} = \frac{\delta L}{L} + 2\frac{\delta W}{W} = (1+2\nu)\frac{\delta L}{L} \end{cases}$$

$\nu = -\frac{1}{2}$ is the incompressible case.

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3°) Mechanical equilibrium

Torque balance to lowest order on the cube of 1°) yields

$$\sigma_{ij} = \sigma_{ji}$$

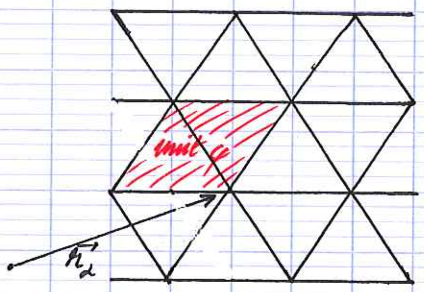
Force balance yields:

$$\nabla_i \sigma_{ij} = 0$$

In practice solving a mechanical problem will consist in solving this eqn w/ the appropriate BCs.

II) Affine deformation of a hyperstatic network.

How can we compute the elastic constants of a medium from its microscopic constituents? Here we show an example in the regular network of chapter II:



We stretch the network homogeneously

$$\Gamma_{ij} = \frac{\delta V}{V}\,\frac{\delta_{ij}}{d}$$

so that $\delta V = V\left[\det(1+\gamma)-1\right]$ is the change in volume.

The work performed reads $\delta W = -\int_0^{\delta V} P\, dV$ with $\sigma_{ij} = -P\delta_{ij}$. Thus:

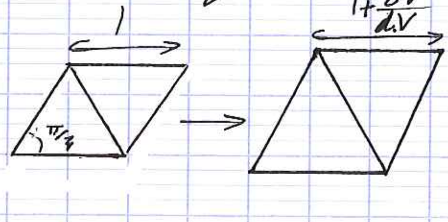
$$\delta W = V\int_0^{\delta V} \sigma_{ij}\, d\gamma_{ij} \qquad \text{(true more generally)}$$

$$= V\int_0^{\delta V} K\,\gamma_{ii}\, d\gamma_{jj}$$

$$= \frac{K}{2}\left(\gamma_{ii}^{\text{final}}\right)^2$$

$$= \frac{K}{2}\,\frac{(\delta V)^2}{V}$$

By transl. symmetry, all unit cells deform in an identical way.



Thus the deformation is affine:

$$\delta \vec{r}_\alpha = \Gamma_{ij}\cdot r_{(\alpha)i}$$

Each unit cell contains $1 + 4\times\frac{1}{2}$ springs, each with an energy $\delta e = \frac{\alpha}{2}\cdot\left(\frac{\delta V}{2V}\right)^2$. Thus $\delta W = 3\cdot\delta e$. Since $V = \sin\frac{\pi}{3} = \frac{\sqrt{3}}{2}$, we have

$$\frac{K}{2}\,\frac{(\delta V)^2}{V} = \frac{\alpha}{8}\cdot\frac{(\delta V)^2}{V^2}$$

$$\Longleftrightarrow K = \frac{\alpha}{4V} = \frac{\alpha}{2\sqrt{3}} \simeq 0{,}4\ \text{pN/nm}$$

$(\xi = 400\,\text{nm})$

In 3D: $K_{3D} \simeq \frac{k_B T \ell_p^2}{\xi^5} \simeq 40\,\text{Pa}$
(scaling)

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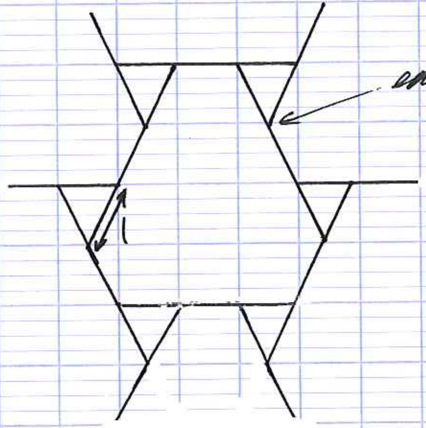
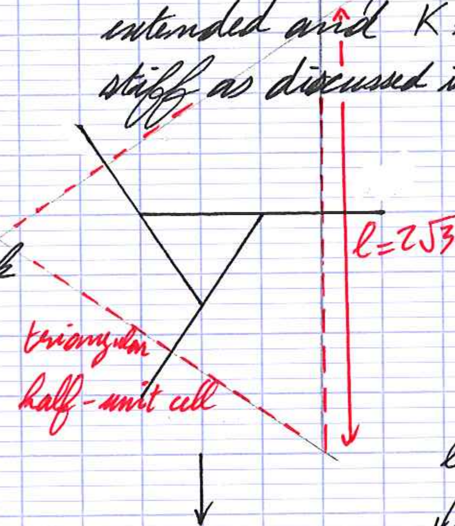
III) Bending-dominated elasticity of a hypostatic network

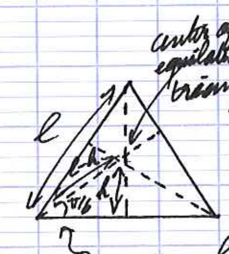
We propose a model of a filament network w/ connectivity below the Maxwell threshold, similar to real gels (presumably):



If we deform the network affinely (consider isotropic stretch), each spring gets extended and $K \simeq \alpha$: very stiff as discussed in ch. I.



Due to its low connectivity however, the spring network can be deformed w/ out stretching any bond by rotating each triangular plaquette.



$\sin\frac{\pi}{6} = \frac{h}{l-h} = \frac{\sqrt{3}}{2}$

$\Rightarrow h = \frac{l}{2\sqrt{3}}$

$\Rightarrow A = \frac{\sqrt{3}}{4} l^2$

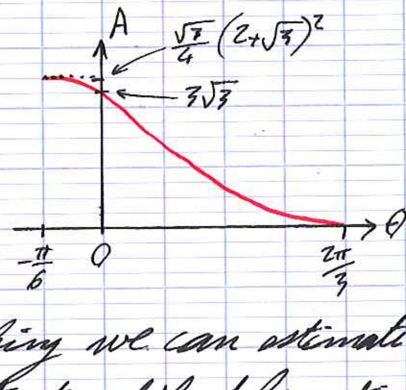
$= 3\sqrt{3} \cdot h^2$

Clearly this decreases the area of the unit cell at no cost in stretching energy:

$$h = \frac{1}{2} + x = \frac{1}{2} + \frac{1}{\sqrt{3}}\cos\left(\frac{\pi}{6}+\theta\right)$$

$$\Rightarrow A = 3\sqrt{3}\left[\frac{1}{2} + \frac{1}{\sqrt{3}}\cos\left(\frac{\pi}{6}+\theta\right)\right]^2$$

$$\Rightarrow \frac{dA}{d\theta} = -6\left[\frac{1}{2} + \frac{1}{\sqrt{3}}\cos\left(\frac{\pi}{6}+\theta\right)\right]\sin\left(\frac{\pi}{6}+\theta\right)$$



However this nonaffine soft mode of deformation bends filaments; if this cost is weak compared to stretching we can estimate the associated cost w/ out changing the structure of the deformation.

We use the same hinge energy as in the simulation:

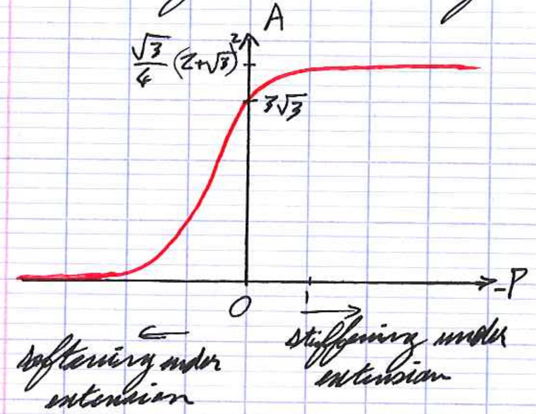
$$e = \frac{k_B T l_p}{\xi} \quad \underbrace{2\sin^2\left(\frac{\theta}{2}\right)}_{= \frac{1-\cos\theta}{2}}$$

Thus for a half-unit cell $E = 3e = 6\,\frac{k_B T l_p}{\xi_{a = 1\text{ here}}} \cdot \sin^2\left(\frac{\theta}{2}\right)$

$$\frac{dE}{d\theta} = 3\, k_B T l_p \sin\theta$$

$$\Rightarrow \quad P = -\frac{dE}{dA} = k_B T l_p \frac{\sin\theta}{\left[1+\frac{2}{\sqrt{3}}\cos\left(\frac{\pi}{6}+\theta\right)\right]\sin\left(\frac{\pi}{6}+\theta\right)}$$

Plotting this similarly to the force-extension diagram of ch. I:



Linear modulus is

$$\frac{dP}{dA}(\theta=0) = \frac{k_B T l_p}{\xi^3} \simeq 6\times10^{-4}\ \mathrm{pN/nm}$$

⚠ This is linear & nonaffine

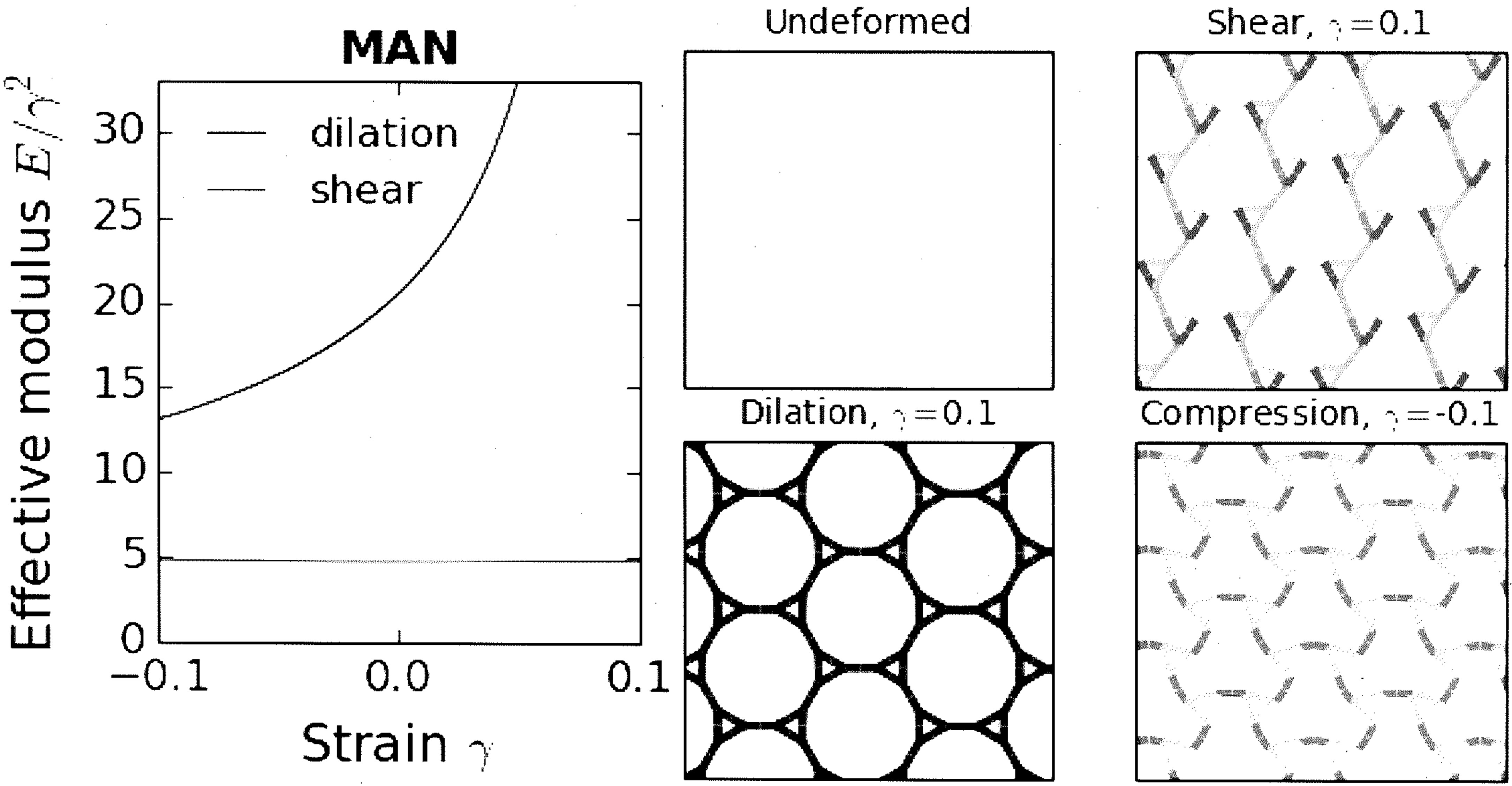
In 3D (scaling)

$$K_{3D} \approx \frac{k_B T l_p}{\xi^4} \simeq 1.6\ \mathrm{Pa}$$

This is indeed much softer than the stretching-dom. net., esp. if the prefactors are taken into account.

IV) Conclusions

- Hypostatic networks avoid costly affine deformations by deforming along nonaffine soft modes.
- In the presence of a stabilizing weak interaction (e.g., bending, or prestress in rubber elasticity), these soft modes acquire a modulus w/out chging their spatial struct.
- Elasticity of hypostatic networks is nonaffine yet linear at small deformation; also bending-dominated (modulus $\propto k_B T l_p$ not $k_B T l_p^2$).

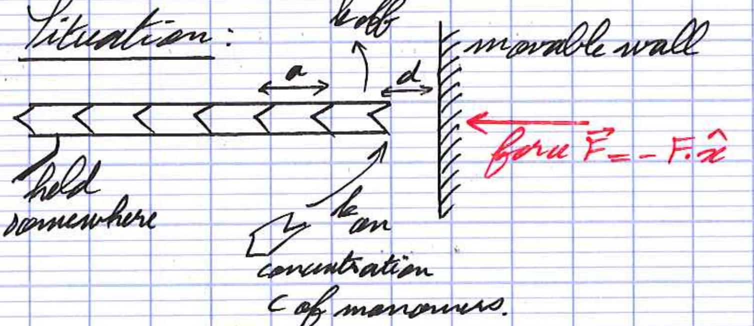

MAN
dilation
shear
Effective modulus E/γ^2
Strain γ
0
5
10
15
20
25
30
−0.1
0.0
0.1
Undeformed
Shear, $\gamma = 0.1$
Dilation, $\gamma = 0.1$
Compression, $\gamma = -0.1$

The brownian ratchet

Actin and other cytoskeletal filaments are very dynamic, getting polymerized & depolymerized from either one of their (non-identical) ends, crosslinked, branched, cut, capped in a controlled fashion by specialized associated proteins. As such, their function in the cell goes well beyond the passive, elastic behaviors described in part I: they can generate force and act as motors for the cell. Here we look at the most simplified model of the simplest of these functions: the brownian ratchet.

<u>Original proposal</u>:
Peskin, Odell, Oster Biophys. J. 65, 316 (1993)

<u>Situation</u>:



At what velocity does the filament push the wall as a f^n of c, F?

We have an infinity of chemical equations:

$$\underbrace{F_n}_{\text{filament of length } n} + \underbrace{M}_{\text{monomer}} \underset{k_{off}}{\overset{k_{on}}{\rightleftharpoons}} F_{n+1}$$

Concentrating on a single filament

$$\frac{d\langle L\rangle}{dt} = a(k_{on}\cdot c - k_{off}) \quad \text{w/out wall}$$
$$= a k_{off}\left(\frac{c}{c^*}-1\right) \quad \text{w/ } c^* = \frac{k_{off}}{k_{on}} \text{ equil. concentrat.}$$

With a wall, the brownian ratchet model proposes that polymerization proceeds with the same rate if $\delta x > a$ and is impossible for $\delta x < a$. Depolym. is unaffected (which is of course an approximation).

At fixed L, the energy associated with the position of the wall is

$$E = F\cdot \delta x$$

Hence $p(\delta x) \propto e^{-\frac{F\cdot\delta x}{k_B T}}$

Thus at a given instant the polymerizal rate is

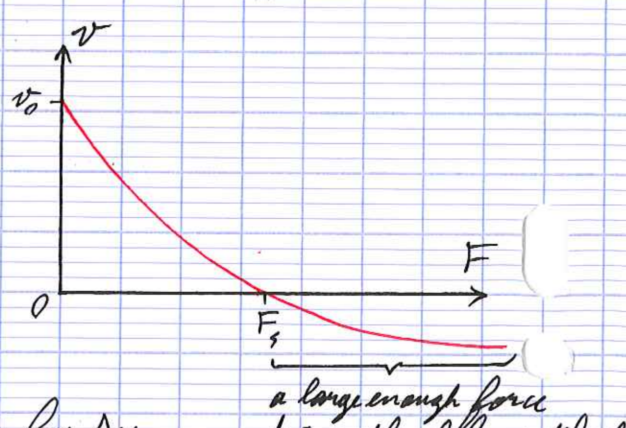
- $k_{off}\frac{c}{c^*}$ w/ proba $\int_a^{+\infty} p(\delta x)\cdot d\delta x$
- 0 w/ proba $\int_0^a p(\delta x)\cdot d\delta x$

And in the end

$$v = \frac{\int_a^{+\infty} e^{-\frac{F\cdot\delta x}{k_BT}} d\delta x}{\int_0^{+\infty} e^{-\frac{F\cdot\delta x}{k_BT}} d(\delta x)}\cdot k_{off}\frac{c}{c^*} + \frac{\int_0^a e^{-\frac{F\cdot\delta x}{k_BT}} d\delta x}{\int_0^{+\infty} e^{-\frac{F\cdot\delta x}{k_BT}} d\delta x}\cdot 0 - k_{off}$$
$$= a k_{off}\left(\frac{c}{c^*}e^{-\frac{Fa}{k_BT}} - 1\right)$$

The stall force reads

$$F_s = \frac{k_BT}{a}\ln\left(\frac{c}{c^*}\right)$$



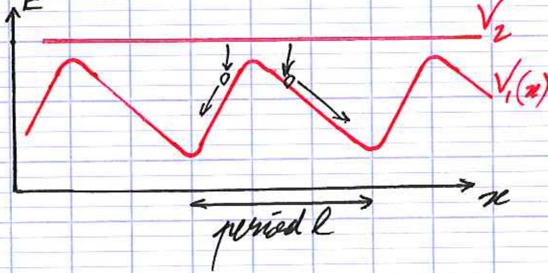
The pushing force is a direct f^{n} of how out-of-eq the monomer solution is. Denoting by $\Delta\mu$ the chem. pot. difference btw actin in solution and in the filament : $F_s = \frac{\Delta\mu}{a}$ (this is a gl thermodynamic truth).

Molecular motors

Looking at the accompanying videos it is clear the the operation of molecular motors consist in a switch btwn two states powered by chemical reactions that change the affinity of the motor head for the track.

References
xvivo.net/animation/the-inner-life-of-the-cell
Vale & Milligan, Science 288: 88 (2000)
Zhang & Thirumalai, Structure 20: 628 (2012)
Jülicher, Ajdari & Prost, Rev. Mod. Phys. 69: 1289 (1997)

This inspires the following minimal model of the motor operation:



Naive picture: When a particle falls from V_2 onto the long slope it shifts to the right by a lot. If it falls onto the short slope it shifts to the left by a little; thus we should have a drift to the right.

We will see that this view is too simplistic: how the system is driven out of eq. matters a lot and can even induce a leftwards flow. We will compute the steady-state motor flow along x and show that it is directly proportional to a qty that quantifies how much detailed balance is violated in the system.

I) Diffusion in an energy potential

For now we only consider motion in the bottom potential $V_1(x)$. The proba of presence of the motor is described by the Fokker-Planck equation.

1°) Biased diffusion and the Fokker-Planck equation.

We assimilate the probability density for the motor to be in x at t to a density of non-interacting motors.

Probability ($\equiv$ mass) conservation: $\partial_t P = -\partial_x J(x,t)$

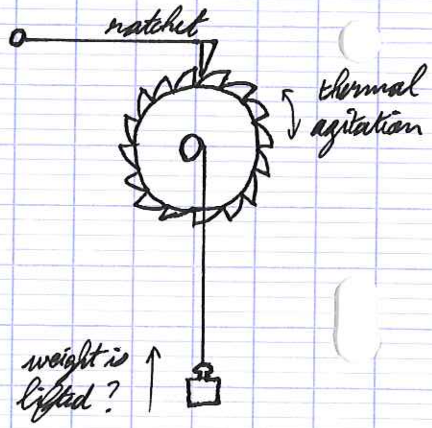
Flux-force relation: $J(x,t) = \underbrace{-D\,\partial_x P}_{\text{Fick's law}} + \underbrace{P \cdot \mu F(x,t)}_{\text{convection current.}}$

Using Einstein's relation $D = \mu k_B T$ we get

$$\partial_t P = D\,\partial_x \left(\partial_x P + \frac{P}{k_B T}\,\partial_x V\right) \quad \text{Fokker-Planck}$$

2°) The Feynman ratchet

Can we get a steady-state current just from moving in a periodic potential? This is equivalent to asking whether Feynman's ratchet can lift a weight:



$$\partial_t P = 0 \implies J = J_0 \text{ constant}$$

$$\iff \partial_x P + \frac{P}{k_B T}\partial_x V = -\frac{J_0}{D}$$

$$\iff \partial_x(\ln P) + \partial_x\left(\frac{V}{k_B T}\right) = -\frac{J_0}{P \cdot D}$$

$$\iff P \propto e^{-\frac{V(x)}{k_B T}} \cdot e^{-\frac{J_0}{D}\int^x \frac{dx'}{P(x')}}$$

Boltzmann distribution if $J_0 = 0$

In a periodic potential at steady-state we must have $\frac{P(\ell)}{P(0)} = 1$, thus

$$\exp\left(\frac{V(0)-V(\ell)}{k_B T}\right) \cdot \exp\left(-\frac{J_0}{D}\int_0^\ell \frac{dx}{P(x)}\right) = 1$$

$$\iff \frac{J_0}{D}\int_0^\ell \frac{dx}{P(x)} = 0 \quad \text{because } V(0) = V(\ell)$$

$$\iff J_0 = 0 \quad \text{since } P(x) > 0.$$

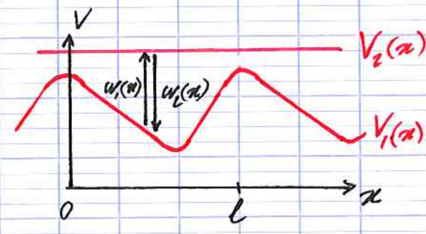
What is the resulting current?

$$J = - D\, \partial_x P - \frac{D}{k_B T} P \cdot \partial_x V$$

$$= D \frac{\partial_x V}{k_B T} P_0 e^{-\frac{V}{k_B T}} - \frac{D}{k_B T} P_0 e^{-\frac{V}{k_B T}} \partial_x V = 0$$

No monotherm motor at equilibrium ⇒ the chemical reactions inducing the switching btw V_1 and V_2 are indispensable to get motion.

II) Motor current



We set the origin of the x's at the maximum of $V_1(x)$ for convenience.
Combining Fokker-Planck and chemical kinetics similar to the last chapter:

$$\partial_t P_1(x,t) = - \partial_x J_1 - w_1(x) P_1 + w_2(x) P_2 \qquad (1)$$

$$\partial_t P_2(x,t) = - \partial_x J_2 + w_1(x) P_1 - w_2(x) P_2 \qquad (2)$$

↑ proba to be in state ② at x and t. ↑ transit rate from ② to ①.

with:

$$J_1 = - D\, \partial_x P_1 - \frac{D}{k_B T} P_1 \partial_x V_1 \qquad (3)$$

$$J_2 = - D\, \partial_x P_2 \qquad (4)$$

We look at the stationary state $\partial_t P_1 = \partial_t P_2 = 0$. $P_1(x)$ and $P_2(x)$ are then l-periodic, as are $V_1(x)$, $w_1(x)$ and $w_2(x)$. The total motor current is $J = J_1 + J_2$. Summing Eqs. (1) and (2) we see that $\partial_x J = 0$, and J is thus a constant:

$$J = \frac{1}{l} \int_0^l J\, dl$$

$$= \frac{1}{l} \int_0^l J_1(x)\, dx + \frac{1}{l} \int_0^l J_2(x)\, dx$$

$$= \frac{1}{l} \int_0^l J_1(x)\, dx - \frac{D}{l} \underbrace{\int_0^l \partial_x P_2\, dx}_{= P_2(l) - P_2(0) = 0}$$

due to P_2's periodicity.

$$J = \frac{1}{l} \int_0^l J_1(x)\, dx \qquad (5)$$

We thus need to compute $J_1(x)$.

1°) Equilibrium situation

Consider thermodynamic equilibrium for the two-state system

(a) How do motors move?

(b) What are the conditions on ω_1, ω_2 for this equil. to exist?

Thermodynamic equilibrium is characterized by:

$$P_1^{eq}(x) \propto \exp - \frac{V_1(x)}{k_B T}$$

$$P_2^{eq}(x) \propto \exp - \frac{V_2(x)}{k_B T} = \text{constant here}$$

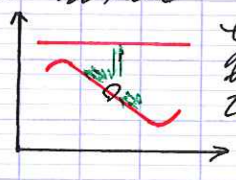
Similarly to the last section this clearly implies $J_1 = J_2 = 0$.
Inserting this into Eq. (1) we moreover get the condition

$$\underline{\omega_1(x) P_1^{eq}(x) = \omega_2(x) P_2^{eq}} \quad \text{"detailed balance"}$$

I.e., a thermodynamic equilibrium can only exist if $\omega_1(x), \omega_2(x)$ satisfy this detailed balance condition, which we can rewrite as

$$\frac{\omega_1(x)\, e^{-\beta V_1(x)}}{\omega_2(x)} = \text{constant}$$

Physically, detailed balance describe a situat° where probability fluxes can simultaneously balance each other locally.



Green arrows
Balanced
2 by 2.

2°) Motor motion

In the presence of an outside energy source (here a continuous supply of ATP), the rates can break detailed balance and generate motion. Choosing $\underline{\omega_2 = \text{constant}}$ for simplicity we quantify this violation through:

$$\gamma(x) = \frac{\omega_1(x) \cdot e^{-\beta V_1(x)}}{\omega_2 \cdot \frac{1}{\ell}\int_0^\ell e^{-\beta V_1(x')}dx'} . \qquad (6)$$

Fourier transforming:

$$\gamma(x) = \tilde{\gamma}_0 + \sum_{n=1}^{+\infty} \tilde{\gamma}_n^c \cos\left(\frac{2\pi n x}{\ell}\right) + \tilde{\gamma}_n^s \sin\left(\frac{2\pi n x}{\ell}\right),$$

where the $\tilde{\gamma}_n^c, \tilde{\gamma}_n^s$ are incompatible with equilibrium and thus quantify the driving of the system.

We consider the limit (relevant for the movies we have shown) where convection in V_1 is much faster than diffusion: $\mu V_1 \gg D$ $\Longleftrightarrow$ $k_B T \ll V$ (i.e., binding much stronger than thermal agitation). We thus propose a small-$k_B T$ expansion of P_1:

$$P_1(x) = P_1^0(x) + k_B T\, \delta P_1(x)$$

Inserting into Eqs (1)-(3) to dominant order in $\frac{1}{k_B T}$, the motion in the potential dominates and the transitions with state ② are negligible:

$$\begin{cases} \partial_x P_1^0 + \frac{1}{k_B T} P_1^0 \partial_x V_1 = 0 \\ P_1^0 \ \ell\text{-periodic} \end{cases},$$

implying (the integration constants are determined from the periodicity):

$$P_1^0(x) = \frac{e^{-\frac{V_1(x)}{k_B T}}}{\int_0^\ell e^{-\frac{V_1(x)}{k_B T}} dx},$$

meaning that the fast convection quickly makes the system sediment into a quasi-equilibrium state. Clearly this leading term cannot induce motor motion, and we thus need to consider the next order:

$$\partial_x J_1 = -w_1 P_1^0 + w_2 P_2 = w_2 \left[P_2(x) - \frac{1}{\ell} \gamma(x) \right] \qquad (7)$$
$$\partial_x J_2 = w_1 P_1^0 - w_2 P_2 = w_2 \left[\frac{1}{\ell} \gamma(x) - P_2(x) \right] \qquad (8)$$

$$J_1 = - D\, \delta P_1 \cdot \partial_x V_1 \qquad (9)$$
$$J_2 = - D\, \partial_x P_2 \qquad (10)$$

Eq. (9) implies that J_1 vanishes in 0 as $\partial_x V_1(0) = 0$. Thus using Eq. (7)

$$J_1(x) = \int_0^x \partial_x J_1(x')\, dx'$$

$$J_1(x) = w_2 \int_0^x \left[P_2(x') - \frac{1}{\ell} \gamma(x') \right] dx \qquad (11)$$

We thus need to compute $P_2(x)$ to obtain J_1 to obtain J.
Combining Eqs. (8) and (10):

$$\partial_x^2 P_2 - \frac{w_2}{D} P_2 = - \frac{w_2}{D\ell} \gamma(x).$$

Thus in Fourier space

$$P_2(x) = \frac{\tilde{\gamma}_0}{\ell} + \frac{1}{\ell}\sum_{n=1}^{+\infty} \frac{1}{1+\frac{D}{\ell^2\omega_2}(2\pi n)^2}\left[\tilde{\gamma}_n^c \cos\left(\frac{2\pi n x}{\ell}\right) + \tilde{\gamma}_n^s \sin\left(\frac{2\pi n x}{\ell}\right)\right]$$

Inserting into Eq. (11):

$$J_1(x) = \omega_2 \int_0^x \left\{ \sum_{n=1}^{+\infty} \frac{-\frac{D}{\ell^2\omega_2}(2\pi n)^2}{1+\frac{D}{\ell^2\omega_2}(2\pi n)^2}\left[\tilde{\gamma}_n^c \cos\left(\frac{2\pi n x}{\ell}\right) + \tilde{\gamma}_n^s \sin\left(\frac{2\pi n x}{\ell}\right)\right]\right\} \frac{dx}{\ell}$$

Clearly $\tilde{\gamma}_0$ does not contribute to the current. Using Eq. (5):

$$J = -\frac{D}{\ell^2}\sum_{n=1}^{+\infty} \frac{(2\pi n)^2}{1+\frac{D}{\ell^2\omega_2}(2\pi n)^2}\left[\tilde{\gamma}_n^c \int_0^\ell \frac{dx}{\ell}\int_0^x \frac{dx'}{\ell}\cos\left(\frac{2\pi n x'}{\ell}\right) + \tilde{\gamma}_n^s \int_0^\ell \frac{dx}{\ell}\int_0^x \frac{dx'}{\ell}\sin\left(\frac{2\pi n x'}{\ell}\right)\right]$$

$$J = -\frac{D}{\ell^2}\sum_{n=1}^{+\infty} \frac{(2\pi n)\,\tilde{\gamma}_n^s}{1+\frac{D}{\ell^2\omega_2}(2\pi n)^2}$$

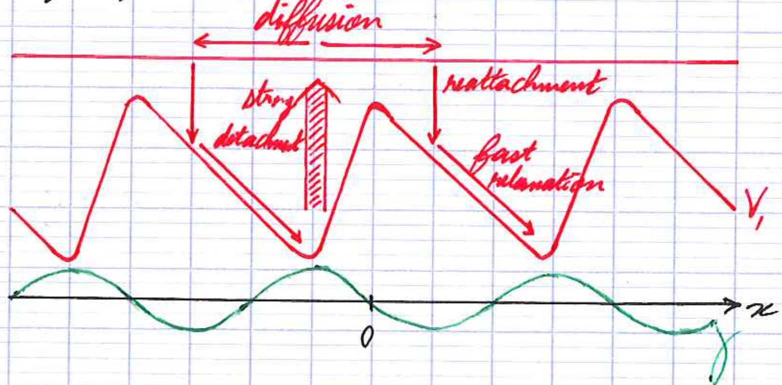
III) Qualitative discussion

Thus two conditions are required for motor motion:

- Out-of-equilibrium transitions btw ① and ② ($\tilde{\gamma}_0$ doesn't count)
- A left-right asymmetry favoring directional motion ($\tilde{\gamma}_n^c$ doesn't count)

Note that the sign of the asymmetry of $\gamma(x)$ is not necessarily the same as that of $V_1(x)$: motion can occur in either direction even w/ a given potential.

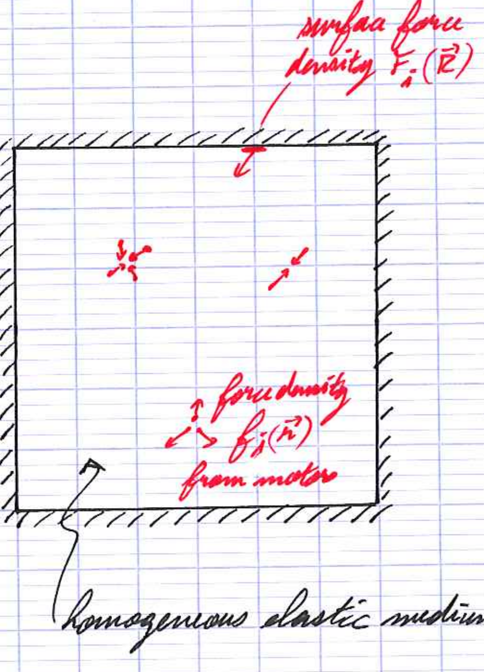
Concretely, if $\tilde{\gamma}_1^s < 0$ we have:



Typical velocities: ~ 200 nm/s ; typical forces: a few pN/motor

Rectifying and amplifying stresses

Biological forces are produced at the microscale (see our chapter on motors), but often effect biological functions at a macro scale (e.g., set the tension of the cell cortex). Here we investigate how the microscopic forces exerted by motors are related to the resulting macro forces.



The problem is as follows: large box in d dimensions w/ fixed boundaries. Many small force dipoles in it (no monopole). What is the overall macroscopic stress Σ_{ij} exerted by the medium on the boundary as a function of the dipole $D_{ij} = \int dV\, x_i f_j$ of microscopic forces?

I) Linear medium: dipole conservation

1°) Relation btw macroscopic stress and macroscopic work

Assume we deform the boundary of the box by a small δT_{ij}, such that the point of the boundary with coordinates $\{X_i\}$ goes to

$$X_i \to X_i + \delta X_i = X_i + \delta T_{ij} \cdot X_j$$

then the work performed by the boundary on the medium is

$$\delta W = -\Sigma_{ij}\, \delta T_{ij}$$

(similar to $-P\delta V$ for isotropic dilation)

do just before 4°) instead.

After Ronceray & ML, Soft Matter 11:1597 (2015)

2°) Mean-stress theorem

In the medium, force balance reads:

$$\partial_j \sigma_{jk} = f_k$$

$$\Rightarrow \int dV\, x_i\, \partial_j \sigma_{jk} = \int dV\, x_i f_k = D_{ik}$$

$$\overset{IBP}{\Longrightarrow} \quad D_{ik} = \oint dS_j\, X_i\, \sigma_{jk} - \int dV\, \sigma_{jk}\, \partial_j x_i$$

$$= \oint dS \cdot X_i F_k - \int dV\, \sigma_{jk}\, \delta_{ij}$$

$$\underline{D_{ik} = \Delta_{ik} - \int dV\, \sigma_{ik}}$$

for all media

with $\Delta_{ik} = \oint dS\, X_i \cdot F_k$ the dipole of the forces exerted by the medium on the boundary.

3°) Dipole conservation in linear media

Δ_{ik} looks like an interesting enough object to characterize surface forces (we will show that it is proportional to Σ_{ik}), but the $\int dV\, \sigma_{ik}$ piece looks like it could be equal to anything; fortunately it is not so if the medium is linear & homogeneous, i.e. $\exists\, K_{ijkl}$ independent on space such that

$$\sigma_{ij} = K_{ijkl}\, \gamma_{kl}$$

Then:

$$\int dV\, \sigma_{ij} = K_{ijkl} \int dV\, \gamma_{kl}$$

$$= \frac{1}{2} K_{ijkl} \left(\int dV\, \partial_k u_l + \int dV\, \partial_l u_k \right)$$

$$= \frac{1}{2} K_{ijkl} \left(\oint dS_k\, u_l + \oint dS_l\, u_k \right)$$

And all displacements at the boundary are zero as the walls are fixed, thus $\int dV\, \sigma_{ij} = 0$ and

$$\underline{\Delta_{ij} = D_{ij}}$$

only in linear media

also true in discrete media & on avg in disordered ≈ w/ homog. disorder.

(c) Relation btw macroscopic force dipole and work

Considering again our macroscopic deformation, the work performed by the boundary can also be expressed by

$$\delta W = \oint dS \cdot dX_i \cdot (-F_i)$$

$$= -\oint dS \cdot \delta \Gamma_{ij} X_j \, F_i$$

$$= -\delta \Gamma_{ij} \oint X_j F_i$$

$$= -\delta \Gamma_{ij} \Delta_{ji}$$

Thus $\Sigma_{ij} = \frac{\Delta_{ij}}{V}$

for all media

Comparing with the expression for the stress and using dipole conservation we get

$$\Sigma_{ij} = -\frac{D_{ij}}{V}$$

The "active stress" is simply the opposite of the microscopic force dipole density.

II) Nonlinear (bucklable) media : dipole amplification

While the above result holds in linear media, motors in an actin gel tend to buckle their surroundings, with dramatic effects on force transmission.

After: Ronceray et al. Proc Natl. Acad. Sci. U.S.A. 113:2827 (2016)

1°) Radial force balance

We can write the stress tensor in spherical coordinates $r, \{\theta_i\}$ where θ_i denotes an angular direction. Then force balance in the radial direction reads:

$$\underline{\frac{1}{r^{d-1}} \frac{d}{dr}\left(r^{d-1}\sigma_{rr}\right) - \frac{1}{r}\sum_i \sigma_{\theta_i\theta_i} = 0}$$

2°) Double-checking our results: linear case.

Using Lamé coefficients

$$\sigma_{ij} = 2\mu\, \gamma_{ij} + \lambda\, \gamma_{kk}\, \delta_{ij}$$

and the strain tensor as a function of radial displacement $u_r(r) = u(r)$:

$$\gamma_{rr} = \partial_r u(r)$$
$$\gamma_{\theta_i\theta_j} = \frac{u(r)}{r}\,\delta_{ij}$$
$$\gamma_{r\theta_i} = 0$$

we get

$$\sigma_{rr} = (2\mu+\lambda)\,\partial_r u + \lambda(d-1)\frac{u}{r}$$
$$\sigma_{\theta_i\theta_i} = \lambda\,\partial_r u + \left[2\mu+\lambda(d-1)\right]\frac{u}{r}$$

Inserting into the force balance equation yields

$$(2\mu+\lambda)\left(\partial_r^2 u + \frac{d-1}{r}\partial_r u - \frac{d-1}{r^2}u\right) = 0,$$

which we re-write as

$$\partial_r\left[r^{1-d}\,\partial_r\left(r^{d-1}u\right)\right] = 0$$

$$\Longrightarrow \quad \partial_r\left(r^{d-1}u\right) = A\cdot r^{d-1}$$

$$\Longrightarrow \quad u = \underbrace{\frac{A}{d-1}\,r}_{} + \frac{B}{r^{d-1}}$$

$\hookrightarrow A = 0$ if u vanishes far away

As a result both γ_{rr} and $\gamma_{\theta\theta}$ are proportional to r^{-d} and:

$$\sigma_{rr} \propto \frac{1}{r^d}$$

$$\Longrightarrow \quad \sigma_{rr} = \sigma_{rr}(r_0)\cdot\left(\frac{r_0}{r}\right)^d$$

Integrating over a sphere:

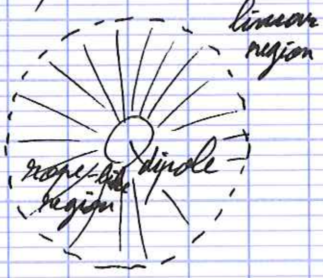
$$\mathcal{E}_r\Delta = \oint r \cdot \sigma_{rr}\, dS$$

$$\propto r \cdot \sigma_{rr} \cdot r^{d-1}$$

Thus $\mathcal{E}_r\Delta\,(r)$ does not depend on r: $\mathcal{E}_r\Delta = \mathcal{E}\Delta$ (all other components of the dipole vanish).

3°) Force amplification in a bucklable medium

For a pulling dipole γ_{rr} is tensile and $\gamma_{\theta\theta}$ is compressive. In regions where $\sigma \gg \frac{F_b}{l^2} = \sigma_b$, the compressed fibers buckle and only tensile stresses are sustained:



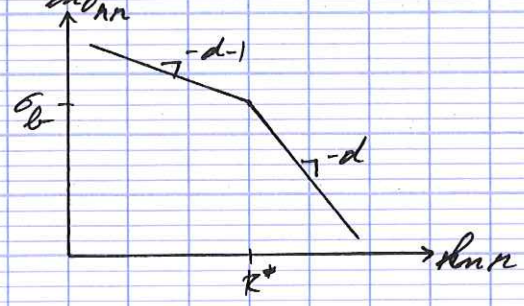
$$\sigma_{\theta\theta} \simeq 0$$

Thus force balance reads

$$\frac{1}{r^{d-1}}\partial_r\left(r^{d-1}\sigma_{rr}\right) = 0$$

$$\Longrightarrow \sigma_{rr} \propto \frac{1}{r^{d-1}}$$

Radial stresses thus decay much more slowly than in a linear medium until they become smaller than σ_b:



Thus

$$r < R^* \qquad \sigma_{rr} \simeq \sigma_{rr}(r_0)\cdot\left(\frac{r_0}{r}\right)^{d-1}$$

$$r > R^* \qquad \sigma_{rr} \simeq \underbrace{\sigma_{rr}(R^*)}_{=\sigma_b}\cdot\left(\frac{R^*}{r}\right)^{d}$$

and $$\sigma_b \approx \sigma_{rr}(r_0) \cdot \left(\frac{r_0}{R^*}\right)^{d-1}$$

$$\Rightarrow \quad \underline{R^* \approx r_0 \left[\frac{\sigma_{rr}(r_0)}{\sigma_b}\right]^{\frac{1}{d-1}}}$$

And $$\sigma_{rr}(r > R^*) = \sigma_{rr}(r_0) \left(\frac{r_0}{r}\right)^d \frac{R^*}{r_0}$$

$$\underline{\sigma_{rr}(r > R^*) = \sigma_{rr}^{lin}(r) \cdot \frac{R^*}{r_0}}$$

Stresses are amplified by an arbitrarily large factor $\frac{R^*}{r_0}$; in practice we have identified cases where the discrepancy btw the measured microscopic and macroscopic dipole can be up to a factor of 20.

III) Discussion

- Motors in a disordered medium exert as many contractile as extensile forces a priori. In addition to amplification we have shown that bucklable media can rectify these forces towards uniform contract.

- The amplification by a factor $\frac{R^*}{r_0}$ is very robust, however R^* does not always go as $\left(\frac{F}{F_b}\right)^{\frac{1}{d-1}}$: anomalous scaling for disordered, bending-dominated networks, saturation at $R_{a.u}$ for a finite density of active units.

- Depleted bending-dominated media have a low buckling threshold, favoring the effects described here.