Cell Mechanics: Boal

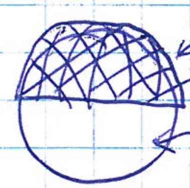
1

- 10^{14} cells in body & ~200 cell types
- Physics of cell shape? movement? tissues?

"Form follows Function" - Louis Sullivan

Architecture:

- thin membrane on a supporting cytoskeleton + rigging (ropes)
- similar to hot air balloon when $P_{in} > P_{out}$
  - system under tension



exterior cell wall

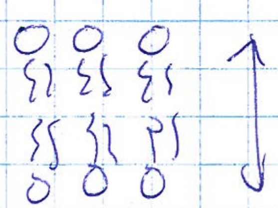
membrane

- Material transport:

optimal layout.

most efficient might be complex web

Bilayers:

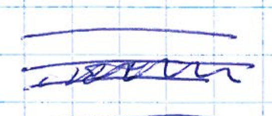


4-5nm

Cell walls:

gram +ve

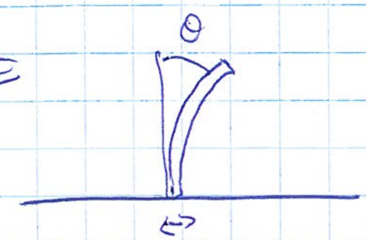
peptidoglycan



gram -ve

Filaments & Sheets

E



$E \sim \theta^2 \sim K \sim d^4$

soft materials $K \sim 100$ x less than conventional 'hard' materials.

Rods & Ropes:

$I = \int x^2 dA$

• cytoskeleton = actin, intermediate filaments, microtubules

bending $E = K_f \frac{L}{2R^2} = YI \frac{L}{2R^2}$ $\boxed{K_f = YI}$

soft: $Y \sim 10^9\ J/m^3$, for circular rod $I \sim \frac{\pi R^4}{4}$

• given diff't R's for biofilaments, K_f spans 5 orders of magnitude in cell

material

rubber $\sim 0.1 \times 10^9\ J/m^3$

Plastic $\sim 1 \times 10^9\ J/m^3$

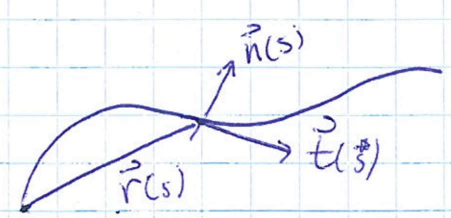
wood $\sim 10 \times 10^9$

Metal $\sim 100 \times 10^9$

Diamond $\sim 1000 \times 10^9$

• Fluctuations: $\xi_p = \frac{K_f}{kT} \sim \frac{1}{T}$

Continuum shapes



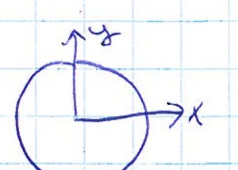
$\vec{t} = d\vec{r}/ds$

$C\vec{n} = d\vec{t}/ds = \frac{d^2 r}{ds^2}$

curvature

& $R_c = \frac{1}{C} \equiv$ radius of curvature

• I:



Hollow

$I = \int dA\, x^2 = \frac{\pi R^4}{4}$

$I = \frac{\pi}{4}(R^4 - R_i^4)$

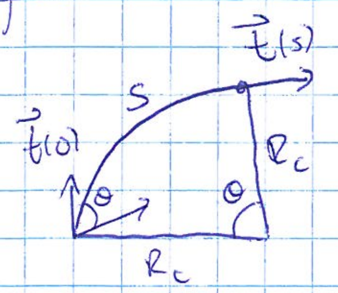
More general

$$E_{bend} = \frac{K_f}{2}\int_0^L ds \left(\frac{\partial \vec{t}}{\partial s}\right)^2 \qquad (K_f = YI)$$

$$\left|\frac{\partial \vec{t}}{\partial s}\right| = C = \frac{1}{R}$$

$$\rightarrow E = \frac{K_f}{2}\frac{L}{R^2}$$

Rigid:



$$s = R_c\,\theta$$

$$E_b(\theta) = \frac{K_f}{2}\frac{s}{R_c^2} = \frac{K_f}{2}\frac{\theta^2}{s}$$

Avg fluctuation:

$$\langle\theta^2\rangle = \int d\Omega\, \theta^2 P(E) \Big/ \int d\Omega\, P(E)$$

$$= \int d\theta \sin\theta\, \theta^2 P(E) \Big/ \int d\theta \sin\theta\, P(E)$$

$$\langle\theta^2\rangle = \left(\frac{2s}{\beta K_f}\right) \underbrace{\int_{-\infty}^{\infty} x^3 e^{-x^2} dx}_{=1/2} \Big/ \underbrace{\int_{-\infty}^{\infty} x e^{-x^2} dx}_{=1/2} \quad (\sin\theta \sim \theta)$$

so

$$\boxed{\langle\theta^2\rangle = \frac{2s}{\beta K_f} = \frac{2s}{\xi_p}}$$

Correlation function:

$$\langle \vec{t}(0)\cdot\vec{t}(s)\rangle = \langle\cos\theta\rangle \approx 1 - \langle\theta^2\rangle/2$$

$$= 1 - s/\xi_p \quad \text{for} \quad \left(\frac{s}{\xi_p} \ll 1\right)$$

In general: $\langle \vec{t}(0)\cdot\vec{t}(s)\rangle = \exp(-s/\xi_p)$ for arb $\frac{s}{\xi_p}$.

(4)

End-to-end distance:

Skip

$$\vec{r}(s) = \vec{r}(0) + \int_0^s d\alpha\, \vec{t}(\alpha)$$

$$\langle \vec{r}_{ee}^{\,2} \rangle = \langle [\vec{r}(L_c) - \vec{r}(0)]^2 \rangle = \int_0^{L_c} du \int_0^{L_c} dv \langle \vec{t}(u) \cdot \vec{t}(v) \rangle$$

$$= 2 \int_0^{L_c} du \int_0^{u} dv \; \exp(-[u-v]/\xi_p)$$

$$= \ldots$$

$$= 2\xi_p L_c - 2\xi_p^2 \left[1 - \exp(-L_c/\xi_p)\right]$$

for $L \gg \xi_p \rightarrow \langle \vec{r}_{ee}^{\,2} \rangle \approx 2\xi_p L_c$

so $|\vec{r}_{ee}| \sim \sqrt{L_c}$

Discrete poly: $\langle \vec{r}_{ee}^{\,2} \rangle \sim N b^2 = L_c b$

Restricted bonds – $\sqrt{\langle r_{ee}^2 \rangle} \sim N^{1/2}$ indep of d

Self Avoidance: $\langle r_{ee}^2 \rangle^{1/2} \sim N^{1/2}$ 1D: o-o-o $\langle r_{ee}^2 \rangle^{1/2} \sim N^1$

general $\boxed{\nu = 3/(2+d)}$ ≡ Flory exponent for $d \leq 4$

$\nu_{ideal} = 1/2$

* Flory derivation p. 190 *

skip

Distributions:

1D: $P(x) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp(-x^2/2\sigma^2)$ $\quad \sigma^2 = Nb^2$

3D: $P(r) = \frac{4\pi r^2}{(2\pi\sigma^2)^{3/2}} \exp(-r^2/2\sigma^2)$ $\quad \sigma^2 = \frac{Nb^2}{3}$

Entropic force:

$P(x) \sim e^{-\frac{k_s x^2}{2kT}}$ for SHO & small x

so $\frac{k_s \cancel{x^2}}{\cancel{2}kT} = \frac{\cancel{x^2}}{\cancel{2}\sigma^2}$ so $\boxed{k_s = \frac{kT}{\sigma^2} = \frac{kTd}{Nb^2}}$

$\boxed{k_s = \frac{kTd}{2\xi_p L_c}} \propto T$

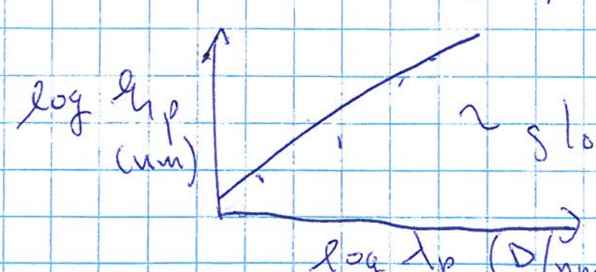
WLC:

ξ_p ~~table~~: See table 2.2 p. 49

Generic biopolymer: $\xi_p \approx \pi Y R^4/4kT$

use mass/length $\equiv \lambda_p = \rho_m \pi R^2$

$\rightarrow \quad \xi_p \approx (Y/4\pi kT\rho_m^2)\,\lambda_p^2$



~ slope ~ 2 $\rightarrow$ $Y \sim 0.5 - 1.5 \times 10^9$ J/m^3

steel ~ 10^{11} J/m^3

Ch 2 Problems:

- Estimation: #2.1 & 2.2 — P347
- Design: #2.5, #2.17
- Phage: #2.6 (P347)

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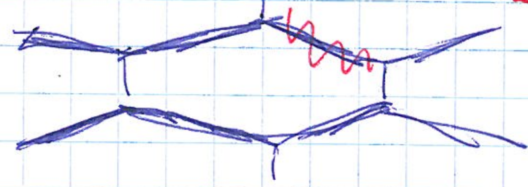
Math: #2.9 (α-chain) (in class P384)

~~#2.14 (Extension)~~

Ch 3 Networks:

peptidoglycan

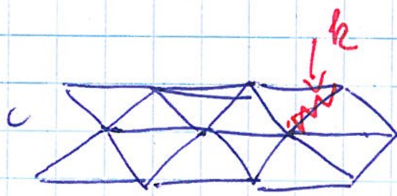


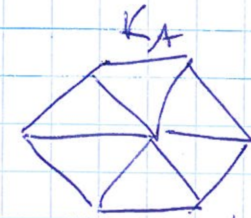
$k_{sp} \sim \frac{kT}{2L\xi}$

mix of soft & stiff filaments

– How does the network behave?

Modes: 2D isotropic





compression/expansion – angle preserving

shear area preserving

Network of springs: $K_A = \frac{\sqrt{3}}{2} k$ & $\mu = \frac{\sqrt{3}}{4} k$ (for 6-fold) @ $T=0$

units = energy/area

for $T \neq 0$ & ext stresses – network deforms from above and change K_A & μ.

General: Strain Tensor

$\vec{u}(\vec{x}_i)$ $\quad$ $\vec{u}(\vec{x}_2)$

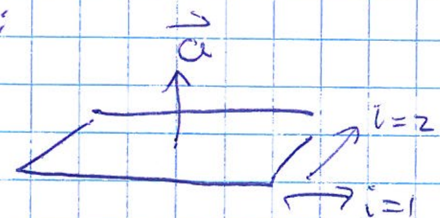
$$u_{ij} = \frac{1}{2}\left[\frac{\partial u_i}{\partial x_j} + \frac{\partial u_j}{\partial x_i} + \underbrace{\sum_k \left(\frac{\partial u_k}{\partial x_i}\right)\left(\frac{\partial u_k}{\partial x_j}\right)}_{\sim 0}\right]$$

here $j = 1, 2$ (or 3) $\rightarrow x, y$ (or z)

- Translation: $u_{ij} = 0$, expansion $u_{xy} = u_{yx} = 0$

$u_{xx} = -u_{yy}$

Stresses:



$$F_i = \sum_j \sigma_{ij} a_j$$

Hook:

$$\sigma_{ij} = \sum_{kl} C_{ijkl} \cdot u_{kl}$$

energy $\rightarrow$ $$\Delta F = \frac{1}{2} \sum_{ijkl} C_{ijkl}\, u_{ij}\, u_{kl}$$

Note not all C_{ijkl} are indep. Symmetries!

isotropic: $C_{ijkl} = C_{jikl} = C_{ijlk}$ & $C_{ijkl} = C_{klij}$

$\rightarrow$ 6 indep in 2D: C_{xxxx} ; C_{yyyy} ; $C_{xxyy} = C_{yyxx}$

$C_{xyxy} = \ldots$; C_{xxxy} ; C_{yyyx}

More symmetries: 6 Fold & 4-Fold

let $\xi = x + iy$ & $\eta = x - iy$

change in x, y $\rightarrow$ $\xi = \xi \exp(i\theta)$ & $\eta = \eta \exp(-i\theta)$

– 6-fold: $\exp\left(\frac{i\pi}{3}\right)$ is invariant ∴ need equal # of η & ξ for non-zero C → all others are zero

need η & ξ an even # of times

so $C_{\eta\xi\eta\xi}$ & $C_{\eta\eta\xi\xi} \neq 0 \Rightarrow$ just 2

so $\Delta F = 2\, C_{\xi\eta\xi\eta}\, u_{\xi\eta}\, u_{\xi\eta} + C_{\xi\xi\eta\eta}\, u_{\xi\xi}\, u_{\eta\eta}$

- Components of tensor transform as products of coordinates:

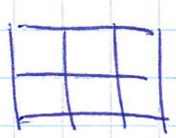
so $\xi^2 = x^2 - y^2 + 2ixy$

so $u_{\xi\xi} = u_{xx} - u_{yy} + 2i u_{xy}$

Gives

$$\Delta F = \underbrace{2C_{\xi\eta\xi\eta}}_{2K_A} \underbrace{(u_{xx}+u_{yy})^2}_{\text{expansion}} + \underbrace{C_{\xi\xi\eta\eta}}_{\substack{\text{shear} \\ 2\mu}} \underbrace{[(u_{xx}-u_{yy})^2 + 4u_{xy}^2]}_{\text{shear}}$$

6-fold $\Delta F = \left(\frac{K_A}{2}\right)(u_{xx}+u_{yy})^2 + \mu\left[\frac{(u_{xx}-u_{yy})^2}{2} + 2u_{xy}^2\right]$

4-fold:  6 indep: $x \to -x$ & $y \to -y$ get rid of odd # C_{ijkl}

and rotate $\pi/2 \Rightarrow x \to -y$ & $y \to x \to C_{xxxx} = C_{yyyy}$

Define:

$K_A = (C_{xxxx} + C_{yyyy})/2$

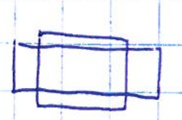
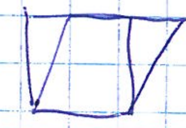
$\mu_p = (C_{xxxx} - C_{xxyy})/2$ (pure shear)

$\mu_s = C_{xyxy}$ (simple shear)

9

S_o ~~4-fold~~

$$\Delta F = \left(\frac{K_A}{2}\right)(u_{xx}+u_{yy})^2 + \frac{\mu_p}{2}(u_{xx}-u_{yy})^2 + 2\mu_s u_{xy}^2$$

 pure shear  simple shear

F=0 Microscopics. write K_A & μ in terms of k

6-fold: (fluctuations only)

$$\Delta U = 3\left(\frac{1}{2}k\delta^2\right) \quad \text{(units of E)}$$

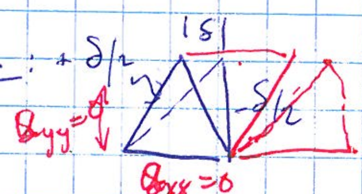
$$A_o = \frac{\sqrt{3}}{2}s_o^2 \qquad \Delta F = \frac{\Delta U}{A_o} = \sqrt{3}\,k\left(\frac{\delta}{s_o}\right)^2$$

Connection: $u_{xx} = u_{yy} = \delta/s_o$ & $u_{xy}=0$ (indep)

Macro

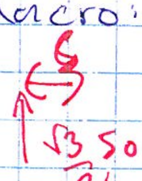
$$\Delta F = 2K_A\left(\frac{\delta}{s_o}\right)^2 = \sqrt{3}\,k\left(\frac{\delta}{s_o}\right)^2 \Rightarrow \boxed{K_A = \frac{\sqrt{3}}{2}k}$$

Shear:



$$\Delta U = 2\times k\,\delta^2/8 \rightarrow \Delta F = \frac{1}{2\sqrt{3}}k\left(\frac{\delta}{s_o}\right)^2$$

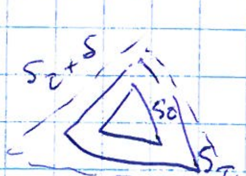
Macro: $u_{xx} = 0$ & $u_{yy}=0$



$$u_{xy} = \frac{\delta}{\sqrt{3}\,s_o} \rightarrow \Delta F = \left(\frac{2\mu}{3}\right)\left(\frac{\delta}{s_o}\right)^2 \qquad \boxed{K_A = 2\mu}$$

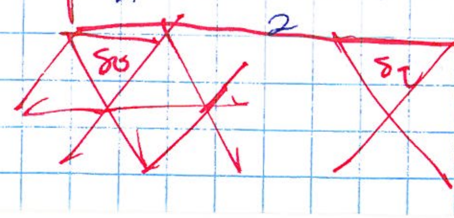
$$\rightarrow \boxed{\mu = \frac{\sqrt{3}}{4}k} \qquad K_A = 2\mu \quad \text{(6-fold)}$$

With Stress: (6-fold) Human erythrocyte)* (do 9a)*



$$\rightarrow \boxed{K_A = \frac{\sqrt{3}}{2}k\left(1-\frac{\tau}{\sqrt{3}k}\right)} \;\&\; \boxed{\mu = \frac{\sqrt{3}}{4}k\left(1+\frac{\sqrt{3}\,\tau}{k}\right)}$$

(stretch)



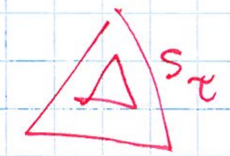
grows w/ τ

resists shear

9a

Energy with stress: apply τ

$$H = E - \tau A$$

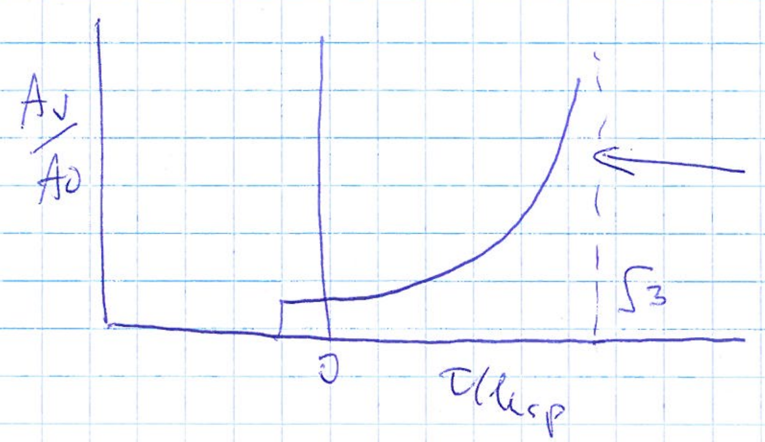


$$A_v = \sqrt{3}s^2/2$$

so energy/vertex: $H_v = 3\,\frac{1}{2}\,k\,(s-s_0)^2 - \sqrt{3}\,\frac{\tau s^2}{2}$

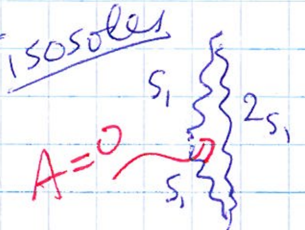
$$\frac{\partial H}{\partial \tau} = 0 \rightarrow \quad s_\tau = \frac{s_0}{(1-\tau/\sqrt{3}k)} \quad ; \quad H^{equ}_{min} = \frac{\sqrt{3}/2\,\tau s_0^2}{(1-\tau/\sqrt{3}k)}$$

good for $\tau > 0$



Compression: equilateral is not the lowest E shape

isosceles



$$\leftarrow \quad E = \frac{k}{2}\left[(2s_1-s_0)^2 + 2(s_1-s_0)^2\right]$$

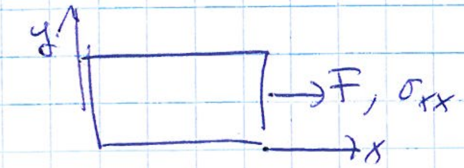
here $H = E$ so $\frac{\partial E}{\partial s_1} = 0$

$$\rightarrow \quad s_1^* = 2s_0/3 \quad \& \quad H^{iso}_{min} = k\,s_0^2/6$$

collapse @ $H^{equ}_{min} = H^{iso}_{m}$

$$\rightarrow \quad \tau_{col} = -\sqrt{\frac{3}{8}}\,k$$

Application to Poisson Ratio



Defn: $\sigma_p = -u_{yy}/u_{xx}$ (usually > 0)

in terms of elastic moduli (2D)

$$\boxed{\sigma_p = \frac{(K_A - \mu)}{(K_A + \mu)}}$$ see Appendix D

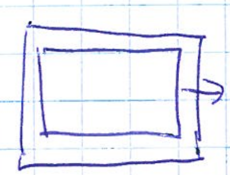
for triangle net @ OT with $\tau = 0 \rightarrow \sigma_p = \frac{(2\mu - \mu)}{3\mu}$

$= 1/3$.

However @ $\tau > 0$:

$$\sigma_p = \frac{1 - (5\tau/\sqrt{3}h)}{3 + (\tau/\sqrt{3}h)}$$

- $\sigma_p < 0$ when $\frac{\tau}{h} \geq \sqrt{3}/5$ $\Rightarrow$ -ve Poisson ratio
  $\Rightarrow$ expands



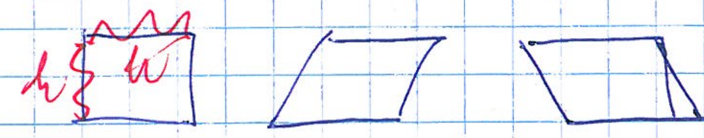
- These calculations are good for uniform length springs (ie. low T or high τ)

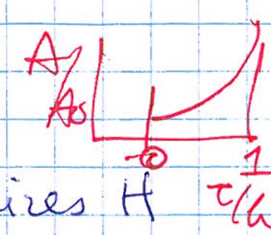
Temp dependence: Give as problem producing graphs for A_v/A_0, $K_A(T)$; $\mu(T)$ (p. 76)

$\rightarrow$ @ finite T shapes distort & fun things happen

VI

4-fold: (nuclear lamina)

@ $T=0$  all have same F

so $\boxed{\mu_s = 0 \;@\; T = 0}$ collapse for $\tau < 0$ 

- Collapse for any $\tau < 0$ since $A=0$ minimizes H
-  for τ & $T=0$ $H = 2\left(\frac{1}{2}k(s-s_0)^2\right) - \tau s^2$
  $\hookrightarrow s_{eq} = \frac{s_0}{1-\tau/k}$
- τ dependence: $\boxed{K_A = \frac{k-\tau}{2}}$; $\boxed{\mu_p = \frac{k+\tau}{2}}$; $\boxed{\mu_s = \tau}$

3 deform: i) ii) iii) 

under $\tau > 0$

Problems:

3.4 – Thermal expansion, 3.5 – real network

3.6 – Laminin network, 3.8 –

3.9: Ideal gas, ~~Area~~ comp modulus $K_A^{-1} = -\frac{1}{A}\left(\frac{\partial A}{\partial P}\right)$

$PV = NkT \rightarrow PA = NkT$ or $A = \frac{NkT}{P}$

$= +\frac{1}{A}\left(\frac{NkT}{P^2}\right) = \frac{1}{P}$

- 3.10: Poisson ratio
- 3.11 – stretch

3.13 – 4-fold net

3.15 – honeycomb net

3.16 – asym 4-fold net

Percolation & Rheology: Viscoelastic materials

Apply strain @ ω:

shear loss modulus

$$\sigma_{xy} = G'(\omega)\, u_{xy}(t) + \frac{G''(\omega)}{\omega} \frac{du_{xy}}{dt}$$

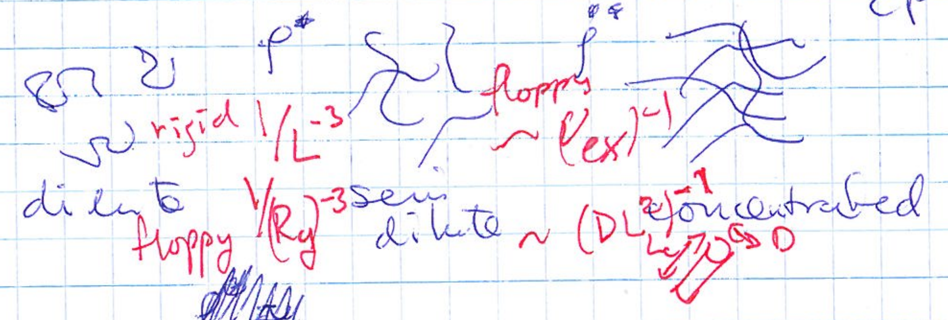
shear storage modulus

(a) $G'(0)$ = shear modulus & $G''(0) = \eta$

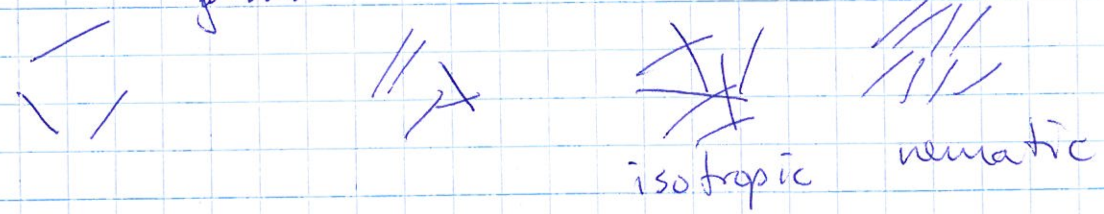
Properties of Viscoelastic materials:

- depend only on $c \equiv$ concentration & $\frac{L_c}{\xi_p}$

$\frac{L}{\xi_p} \gg 1$



$\frac{L}{\xi_p} \ll 1$



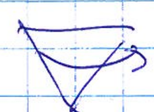
<u>response</u>:

relaxation modulus

$$\sigma_{xy} = \int_{-\infty}^{t} G(t-t')\, \frac{du_{xy}}{dt'}\, dt'$$

· if one waits $\sigma_{xy} \to 0$ as system relaxes

<u>Meas^t</u>:



$$u_{xy}(t) = u_{xy}^{0} \sin\omega t$$

$$\frac{du_{xy}}{dt} = \omega u_{xy}^{0} \cos\omega t$$

$$\to \quad \sigma_{xy}(t) = u_{xy}^{0}\Big[\underbrace{\omega \int_0^\infty G(\tau) \sin\omega\tau\, d\tau}_{G'(\omega)}\Big] \sin\omega t$$

$$+\, u_{xy}^{0}\Big[\underbrace{\omega \int_0^\infty G(\tau) \cos\omega\tau\, d\tau}_{G''(\omega)}\Big] \cos\omega t$$

· Fluid: $G'(0) = 0$

· <u>Dense</u>: isotropic, floppy polymer (homework)

$$\mu \sim \rho\, k_B T$$

density