

3b. Stiffness of Cytoskeletal

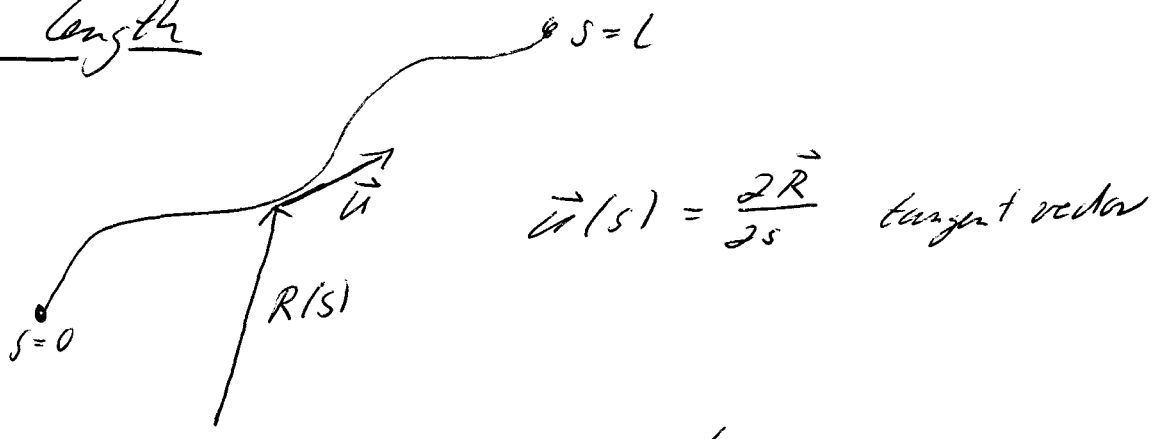
Filaments

- Lit:
- Doi and Edwards, *Theory of Polymer Dynamics*, Chapt. 88
 - Käs et al., *Biophys. J.*, Vol 70, 609-625, Feb 1996
 - Isambert et al., *J. Biol. Chem.*, Vol 270, 11437-44, May 1995
 - Legoff et al., *PRL*, Vol 88, 2002

Fundamental Problem:

- synthetic ~~polymers~~ polymers are very flexible
⇒ they only form mechanically stable networks at high volume fraction
- nature needs networks with large mesh sizes
⇒ biopolymers are much stiffer
(DNA $\times 10$, Cytoskeleton $> \times 100$)

Persistence length



bending energy:
$$U_{bend} = \frac{1}{2} k_c \int_0^L \left(\frac{d\vec{u}}{ds} \right)^2 ds$$

distribution of \vec{u} :
$$\Psi(\vec{u}) \sim e^{-U_{bend}/k_B T} = e^{-\frac{1}{2} L_p \int_0^L \left(\frac{d\vec{u}}{ds} \right)^2 ds}$$

\Rightarrow Persistence length:
$$L_p = \frac{k_c}{k_B T}$$

correlation length:

$$\langle \vec{u}(s) \cdot \vec{u}(0) \rangle = e^{-s/L_p}$$

Kratky - Porod model:



$$\overline{R_{end}^2} = 2L L_p - 2L_p^2 (1 - e^{-L/L_p})$$

better way to measure L_p by end-to-end distance see Le Goff

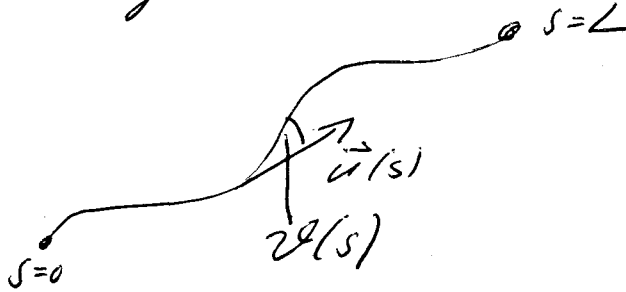
show transparency!

3

analyzing the thermal fluctuations:

~~Fourier decomposition of $u(s)$~~

tangential angle $\vartheta(s)$:



$$U_{\text{bend}} = \frac{kc}{2} \int_0^L \left(\frac{\partial \vartheta}{\partial s} \right)^2 ds$$

free filament ends: $\frac{\partial \vartheta}{\partial s} \Big|_{s=0,L} = 0$

Fourier expansion: $\vartheta(s) = \sum_q a_q \cos(qs)$

$$q = \frac{\pi n}{L} \quad n = 1, 2, 3, \dots \Rightarrow \lambda = \frac{\pi}{q}$$

$$\langle U_{\text{bend}}(q) \rangle = \frac{kc}{2} \left\langle \int_0^L \left(\frac{\partial}{\partial s} a_q \cos(qs) \right)^2 ds \right\rangle$$

$$= \frac{kc}{4} \langle q^2 \rangle \langle a_q^2 \rangle = \frac{ksT}{2}$$

equipartition theorem

values for L_p :

microtubules	actin + phalloidin	actin	vimentin
1-3 mm	16 μm	7 μm	300 nm

3.6. Rheological Properties of Cytoskeletal Filaments

Lit. : • D. Morse et al, Viscoelasticity of tightly entangled solution of semiflexible polymers, Phys. Rev. E, 58, R1237 - R1240, 1998

• F.C. MacKintosh et al, Phys. Rev. Lett, 75 4425, 1995

• Doi and Edwards, Theory of Polymer Dynamics, Chapt. 7.3

Linear viscoelasticity :

polymer solution is like a bowl of spaghetti: it flows for ~~slow~~^{slow} deformations and resists elastically for fast deformations = Viscoelasticity
show actin rheology!

$$\sigma_{\alpha\beta}(t) = (\kappa_{\alpha\beta}(t) + \eta_{\alpha\beta}(t)) \dot{\gamma}_{\alpha\beta}$$

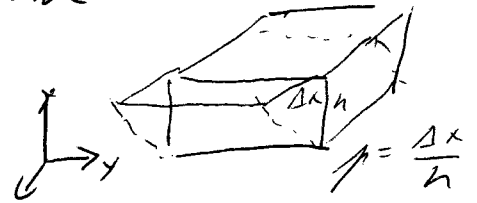
stress (pressure) tensor
viscosity
velocity gradient tensor

(5)

$$\sigma_{\alpha\beta}(t) = \int_{-\infty}^t G(t-t') (K_{\alpha\beta}(t') + K_{\beta\alpha}(t'))$$

for $K_{\alpha\beta}$ small justifying a linear relation

$G(t)$ shear relaxation modulus:



for shear flow: $v_x = K(t)y$ $v_y = 0$ $v_z = 0$

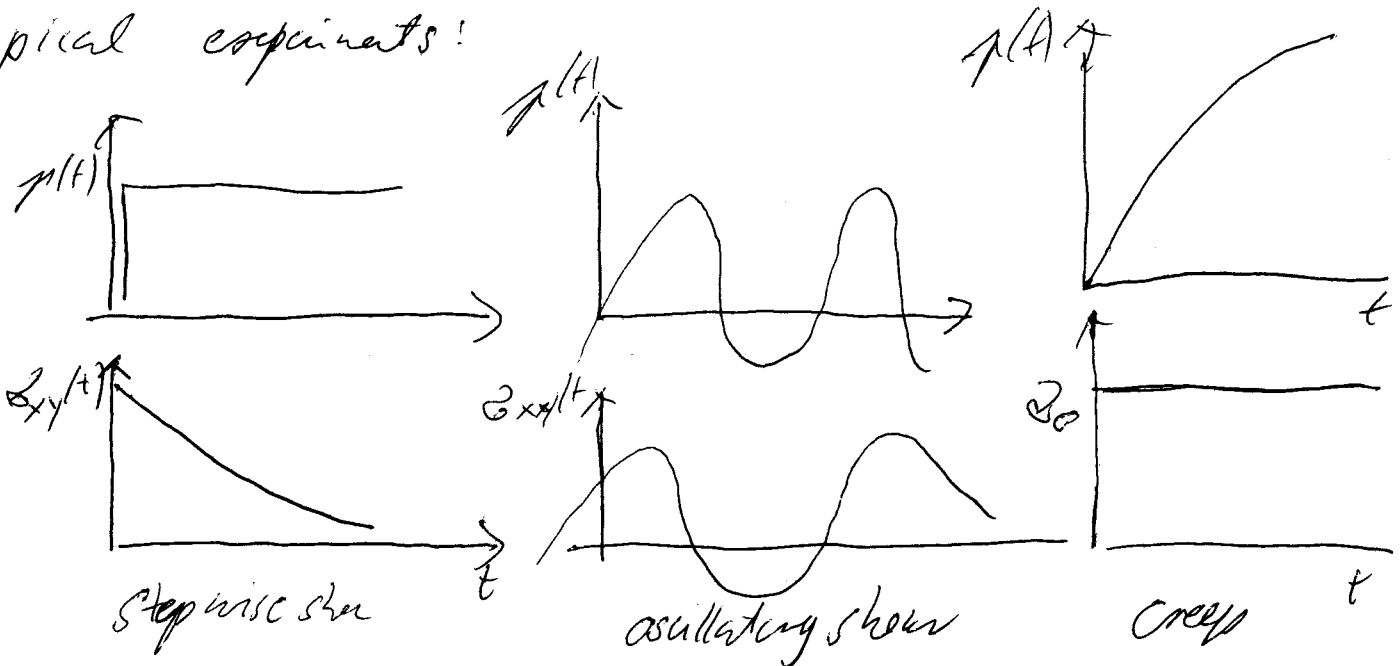
$$\Rightarrow \sigma_{xy}(t) = \int_{-\infty}^t dt' G(t-t') K(t')$$

shear strain:

$$\gamma(t) = \int_0^t dt' K(t')$$

$$\Rightarrow \sigma_{xy}(t) = \int_{-\infty}^t dt' G(t-t') \frac{\partial \gamma(t')}{\partial t'}$$

typical experiments:



stepwise: $\mu(t) = \begin{cases} 0 & (t < 0) \\ \mu_0 & (t > 0) \end{cases}$

(6)

$$\sigma_{xy}(t) = G(t) \mu_0$$

Oscillating:

$$\mu(t) = \mu_0 \cos \omega t$$

\downarrow storage modulus \downarrow loss modulus

$$\Rightarrow \sigma_{xy}(t) = (G'(\omega) \cos \omega t - G''(\omega) \sin \omega t) \mu_0$$

$$= \mu_0 \operatorname{Re} (G^*(\omega) e^{i\omega t})$$

$$G^*(\omega) = G'(\omega) + i G''(\omega) \quad \text{complex storage modulus}$$

$$G^*(\omega) = i\omega \int_0^{\infty} e^{-i\omega t} G(t) dt$$

Creep

$$\sigma(t) = \sigma_0$$

$$\mu(t) = \sigma_0 \left(\frac{t}{g_0} + \frac{g_1}{g_0^2} \right)$$

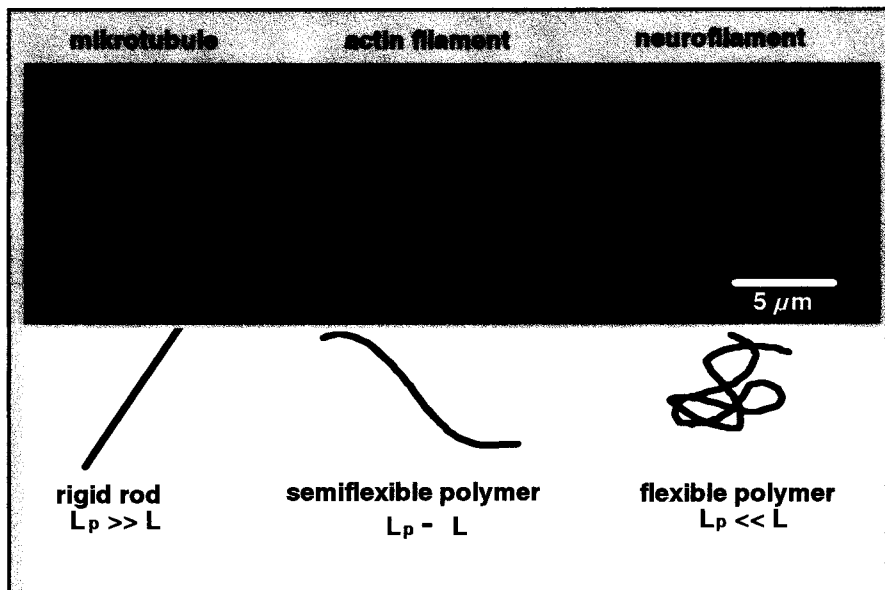
\downarrow steady-state compliance

mit $g_0 = \int_0^{\infty} dt G(t) = \tau_0$ (steady state viscosity) $g_1 = \int_0^{\infty} t G(t) dt$

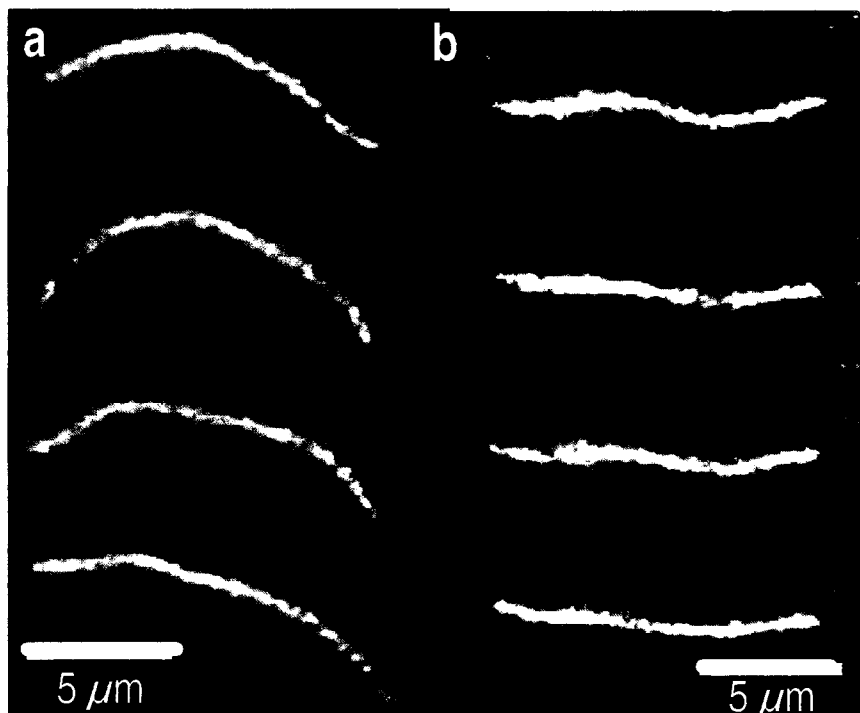
$t \rightarrow 0$:

$$\sigma_0 = g_0 \frac{d\mu}{dt}$$

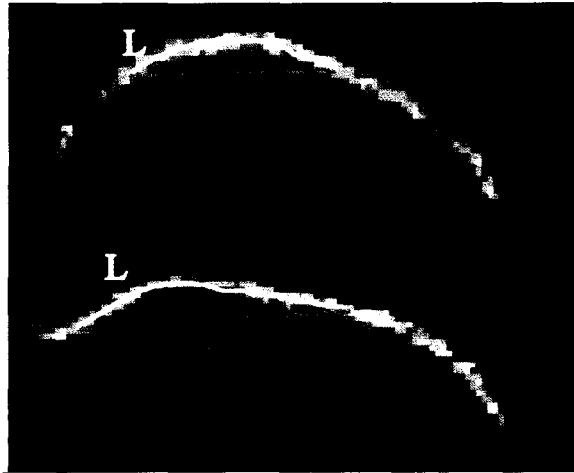
PERSISTENCE LENGTH OF ACTIN FILAMENTS



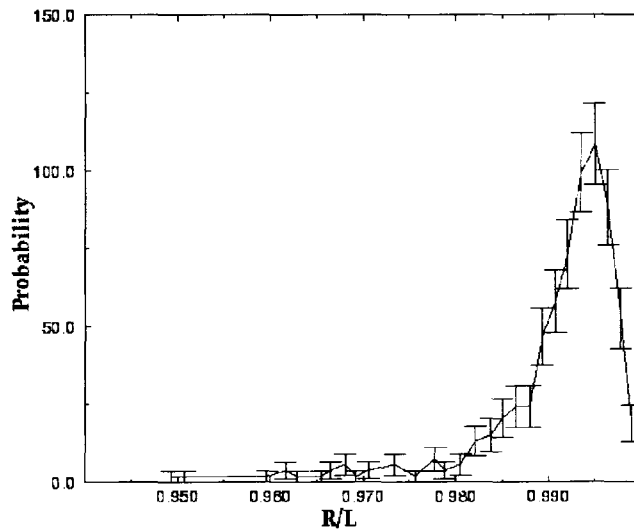
Magnitude of Brownian motions is a measure for stiffness:



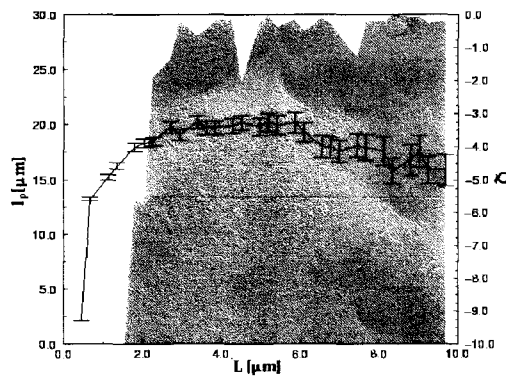
the end-to-end distance R as a function of the arc-length L determines the persistence length L_p :



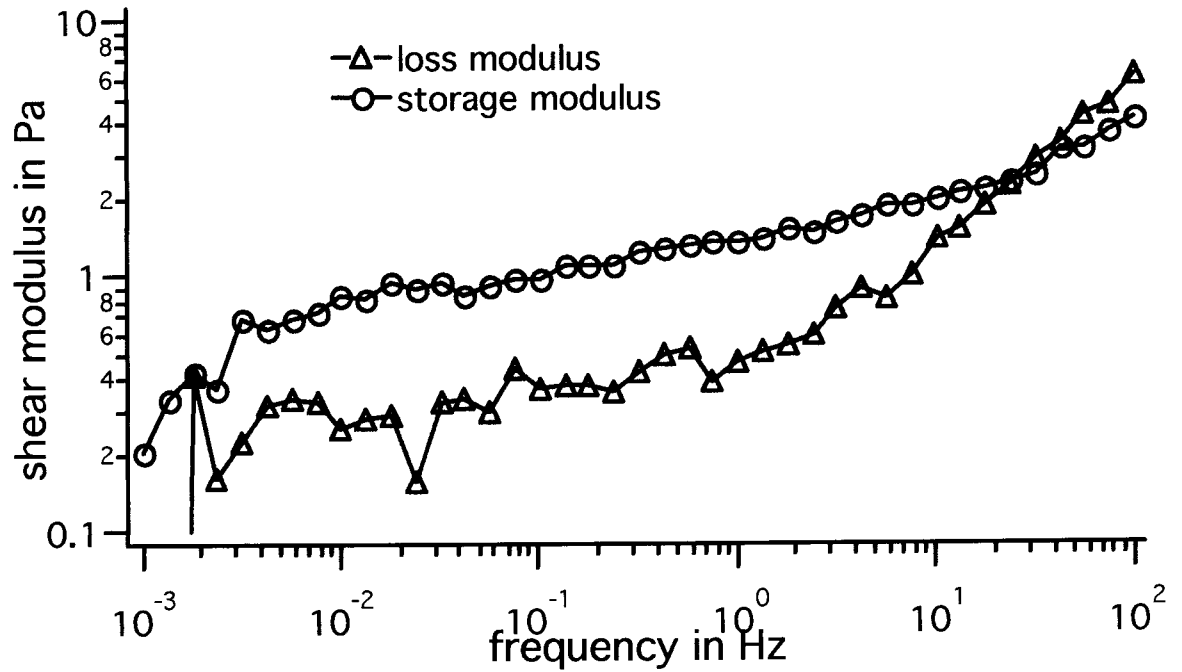
distribution of the end-to-end distance R (\rightarrow J. Wilhelm et al.) :



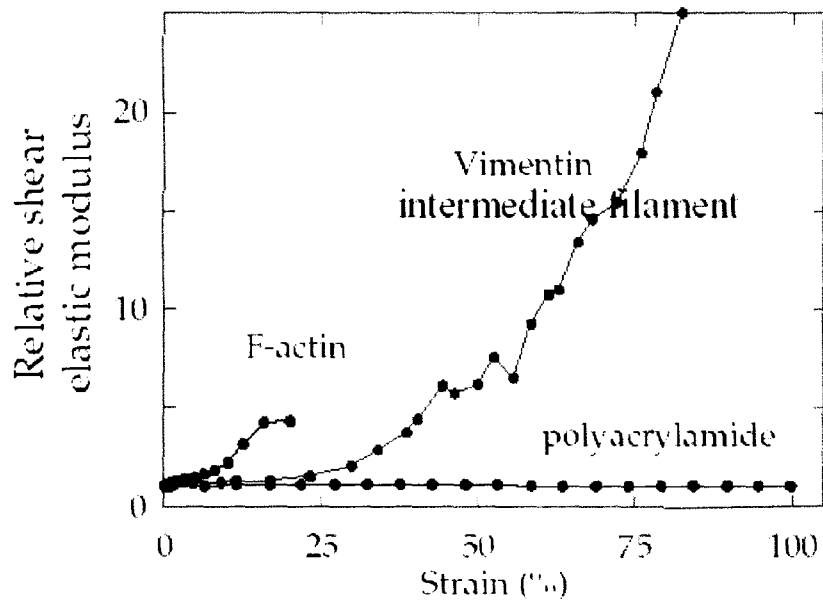
persistence length L_p as a function of the wavelength



Viscoelastic Behavior of Actin Networks I



Cytoskeletal polymer gels display strain-hardening not seen in synthetic gels



Strain hardening