Three microstructural models for the cytoskeleton

Cellular solids

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Tensegrity

Biopolymer

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Gibson & Ashby, 1988

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The cytoskeleton as a homogeneous, isotropic, elastic material.

Fig. 1. The cytoskeleton of a macrophage lamellipodium as seen by electron microscopy. The fibrous structure is mainly comprised of actin filaments. (John Hartwig, http://expmed.bwh.harvard.edu)
Cellular Solids Model

(Gibson & Ashby, 1988, Satcher & Dewey, 1997)

\[ \Phi \sim (a/L)^2 \text{ (solid fraction)} \]

\[ \delta \sim FL^3/(E_p I) \text{ from bending analysis} \]

where \( I \sim a^4 \)

\[ \sigma \sim F/L^2 \]

\[ \varepsilon \sim \delta/L \]

\[ E_n = \sigma/\varepsilon = c_1 E_f I/L^4 \text{ (network modulus)} \]

\[ E_n/E_f = c_1 \Phi^2 \text{ or } G_n \sim E_f \Phi^2 \]

\( a = \text{radius of filaments} \)

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The Architecture of Life

A universal set of building rules seems to guide the design of organic structures—from simple carbon compounds to complex cells and tissues

by Donald E. Ingber

Life is the ultimate example of complexity at work. An organism, whether it is a bacterium or a baboon, develops through an incredibly complex series of interactions involving a vast number of different components. These components, or subsystems, are themselves made up of smaller molecular components, which independently exhibit their own dynamic behavior, such as the ability to catalyze chemical reactions, generate new energy, and transport materials.

Finally, more philosophical questions arise: Are these building principles universal? Do they apply to structures that are molded by very large scale forces as well as small-scale ones? We do not know. Snellen, however, has proposed an intriguing model of the atom based on tensegrity that takes off where the French physicist Louis de Broglie left off in 1923. Fuller himself went so far as to imagine the solar system as a structure composed of multiple nondeformable rings of planetary motion held together by continuous gravitational tension. Then, too, the fact that our expanding (tensing) universe contains huge filaments of gravitationally linked galaxies and isolated black holes that experience immense compressive forces locally can only lead us to wonder. Perhaps there is a single underlying theme to nature after all. As suggested by early 20th-century Scottish zoologist D’Arcy W. Thompson, who quoted Galileo, who, in turn, cited Plato: the Book of Nature may indeed be written in the characters of geometry.

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Don Ingber, Scientific American
Tensegrity Model

\[ U \sim \int_0^{L_1} \sigma_{f1} \varepsilon_{f1} a^2 \, dx + \int_0^{L_2} \sigma_{f2} \varepsilon_{f2} a^2 \, dx \]

Work done = \Delta stored elastic energy

\[ F \delta \sim L a^2 \left( \frac{\delta}{L} \right)^2 \left( 2 \sigma_{f0} + E_f \right) \]

\[ E_n \sim \frac{\sigma_n}{\delta/L} \propto \left( 2 \sigma_{f0} + E_f \right) \left( \frac{a}{L} \right)^2 \propto \left( 2 \sigma_{f0} + E_f \right) \Phi \]
Tensegrity Model

\[ E = \frac{\sigma_c \Phi}{3} \frac{1 + 4\varepsilon}{1 + 12\varepsilon} \]

Where \( \sigma_c \) is the prestress in the individual tensile elements and \( \varepsilon \) is the initial strain in each.

Or, in the limit of \( \varepsilon \to 0 \),

\[ G_n \sim \frac{P}{3} \]

where \( P \) is the pre-stress in the tensile elements per unit total cross-sectional area \( (P=\pi\sigma_c a^2/L^2) \).

See Stamenovic for a full derivation.
Biopolymer Models

For a single segment of polymer between cross-links (Isambert and Maggs, 1997, Maggs, 1999, Storm, et al., 2005)

\[ F = \frac{l_p}{l^4} K_b \delta \]

\[ \varepsilon_n = \frac{\delta}{l} \]

\[ \sigma_n \sim F \cdot \frac{\text{filaments}}{\text{area}} \sim \frac{F}{\xi^2} \]

Low cross-link density

\[ E_n = \frac{\sigma_n}{\varepsilon_n} \sim \frac{l_p K_b}{l^3 a^2} \Phi \]

Maximum cross-link density \((l \sim \xi)\)

\[ E_n = \frac{\sigma_n}{\varepsilon_n} \sim \frac{l_p K_b}{a^5} \Phi^{5/2} \]

\[ l_p = \text{persistence length} \]

\[ l = \text{distance between entanglements or cross-links} \]

\[ \xi = \text{filament spacing} \]

\[ \varepsilon_n = \text{network strain} \]

\[ E_n = \text{network elastic modulus} \]

\[ \delta = \text{change in distance between entanglements/cross-links} \]

\[ \Phi = \text{solid fraction} \]
The initial shear modulus is given by

\[ G_0 = \frac{n k_B T r_0}{3 l_p} \left( \frac{1}{4(1-r_0/L_c)^2} \right) \left( \frac{L_c}{l_p} - 6(1 - r_0/L_c) \right) \left( \frac{L_c}{l_p} - 2(1 - r_0/L_c) \right) \]

- \( n \) = filament density
- \( l_p \) = persistence length
- \( r_0 \) = rest junction-to-junction distance
- \( L_c \) = contour length

\[ n = \frac{\# \text{filaments}}{\text{vol}} = \Phi/(\alpha^2 L_c) \]
Scaling behaviors for the three models

**Tensegrity**
Predicts a linear dependence on prestress (alone!)
Athermal
No ability to change cross-link density
No role for cross-link mechanics
Viscoelasticity?
Not valid in the limit of zero prestress

**Cellular Solids**
Filament bending stiffness dominates
Maximal cross-link density
Athermal
No role for cross-link mechanics
Viscoelasticity?

**Biopolymer**
Thermal (WLC at high extensions)
Viscoelastic. Captures $\frac{3}{4}$ power law at high frequency
Cross-link density and mechanics?

\[ G' \sim \sigma_n \]

\[ G' \sim E_f \Phi^2 \]

\[ G' \sim K_b^2 \Phi^1 \rightarrow K_b^2 \Phi^{5/2} \]