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Affine and non-affine deformations quantified in cytoskeletal networks through three-dimensional form-finding model

Yifan Wang[a], Jinghai Gong[a,*], Denis Wirtz[b], Benjamin W. Schafer[b]

[a] School of Naval Architecture, Ocean and Civil Engineering, Shanghai Jiao Tong University, Shanghai 200240, China
[b] Department of Civil Engineering, Johns Hopkins University, 3400 North Charles Street, Baltimore, MD 21218, USA

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ABSTRACT

Actin filaments and cross-linkers are main components of cytoskeletal networks in eukaryotic cells, and they support bending moments and axial forces respectively. A three-dimensional form-finding model is proposed in this work to investigate affine and non-affine deformations in cytoskeletal networks. In recent studies, modeling of cytoskeletal networks turns out to be a key piece in the cell mechanics puzzle. We used form-finding analysis to compute and analyze cytoskeletal models. A three-dimensional model is much more flexible and contains more elements than a two-dimensional model, and non-linear finite element analysis is difficult to converge. Thus, vector form intrinsic finite element analysis is employed here for valid results. The three-dimensional model reveals new behaviors beyond earlier two-dimensional models and better aligns with available data. Relative density of actin filaments and height of the form-finding model both play important roles in determining cytoskeletal stiffness, positively and negatively, respectively. Real cytoskeletal networks are quite mixed in terms of affine and non-affine deformations, which are quantified by internal strain energy in actin filaments and cross-linkers. Results are also influenced by actin filament relative density and height of the model. The three-dimensional form-finding model does provide much more room for intensive studies on cytoskeletal networks. In our future study, microtubules, fluidics, viscoelastic-plastic cross-linkers and even the whole cell model may be taken into account gradually to improve the cytoskeletal form-finding model.

1. Introduction

Affine stretching and non-affine bending both affect actin cytoskeleton network of protein-polymers. Since the protein-polymers are responsible for the mechanical stability of a cell, the influences may spread to the whole cell. However little is known about the boundary between affine deformation and non-affine deformation. Tensegrity model and open-cell foam model are important models of cytoskeletal networks. Deformations in these two types of models appear to be either axial (tensegrity) or bending (open-cell foam). Tensegrity model presents 100% affine as all the deformations are axial, and Young's modulus E for the model can be written as $E = s_0^2 T/(s_x - s_0)\cdot W\rho_0/\int_{s_0}^{s_x} T dx$, where W is the strain energy per unit mass and ρ_0 is the density of the model, which experiences elongation from length s_0 to length s_x caused by a small applied tension T acting in the x direction (Ethier and Simmons, 2007). Open-cell foam appears to be 100% non-affine, which are all bending deformations, and the effective Young's modulus of an open-cell foam model can be formulated as $E = 1.009E_s\rho^2/(1 + 1.514\rho)$ wherein ρ is the relative density of the foam and E_s is the Young's modulus of the solid from which the foam is made (Zhu et al., 2000). Form-finding model (Gong et al., 2013) shows a more complex relation and demonstrates how affine and non-affine play an important role in the solution. However it was established on a two-dimensional surface and seemed to be a little bit stiffer than reality in general, therefore a three-dimensional form-finding model is developed on the basis of two-dimensions in this work.

There exists controversy about whether affine or non-affine deformation is dominating in actin cytoskeleton network. Bai and Missel determined the effect of stiffer impurity filaments generally on the affine to non-affine crossover in the softer filament matrix and found that the stiffer impurity filaments make affine network slightly more affine, while highly non-affine network even more non-affine (Bai et al., 2011). Onck and Koeman showed that stiffening is caused by non-affine network rearrangements that govern a transition from a bending-dominated response to a stretching-dominated response (Onck et al., 2005). Head and Levine identified a dimensionless scalar quantity, being a combination of the material length scales that specifies to which regime a given cytoskeleton belongs and confirmed that the degree of

* Corresponding author.
E-mail address: gongjh@sjtu.edu.cn (J. Gong).

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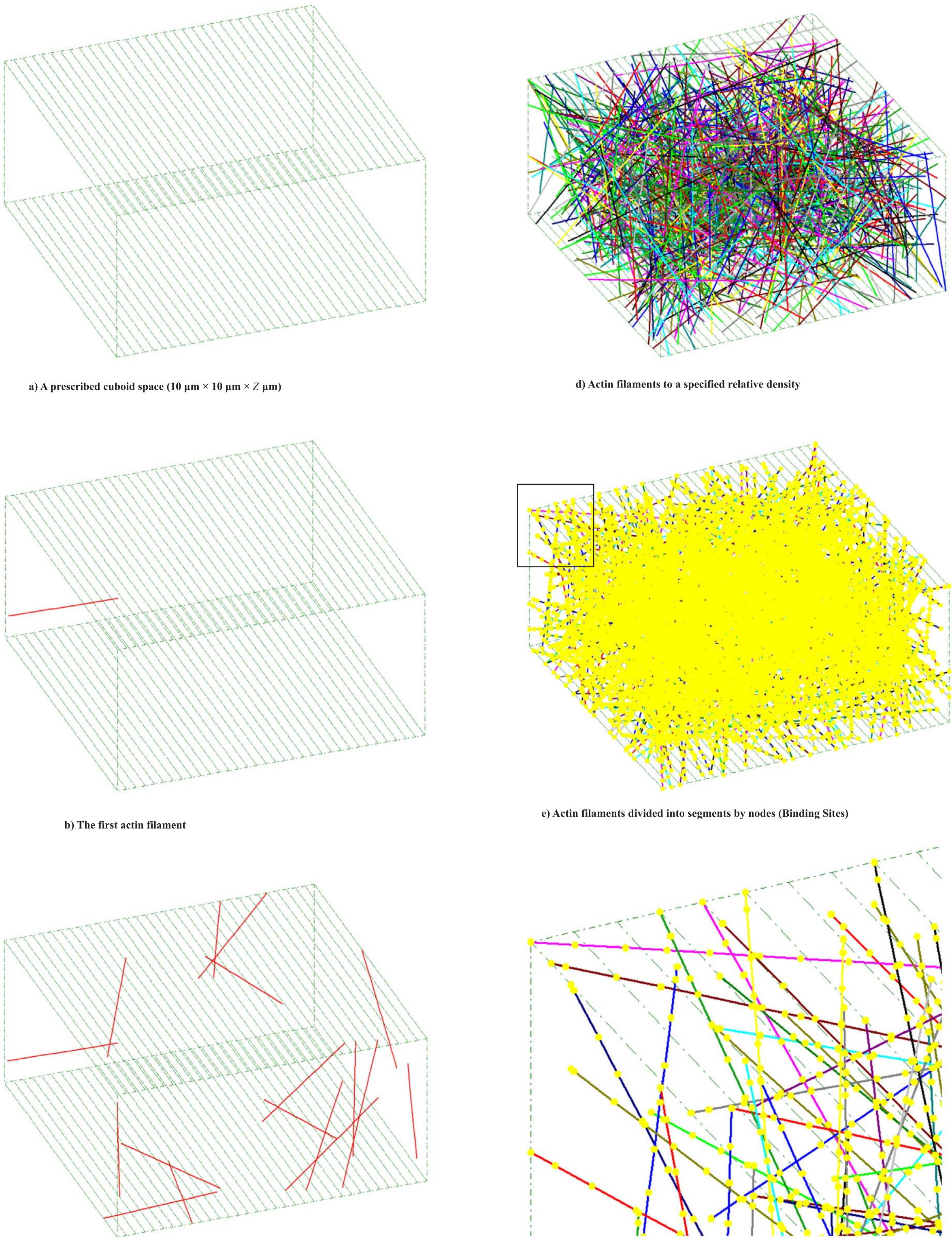
affinity under strain correlates with the distinct elastic regimes (Head et al., 2003).

Existing models have been expected to be found in either affine or non-affine deformations. It is assumed that deformations of the system is homogeneous down to the length scale of crosslinks for models considering only entropic stretching of filaments, that is, the deformation field is affine, e.g. the tensegrity model. For models relying on dynamic bending of filaments, the deformation must necessarily be



a) A prescribed cuboid space (10 μm × 10 μm × Z μm)

b) The first actin filament

c) More actin filaments

d) Actin filaments to a specified relative density

e) Actin filaments divided into segments by nodes (Binding Sites)

f) A high-magnification inset of the boxed regionine

Fig. 1. Process of building a three-dimensional form-finding model