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Surface effects on the mechanical characteristics of microtubule networks in living cells

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ABSTRACT

In this article, a new explicit formula is presented for the length-dependent persistence length of microtubules with consideration of surface effects. Further, surface effects on the buckling characteristics of microtubule systems in viscoelastic surrounding cytoplasm are investigated using a modified Timoshenko beam model. Closed-form solutions are presented for the buckling growth rates of double-microtubule systems. Both normal and shearing behaviors of microtubule associated proteins are taken into consideration. The comparison of present results with the available experimental data in the open literature shows that the present formulation provides more accurate results than those obtained by the classical beam theory. It is observed that the surface effect plays a prominent role in the bending and buckling behaviors of microtubules. Further, surface effects are more significant at higher buckling modes.

1. Introduction

Eukaryotic cytoskeleton plays an important role in the mechanical behavior of cells with complex structures. The cytoskeleton is a self-organized network consists of three main types of protein filaments, namely, microtubules, intermediate filaments and actin filaments. The stiffest elements of cytoskeleton are microtubules (MTs) which are commonly organized by the centrosome. The flexural rigidities of intermediate and actin filaments are much smaller than that of microtubule (about 100 times smaller) (Gittes et al., 1993). MTs are long, hollow cylinders having outer and inner radii of about 12.5 and 7.5 nm, respectively. In cells, the length of MTs ranges from 1 to 10 μm, while in axons MT's lengths may vary from 50 to 100 μm (Bray, 2001). MTs are made of α- and β-tubulin protein heterodimers that bind head-to-tail in protofilaments. Tubulins are organized in thirteen parallel protofilaments to form a single microtubule. MTs have crucial roles in many cellular processes (Alberts et al., 1994), such as forming the mitotic spindle, directing and facilitating intracellular motions of organelles, and support kinesins to convert chemical energy into mechanical work. It is also reported that MTs can be used as targets for anticancer drugs (Jordan and Wilson, 2004). Due to these roles in various cellular functions, the investigation of mechanical properties of MTs is an important problem.

Recently, continuum based modeling of MTs has been widely used in order to study their mechanical behaviors. One main reason for this is that controlled experiments on MTs are relatively difficult to perform. Inspired by development of elastic shell models for carbon nanotubes (CNTs), the classical shell theory has been used for the determination of vibrational frequencies of microtubules (Wang et al., 2006). Li (2008) proposed an Euler–Bernoulli beam model to study the influences of surrounding filament network and cytosol on the microtubule buckling. Also, Huang et al. (2008) studied surface deflection of a microtubule loaded by a concentrated radial force. Based on the nonlocal Timoshenko beam theory, small scale effects on the persistence lengths and buckling growth rates of MTs were investigated by Gao and Lei (2009). In another work, Tounsi et al. (2010) employed a parabolic shear deformable beam model to investigate the length-dependence of flexural rigidity and Young's modulus of microtubules. Civalek et al. (2010) examined the effects of small length scale on the free vibration and bending of cantilever microtubules. Civalek and Akgöz (2010) presented the nonlocal vibration characteristic of MTs by employing the Euler–Bernoulli beam model and differential quadrature method (DQM). They also investigated the buckling analysis of protein microtubules using strain gradient elasticity theory (Akgöz and Civalek, 2011). Based on an atomistic-continuum model, the stability behavior of MTs was studied by Xiang and Liew (2011). Further, using first-order shear deformation shell theory, the wave propagation in microtubules has been studied by Daneshmand et al.

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(2011). These interesting research works are limited to studying the mechanical properties of MTs without taking into account surface effects. The surface energy of an elastic solid is related to a few layers of atoms near its surface and thus the ratio of surface energy to bulk energy is extremely small in the classical elasticity theory. However, reduction in the structural size to micro/nanometer regime leads to a significant increase in the surface-to-bulk energy ratio (Gurtin et al., 1998; Dingreville et al., 2005). Hence, the surface effects on the mechanical characteristics of micro/nano-structural elements such as nanowires (Wang and Feng, 2009), carbon nanotubes (Farshi et al., 2010), nanofilms (Zhang et al., 2012) and microtubules should be taken into consideration. The strain gradient theory and nonlocal continuum mechanics are free from these effects. In addition, the deformation of microtubules is almost beam-like. Therefore, as anticipated, the results of Timoshenko beam model are close to those of the 2D orthotropic shell model (Heireche et al., 2010). In many cases, except for the systems where the anisotropic elastic properties of MTs are important, the Timoshenko beam model is employed because of its mathematical simplicity compared to the 2D shell model. Hence, the mechanical behavior of MTs including surface effects can be well described by a modified Timoshenko beam model using surface elasticity theory.

On the other hand, in a neuron (nerve cell) MTs are connected to each other by microtubule associated proteins (MAPs) to form complex microtubule systems (Hameroff and Penrose, 1996). Hence, there is a strong scientific need to increase the level of knowledge in the mechanical properties of complex microtubule systems. From the literature survey, it is cleared that the surface effect on the buckling and bending behaviors of microtubule networks embedded in a viscoelastic surrounding cytoplasm is not studied previously. This motivates us to investigate these problems here. A new closed-form solution is presented for the length-dependent persistence length of cantilever MTs. Further, exact solutions are obtained for the buckling analysis of microtubule networks in viscoelastic surrounding cytoplasm including both surface and shear effects. The presented approach is validated by comparing the results with experimental data and analytical solutions available in the open literature. The results reveal that surface energy has a significant effect on the mechanical behavior of MTs.

2. Persistence length of microtubules with consideration of surface effects

Consider a microtubule (MT) of length L with inner and outer surface layers as shown in Fig. 1. The inner and outer radii of MT are denoted by R_i and R_o, respectively. Let the thickness of inner and outer surface layers be t_i and t_o, respectively.

Based on the surface elasticity theory (Gurtin et al., 1998), the influence of surface energy on the mechanical behavior of micro/nano-structural elements is taken into account by assuming the solid surface as a layer of zero thickness that is bonded to the bulk material without slipping. The surface elastic modulus is defined as $E^s = E_o t_o = E_i t_i$ where E_i and E_o are the Young's modulus of inner and outer surface layers, respectively. The surface stress tensor ($\sigma^s_{\alpha\beta}$) can be obtained from the surface energy density (Λ) as follows (Cammarata, 1994):

$$\sigma^s_{\alpha\beta} = \Lambda\delta_{\alpha\beta} + \frac{\partial\Lambda}{\partial\varepsilon^s_{\alpha\beta}} \tag{1}$$

where $\varepsilon_{\alpha\beta}$ is the surface strain tensor and $\delta_{\alpha\beta}$ represents the Kronecker delta. Using the above equation, the linear one-dimensional constitutive relation of surface layers can be expressed as:

$$\sigma^s = \tau^s + E^s\varepsilon^s, \quad \tau^s = \left(\Lambda + \frac{\partial\Lambda}{\partial\varepsilon^s}\right)\Bigg|_{\varepsilon^s=0} \tag{2a,b}$$

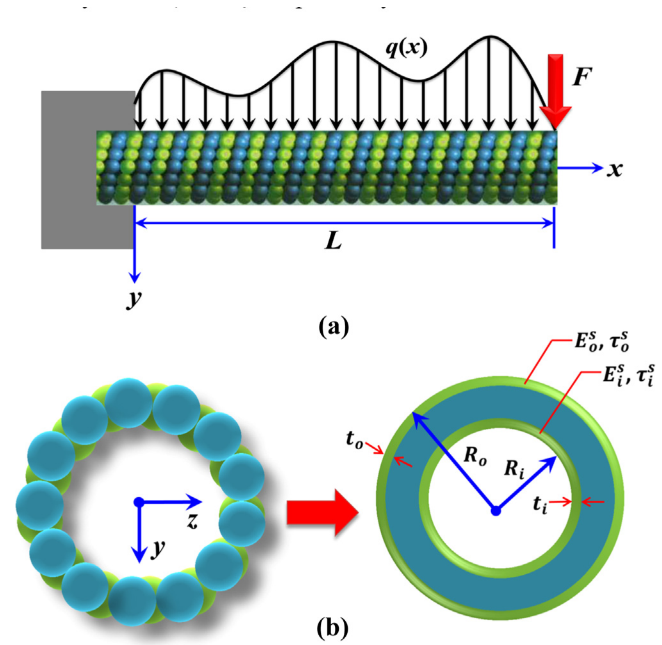

Fig. 1. (a) Schematic representation of a cantilever microtubule under a concentrated force. (b) Cross-section view of the microtubule.

Here τ^s is the surface residual stress when the bulk material is free of any strains. It has been shown that there are two important additional effects on the bending, vibration and buckling responses of micro/nano-beams due to surface energy (Wang and Feng, 2009; Farshi et al., 2010). The first surface effect is an increase in the flexural rigidity of the beam. The second effect is the influence of residual surface tension on the transverse load. The first surface effect can be mathematically expressed as:

$$(EI)^* = \frac{\pi}{4}E(R_o^4 - R_i^4) + \pi E^s(R_o^3 + R_i^3) \tag{3}$$

The surface elastic modulus is extremely small compared with the Young's modulus of the bulk material ($E^s \ll E$), but the surface elastic modulus is multiplied by R_i^3 while, the bulk elastic modulus is multiplied by R_i^4. Thus, both terms of Eq. (3) have the same order of magnitude at micro/nano scale and the effect of surface elastic modulus cannot be ignored. According to the Laplace–Young equation (Gurtin et al., 1998), the stress jump across both inner and outer surface layers can be written as:

$$\left\langle \sigma^+_{ij} - \sigma^-_{ij} \right\rangle n_i n_j = \sigma^s_{\alpha\beta}\kappa_{\alpha\beta} \tag{4}$$

where $\kappa_{\alpha\beta}$ and n_i represent the curvature and unit normal vector of the surface, respectively. In the above equation, Latin subscripts range from 1 to 3, but Greek indices take the values of 1 or 2. Using Eq. (4), the following relationship can be obtained for the distributed normal pressure caused by residual surface stress.

$$q(x) = H\frac{\partial^2 w}{\partial x^2}, \quad H = 4\tau^s(R_o + R_i) \tag{5a,b}$$

where $w(x)$ is the transverse deflection at point x on the mid-plane. As seen from Eq. (5a,b), the vertical surface load distributed along the length of MT (as shown in Fig. 1) depends on the current curvature of surface layers. Based on the Timoshenko beam