



Wave propagation in protein microtubules modeled as orthotropic elastic shells including transverse shear deformations

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ABSTRACT

Wave propagation along the microtubules is one of the issues of major concern in various microtubule cellular functions. In this study, the general wave propagation behavior in protein microtubules is investigated based on a first-order shear deformation shell theory for orthotropic materials, with particular emphasis on the role of strongly anisotropic elastic properties of microtubules. According to experimental observation, the first-order shear deformation theory is used for the modeling of microtubule walls. A general displacement representation is introduced and a type of coupled polynomial eigenvalue problem is developed. Numerical examples describe the effects of shear deformation and rotary inertia on wave velocities in orthotropic microtubules. Finally, the influences of the microtubule shear modulus, axial external force, effective thickness and material temperature dependency on wave velocities along the microtubule protofilaments, helical pathway and radial directions are elucidated. Most results presented in the present investigation have been absent from the literature for the wave propagation in microtubules.

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1. Introduction

Microtubules are one of the filamentous structures commonly found in the cytoplasm of eukaryotic cells. They are essential for many fundamental biological processes including cell motility (Hyams and Lloyds, 1994), cell division and intracellular transport (Schliwa and Woehlke, 2003; Yildiz et al., 2004). Microtubules consist of strings of $\alpha\beta$ -tubulin heterodimers, so-called protofilaments, which are arranged in parallel forming a hollow cylindrical nanotube with outer and inner diameters of about 25 and 17 nm, respectively (Alberts et al., 2005).

Mechanical properties of microtubules are important for understanding their role in various cellular functions and are particularly useful in designing molecular shuttles (Nitta and Hess, 2005). Our understanding of mechanical behaviors has been greatly advanced by the emergence of new experimental techniques, such as laser trap and high resolution microscopy, but there are still more behaviors to be studied that depend largely on techniques with improved time and spatial resolution (Nan et al., 2008). In particular, the last reference shows that time resolutions in the order of μ s are necessary to capture accurate aspects of motor stepping “in vivo”. Moreover, they reported that the rise

time for kinesin steps in vitro is typically 20–50 μ s. Priel et al. (2005) showed that the wave may propagate at a speed of 2 nm/ps ($=2000$ m/s) along microtubule associated protein 2 (MAP2) with the length of 1 nm (the order of magnitude for wave traveling time $=10^{-12}$ s). Meanwhile, theoretical models have also been developed for predicting the microtubules mechanics in recent years, including prediction of flexural rigidity (Tuszynski et al., 2005; van Mameren et al., 2009; Ghavanloo et al., 2010a; Donhauser et al., 2010), elastic buckling (Wang et al., 2006; Li, 2008; Yi et al., 2008; Chelminiak et al., 2010) and mechanical vibration (Sirenko et al., 1996; Kasas et al., 2004b; Portet et al., 2005; Tounsi et al., 2010; Ghavanloo et al., 2010b).

Wave propagation along microtubules is one of the major issues in various cellular functions of the microtubule such as mechanical rigidity of cells, cell motility and intracellular transport. There are several reasons to study universal properties of wave propagation in microtubules:

- The motion of some cells is essentially related to bending propagation in cilia and flagella and it is relevant to understand wave propagation along microtubules as the core constituents of cilia and flagella (Brokaw, 1988).
- Experimental observations indicate the presence of moving bending modes due to either the force generation by dynein arms (Hamasaki et al., 1995) or even the emergence of bending waves in interface microtubules close to the cell periphery (Neujahr et al., 1998).

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