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TWO-DIMENSIONAL SHELL VIBRATION OF MICROTUBULE IN LIVING CELL

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ABSTRACT

The mechanical behavior of a eukaryotic cell is mainly determined by its cytoskeleton. Microtubules immersed in cytosol are a central part of the cytoskeleton. Cytosol is the viscous fluid in living cells. The microtubules permanently oscillate in the cytosol. In this study, two-dimensional vibration of a single microtubule in living cell is investigated. The Donnell's shell theory equations for orthotropic materials is used to model the microtubule whereas the motion of the cytosol is modeled as Stokes flow characterized by a small Reynolds number with no-slip condition at microtubule-cytosol interface. The stress field in the cytosol induced by vibrating microtubule is determined analytically and the coupled vibrations of the microtubule-cytoplasm system are investigated. A coupled polynomial eigenvalue problem is developed in the present study and the variations of eigenvalues of coupled system with cytosol dynamic viscosity, microtubule circumferential Young's modulus and circumferential wave number are examined.

INTRODUCTION

The mechanical behaviour of an eukaryotic cell are mainly determined by its cytoskeleton. The cytoskeleton consists of microtubules, actin filaments and intermediate filaments. Among these components, microtubules are the most important component of eukaryotic cytoskeleton and play an essential role in mechanical stability and maintaining the shape of cells. A Microtubule is a long (up to 50 μm) hollow cylindrical polymer of tubulin heterodimers with outer and inner diameters about 25 nm and 17 nm, respectively. The microtubules permanently oscillate driven by the thermal energy of the cytoplasm. Therefore, considerable attention has also been focused on the vibration analysis of the microtubule [1-4].

Elastic vibrations of microtubules in fluid have been investigated based on an isotropic continuum model [1]. The effect of viscous damping of the surrounding medium on the microtubules vibrations has been studied by using a simple model [2]. The free vibration of microtubules using the finite element method with radial deformation has been investigated [3]. The effect of surrounding medium has been neglected in their analysis. An orthotropic elastic shell model has also been developed for microtubules and has been employed to study the free vibration of microtubules [4-5]. Recently, dynamic behavior of microtubules in cytosol has been studied [6]. An orthotropic shell-Stokes flow model with a slip boundary condition has been developed to explore the dynamic behaviors of microtubules in cytosol. An isotropic membrane shell is used in the present paper for modeling of the microtubule. The fluid around microtubules is assumed to be an ideal fluid with an infinitely large Reynolds number [1].

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It is worth to note that the microtubules in living cells are surrounded by cytoplasm which exhibits both viscosity from cytosol and elasticity from solid cytoskeleton network [7]. Hence, it is necessary to consider the coupled effect of the viscous cytosol to investigate the microtubule vibration behavior in living cell. To address the abovementioned controversy in the structural role of microtubules in living cells, this paper describes a mechanical model for microtubule vibration, considering the coupled effect of the viscous cytosol. Since the length of the microtubule is much larger than its radius we shall focus on the circumferential vibration of microtubule surrounded by cytoplasm. Furthermore, the cytosol motion can be assumed to take place in a plane perpendicular to the axis of the microtubule. In the present paper, the microtubule is modeled by based on Donnell's shell theory equations for orthotropic materials whereas the motion of the cytosol is considered as Stokes flow characterized by a small Reynolds number. No-slip boundary condition is also specified on the microtubule surface. The governing equations of the microtubule elastic deformation and the cytosol viscous flow are derived separately and then coupled through the interface between the microtubule and the surrounding cytosol. As the first step, the stress field in cytosol induced by vibrating microtubule is determined analytically. Then the natural frequencies and damping of the coupled cytoplasm-microtubule vibration are examined.

SHELL MODELLING OF MICROTUBULE

A long elastic microtubule surrounded by cytoplasm is shown in Fig. 1. The elastic filament network and cytoplasm can be modeled as a viscoelastic medium with elastic modulus E_c and viscosity μ. The microtubule is modeled as a long hollow cylinder. The elastic vibration of a microtubule in plane perpendicular to the axis of the microtubule can be modeled by using the Donnell's shell theory,

$$\frac{\partial^2 v}{\partial \theta^2} - \frac{\partial w}{\partial \theta} + \frac{R_m^2(1-\upsilon_x\upsilon_\theta)}{E_\theta h} f_\theta = \rho \frac{R_m^2(1-\upsilon_x\upsilon_\theta)}{E_\theta}\frac{\partial^2 v}{\partial t^2}, \tag{1}$$

$$\frac{\partial v}{\partial \theta} - w - \frac{1}{12}\left(\frac{h}{R_m}\right)^2 \frac{\partial^4 w}{\partial \theta^4} + \frac{R_m^2(1-\upsilon_x\upsilon_\theta)}{E_\theta h}(f_r - \xi w) = \rho \frac{R_m^2(1-\upsilon_x\upsilon_\theta)}{E_\theta}\frac{\partial^2 w}{\partial t^2}, \tag{2}$$

where θ is circumferential angular coordinate; v and w are circumferential and radial displacements, respectively; t is time; ρ is the mass density, h is the thickness, R_m is the mean radius, υ_x and υ_θ are Poisson's ratios in the axial and circumferential directions and E_θ is the Young's modulus in circumferential direction of the microtubule. In addition, ξ is an equivalent elastic medium constant ($\xi \approx 2.7E_c$), and f_θ and f_r are the circumferential and radial external tractions, respectively. The external tractions acting on the microtubule in the circumferential and radial displacement are the interaction force per unit axial length between the microtubule and the cytosol. This force can be determined by obtaining the stress field in cytosol induced by microtubule vibrations.

The displacements in each direction can be expressed as the series of functions with n circumferential nodes,

$$v(\theta,t) = \sum_{n=0}^{\infty} v_n(\theta,t)$$
$$w(\theta,t) = \sum_{n=0}^{\infty} w_n(\theta,t) \tag{3}$$

In this paper, we consider the case $n \geq 1$. Each function in (3) can be expressed as

$$v_n(\theta,t) = \sin(n\theta)\, q_{nv}(t) \tag{4}$$

$$w_n(\theta,t) = \cos(n\theta)\, q_{nv}(t) \tag{5}$$

where $q_{nv}(t)$ and $q_{nw}(t)$ are generalized coordinates. Before inserting (4-5) into (1-2), in the next section, we have to formulate and obtain the stress field in viscous cytosol to determine the interaction forces between cytosol and microtubule.

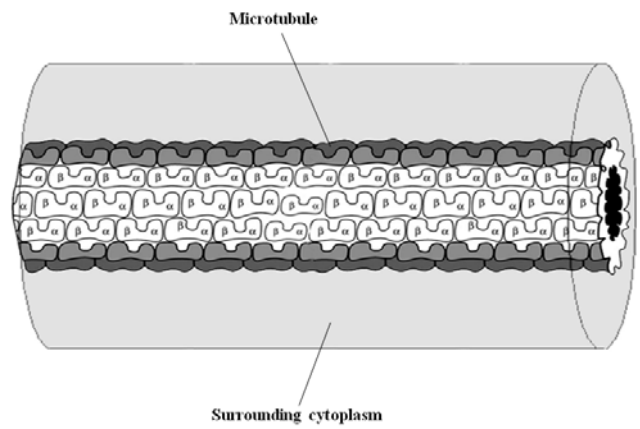

Fig. 1: A schematic picture of a microtubule immersed in cytoplasm, α and β are tubulin dimers that form microtubule

DYNAMIC EQUATIONS OF CYTOSOL MOTION

The cytosol is the liquid that fills the entire cytoplasmic region and can be modeled as a viscous fluid. To obtain the cytoplasm equations of motion, we use the Navier-Stokes equations for incompressible fluids in cylindrical coordinates. The induced cytoplasm flow velocity is assumed to be low; therefore, the inertia terms in Navier-Stokes equations are neglected. Moreover, assuming the axial displacement of the microtubule to be negligible, we use the cytoplasm deformation state in the r-θ plane. Regarding to these assumptions, the momentum-balance equation for the cytoplasm motion can be described by the well-known Stokes equations

$$\frac{\partial p}{\partial r} = \mu\left(\frac{\partial^2 v_r}{\partial r^2} + \frac{1}{r^2}\frac{\partial^2 v_r}{\partial \theta^2} + \frac{1}{r}\frac{\partial v_r}{\partial r} - \frac{v_r}{r^2} - \frac{2}{r^2}\frac{\partial v_\theta}{\partial \theta}\right), \tag{6}$$

$$\frac{1}{r}\frac{\partial p}{\partial \theta} = \mu\left(\frac{\partial^2 v_\theta}{\partial r^2} + \frac{1}{r^2}\frac{\partial^2 v_\theta}{\partial \theta^2} + \frac{1}{r}\frac{\partial v_\theta}{\partial r} - \frac{v_\theta}{r^2} + \frac{2}{r^2}\frac{\partial v_r}{\partial \theta}\right), \tag{7}$$

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whereas the continuity equation takes the form

$$\frac{\partial v_r}{\partial r}+\frac{v_r}{r}+\frac{1}{r}\frac{\partial v_\theta}{\partial \theta}=0 \tag{8}$$

To obtain the cytoplasm stress field, the continuity and momentum equations must be simultaneously solved for pressure and velocity. To reduce the general formulations given in (6-8) into a single governing equation in terms of a single unknown variable, we use the stream function ψ ,

$$v_r=\frac{1}{r}\frac{\partial \psi}{\partial \theta} \qquad v_\theta=-\frac{\partial \psi}{\partial r} \tag{9}$$

After substituting the stream function ψ from (9) into (6-8), the following equation is obtained,

$$\nabla^4\psi=0\,. \tag{10}$$

Assuming no-slip condition at the interface between the microtubule and the cytosol, the velocity of the cytosol at the interface where $r=R$ is written as

$$v_r(R,\theta)=-\frac{\partial w}{\partial t} \tag{11}$$

$$v_\theta(R,\theta)=-\frac{\partial v}{\partial t} \tag{12}$$

In addition, the induced viscous flow of the cytosol decays spatially away from the microtubule and vanishes at far from the microtubule:

$$\lim_{b\to\infty} v_r(b,\theta)=\lim_{b\to\infty} v_\theta(b,\theta)=0 \tag{13}$$

This boundary value problem (10-13) can be solved analytically. Its solution has the form

$$\psi=\begin{cases}\left[b_{11}r+b_{12}r\ln r+\dfrac{b_{13}}{r}+b_{14}r^3\right]\sin\theta & \text{for } n=1\\ \left[b_{n1}r^n+b_{n2}r^{2+n}+b_{n3}r^{-n}+b_{n4}r^{2-n}\right]\sin n\theta & \text{for } n\ge 2\end{cases} \tag{14}$$

where b_{ni} (i =1,2,3 and 4) are coefficients to be determined. Substituting (14) into (10) and using boundary conditions, we obtain

$$\begin{cases}v_r=-\left[\dfrac{R^2}{r^2}\dfrac{dq_{1w}}{dt}\right]\cos\theta\\ v_\theta=-\left[\dfrac{R^2}{r^2}\dfrac{dq_{1w}}{dt}\right]\sin\theta\end{cases} \quad \text{for } n=1 \tag{15}$$

$$\begin{cases}v_r=n\left[b_{n3}r^{-(n+1)}+b_{n4}r^{-(n-1)}\right]\cos n\theta\\ v_\theta=-\left[-nb_{n3}r^{-(n+1)}+(2-n)b_{n4}r^{-(n-1)}\right]\sin n\theta\end{cases} \quad \text{for } n\ge 2 \tag{16}$$

where

$$b_{n3}=\frac{R^{n+1}}{2}\left(\frac{n-2}{n}\frac{dq_{nw}}{dt}-\frac{dq_{nv}}{dt}\right) \tag{17}$$

$$b_{n4}=\frac{R^{n-1}}{2}\left(\frac{dq_{nv}}{dt}-\frac{dq_{nw}}{dt}\right) \tag{18}$$

The stress components relate to the velocities by

$$\begin{cases}\sigma_{rr}=\dfrac{4\mu}{r}\cos\theta\dfrac{dq_{1w}}{dt}\\ \tau_{r\theta}=\dfrac{4\mu}{r}\sin\theta\dfrac{dq_{1v}}{dt}\end{cases} \quad \text{for } n=1\,, \tag{19}$$

$$\begin{cases}\sigma_{rr}=\dfrac{2\mu n}{r}\left[\dfrac{dq_{nv}}{dt}+\dfrac{1}{n}\dfrac{dq_{nw}}{dt}\right]\cos n\theta\\ \tau_{r\theta}=\dfrac{2\mu n}{r}\left[\dfrac{dq_{nv}}{dt}+\dfrac{1}{n}\dfrac{dq_{nw}}{dt}\right]\sin n\theta\end{cases} \quad \text{for } n\ge 2 \tag{20}$$

To investigate the coupling effects of the elastic deformation of the microtubule, the filament network and the viscous flow of the cytosol, we assume that the surface traction of cytosol along the interface is equal to external tractions exerted on microtubule in opposite

$$\begin{aligned}f_\theta&=-\tau_{r\theta}(R,\theta)\\ f_r&=-\sigma_{rr}(R,\theta)\end{aligned} \tag{21}$$

Using these equations, we will solve the problems in the next sections.

EIGENVALUE PROBLEM

Substituting (4-5) and (19-21) into (1-2), one can obtain a microtubule-cytoplasm system of equations,

$$A\begin{bmatrix}1&0\\0&1\end{bmatrix}\begin{pmatrix}\ddot q_{1v}\\ \ddot q_{1w}\end{pmatrix}+B\begin{bmatrix}1&0\\0&1\end{bmatrix}\begin{pmatrix}\dot q_{1v}\\ \dot q_{1w}\end{pmatrix}+\begin{bmatrix}1&-1\\-1&1+k+C\end{bmatrix}\begin{pmatrix}q_{1v}\\ q_{1w}\end{pmatrix}=\begin{pmatrix}0\\0\end{pmatrix} \quad \text{for } n\ge 2 \tag{22}$$

$$A\begin{bmatrix}1&0\\0&1\end{bmatrix}\begin{pmatrix}\ddot q_{nv}\\ \ddot q_{nw}\end{pmatrix}+\frac{B}{2}\begin{bmatrix}n&1\\n&1\end{bmatrix}\begin{pmatrix}\dot q_{nv}\\ \dot q_{nw}\end{pmatrix}+\begin{bmatrix}n^2&-n\\-n&1+kn^4+c\end{bmatrix}\begin{pmatrix}q_{nv}\\ q_{nw}\end{pmatrix}=\begin{pmatrix}0\\0\end{pmatrix} \quad n\ge 2 \tag{23}$$

where

$$A=\rho\frac{(1-\upsilon_x\upsilon_\theta)}{E_\theta}R_m^2 \qquad B=\frac{4\mu(1-\upsilon_x\upsilon_\theta)}{RhE_\theta}R_m^2$$

$$C=\frac{\xi(1-\upsilon_x\upsilon_\theta)}{hE_\theta}R_m^2 \qquad k=\frac{1}{12}\left(\frac{h}{R_m}\right)^2 \tag{24}$$

To obtain the free-vibrations problem, we make the standard substitution

$$q_{nv}(t)=V_n\exp(\lambda t)\,, \tag{25}$$

$$q_{nw}(t)=W_n\exp(\lambda t)\,, \tag{26}$$

into the transient response equations. Using (25-26) in (22-23) one can obtain a system of equation of the form

$$\begin{bmatrix}Q_{11}&Q_{12}\\Q_{21}&Q_{22}\end{bmatrix}\begin{pmatrix}V_n\\W_n\end{pmatrix}=\begin{pmatrix}0\\0\end{pmatrix}. \tag{27}$$

For nontrivial solution of (30), one requires

$$\det([Q])=0 \tag{28}$$

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This is the characteristic equation of the system. For different values of the parameters and $n \geq 1$, there are three forms for the roots of the characteristic equation(Ω_i),

1)

$$\Omega_1 = -\lambda_1 + i\lambda_2, \quad \Omega_2 = -\lambda_1 - i\lambda_2, \quad \Omega_3 = -\lambda_3 + i\lambda_4, \quad \Omega_4 = -\lambda_3 - i\lambda_4, \tag{29}$$

2)

$$\Omega_1 = -\lambda_1, \quad \Omega_2 = -\lambda_2, \quad \Omega_3 = -\lambda_3 + i\lambda_4, \quad \Omega_4 = -\lambda_3 - i\lambda_4, \tag{30}$$

3)

$$\Omega_1 = -\lambda_1, \ \Omega_2 = -\lambda_2, \ \Omega_3 = -\lambda_3, \ \Omega_4 = -\lambda_4, \tag{31}$$

where λ_i ($i = 1-4$) are real, positive numbers.

RESULTS AND DISCUSSION

A single microtubule is analyzed to determine the vibration characteristics and the influences of the viscous cytosol. Here, we use the parameters of material and geometry as the microtubule inner radius $R_i = 11.5$ nm, wall thickness $h = 2.7$ nm and the mass density $\rho = 1.47$ g/cm^3 for 14-protofilamment microtubules [1]. Thus, the outer radius in our calculation is $R = 14.2$ nm and the mean radius R_m is approximately 12.8 nm. The Poisson's ratio in circumferential and axial direction is another parameter needed in calculation. In general, the value of this parameter for different materials lies in the range (0, 0.5). Since our results depend only weakly on Poisson's ratio ($\upsilon_x \upsilon_\theta \approx 10^{-3}$), we choose the values $\upsilon_x = 0.3$ and $\upsilon_\theta = 0.3 \times 10^{-3}$ in next calculations. Other parameters required for numerical evaluation have been given in the literature for different range of magnitudes. The effects of main parameters including the microtubule circumferential Young's modulus and dynamic viscosity of the cytosol on the coupled cytosol-microtubule dynamics are studied here.

The longitudinal and circumferential Young's modulus of the microtubule is the most difficult parameters to obtain among the parameters needed for the numerical computation, because no direct measurement seems to be possible. So far, different methods have been investigated for determining the longitudinal and circumferential Young's modulus of the microtubules. The circumferential elastic modulus is lower than the longitudinal elastic modulus by a few orders of magnitude. The magnitude of the circumferential Young's modulus of microtubules E_θ has been reported by Tuszynski et al. [8] to be in the range of $1 \leq E_\theta \leq 4$ MPa. Therefore, the four eigenvalues of the cytosol-microtubule system λ_1, λ_2, λ_3 and λ_4 are plotted in Fig. 2 for different value of circumferential Young's modulus of microtubules E_θ in the rang $1 \leq E_\theta \leq 4$. In this figure, the other parameters are fixed as the dynamic viscosity $\mu = 1 \times 10^{-3}$ N.s/m^2 and the circumferential wave numbers n=1. It can be seen from Fig. 2 that the second and the fourth eigenvalues λ_2 and λ_4 are very close (almost coincident) for different values of microtubule circumferential Young's modulus. It is well known that in general, the eigenvalues of a system increases when its stiffness increases. As it can be seen from Fig. 2, the eigenvalues of the cytosol-microtubule system increase when the microtubule circumferential Young's modulus increases.

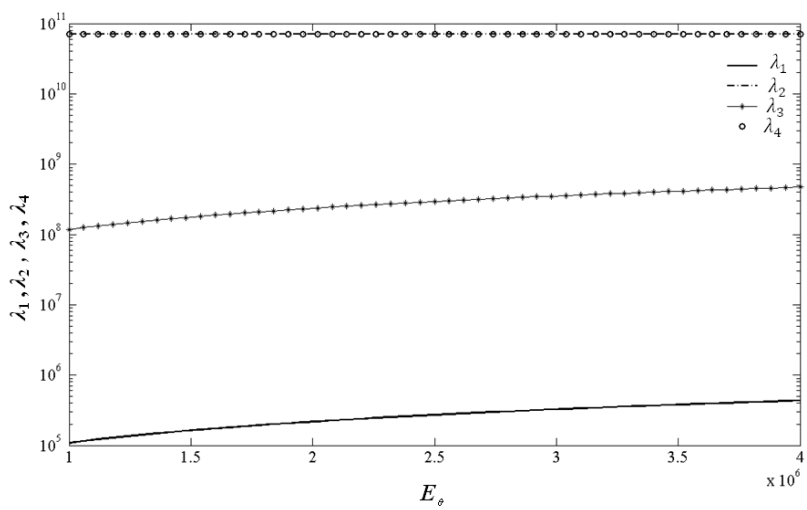

Fig. 2: Effect of the microtubule circumferential Young's modulus on the coupled eigenvalues of the microtubule-cytoplasm system for $\mu = 1 \times 10^{-3}$ Pa.s and $n = 1$.

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For the circumferential Young's modulus of microtubules in the range $1 \le E_\theta \le 4$ and the circumferential wave numbers $n \ge 2$, the eigenvalues of the coupled cytosol-microtubule system are a complex conjugate pair Ω_3 and Ω_4 and two real eigenvalues Ω_1 and Ω_2. The effect of the microtubules circumferential Young's modulus on the eigenvalues of the coupled cytosol-microtubule system is investigated in Fig. 3 and Fig. 4 for cytosol viscosity $\mu = 1\times10^{-3}$ N.s/m^2. It is observed that

a) λ_1, λ_3 and λ_4 are monotonically increasing as the microtubule circumferential Young's modulus increases for different circumferential wave numbers.

b) The second eigenvalue λ_2, in various circumferential wave numbers is not almost sensitive to the microtubule circumferential Young's modulus.

c) For the specific Young's modulus, λ_4, λ_3, λ_2 and λ_1 increase as the circumferential wave number increases.

d) The effect of the circumferential wave number on λ_1 and λ_3 is much larger than λ_2 and λ_4.

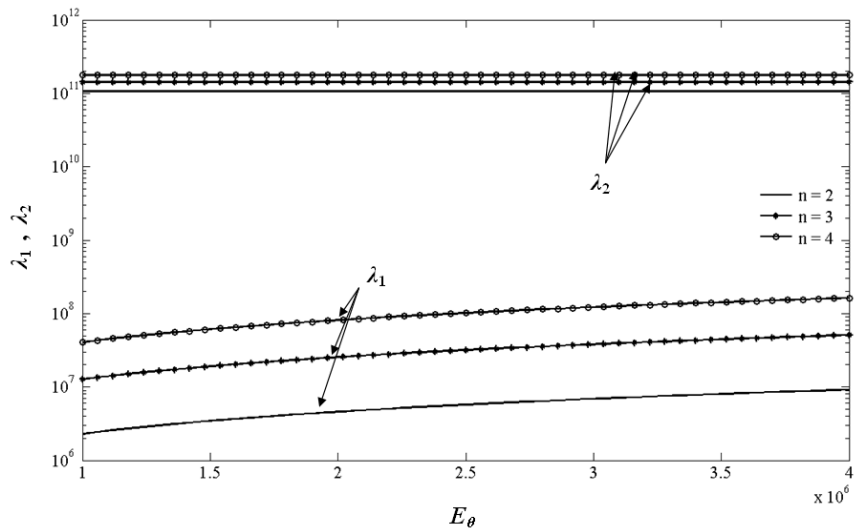

Fig. 3: Effect of the microtubule circumferential Young's modulus on λ_1 and λ_2 for $\mu = 1\times10^{-3}$ Pa.s and different circumferential wavenumber.

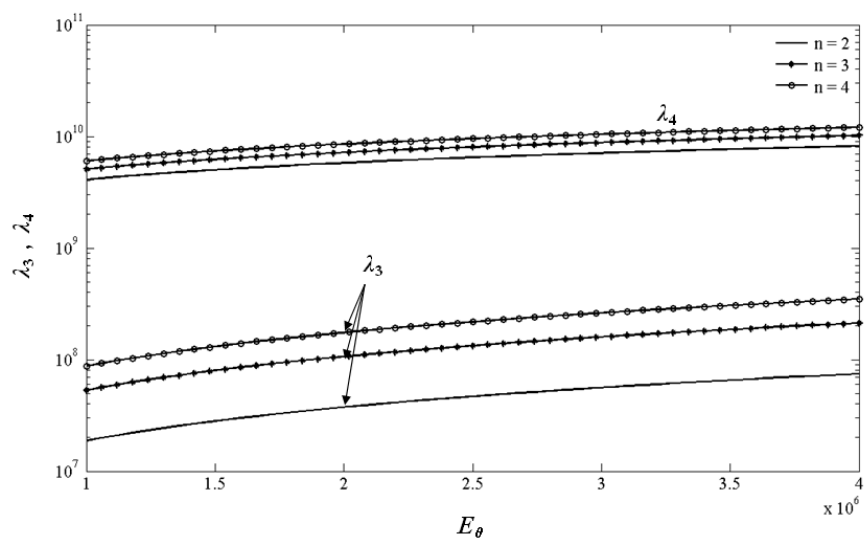

Fig. 4: Effect of the microtubule circumferential Young's modulus on λ_3 and λ_4 for $\mu = 1\times10^{-3}$ Pa.s and different circumferential wavenumber.

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Viscous damping by surrounding cytosol may quench excitation of vibrations. The role of surrounding cytoplasm is characterized by parameter μ . For the cytosol viscosity μ in the range $1\times10^{-3} \le \mu \le 8.5\times10^{-3}$ N.s/m^2, the variations of the four eigenvalues λ_4, λ_3, λ_2 and λ_1 for a specified circumferential Young's modulus of microtubule E_θ=1MPa and n=1 are plotted in Fig. 5. In this figure, it can be seen that the first and the second eigenvalues λ_1 and λ_2 for different values of cytosol viscosity are almost identical and with increasing the viscosity, λ_1 and λ_2 smoothly increase and λ_3 and λ_4 smoothly decrease. Moreover, it should be noted that for n=1 the roots of characteristic equation are pure real (31).

For the cytosol viscosity μ in the range $1\times10^{-3} \le \mu \le 8.5\times10^{-3}$ N.s/m^2 and the circumferential wave numbers $n \ge 2$, the eigenvalues of the coupled cytosol-microtubule system are a complex conjugate pair Ω_3 and Ω_4 and two real eigenvalues Ω_1 and Ω_2. The effect of the viscosity of the cytosol on the eigenvalues of the coupled cytosol-microtubule system is investigated in Figs. 6 and 7 for circumferential Young's modulus of microtubule E_θ=1MPa.

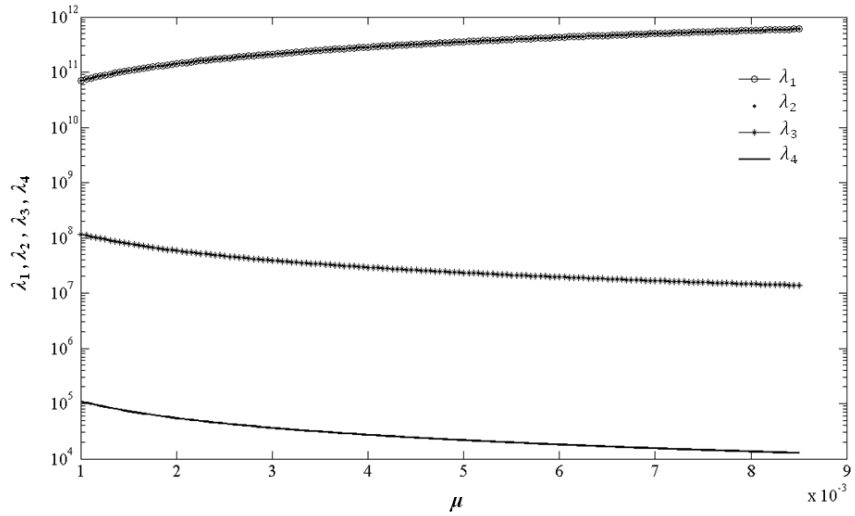

Fig. 5: Effect of the cytosol viscosity on the coupled eigenvalues of the microtubule-cytoplasm system for E_θ=1MPa, and $n=1$.

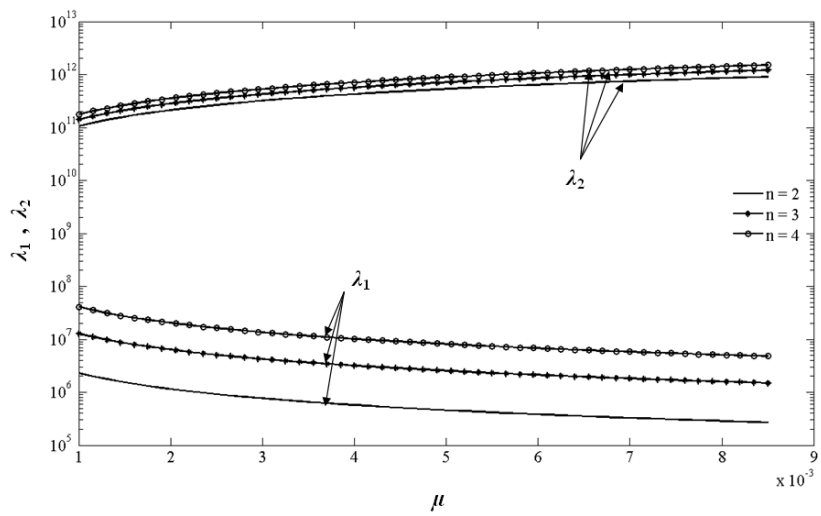

Fig. 6: Effect of the cytosol viscosity on λ_1 and λ_2 for E_θ=1MPa and different circumferential wavenumber.

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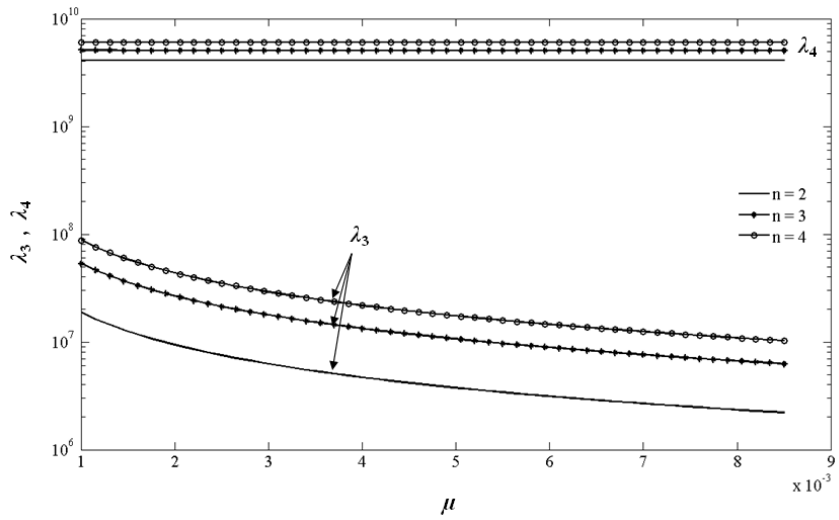

Fig. 7: Effect of the cytosol viscosity on λ_3 and λ_4 for E_θ=1MPa, and different circumferential wavenumber.

It is observed that

a) Both λ_1 and λ_3 are monotonically decreasing as cytosol viscosity increases for different circumferential wave numbers.

b) λ_2 is smoothly increasing as cytosol viscosity increases for different circumferential wavenumbers.

c) The frequency of oscillation, λ_4, in various circumferential wavenumbers is not almost sensitive to the cytosol viscosity.

d) For the specific cytosol viscosity, λ_4, λ_3, λ_2 and λ_1 increase as the circumferential wave number increses.

e) The effect of the circumferential wave number on λ_1 and λ_3 is much larger than λ_2 and λ_4.

CONCLUSION

Two-dimensional free vibration of a microtubule in living cell was presented based on Donnell's shell theory equations for orthotropic materials. The cytosol was modeled as a viscous fluid. The motion of the cytosol was modeled as Stokes flow with no-slip condition at microtubule-cytosol interface. The microtubule motion was coupled with the cytosol through interface continuity conditions. The dynamic equations of cytosol was solved analytically and then the coupled cytosol-microtubule equations of motion were obtained and presented in matrix forms, which were suitable for the prediction of the change of the coupled eigenvalues. It should be noted that the effect of the cytosol on the equations of motion appears as the damping terms. The variations of the eigenvalues with cytosol dynamic viscosity, microtubule circumferential Young's modulus and circumferential wave number were examined. The numerical results show that the dynamic behavior of the microtubule surrounded by cytosol is very sensitive to the cytosol viscosity. Moreover, the eigenvalues increase with the growing circumferential wave number *n* and increasing the microtubule circumferential Young's modulus.

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