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Viscous Damping of Vibrations in Microtubules

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Abstract. Pokorný et al. have recently suggested that metabolic processes drive microtubules in a cell to vibrate at Megahertz frequencies, but the theory does not explicitly consider dissipative effects which will tend to damp out the vibrations. To examine the effects of viscous damping on the structure, we determine viscous forces and rate of energy loss in a cylinder undergoing longitudinal oscillations in water. A nondimensional expression is obtained for the viscous drag on the cylinder. When applied to a microtubule, the results indicate that viscous damping is several orders of magnitude too large to allow resonant vibrations.

Key words: microtubules, radiofrequency signal, relaxation time, vibrations, viscous damping

1. Introduction

Pokorný et al. have recently proposed that metabolic processes drive microtubules in living cells into oscillations in the MHz frequency range [1]. A subsequent paper reported weak narrowband electrical signals from yeast cells at frequencies between 8–9 MHz, which the investigators interpreted as confirmation of the theory [2].

Notably missing from this theory, however, is an explicit consideration of viscous damping by the surrounding medium, or other dissipative processes which have to be present, at some level. We estimate the magnitude of these effects by developing a simple model.

2. The model

We calculate the viscous force on a uniform cylinder of radius R immersed in a fluid, which is undergoing forced sinusoidal oscillation at radian frequency ω in a longitudinal mode. The cylinder is immersed in a fluid of density ρ and kinematic viscosity ν. The cylinder is acted on by a shear stress (axial force per unit surface area) τ

$$\tau = \mu \frac{\partial u}{\partial r}\bigg|_{r=R} \quad (1)$$

where μ is the dynamic viscosity which is equal to $\nu\rho$. The momentum equation in cylindrical coordinates can be written

$$\nu\left(\frac{\partial^2 u}{\partial r^2}+\frac{1}{r}\frac{\partial u}{\partial r}\right)=\frac{\partial u}{\partial t} \tag{2}$$

where u is the axial component of the velocity. We assume no-slip (stick) boundary conditions at the cylinder's surface where $r = R$

$$u(R,t)=U_0\cos(\omega t) \tag{3}$$

In addition, the velocity is bounded far from the cylinder:

$$u(\infty,t)=0. \tag{4}$$

This boundary value problem is analogous to that of heat diffusion in a solid around a cylinder with an oscillating temperature [3]. Its solution has the form

$$u(r,t)=\Re\{U_0\exp(i\omega t)g(r)\}. \tag{5}$$

Substituting Equation (5) into Equation (2) yields

$$\frac{d^2 g}{dr^2}+\frac{1}{r}\frac{dg}{dr}-\frac{i\omega}{\nu}g=0 \tag{6}$$

whose solutions are modified Bessel's function of the zeroeth order

$$K_0\left(r\sqrt{\frac{i\omega}{\nu}}\right),\ I_0\left(r\sqrt{\frac{i\omega}{\nu}}\right) \tag{7}$$

We reject the I_0 solution which diverges at infinite r. The solution is then

$$u(r,t)=\Re\left\{U_0\exp(i\omega t)AK_0\left(r\sqrt{\frac{i\omega}{\nu}}\right)\right\} \tag{8}$$

where A is determined from the boundary condition on the surface of the cylinder, i.e.

$$U_0\cos(\omega t)=\Re\left\{U_0\exp(i\omega t)AK_0\left(r\sqrt{\frac{i\omega}{\nu}}\right)\right\}. \tag{9}$$

Finally, the velocity profile $u(r,t)$ is given by

$$u(r,t)=\Re\left\{U_0\exp(i\omega t)\frac{K_0\left(r\sqrt{\frac{i\omega}{\nu}}\right)}{K_0\left(R\sqrt{\frac{i\omega}{\nu}}\right)}\right\}. \tag{10}$$

Inserting into Equation (1) and evaluating gives

$$\tau=-U_0\Re\{\exp(i\omega t)\}\mu\left(\frac{i\omega}{\nu}\right)^{1/2}\frac{K_1\left(R\sqrt{\frac{i\omega}{\nu}}\right)}{K_0\left(R\sqrt{\frac{i\omega}{\nu}}\right)}. \tag{11}$$

For convenience, we evaluate the shear stress in normalized form ($\tau R/\mu U_0$ vs. $R\sqrt{\omega/\nu}$), and plot its magnitude and phase Figure 1. The viscous force F on the cylinder is then given by the product of the shear stress τ and the surface area S of the cylinder, i.e.

$$F = S\tau = 2\pi RL\tau. \tag{12}$$

The shear stress always lags the velocity, by angles ranging from 180° to 135° depending on the frequency. In this system the Reynolds number (Re) is low ($\ll 1$) but the solution does not depend on Re.

Figure 1 also shows the corresponding solution for an oscillating slab (Stokes' second problem), which is found in standard textbooks, e.g. [4]. In nondimensional quantities, this solution is simply

$$\frac{\tau R}{\mu U_0} = R\sqrt{\frac{\omega}{\upsilon}} \tag{13}$$

where there is a phase angle of 135° between the velocity and viscous force. The two solutions approach each other when $R\sqrt{\omega/\nu} > 1$. In effect, as the frequency increases, the thickness of the layer of moving fluid near the cylinder becomes small relative to its radius, and the cylindrical problem reduces to Stokes' second problem for a slab.

3. Application to the microtubule

We assume that the medium has the material properties of water at 37°C ($\mu = 695\times10^{-6}$ N–s m^{-2} and $\nu = 7.00\times10^{-7}$ m^2 s^{-1}) and choose a radius $R = 12.5$ nm appropriate for a microtubule. Assuming a resonant frequency of 10 MHz (which is towards the lower end of the proposed range of vibrations in [1]) the nondimensional quantities are $R\sqrt{\omega/\nu} = 0.118$ and $\mu U_0 = 0.42$. Under these conditions, the viscous drag on the cylinder three times larger than would be experienced by a slab of the same surface area.

These results can be interpreted most simply by assuming that the viscous force is exactly out of phase with the velocity of the cylinder (the calculated phase lag is 162°). The system is then equivalent to the simple mass-spring-dashpot oscillator of elementary mechanics. The rate of energy loss per unit length of the cylinder, due to viscous drag, is simply

$$\frac{dE(t)}{dt} = -2\pi R\tau U(t) \tag{14}$$

This is proportional to the kinetic energy $E(t)$ per unit length

$$E(t) = \frac{1}{2}\pi R^2 \rho_{cyl} U^2(t) \tag{15}$$

where ρ_{cyl} is the mass density of the cylinder. This implies that energy is lost to dissipative forces as a single exponential process with relaxation time constant T:

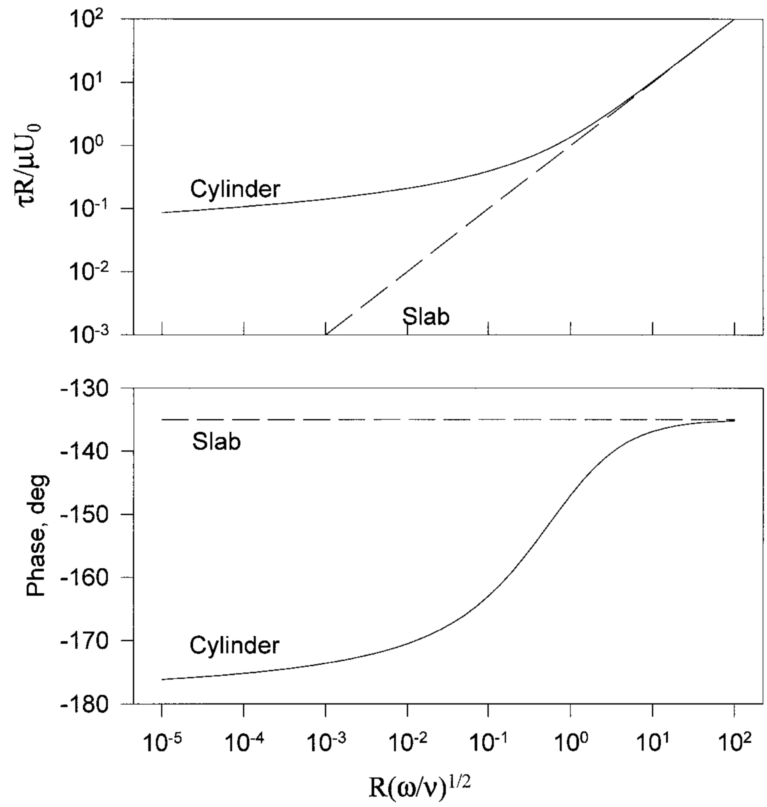

Figure 1. Calculated magnitude and phase of viscous drag on a cylinder undergoing longitudinal oscillation. The quantities plotted are normalized units, which are defined in the text.

$$T = \frac{-E}{dE/dt} = \frac{rho_{cyl}R^2}{2(0.42)\mu} \approx 0.26 \text{ ns.} \quad (16)$$

The relaxation time in the cylinder is more than three orders of magnitude smaller than the period of the postulated resonance. The damping is so strong that it is not meaningful to speak of 'resonance' at all.

Similar considerations rule out storage of energy in the microtubule sufficient to sustain oscillations. Pokorný et al. propose that the energy for the oscillations of the microtubule is supplied by metabolic processes, i.e. hydrolysis of GTP when tubulin heterodimers are added to the structure. The amount of energy that is added by such processes can be estimated from a typical growth rate of a microtubule of 1 μm min^{-1}, which corresponds to addition of about 30 tubulin dimers per second to the structure [5]. If we accept Pokorný's estimate that the incorporation of tubulin heterodimers adds 7.1 kJ mol^{-1} to the microtubule [6], we estimate that approximately 10^{-19} watts can be supplied to the structure. However, the amount of energy stored in an oscillator driven with a power P and relaxation time T is of the order of $P\ T$. This implies that the average stored energy in the microtubule from metabolic processes associated with addition of heterodimers will be about eight orders of magnitude below kT, and any resulting oscillations would be swamped by random thermal agitation. We have not considered transverse oscillations, but since they would result in displacement of more of the surrounding water, we would anticipate higher viscous losses.

4. Discussion

Pokorný et al. have reported electrical signals from yeast cells at 8.18 MHz with extremely sharp bandwidth ($<$ 0.01 MHz), which they attribute to microtubule oscillations [2].

We question the reliability of these observations on several accounts. The signals were very small and they occurred in a part of the spectrum that is widely used for communications. (In particular, there is a major communications band between 8.100 and 8.195 MHz). Narrow band signals in the Megahertz range are characteristic of technological, not biological sources. Moreover, signals were sometimes observed from pure sucrose solution [2], which further clouds their significance.

Retrieving resonances in the microtubule would require an extraordinarily weak coupling between the cylinder and the surrounding fluid. In hydrodynamic terms, this would correspond to nearly perfect ‘slip’ boundary conditions at the surface. This is strongly disagrees with standard theories of hydrodynamics of colloidal particles and biological macromolecules, some of which (e.g. the Debye theory for dielectric relaxation) have been relied on for generations of scientists to interpret experimental data (e.g. [7, 8]). It also disagrees with other theoretical studies on dynamics of microtubules (e.g. [9]) which assume stick boundary conditions, and which refer to extensive experimental data on the motional dynamics of microtubules. Near-perfect slip boundary conditions would have resulted in bizarre experimental results that could not be interpreted by the theory.

Perhaps some internal modes of vibration in the microtubule might not be as strongly coupled to the surrounding fluid as are vibrations of the whole structure. However, dissipative processes must still occur, and any reasonable theory must take them into account. The theory [1] assumes a one-dimensional model and explicitly does not consider internal modes.

Other experimenters have reported sharp resonances or resonance-type effects of radiofrequency energy on biological structures in aqueous surroundings (e.g. [10, 11]). However these results were ultimately nonreproducible and presumably artifact. Theories developed to interpret those findings also neglected dissipative effects. Many things seem possible if one does not consider losses in a system.

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