American Journal of Modern Physics
2014; 3(1): 1-11
Published online July 20, 2014 (http://www.sciencepublishinggroup.com/j/ajmp)
doi: 10.11648/j.ajmp.s.20140301.11
ISSN: 2326-8867 (Print); ISSN: 2326-8891 (Online)

Calculation of vibration modes of mechanical waves on microtubules presented like strings and bars

Atanas Todorov Atanasov

Dept. of Biophysics, Medical Faculty, Trakia University, Armeiska Str. 11, 6000 Stara Zagora, Bulgaria

Email address:
atanastod@abv.bg

To cite this article:
Atanas Todorov Atanasov. Calculation of Vibration Modes of Mechanical Waves on Microtubules Presented like Strings and Bars. *American Journal of Modern Physics.* Special Issue: High Energy Physics. Vol. 3, No. 1, 2014, pp. 1-11.
doi: 10.11648/j.ajmp.s.20140301.11

Abstract: The study describes a physical model of vibrating microtubules in living cells, presented as strings and bars. Calculated are proper-frequencies of first four vibration modes of transverse and longitudinal waves on microtubules. For microtubules with length 1-30μm and shear modulus 5.0×10^6 N/m^2 the proper-frequencies of standing transverse waves fall in diapason of 1×10^3 - 5×10^7 Hz. For microtubules with same length and Young's modulus 10^8–10^9 N/m^2 the proper-frequencies of standing longitudinal waves fall in diapason of 5×10^6 - 3×10^9 Hz. These calculated diapasons of frequencies overlap with experimentally registered diapasons of frequencies of mechanical and electric vibrations in bacteria, yeast cells, erythrocytes, infuzorii and soma cells. Some theoretical problems related to the present model are discussed.

Keywords: Microtubules, String, Bar, Frequency, Transverse, Longitudinal, Waves

1. Introduction

The living cells and their structures have vibrations in all frequency diapason - mechanical, acoustical, electrical, electromagnetic, ultraviolet, infrared and visible [1, 2, 3, 4]. By vibration, the living cells can transfer mass, energy and information (signals) between them and inside [5, 6]. Endogenous mechanical and electromechanical vibrations of some cell structures like membranes and microtubules may have fundamental function in organization of living organisms, including intensity of biochemical reactions, cell growth and building of morphological structures, cellular transport, long range control of cellular functions and sensor functions in cells [7, 8, 9, 10, 11]. The microtubules determine the topology of the cells during the entire cell cycle [12, 13]. Certain authors attribute the participation of microtubules in the logical functions of the brain and consciousness [14, 15]. The possibility that microtubules carry power and information by mechanical and electromechanical vibration of their building macromolecules is under investigation. In this regard various theoretical models have been made, connecting the modes of measured vibrations emitted by the cells with the function of the microtubules. In the same sense, the aim of this study is i) to calculate the modes of mechanical vibrations in microtubules, using model in which they are presented as strings and bars and ii) to compare the calculated frequencies with experimentally measured frequencies of mechanical and electromechanical vibrations and signals emitted from living cells.

2. Experimentally Registered Mechanical and Electrical Vibrations and Signals Emitted from Living Cells

The experimentally registered vibrations and signals are received predominantly on some type of cells (bacteria, yeast, infuzorii, erythrocytes and soma cells). Experimentally measured frequencies of mechanical and electrical vibration in these types of cells don't exceed 10^7 Hz, despite of that the calculated frequencies in theoretical models of other authors reach till to 10^{11} Hz [7, 16, 17, 18]. However, the external electric and electromagnetic fields (microwaves) with frequencies 10^5 -10^{11} Hz have clear expressed non-thermal biological effect on cells, tissues and organisms [19, 20, 21] showing that the cells and their structures are capable of absorbing and resonate the vibration in this frequency range.

2.1. Bacterial Cells

Matsuhashi et al. [22] have measured production of sound waves by bacterial cells and the response of bacterial cells to sound. Some bacterial cells like *Escherichia coli*, *Proteus vulgaris*, *Bacillus subtilus*, *Streptococcus lauceliedis gr. B* and *Neisserra gonorrahae* are very sensitive to vibrations in the range of 9000-9045 Hz. The bacteria *E. coli* death after 60 minutes treatment at vibrations with frequency 9000 Hz [23]. A frequency about 9 kHz has lethal effect on bacteriophages [9]. Reguera [4] has discussed the role of mechanical (acoustic) vibration on microbial cell-cell communications, and arises the hypothesis that these vibrations can be base of informational exchange (signals) between living cells.

2.2. Yeast Cells

Pokorný et al. [17] have suggested that the metabolic processes drive microtubules in yeast *Saccharomyces cerevisiae* to vibrate at MHz frequencies. A subsequent paper reported weak narrowband electrical signals from these cells at frequencies between 8-9 MHz.

Local nanomechanical membrane motion with amplitude of oscillations 3-4 nm of yeast cells was measured by Pelling et al. [24]. They found oscillations fall in the frequency range of 0.9 -1.6 kHz. These frequencies were temperature dependent. The temperature, which modulates the metabolic activity of the cells and its intracellular vibrations, affected the specific frequencies, but not the intensity of the yeast's oscillatory motion. After application of sodium azide, which switches off ATP production in the mitochondria, but does not change the mechanical properties of the cell membrane, the cells do not display oscillatory motion.

Later, Cifra et al. [25] have measured local nanomechanical oscillations of synchronized yeast cells (cold sensitive beta-tubulin mutant of *Saccharomyces cerevisiae*) in the range of 0- 3 kHz. The same authors have measured electrical oscillations of these cells in the frequency bandwidth from 1280 to 1400 Hz. The authors supposed that, if the vibrations are exited in the cytoskeleton, they may cause vibration of the cell membrane, because of the bonding of cytoskeleton to the cell membrane. Jelínek et al. [27] discussed the possibility of using of device to detect electromagnetic emission of yeast cells at frequency of about 42 GHz.

Pokorný et al. [3] have measured on the synchronized yeast cells (cold sensitive beta-tubulin mutant) mechanical vibrations of the yeast membranes, at about 800 Hz at the temperature of 28°-30°C. The same authors have detected electrical oscillations in the frequency range of 400-1600 Hz in synchronized and non-synchronized yeast cells.

2.3. Erythrocytes

Nanoscale oscillations of membranes of human erythrocytes with frequency up to 30 Hz were measured by point dark spectroscopy [27, 28, 29]. The dominant component of membrane fluctuations is metabolically excited and depends on a dynamic mechanochemical coupling of the membrane-skeleton network [30]. Oscillations of the membrane of erythrocytes are correlated in a certain time period and conditioned by energy supply (from intracellular MgATP). The actin's ATPase, located at the end of short actin filament in spectrin submembrane skeleton, is responsible for the MgATP stimulation of red blood cell fluctuations. Mechanism of transformation of chemical to vibration energy is not yet revealed. Levin and Korenstein [27] conclude that the low frequency fluctuations of the cell membrane in erythrocytes may be a general property of all living cells. Interactions between red blood cells up to a distance of about 1 μm were observed by Rowlands [31]. These interactions are metabolically dependent and are weakened or disappears if the cell membrane is disorganized or if the quasi-static membrane potential is considerably lowered.

2.4. Infuzorii

Mechanical vibrations in diapason of 1.2-7.2 kHz can rupture the cell structures of infuzorii *Paramecium caudatus*, *P. bursaria*, *P. solkensi*, *P. aurelia* and *P. trichium* [32]. In review paper of Romanoff [9] is shown that there is a resonance mechanism of influence of the mechanical and acoustic vibrations on the cell structures of infuzorii.

3. Effects of Electromagnetic Fields on Microtubules and Cells

3.1. Effect of External Electric Field on Microtubules

Kirson et al. [33] have showed that the electric vibrations with frequencies about 10^5 Hz can disrupt the mitotic spindle of the soma cells. The organization of the mitotic spindle in the cytokinetic phase of cell division can be disturbed by external electric field with intensity of 100-200V/m and frequency of 100-300 kHz, accordingly data by Kirson et al. [34] and Cucullo et al. [35]. The forces exerted by the external field on tubulin-heterodimers prevent their correct orientation and attraction to the close vicinity of the tip and, therefore disrupt polymerization of microtubules. The cells (*e.g.* melanoma cells) are arrested in mitosis by external electric field and/or the cells are disintegrated [3]. Minoura and Muto [36] have showed that the electric signals with intensity of electric field 5×10^4 -1.9×10^5 V/m and frequencies of 1×10^4 -3×10^5 Hz can oriented microtubules parallel to the field line, because of the high dipole moment induced along their long axis.

3.2. Effect of Microwaves on Microtubules and Cells

Microwaves are part of the electromagnetic spectrum ranging in frequency from 3×10^8 to 3×10^{11}Hz. This non-ionizing electromagnetic radiation is absorbed at molecular level and manifests as changes in vibration energy of the molecules or heat [19, 20, 21]. The non-thermal absorption of microwaves is a resonant that is consequence

of the resonant interaction of the electromagnetic field with the intrinsic cell and tissue oscillators. There are many experiments which indicate electrodynamic activity of variety of cells, expecting the microtubules to be the source of this activity [37, 38]. Because of the microtubule's subunits (tubulin-heterodimers) are elementary electric dipoles, the vibration of microtubules generate electromagnetic field around space [39]. Instead of that the radiation rate of the single cell is lower than 10^{-20}W, the interactions of external electromagnetic field with cell's oscillators have macroscopic biological effects on cells membranes, tissues and hole organisms in frequencies between 30GHz and 80GHz [19, 20, 40]. For example, microwaves in the frequency diapason of 54-76 GHz affect conductance, capacitance and ion transport across lipid bilayer of cell's membranes as well as the ionic channel current in cells [41]. At 41.8 GHz the microwaves affect growth rate of yeast cells [21]. The mechanism of action of external electromagnetic field on cells could be based on forced-vibration of free ions on both sides of plasma cell membrane [42].

4. Some Structural, Elastic, Electric and Vibration Characteristics of Microtubules

Microtubules are the main constituents of the cellular cytoskeleton together with microtubule associated proteins, intermediary and actin filaments. Microtubules are dynamical instability structures because of it leads to reorganization of the cytoskeleton and therefore cellular morphology and functions. However, in highly differentiated cells like neurons there is a stable population of cytoskeletal microtubules. In most cells the majority of microtubules emanate from a microtubule-organizing center (centrioles) and radiates to the membrane and other structures of cells [12, 13]. Microtubules are cylindrical polymers composed from tubulin dimers molecules with protein density ~1250 kg/m^3 [43]. Porter et al. [18] have calculated the microtubules density to be about 1000 kg/m^3. Each tubulin subunit is an 8 nm by 4 nm by 5 nm heterodimer which consists of two slightly different classes of 55,000 dalton monomers known as alpha and beta tubulin [44, 45]. The tubulin dimer subunits within microtubules are arranged in a hexagonal lattice. Microtubules cylinder are comprised of 13 longitudinal protofilaments. They resemble hollow tubes with 15 nm inner and 25 nm of outer diameter [46]. Microtubules are rigid polymers that contribute the mechanical and elastic properties of cells. Microtubules resist various internal and external forces to maintain cell shape and they support motor proteins to generate the force required for cell movement and changes in shape. The most important elastic characteristics of single microtubule are rupture stress modulus, about 0.4-0.5 N/m^2 [47, 18]; shear stress modulus, in the range of 5.0×10^6 N/m^2 [48, 49]; shear modulus between microtubules in intact cells, about 10^3 N/m^2 [50]; Young's modulus, between 10^6 -10^9 N/m^2 [48, 50]; flexural rigidity of microtubules (34-62)$\times10^{-24}$ Nm^2 [51], elastic coefficients of microtubules, in the range of 10^{-2} - 4.5 N/m [18], bending modulus for individual microtubules 7×10^{-23} Nm^2 [50]; average midpoint bending stiffness of intact cells 7×10^4 N/m [50], spring constant, about 0.1 N/m [52, 53] and others. Microtubules have an anisotropic structure, because of the longitudinal interactions between alpha and beta tubulin-subunits. Along protofilaments the microtubules are relatively stronger than the lateral interactions (in circumferential direction). As a consequence of this anisotropic structure the ratio between Young's modulus and shear modulus of microtubules varies between 10 -10^6 folds [48, 54; 55]. Some microtubules are over a hundred microns long, while others are only a single microns or even shorter [56, 57]. The persistent length of microtubules is about 6mm [58]. The microtubules high stiffness on length scales associated with the cell size aids in their role of maintaining mechanical stability of the cell. Microtubules are highly polar structures. Minoura and Mito [36] infer from dielectric measurements a net charge of tubulin's molecules to be 10-20 negative electron's charges per tubulin-dimmer, which corresponds to 3250e$^-$ - 32 500e$^-$ charges per μm length of the microtubules. Sträcke et al. [59] estimate the lower linear charge density of tubulin molecules to be minimum 280 e$^-$/μm. Each tubulin-subunit has an electrical dipole moment of 1740 Debye. These high charge density and dipole moment of microtubules allows an active directional control of microtubules by internal and external electric fields [55, 60].

Microtubules have many static, dynamic and vibration properties. Firstly, Fröhlich [7] suggested that by means of strong fluctuations of membrane electrical field and its coupling with the highly polarizable membrane and cell structure, typical vibration with frequencies related to optical phonons would lie in the GHz-THz region. Later, many investigators like Sirenko et al. [16], Pokorný et al. [17], Porter et al. [18], using others theoretical models, have calculated the modes of mechanical and electromechanical vibrations (longitudinal, radial and torsion) in the microtubules to fall in the range of 10^7 – 10^{11} Hz, with velocities of phonons in the range of 100-1300 m/s, and wavelength in the range of 10^{-5} -10^{-9} m [16, 17, 18]. One problem exists, that the predicted frequencies in these theoretical models still await experimental confirmation. The other problem is, that the calculated modes of vibrations and corresponding frequencies differs some orders of magnitude from experimentally measured mechanical and electrical vibration in cells (predominantly, in bacteria, yeast cells and erythrocytes). The registered mechanical vibrations fall mainly in low-frequency diapason of 30- 10^6 Hz [61, 62], while the registered electromechanical vibrations fall predominantly in high-frequency diapason of 10^7 - 10^{10} Hz and over [17, 26, 37, 62].

5. Models and Modeling

Various approximations and models have been used to determine microtubule vibration modes [63, 64]. In more models, the microtubules are presented as a cylinder, cylindrical shells or tube [53, 64]. Amos [65] and Pokorný et al. [17] used model of microtubules as a lattice of monomers, while the other authors like Metoz et al. [66] and Porter et al. [18] used model of microtubules as a lattice of dimmers. Using the elastic and electric characteristics of microtubules and tubulin-dimers, predominantly the stretching, longitudinal, torsional, breathing and beam-bending modes are calculated [17, 63, 67]. Saha et al. [68] considers the possibility of stochastic resonance in tubulin- dimmers. Because of viscosity of cytoplasm the exited vibrations dissipate part of energy, which tend to damp out the vibrations [69].

From most common physical observations, because of the time of relaxation of water molecules is about 10-13s [52], the viscous damping of microtubules vibrations would depend on the difference between the frequency of vibration of microtubules and the frequency of relaxation of the water molecules. This means that with the approaching of the vibration frequencies of the microtubules to the frequency of relaxation of the water molecules, the viscous dumping will increase. Longitudinal (axial) modes are expected to have the lowest viscous damping due to smallest displacement of surrounding water, which is present *in vivo*, and viscoelastic transition of cellular water [64]. However, the experimentally registered cell vibration modes in the range of 30 -10^7 Hz show that viscous dumping is not able to dissipate fully vibration of the cells in this relatively low-frequency diapason. The lack of experimentally registered vibrations over 10^7 Hz perhaps, is due to viscous dumping, but it is possible that the cells do not have enough energy to cause vibration of this frequency. For example, radiations of cells with microwaves at 30-80 GHz (which lead to non-thermal effects in cells) have shown that the cell structures can vibrate in this frequency diapason in the presence of sufficiently intensive energy source.

Our model represent a classical model, based on theory of mechanical vibrations of string and bars, by which can be calculated the natural frequencies of vibration and standing waves modes [70] on the tubules. In the model is not taken under consideration the viscous dumping of vibrations.

Arguments that allow us to present microtubules by strings and bars are connected to their geometric and elastic characteristics: i/ the big persistent length of microtubules, about 6mm [58]; ii/ the big ratio between length and external diameter of microtubules. For example: the ratio between length of microtubules, equals to minimum and maximum length of eukaryotic cells (1- 30μm) and external (outer) diameter of microtubules (25 nm) is 10^2 -10^3 fold; iii) microtubules are presented like fixed to the membrane or

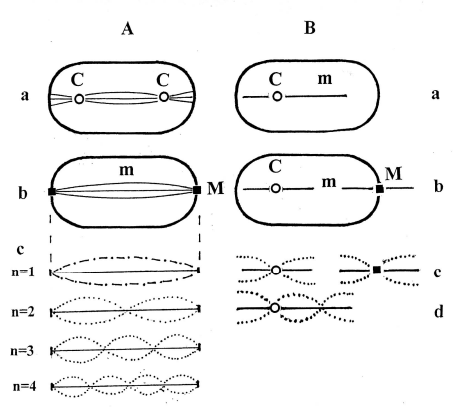

Figure 1. *Schematic presentation of microtubules in cells like strings and bars: A(a,b)-microtubules fixed to microtubules-organizing center (centrioles) or to membrane of the cells; A(c)- scheme of standing waves on microtubules for 1, 2, 3 and 4 mode; B(a,b)-microtubules fixed to the microtubule-organizing center (centriole) or to the membrane; B(c,d)-scheme of standing waves on microtubule-bar. Figure legend: C-centriole, M-membrane, m-microtubules.*

microtubule-organizing center (centrioles) [71] anisotropic strings and bars with length- L(m), surface area of S (m^2), shear modulus of Ғsh (N/m^2), Young's modulus of Ғy (N/m^2) and density of ρ (kg/m^3)- Fig. 1.

The role of vibrator, which excite vibration of microtubules, can be every one from the commonly accepted and discussed in the scientific literature energizing source of the microtubules - mechanical vibration and electric field of the membrane, efflux of energy from mitochondria to microtubules, external mechanical and electromagnetic waves, ATP sources and others [64].

Accordingly Newton's equation [70, 72] the speed of a wave v (m/s) of excited vibrations on string and bar is equals to:

$$v=(Ғ/\rho)^{½} \quad (1)$$

where Ғ is the elastic modulus of the string or bar.

For transverse waves, the elastic modulus Ғ is equals to the shear modulus Ғsh and Eq.(1) gives the form.

$$v=(Ғsh/\rho)^{½} \quad (2)$$

For longitudinal waves, the elastic modulus Ғ is equals to the Young's modulus Ғy and Eq.(1) gives the form:

$$v=(Ғy/\rho)^{½} \quad (3)$$

The relation among the speed of the waves v(m/s), the wavelength λ(m) and frequency f(Hz) of vibration is given by the ratio:

$$\lambda=v/f \quad (4)$$

To simplicity the model we consider harmonic (sinusoidal) waves on microtubules, which vibrate independently each from other.

6. Theory and Calculation of Vibration Modes of Transverse Waves on String and Bar

6.1. Theory of Transverse Waves on Microtubules-String

Let us consider that the microtubules are presented as strings. The waves traveling to the strings will be particularly reflected to solid walls and a large fraction of the energy will be reflected. As a result, a standing waves will be formed with nodes (the points of zero motion) placed on solid walls -membranes or centrioles of the cell (see Fig.1). When the vibrator, pushes in resonance with the wave pulses on the strings, a large standing waves will be formed. Our purpose is to calculate the vibration modes and corresponding proper frequencies of standing transverse waves traveling to the microtubule-string. Let us now consider that the cells and resonating microtubules have the same length equals to L(m), accordingly Fig.1A(a, b).The distance between adjacent nodes is λ/2. As a result, the strings can resonate when its length (L) is equal a whole number (n) of half wavelengths (λ/2) long:

$$L=n\lambda/2 \text{ where } n=1, 2, 3,\ldots.. \quad (5)$$

Since the wavelength is related to the frequency by Eq. 4, we see at once that a string of fixed length (L) will resonate with resonant frequencies (f, Hz) as function of mode (n) given by relation:

$$f(n) =v/(2L/n)=n(v/2L) \text{ where } n=1, 2, 3 \text{ etc. is mode's number} \quad (6)$$

In Equation (6) the speed of waves v (m/s) is computed by Eq.2. The first four vibration modes on strings are indicated in part 'c' of Fig.1A.

6.2. Theory of Transverse Waves on Microtubules-Bar.

Let us now consider that the microtubules are presented as bars. If a bar clamped at its center is struck at its end, as shown in Fig.1B(b), the microtubule-bar will vibrate. The mode of vibration is indicated in part 'c' of Fig.1B. The center of the bar must be a node, because it is tightly clamped in place. Since the ends of the bar are not held rigidly, we expect antinodes near them. If we assume the ends to be antinodes, the length of the bar L(m) is one-half wavelength λ/2, because of the distance between two successive antinodes is λ/2. Knowing that λ= 2L, we could calculate the frequency f (Hz) of vibration of the bar, if the speed of waves (computed by Eq.2) is equals to v(m/s):

$$f=v/2L \quad (7)$$

If the bar had been clamped as in Figure 1B(a), at a distance L/4 from its end, the vibration would have appeared as in part 'd' of Fig.1B. Once again, the ends would approximate antinodes, and the clamp point would be a node. In this case λ=L and the frequency of vibration can be given by the relation:

$$f=v/L \quad (8)$$

6.3. Calculation of Vibration Modes of Standing Transverse Waves on Microtubules Presented as Strings and Bars. Comparison with Experimental Data

Because of many experimental data for mechanical vibration are made on yeast cells, we give the length of microtubules to be in order of length of this type of cells. Accordingly Tyson et al. [73] the length of yeast at birth varied in interval of 5-14 μm, while the length of yeast at division is between 10-28μm. Accordingly Fantes [74] the mean diameter of yeast cells is 3.5 μm. In our model we gives the length of microtubules L(m) to fall in window of 1-30μm.

The microtubules-strings can resonate when its length (L) is equal a whole number (n) of half wavelengths (λ/2) long, accordingly equation L=n λ/2. On Figure 1A(c) are shown wavelength of standing waves on microtubules for modes n=1, n=2, n=3 and n=4. (For n=1 the wavelength is λ=2L; for n=2 the wavelength is λ=L; for n=3 the wavelength is λ=2L/3 and for n=4 the wavelength is λ=L/2).

Giving in the mind that length of strings is equal to 1-30 μm, for n=1 the calculated wavelength will be:

$$\lambda=2L=(2\text{-}60)\mu m \quad (9)$$

For transverse waves, the elastic modulus is equals to shear modulus Ғsh= 5.0-1×10^6 N/m^2 [48, 49]. For density of microtubules ρ = 1250 kg/m^3 the speed of waves on strings and bars will be in interval of:

$$v=(Ғsh/\rho)^{½}=(6.324\times10^{-2}\text{–}28.3)m/s \quad (10)$$

where the speed 6.324×10^{-2} m/s corresponds to low value of shear modulus Ғsh= 5.0 N/m^2 and the speed 28.3 m/s corresponds to high value of shear modulus Ғsh=1×10^6 N/m^2.

For λ =2L for first mode n=1 of strings and bar clamped at its center, the resonant frequencies f(n) given by Eq.6 will be in interval given by the equation:

$$f(1)=v/2L=(6.324\times10^{-2}/\lambda\text{–}28.3/\lambda)m/s \quad (11)$$

For λ =2μm, the calculated frequencies fall in the interval of:

$$f(1)=(3.162\times10^4\text{–}1.415\times10^7)Hz \quad (12)$$

For λ =60μm, the calculated frequencies fall in the interval of:

$$f(1)=(1.054\times10^3\text{–}4.714\times10^5)Hz \quad (13)$$

For bar clamped at a distance L/4 from its end, the diapason of frequencies will be 2 fold higher than for strings i.e.:

$$f(1)=(6.324\times10^4\text{–}2.83\times10^7)Hz \quad (14)$$

and

$$f(1)=(2.108\times10^{3}–9.428\times10^{5})\text{Hz} \quad (15)$$

For modes n= 2, 3, 4 of strings, the calculated frequencies f(2), f(3) and f(4) will be 2, 3 and 4 fold higher than the basic frequency-f(1). The all calculated vibration modes and corresponding frequencies of transverse waves for first four modes for strings and bars are given in Table 1.

For modes n=1, 2, 3, 4 and low shear modulus of Ғsh=5.0 N/m^2, the calculated on Table 1 interval of frequencies (1×10^3 - 3×10^4 Hz) of transverse waves overlaps with experimentally registered interval of frequencies (10^3 -10^4 Hz) of mechanical and electric vibrations from bacteria, yeast and infuzorii [3, 4, 9, 23, 24, 25, 32, 61]. The calculated interval of frequencies includes also the frequencies (1×10^4 -3×10^5Hz) of external electric signals and fields (with intensity 5×10^4 -1.9×10^5 V/m) that can disrupt the mitotic spindle of the cells in the cytokinetic phase of cell division [33, 34, 35, 36]. Indeed, the tubulin-subunits has minimum electric charge equals to ten electron charges q =$10e^-$ and rupture modulus of Ғr = 0.4-0.5 N/m^2 [18, 47].

Table 1. *Calculation of vibration modes and proper- frequencies of standing transverse waves on microtubules-strings and bars*

Mode number n	Shear modulus 5.0 N/m^2 (speed of waves 6.32×10^{-2} m/s)		Shear modulus 1×10^6 N/m^2 (speed of waves 28.2 m/s)	
	For L=1μm (λ=2μm)	For L=30μm (λ=60μm)	For L=1μm (λ=2μm)	For L=30μm (λ=60μm)
1.	3.14×10^4 Hz	1.05×10^3 Hz	1.41×10^7 Hz	4.75×10^5 Hz
2.	6.32×10^4 Hz	2.10×10^3 Hz	2.87×10^7 Hz	9.50×10^5 Hz
3.	9.48×10^4 Hz	3.15×10^3 Hz	4.24×10^7 Hz	14.25×10^5 Hz
4.	12.65×10^4 Hz	4.20×10^3 Hz	5.66×10^7 Hz	19.00×10^5 Hz

The mitotic spindle can be disrupted if the ratio between electric force (Fe) acting on tubulin-dimers with surface area of s =2.0×10^{-17} m^2 (or acting on single microtubules with surface area of S=6.25×10^{-16} m^2) is higher than value of rupture modulus Ғr i.e. must be met inequalities: i) Fe/s > Ғr and ii) Fe/S> Ғr.

The electric force (Fe) is equals to product between electric charge (q, C) of tubulin-dimers (q=$10e^-$ =16×10^{-19}C) and intensity of external electric field (E ~200V/m), acting on microtubules i.e: Fe = qE =3.2×10^{-16}N. For calculated electric force Fe ~3.2×10^{-16} N, the ratio between the force and surface area of tubulin-dimer Fe/s (and ration between the force and surface area of microtubules Fe/S) fall in the interval of F/S –F/s = 0.512 -20 N/m^2. The comparison shows that the equations i) and ii) are valid, i.e. F/S ≈ Ғr ≈0.512 N/m^2 and F/s =20 N/m^2 > Ғr. The equations i) and ii) show than the intensity of external electric field is sufficient to disrupt microtubules. The frequency of external destroying electric field (5.0×10^5 Hz) is near to the frequency (3×10^5 Hz) of calculated mechanical vibration of microtubules.

The assumption of a number of authors [7, 8, 9, 10] that the vibrations of microtubules may act on intensity of biochemical reactions allow as to assume, that the maximum frequencies of mechanical vibration of microtubules don't exceed the maximum frequencies of mechanical vibration of enzyme molecules in cells ~ 10^7 Hz [11].

For modes n=1, 2, 3, 4 and high shear modulus Ғsh =10^6 N/m^2, the calculated on Table 1 interval of frequencies (5×10^5 - 5×10^7 Hz) are near to maximum frequencies of mechanical vibration of enzyme molecules ~ 10^7Hz and include the experimentally registered frequencies of electric signals (8-9 MHz) in yeast cells, due to the metabolic processes in yeast [17].

In summary, calculated interval of frequencies of transverse mechanical waves on microtubules fall in relatively low-frequency diapason (1×10^3-5×10^7 Hz) in which are located the frequencies of the vibrating enzyme molecules. This interval is about 10^4 -10^8 folds lower than predicted maximum frequencies of vibrating cell structures and microtubules ~10^{11} Hz, calculated from Fröhlich [7, 8], Sirenko et al. [16], and Cifra et al. [37, 62].

7. Theory and Calculation of Vibration Modes of Longitudinal Waves on String and Bars

7.1. Theory of Longitudinal Waves on Microtubules-Strings

Waves where the motion of the particles is along the direction of wave propagation, is called a longitudinal wave. If a compressive or extensive wave is sent down a string, the wave and its energy are usually reflected at the end of the string. This reflected wave can interfere with the later waves being sent down string from the source. If the proper relation is maintained between the frequency of the driving source oscillating the end of the string and the various parameter parameters of the string, resonance will occur. The resonating cellular membranes or centrioles can play role of driving source. As with resonance on a string, the position of the driving source will be closed to a node. If the other end of the string is fixed solidly to a wall (membrane) or some other cellular object (centriole), that end must also be a node. The resonance motion of the string must then appear as shown in the graphs of Fig.1. The distance between adjacent nodes is λ/2. Also, at resonance, the strings must be a whole number of half wavelengths long. That is in resonance the ratio between length of string L(m) and wavelength λ(m) of standing wave will be:

$$L=n\lambda/2 \quad \text{where } n=1,2,3,4\ldots \quad (16)$$

This relation, when combined with the relation between wavelength and frequency (λ=v/f), tell us at once the string resonance frequencies will be:

$$f(n)=n(v/2L) \quad \text{where } n=1,2,3,4\ldots \quad (17)$$

For longitudinal waves the elastic modulus is equals to Young's modulus (Fy) and the speed of waves will be:

$$v = (Fy/\rho)^{1/2} \quad (18)$$

7.2. Theory of Longitudinal Waves on Microtubule-Bar

The elastic bar acts like a very stiff string. The blow on the end of the bar sends a compressive or extensive wave down the bar. This wave is quite complex in form and is actually a large group of waves of various frequencies. The bar will resonate to only certain frequencies and hence it selects the proper frequency to which it will resonate. The wave in the bar must have a node at its center and antinodes at its end. The lowest resonant frequency mode of motion is shown on Fig.1B (c). In this case the bar is one-half wavelength long i.e. L= λ/2 (Fig.1B (b). If the speed v(m) and wavelength λ(m) of waves are known, the frequency of vibration can be computed by ratio:

$$f=v/\lambda=v/2L \quad (19)$$

For longitudinal waves, the elastic modulus is equals to the Young's modulus and the speed of waves will be:

$$v=(Fy/\rho)^{1/2} \quad (20)$$

If the bar had been clamped as in Fig.1B (a), at a distance L/4 from its end, the vibration would have appeared as in part 'd' of Fig. 1. Once again, the ends would approximate antinodes, and the clamp point would be a node. In this case λ=L and the frequency of vibration can be given by the relation:

$$f=v/L \quad (21)$$

7.3. Calculation of Vibration Modes of Standing Longitudinal Waves on Microtubules Presented as Strings and Bars. Comparison with Experimental Data

Giving in the mind that the Young's modulus of microtubules is in interval of 10^8 -10^9 N/m^2 [48, 55] and the density of microtubules is about 1250 kg/ m^3, we can calculate the diapason of speed of longitudinal waves on strings and bars:

$$v=(Fy/\rho)^{1/2} =(2.828\times10^2–8.944\times10^2)\text{m/s} \quad (22)$$

In relation (22) the speed 2.828×10^2 m/s corresponds to low Young's modulus 1×10^8 N/m^2 , while the speed 8.944×10^2 m/s corresponds to high Young's modulus 1×10^9 N/m^2 of microtubules.

The strings can resonate when its length (L) is equal a whole number (n) of half wavelengths (λ/2) long, accordingly equation L=n λ/2. On Figure 1 are shown microtubules and possible wavelength traveling on them for modes n=1, 2, 3, 4. (For n=1 the wavelength is λ=2L; for n=2 the wavelength is λ=L; for n=3 the wavelength is λ=2L/3; for n=4 the wavelength is λ=L/2).

Giving in the mind that the length of strings is equal to (1-30) μm, for first mode n=1 the calculated wavelengths will be:

$$\lambda=2L=(2.0\text{-}60)\mu\text{m} \quad (23)$$

For n=1 the resonant frequencies f(n) for strings and bar clamped at its center will be in the interval of:

$$f(1)=v/2L=(2.828\times10^2/\lambda\text{-}8.944\times10^2/\lambda)\text{m/s} \quad (24)$$

For λ = 2 μm the calculated frequencies fall in the interval of:

$$f(1)=(1.414\times10^8–4.472\times10^8)\text{Hz} \quad (25)$$

For λ = 60 μm the calculated frequencies fall in the interval of:

$$f(1)=(4.71\times10^6–1.49\times10^7)\text{Hz} \quad (26)$$

For bar clamped of a distanceL/4 from its end, the frequencies will be 2 fold higher i.e.

$$f(1)=(2.828\times10^8–8.994\times10^8)\text{Hz} \quad (27)$$

and

$$f(1)=(9.42\times10^8–2.98\times10^7)\text{Hz} \quad (28)$$

For modes of n= 2, 3, 4 the calculated frequencies f(2), f(3) and f(4) will be 2, 3 and 4 fold higher than basic frequency f(1). The calculated vibration modes and corresponding frequencies of longitudinal waves for first four modes are given on Table 2.

The calculated on Table 1 interval of frequencies (4.71×10^6- 1.788×10^9) Hz overlaps with previously calculated from Pokorny et al.[3, 6, 17] proper-frequencies of microtubule vibrations f ~ 10^7 -10^{10} Hz. The calculated from us speed of waves and calculated from other authors speed [6, 16, 17] lies in same diapason of 100-1000 m/s.

Table 2. *Calculation of vibration modes and proper- frequencies of standing longitudinal waves on microtubules-strings and bars*

Mode number n	Young's modulus 1×10^8 N/m^2 (speed of waves 2.828×10^2 m/s)		Young's modulus 1×10^9 N/m^2 (speed of waves 8.944×10^2 m/s)	
	For L=1μm (λ=2μm)	For L=30μm (λ=60μm)	For L=1μm (λ=2μm)	For L=30μm (λ=60μm)
1.	1.414×10^8 Hz	4.71×10^6 Hz	4.472×10^8 Hz	1.49×10^7 Hz
2.	2.828×10^8 Hz	9.42×10^6 Hz	8.944×10^8 Hz	2.98×10^7 Hz
3.	4.242×10^8 Hz	1.41×10^7 Hz	1.341×10^9 Hz	4.47×10^7 Hz
4.	5.656×10^8 Hz	1.88×10^7 Hz	1.788×10^9 Hz	5.96×10^7 Hz

For microtubules with length 30μm (and λ=60 μm) the calculated frequencies (4.71×10^6 – 5.96×10^7 Hz) overlaps with frequencies of electric signals (8-9 MHz) emitted from yeast cells [17, 49].

The recent investigations show that the microtubules interact directly with numerous membrane proteins and form scaffolds. These include proteins as diverse as ion channels,

receptors, ion pumps and others [75]. However, the activity of ion pumps can be regulated by a subset of specifically modified tubulin, namely acetylated tubulin [76]. These show the presence of a possible functional relationship between microtubules and ion channels. The microtubules are associated with the membrane and vibrate with same frequencies with it and respectively, with ion channels in membrane. For example: ion channels allow the movement of ions at rates of the order about10^7-10^9 ions per second [77, 78, 79]. The microtubules have the same frequency of vibration ~2×10^7-2×10^9 Hz.

Coupling mechanism between rate of ion transfer trough membrane and frequency of longitudinal microtubule's vibration could be transmembrane electric field with extremely high intensity ~10^6-10^7 V/m, which act simultaneously over microtubules and ion channels in membranes and synchronized their working frequencies.

8. Discussion

The interval of calculated on Table 1 and Table 2 frequencies falls between 10^3–10^9 Hz. The frequencies of microtubule's vibration higher than 10^9 Hz can be received for very short bars with length some tubulin-dimer molecules. For example, bar with length of single tubulin-dimer 8×10^{-9} m, Young modulus 10^8-10^9 N/m^2 and speed of longitudinal waves on it 2.828×10^2 - 8.944×10^2 m/s would have vibration frequencies of longitudinal waves in diapason of 10^{10}-10^{11} Hz. In same diapason fall the Fröhlich frequencies [7, 8] and microwaves ~3×10^8 to 3×10^{11} Hz [19, 20, 21]. The frequencies lower than 10^3 Hz can be received for very low elastic modulus, equal to values of rupture stress modulusp ~0.4-0.5 N/m^2 and very long microtubules ~10-30 μm. For example, the speed of waves corresponding to rupture stress modulus 0.4-0.5 N/m^2 and density of microtubules 1250 kg/m^3 falls in the interval of 1.78×10^{-2} -2.0×10^{-2} m/s. In this case, the interval of calculated frequencies is 600-2000 Hz and overlaps with observed from Pokorný et al. [3] mechanical vibrations (with 800 Hz) yeast membranes and electrical oscillations (with frequency 400-1600Hz) of membrane of synchronized and non-synchronized yeast cells. Thus, the calculated proper-frequencies of theoretical possible transverse waves fall in relatively low frequency diapason of 6×10^2-10^7 Hz and overlaps with experimentally registered frequencies (from 30Hz to 10^7 Hz) of mechanical and electromechanical vibrations in cells (see Fig. 2). The proper-frequencies of theoretical possible longitudinal waves fall in relatively high diapason of 10^6-10^{11} Hz and overlap with some experimentally measured and predicted electric vibrations in cells, as well as the frequency of the external electric and electromagnetic fields (10^5 to 3×10^{11} Hz) with non-thermal effects on cells (Figure 2). This interrelationship between elastic modulus, type of vibration and diapason of frequencies could be presented on Scheme 1, and can be explained by the molecular structure of microtubules [37, 62]. The microtubules have an anisotropic structure, because of the longitudinal interactions between alpha and beta tubulin-subunits. In the propagation of transverse waves on microtubules, whole molecules of tubulin-subunits can be displaced from their equilibrium positions without changing their conformation. Their replacement however may be accompanied with a conformational transition of molecules from α to β state. When whole molecules are displaced without conformational transitions, transverse waves propagate as mechanical waves without the electrical component. If simultaneously with the transversely shift of the molecules of tubulin-subunits perform conformational transitions from α to β state, the transverse waves propagate as mixed type - electromechanical and electrical oscillations.

Scheme 1. Connections between elastic modulus, type of waves and frequency diapason of vibrating microtubules.

SHEAR MODULUS→ transverse vibrations→ mechanical and electric waves→ frequency diapason of 6×10^2 - 10^7 Hz.

YOUNG MODULUS→longitudinal vibrations→ electromagnetic waves→ frequency diapason of 5×10^6 – 10^{11} Hz.

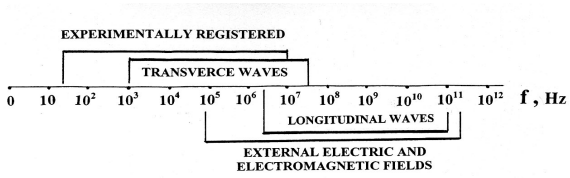

Figure 2. *Scaling of calculated and experimentally registered frequencies of vibration in cells (bacteria, yeast, infuzorii and erythrocytes), and frequencies of external electric and electromagnetic fields with non-thermal effects on cells.*

Unlike the transverse waves, the longitudinal waves are obviously connected with conformational change of tubulin-heterodimer from α to β state and vibration of dipole moment of heterodimers. Because of the high dipole moment of tubulin molecules, it is possible during their vibration to generate at the same time electrical, electromechanical and electromagnetic oscillations in the space around them.

9. Conclusion

The study describes a physical model of vibrating microtubules in living cells, presented as strings and bars. The calculated modes of transverse and longitudinal waves on microtubules are based on experimentally measured mechanical characteristics of microtubules. The vibrating microtubules can have wide spectrum of physical effects on cellular processes (influence on architecture of the cells, transport of matter, energy and information in membrane and cytoplasm of the cells (and between cells), acceleration of diffusion, biochemical and metabolic processes and others).

The importance of the model due to the possibility to explain different cellular processes, using clear physical model and calculations based on the classical physics.

The proposed model can be future developed, firstly, to develop the participation and effect of microtubules vibration on the mechanism of cell mitosis and dividing of cells by binary, accordingly the scheme given on Fig.1, A (a, b).

Secondly, the proposed model can explain (by flow of energy between vibrating microtubules) the communication between the centrioles and nucleus, the centrioles and mitochondria and between others cellular structures with participation of microtubules and centrioles, accordingly model given on Fig.1 (B, a).

By vibrating microtubules, it can explain (Fig.1, B, b) the communication mechanisms and flow of information between cellular sensor structures (for example, between sensor cilia and centrioles) in photoreceptors, mechanoreceptors and chemo-receptors.

Because of the cellular, tissues and organ architecture depend on microtubules distribution and organization in cytoplasm of the cells, the model can be developed for cell-cell communications and particularly in the case of tumor processes in tissues and organs of the body (Fig.1, B, b).

References

[1] A. G. Gurwitsch and L. D. Gurwitsch, Die Mitogenetische Strahlung, Jena, Fischer, Germany, 1959.

[2] R. VanWijk, "Bio-photons and biocommunication," J. Sci. Explor., vol.15, pp.183-197, 2001.

[3] J. Pokorný, J. Hašek, J. Vaniš and F. Jelínek, "Biophysical aspects of cancer-electromagnetic mechanism," Indian. J. Exp. Biol., vol. 46, pp. 310-321, 2008.

[4] G. Reguera, "When microbial conversations get physical," Trends. Microbiol., vol. 19, pp.105-113, 2011.

[5] G. Albrecht-Buehler,"Changes of cell behavior by near-infrared signals," Cell. Mobil. Cytoskeleton," vol.32, pp. 299-304, 1995.

[6] J. Pokorný, J. Hašek, J. Vaniš and F. Jelínek. "Electromagnetic field of microtubules: effects on transfer of mass particles and electrons," J. Biol. Phys., vol. 31, pp. 501-514, 2005.

[7] H. Fröhlich,"Long-range coherence and energy storage in biological systems," Int. J. Quantum Chem., vol. 2, pp. 641-649, 1968.

[8] H. Fröhlich, "Evidence for coherent excitation in biological system," Int. J. Quantum Chem., vol. 23, pp.1589-1595,1983.

[9] C. H. Romanoff, Biological action of mechanical vibrations. Ed. 'Nauka', S. Peterburg, Russia, 1983.

[10] B. Martinac, "Mechanosensitive ion channels: molecules of mechanotransduction," J. Cell. Sci., vol. 117, pp.2449-2460, 2004.

[11] L. V. Beloussov and I. Y. Volodyaev, "From molecular machines to macroscopic field: an accent to characteristic times," Europ. J. Biophys., vol. 1, pp. 6-15, 2013.

[12] W. F. Marshall and J. L. Rosenbaum, "Cell division: the renaissance of the centriole," Curr. Biol., vol. 9, pp.R218-R220, 1999.

[13] J. L. Salisbury, "A mechanistic view on the evolutionary origin for centrin-based control of centriole duplication," J. Cell. Physiol., vol. 213, pp. 420-428, 2007.

[14] M. Jibu, S. Hagan , S. R. Hameroff, K. H. Pribram and K. Yasue, "Quantum optical coherence in cytoskeletal microtubules: implications for brain function," BioSystems vol.32:, pp.195-209, 1994.

[15] N. J . Woolf and S. R. Hameroff, " A quantum approach to visual consciousness," TRENDS Cogn. Sci., vol. 5, pp. 472-478, 2001.

[16] Y. M. Sirenko, M. A. Stroscio and K. W. Kim, " Electric vibrations of microtubules in a field," Phys. Rev. E-APS., vol. 53, pp. 1003-1010, 1996.

[17] J. Pokorný, F. Jelinek, V. Trkal, I. Lamprecht and R. Hölzel, "Vibration in microtubules," J. Biol. Phys., vol. 23, pp. 171-179, 1997.

[18] S. Porter, J. A. Tuszyński, C. W. V. Hogue and J. M. Dixon, "Elastic vibrations in seamless microtubules," Eur. Biophys. J., vol.34, pp. 912-920, 2005.

[19] A. G. Pakhomov, Y. Akyel, O. N. Pakhomova, B. E. Stuck and M. R. Murphy, "Current state and implications of research on biological effects of millimetre waves: a review of the literature," Bioelectromagnetics, vol.19, pp.393-413, 1998.

[20] S. Banik, S. Bandyopadhay and S. Ganguly, "Bioeffects of microwaves-a brief review," Bioresource technology, vol. 87, pp.155-159, 2003.

[21] V. I. Fedorov, S. S. Popova and A. N. Pisarchik, "Dynamic effects of submillimeter wave radiation on biological objects of various levels of organization," IRMMW, vol. 24, pp.235-1254, August 2003.

[22] M. Matsuhashi, A. N. Pankrushina, S. Takeuchi, H. Ohshima, H. Miyoi, K. Endoh, K. Murayama, H. Watanabe, S. Endo, M. Tobi, Y. Mano, M. Hyodo, T. Kobayashi, T. Kaneko, S. Otani, S. Yoshimura, A. Harata and T. Sawada, "Production of sound waves by bacterial cells and the response of bacterial cells to sound," J. Gen. Appl. Microbiol., vol. 44, pp. 49-55, 1998.

[23] T. F. Anderson, S. Boggs and B. C. Winters, "The relative sensitivities of bacterial viruses to intense sonic vibration," Science (NY), vol.108, pp.18, 1948.

[24] A. E. Pelling, S. Sehati, E. B. Gralla, J. S. Valentine and L. K. Gimzewski, "Local nanomechanical motion of the cell wall of Saccharomyces cerevisiae," Science, vol. 305, pp. 1147-1150, 2004.

[25] M. Cifra, J. Vaniš, O. Kučera, J. Hašek, I. Frýdlová, F. Jelínek, J. Šaroch and J. Pokorný, "Electric vibrations of yeast cell membrane," Bioelectrochemistry, vol. 51, pp. 142-148, 2007.

[26] F. Jelínek, J. Šaroch, O. Kučera, J. Hašek, J. Pokorný, N. Jaffrezic-Renault and L. Ponsonnet, "Measurement of electromagnetic activity of yeast cells at 42 GHz," Radioengineering, vol. 16, pp. 36-39, 2007.

[27] A. Levin and R. Korenstein, "Membrane fluctuations in erythrocytes and linked to MgATP-dependent dynamic assembly of the membrane skeleton" Biophys. J., vol. 60, pp.733-737, 1991.

[28] S. Tuvia, A. Bitler and R. Korenstein, " Mechanical fluctuations of the membrane-skeleton and dependent on F-actin ATPase in human erythrocytes," J. Cell. Biol., vol.141, pp. 1551-1561, 1998.

[29] S. Tuvia, A. Moses, N. Gulayev, S. Levin and R. Korenstein, "ß-Adrenergic agonists regulate cell membrane fluctuation of human erythrocytes," J. Physiol., vol. 516, pp.781-792, 1999.

[30] A. Bitler and R. Korenstein, "Nano-scale fluctuations of red blood cell membrane reveal nonlinear dynamics," Biophys. J., vol. 86, pp. 582, 2004.

[31] S. Rowlands, The interaction of living red blood cells. In Biological Coherence and Response to External Stimuli, Fröhlich , H. Ed. Springer, Berlin, Heidelberg, New York, 1988, pp.171-191.

[32] K. W. Ockelmann and O. Vahl, "On the biology of the polychaete Glycera alba, especially its burrowing and feeding," Ophelia, vol. 8, pp. 275-294, 1970.

[33] E. D. Kirson, Z. Gurvich, R. Schneiderman, E. Dekel, A. Itzhaki, Y. Wasserman, R. Schatzberger and Y. Palty, "Disruption of cancer cell replication by alternating electric fields," Cancer Res., vol. 64, pp. 3288, 2004.

[34] E. D. Kirson, V. Dbalý, F. Tovariš, J. Vymazal, J.F. Soustiet, A. Itzhaki, D. Mordechovich, S. Steinberg-Shapira, Z. Gurvich, R. Schneiderman, Y. Wasserman, M. Salzberg, B. Ryftel, D. Goldsher, E. Dekel and Y. Palti, "Alternating electric fields arrest cell proliferation in animal tumor models and human brain tumors," Proc. Natl. Acad. Sci. USA, vol. 2104, pp. 10152, 2007.

[35] L. Cucullo, G. Dini, K. L. Hallene, V. Fazio, E. V. Ilkanich, C. H. Igboechi, K. M. Kight, M. K. Agarval, M. Garrity-Moses and D. Janirgo, "Very low intensity alternating current decreases cell proliferation," Glia, vol. 51, pp. 65, 2005.

[36] I. Minoura and E. Muto, "Dielectric measurement of individual microtubules using the electroorientation method," Biophys. J., vol.90, pp.3739-3748, 2006.

[37] M. Cifra, J. Pokorny, D. Havelka and D. Kucera, "Electric field generated by axial longitudinal vibration modes of microtubule," BioSystems, vol.100, pp. 122-131, 2010.

[38] D. Havelka, M. Cifra, O. Kučera, J. Pokorný and J. Vrba, "High-frequency electric field and radiation characteristics of cellular microtubule network," J. Theoret. Biol., vol.286, pp. 31-40, 2011.

[39] A. Mershin, A. A. Kolomenski, H. A. Schuessler and D. V. Nanopoulus, "Tubulin dipole moment, dielectric constant and quantum behaviour: computer simulations, experimental results and suggestions," Biosystems, vol.77, pp. 73-85, 2004.

[40] M. A. Rojavin and M. C. Ziskin, "Medical application of millimetre waves," Q.J. Med., vol.91, pp. 57-66, 1998.

[41] S. I. Alekseev and M. C. Zickin, "Millimeter microwave effect on ion transport across lipid bilayer," Bioelectromagnetics, vol.16, pp. 124-131, 1995.

[42] D. J. Panagopoulos, A. Karabarbounis and L. H. Margaritis,"Mechanism for action of electromagnetic fields on cells," Biochem. Biophys. Res. Commun., vol. 298, pp. 95-102, 2002.

[43] C.R. Cantor and P. R. Schimmel, Biophysical Chemistry, Part I: The Conformation of Biological Macromolecules, Ed. by W.H. Freeman and Company, San Francisco, 1980.

[44] E. Nogales, S. C. Wolf and K. H. Dowing "Structure of the tubulin dimer by electron crystallography," Nature, vol.391, pp. 199-203, 1998.

[45] J. Lowe, H. Li, K. H. Downing and E. Nogales, "Refined structure of α/β tubulin of 3.5A resolution," J. Mol. Biol., vol. 313, pp.1045-1057, 2001.

[46] E. M. Mandelkow, R. Schulthesiss, R. Rapp, M. Muller and E. Mandelkow, "On the surface lattice of microtubules, helix starts, protofilaments number, seam and handedness," J. Cell Biol., vol.102, pp. 1067-1073, 1986.

[47] P. A. Janmey, U. Euteneuer, P. Traub and M. Schliwa, "Viscoelastic properties of vimentin compared with other filamentous biopolymer network," J. Cell Biol., vol. 113, pp. 155-165, 1991.

[48] A. Kis, S. Kasas, B. Babić, A. J.Kulik, W. Benoît, G.A.D. Briggs, C. Schönenberger, S. Catsicas and L. Forró, "Nanomechanics of microtubules," Phys. Rev. Lett., vol.89, pp. 248101-248104, 2002.

[49] J. Pokorný, "Excitation of vibrations in microtubules in living cells," Bioelectrochemistry, vol. 63, pp. 321-326, 2004.

[50] J. A. Tolomeo and M. C. Holley, "Mechanics of microtubule bundles in pillar cells from inner ear," Biophys. J., vol. 73, pp. 2241-2247, 1997.

[51] E. Mickey and J. Howard, "Rigidity of microtubules is increased by stabilizing agents," J. Cell. Biol., vol. 130, pp. 909-917, 1995.

[52] R. P. Feynman, R. B. Leighton and M. Sands, The Feynman Lecture on Physics. Addison-Wesley Publishing Co. Inc., Reading, MA, 1964.

[53] P. J. Pablo, I. A. T. Schaap, F. C. MacKintosh and C. F. Schmidt, "Deformation and collapse of microtubules on nanometer scale," Phys. Rev. Lett., vol.91, pp. 098101(1)-098101(4), 2003.

[54] F. Pampaloni, G. Lattanzi, A. Jonas, T. Surrey, E. Frey and E.L. Florin. "Thermal fluctuations of grafted microtubules provide evidence of a length-dependent persistence length," Proc. Natl. Acad. Sci. USA, vol.103, pp. 10248-10253, 2006.

[55] M. Kikumoto, M. Kurachi, V. Tosa and H. Tashiro, "Flexural rigidity of individual microtubules measured by a buckling force with optical traps," Biophys. J.,vol. 90, pp. 1687-1696, 2006.

[56] W. Yu and P. W. Baas, "Changes in microtubule number and length during axon differentiation," J. Neurosci., vol.14, pp. 2818-2829, 1994.

[57] P. W. Baas, C. V. Nadar and A. M. Kenneth, "Axonal transport of microtubules: the long and short of it," Traffic, vol.7, pp. 490-498, 2006.

[58] D. Boal and D. H. Boal, Mechanics of the Cell. Cambridge Univ. Press © David Boal, 2012.

[59] R. Sträcke, K. J. Böhm, L. Wollweber, J. A. Tuszynski and E. Under, "Analysis of the migration behaviour of single micr tubules in electric fields," Biochem. Biophys. Res. Commun., vol. 292, pp. 602-609, 2002.

[60] T. Kim, M. T. Kao, E. F. Hasselbrink and E. Mehöfer, "Nanomechanical model of microtubule translocation in the presence of electric field," Biophys. J., vol. 94, pp. 3880-3892, May 2008.

[61] A. E. Pelling, S. Sehati, E. B. Gralla and L. S. Gimzewski, "Time dependence of the frequency and amplitude of the local nanomechanical motion of yeast," Nanomedicine, vol. 1, pp. 178-183, 2005.

[62] M. Cifra, D. Havelka, O. Kučera and J. Pokorný, "Electric field generated by higher vibration modes of microtubule," In 15th Conference on Microwave Techniques – COMITE 2010.

[63] J. Tuszynski, J. Brown, E. Crawford, E. Carpenter, M. Nip, J. Dixon and M. Sataric, "Molecular dynamics simulations of tubulin structure and calculations of electrostatic properties of microtubules," Math. Comput. Model, vol.41, pp. 1055-1070, 2005.

[64] M. Cifra, D. Havelka and M. A. Deriu "Electric field by longitudinal axial microtubule vibration modes with high spatial resolution microtubule model," Journal of Physics: Conference Series 329: 012013-01226. 90th International Fröhlich's Symposium, IOP Publishing Ltd, 2011.

[65] L. A. Amos, "The microtubule lattice-20 years on," Trends. Cell. Biol., vol. 5, pp. 48-51, 1995.

[66] F. Metoz, I. Amal and R.H. Wade, "Tomography without Tilt: Tree-Dimensional Imaging of Microtubules/Motor Complexes," J. Struct. Biol., vol. 118, pp.159-168, 1997.

[67] K. R. Foster and M. H. Repacholi, "Biological effects of radiofrequency fields: does modulation matter?," Radiation Research, vol. 162, pp. 219-225, August 2004.

[68] A. A. Saha, T. J. A. Craddock and J. A. Tuszynski, "An investigation of the plausibility of stochastic resonance in tubulin dimmers," BioSystems, vol.107, pp. 81-87, 2012.

[69] K. F. Foster and J. W. Baish, "Viscous damping of vibrations in microtubules," J. Biol. Phys., vol. 26, pp. 255-260, 2000.

[70] F. Bueche, Principles of physics. Fourth Ed. McGraw-Hill International Book Company, UK, 1982.

[71] J. L. Carminati and T. Stearns, "Microtubules orient the mitotic spindle in yeast through dynein-dependent interactions with the cell cortex," J. Cell. Biol., vol. 138, pp. 629-641, 1997.

[72] I. V. Savelev, Lecture of fundamental physics. Part 1-3, 'Science' Ed., Moscow, Russia, 1977.

[73] C. B. Tyson,P. G. Lord and A. E. Wheals "Dependency of size of Saccharomyces cerevisiae cells on growth rate," J. Bacteriol. Vol. 138, pp. 92-98, 1979.

[74] P. A. Fantes, "Control of cell size and cycle time in Schizosaccharomyces pombe." J. Cell Sci., vol. 24, pp.51-67, 1977.

[75] A. T. Atanasov, "Method for tentative evaluation of membrane permeability coefficients for sodium and potassium ions in unicellular organisms," Open J. of Biophysics, vol. 3, PP.91-98, 2013.

[76] C. Goswami and T. Hucho, "Novel aspects of submembraneous microtubule cytoskeleton," FEBS Journal, vol. 275, pp. 4653, 2008.

[77] I. B. Levitan, "Modulation of ion channels in neurons and other cells," Ann. Rev. Neurosci. vol.11, pp. 119-136, 1988.

[78] B. Hille, Endplate channels and other electrically inexitable channels. In: Ionic Channels of Excitable membranes. pp. 117-147. Sinauer Associated Inc., Sunderland MA, USA, 1984.

[79] C. Miller, "Trapping single ions inside ion channels," Biophys. J., vol. 52, pp. 123-126, 1987.