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Survey

SURVEY

Microtubules: a network for solitary waves**

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Abstract: In the present paper we deal with nonlinear dynamics of microtubules. The structure and role of microtubules in cells are explained as well as one of models explaining their dynamics. Solutions of the crucial nonlinear differential equation depend on used mathematical methods. Two commonly used procedures, continuum and semi-discrete approximations, are explained. These solutions are solitary waves usually called as kink solitons, breathers and bell-type solitons.

Keywords: molecular motors; non-linear dynamics; solitons; non-linear differential equations.

INTRODUCTION

A cell is defined as eukaryotic if it has a membrane-bound nucleus**.** Such cells are generally larger and much more sophisticated than prokaryotic cells due to the many different types of specialized organelles present in most eukaryotic cells. Plant and animal cells are eukaryotic while bacteria cells are prokaryotic.

In eukaryotes, intracellular protein filament networks exist. The two predominant types are filamentous actin (F-actin)[1] and microtubules (MTs). In this paper we deal with the later only.

All eukaryotic cells produce two kinds of tubulin proteins. Alpha and beta tubulins spontaneously bind one another to form a functional subunit that we call a heterodimer, or a dimer for short. When intracellular conditions favour assembly, the dimers assemble into long structures called protofilaments (PFs). Microtubules are usually formed of 13 PFs, as shown in Fig. 1. Hence, MTs are long cylindrical polymers whose lengths vary from a few hundred nanometers up

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to meters in long nerve axons.[2] Each dimer is an electric dipole whose mass is $m = 1.8\times10^{-22}$ kg. Its length is $l = 8$ nm, while the remaining two dimensions are 6.5 and 4.6 nm.[3] The component of its electric dipole moment in the direction of PF and charge displacement are: $p = 337\ D = 1.13\times10^{-27}$ C m and $d \approx 4$ nm, respectively.[4]

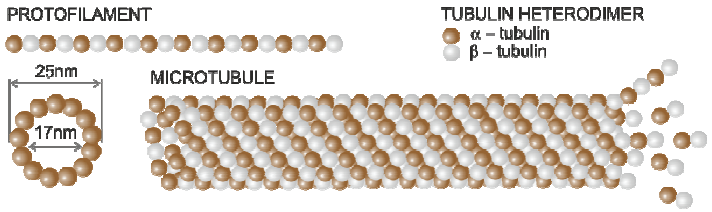

Fig. 1. A tubulin dimer, a protofilament and a microtubule.[5]

MTs are the major part of cytoskeleton.[6] They are long structures that spread between a nucleus and a cell membrane. MTs are involved in nucleic and cell division and organization of intracellular structure. They also serve as a network for motor proteins. This is shown in Fig. 2. One can see that there are two distinct families of microtubule associated motor proteins move along microtubules, carrying molecular and vesicular cargo. Dynein motors move from the microtubule plus end toward the minus end, while most members of the kinesin family move in the opposite direction. Particular cargos associate preferentially with particular motors, often through adapter molecules.[7] Experimental results show that mean squared displacement is approximately $\langle x^2 \rangle \sim t^{1.5}$, where t is time.[7]

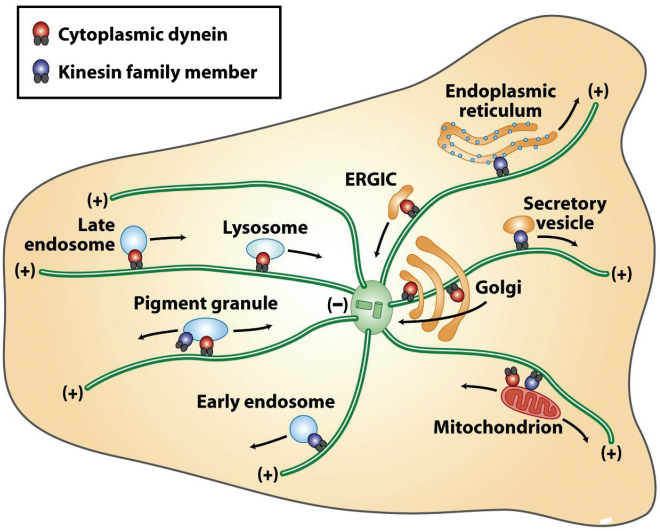

Fig. 2. Microtubule as a network for motor proteins in a eukaryotic cell.[5]

Cellular motors with dimensions of less than 100 nm convert chemical energy into useful work. These small systems have the fundamental role of dissipation in biological systems, which has been confirmed by both the theoretical and the experimental investigations.[8] The molecular machines dissipate continuously, thus they operate as irreversible systems.[8]

Motor proteins move with a velocity of 0.1–2 μm/s.[9] More precise *in vivo* experimental value, for an individual Kinesin-1 motor, is 0.78±0.11 μm/s.[10] Also, these motors display an average run length of 1.17±0.38 mm, which agrees well with in vitro measurements.[10] For this activity they use the energy derived from repeated cycles of adenosine triphosphate (ATP) hydrolysis. One ATP molecule is hydrolyzed for each step of motor protein. The step of motor protein is 8nm distance, as this is nothing but the length of a single dimer. Energy released during ATP hydrolysis is about 14 kcal/mol*, which corresponds to activation energy of the motor proteins.[9]

It was pointed out that MT was a hollow cylinder. This should not yield to a possible wrong conclusion that motor proteins move through it. Quite opposite, they "walk" along PFs carrying their cargos, as shown in Fig. 3. The figure shows so-called two-headed motors but two-legs might be more appropriate term. Theoretical formalisms for kinesin motility of both one-headed[11] and two-headed motors[12] exist.

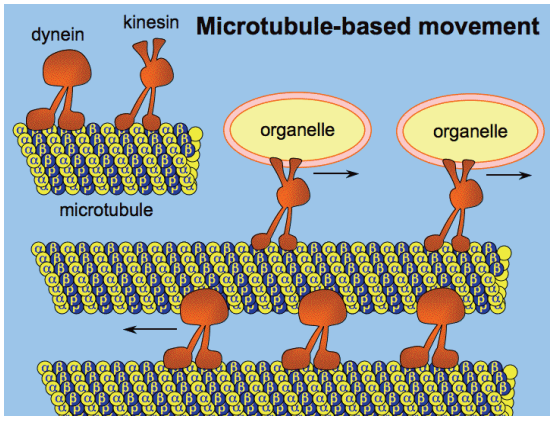

Fig. 3. Motor proteins move along MTs carrying cargo.[5]

It was pointed out that kinesins and dyneins are microtubule-based protein motors that can utilize the free energy of ATP hydrolysis to carry a cargo unidirectionally along a microtubule. The first kinesin was found in mid-1980.[12] From then a big progress has been performed. Probably the most exhaustive and useful review paper is the one that includes more than 2000 references.[13]

* 1 kcal = 4186 J

MTs in non-neuronal cells are unstable structures. They explore intracellular space by switching between phases of growth and shrinkage. The size fluctuation, *i.e.*, repeated growth (polymerization) and shrinkage (depolymerisation), of MT has been called as dynamic instability.[14,15] This means that populations of MTs usually consist of some that are shrinking and some that are growing. Hence, they exhibit dynamic instability behaviour existing in phases of elongation or rapid shortening. MTs grow steadily at plus end and then shrink rapidly by loss of tubulin dimers at the minus end. The rapid disassembly is referred to as catastrophe. Therefore, a population of MTs exhibits a bulk steady state, while a single MT never reaches a steady state length but persists in prolonged states of polymerization and depolymerization.[14] Many anti-cancer drugs, *e.g.*, taxol (paclitaxel) prevent growth and shrinkage of microtubules and thus prevent cell proliferation.[16]

The meanings of the plus and the minus ends should be explained in some more details. MT polymerizes more quickly from the plus end, which is terminated by the β-subunit, *i.e.*, β-monomer. The other end, growing more slowly, is known as the minus end, and is terminated by the α-subunit. These dynamics ends do not correspond to electric ones. Namely, the dimers are electric dipoles and, consequently, the whole MT can be seen as a giant dipole, with its electric plus and minus ends. The electric plus end corresponds to the minus dynamics one and *vice versa*.

One can find different values for velocities of elongation and shortening in literature depending on tubular concentration in the cell. Some values of the growth rate occurred in the plus end and the shrinkage rate occurred in the minus end are 1.9 and 9.7 μm/min,[17] respectively, as well as 7.2 and 17.3 μm/min.[18] Notice that the shrinkage rate is bigger than the growth rate.

Direct observation of the growth and shrinkage of MTs is possible. This can be done using single molecule Förster resonance energy transfer (FRET) method.[19] Using FRET it was shown that there exist multiple dwell times of microtubules in the polymerized and depolymerized states with an average value of 220 and 430 ms, respectively.[19] In the interphase the half lifetime of individual unstable MT is 5–10 min.[9]

MTs existing in neuronal cells are uniquely stable and, consequently, neurons, once formed, don't divide.[2] This stability is crucial as there are evidences that neuronal MTs are responsible for processing, storage and transduction of biological information in a brain.[2,20]

NONLINEAR DYNAMICS OF MICROTUBULES

To study dynamics of MTs we need an appropriate model. The dimers are electric dipoles and the whole MT can be regarded as ferroelectric. That was assumed for the first nonlinear model of MT.[21]

The tubulin polymerization process involves two types of contacts between the dimers. These are head-to-tail binding of dimers, resulting in protofilaments, and interactions between parallel protofilaments, which complete the MT wall. Since the longitudinal contacts along PFs appear to be much stronger than those between adjacent PFs,[22,23] we construct a simplified Hamiltonian of MT, which is, practically, Hamiltonian for a single PF only. However, the influence of the neighbouring PFs is taken into consideration through the electric field. Namely, each dimer exists in the electric field coming from the dimers belonging to all PFs. Also, the nearest neighbour approximation is assumed.

There is one additional approximation. The dimers oscillate performing both radial and longitudinal oscillations. Hence, there are a few degrees of freedom, theoretically six, but all existing models assume only one degree of freedom per dimer, though some attempts to use two degrees of freedom are in progress. Thus, according to the chosen coordinates describing dimers` oscillations we can talk about either radial or longitudinal model. The latter one we call as *u*-model.[24,25] Notice that the *u*-model assumes radial oscillations of the dimers but the coordinate *u* is the projection of the top of the dimer on the direction of PF. There is a real longitudinal model assuming longitudinal displacements of the dimers that we call as *z*-model.[26] Both *u*- and *z*-models bring about equal differential equations but meanings of the coordinates *u* and *z* are different.

The second kind of the model is a radial one[27] and we call it as φ-model for short. Of course, the angle φ determines the radial displacement of the dimer representing the angle between the dimer and the direction of PF.

The equation describing the *u*- and *z*-models comprises a term which does not exist in the one coming from the φ-model. Hence, it is more complicated and interesting and, in what follows, we concentrate on the *u*-model only.

Each model requires a simplified picture according to which we write Hamiltonian describing the physical system. Also, an elementary mass, *i.e.*, the smallest particle whose internal structure is neglected, should be indicated. The *u*-model, as well as all the models mentioned above, assumes that the dimer is the elementary particle. The simplified picture, allowing us to write the Hamiltonian, could be the one in Fig. 4. The figure shows a segment of MT with three PFs clearly indicated.

The Hamiltonian for the *u*-model is:

$$H = \sum_n \left[\frac{m}{2}\dot{u}_n^{\,2} + \frac{k}{2}\left(u_{n+1} - u_n\right)^2 - \frac{1}{2}Au_n^2 + \frac{1}{4}Bu_n^4 - Cu_n \right], \; C = QE \qquad (1)$$

where dot means the first derivative with respect to time, m is a mass of the dimer, k is an intra-dimer stiffness parameter, $Q > 0$ represents the excess charge within the dipole, $E > 0$ is internal electric field and the integer n determines the position of the considered dimer in PF.[21,24,25] The first term represents the kinetic

energy of the dimer. The second one is the potential energy of the chemical interaction between the neighbouring dimers belonging to the same PF, where, obviously, the nearest neighbour approximation is used, as explained above. The next two terms represent *W*-potential, which was introduced due to the fact that MT is ferroelectric and A and B are parameters that should be determined or, at least, estimated.[21,24,25] The very last term is coming from the fact that the dimer is the electric dipole existing in the field of all other dimers. The last three terms together can be called as the combined potential which looks like unsymmetrical *W*-potential.

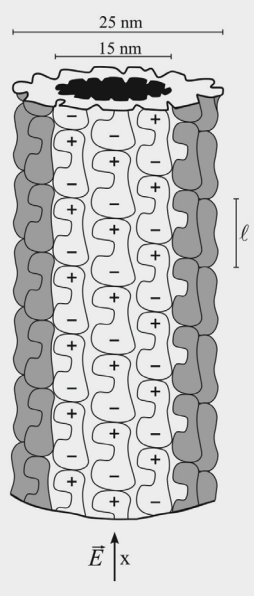

Fig. 4. Microtubule.

Our final goal is the function $u_n(t)$, describing nonlinear dynamics of MT. In principle, this can be done in two main steps. The first one is derivation of the equation coming from Eq. (1) and the second step is its solution. To obtain the required equation we introduce generalized coordinates q_n and p_n defined as $q_n = u_n$ and $p_n = m(\mathrm{d}u_n/\mathrm{d}t)$. Using well-known Hamilton's equations of motion $\mathrm{d}p_n/\mathrm{d}t = -\partial H/\partial q_n$ and $\mathrm{d}q_n/\mathrm{d}t = \partial H/\partial p_n$ we obtain the following discrete differential equation that should be solved:

$$m\ddot{u}_n - k\,(u_{n+1} + u_{n-1} - 2u_n) - Au_n + Bu_n^3 - C = 0 \qquad (2)$$

Therefore, nonlinear dynamics of MTs has been described by Eq. (2). Obviously, nonlinearity is coming from the 4th degree term in the *W*-potential.

Our next task is solution of Eq. (2). We are not going through all the tedious derivations. Instead, two known approaches will be explained briefly. It is interesting that the final results depend on applied mathematical procedures.

Some approximations used in derivation of Eq. (2) were introduced above. We now explain the two mathematical methods for solving this equation. Practically, these two approaches are two approximations. In other words, the approximations mentioned above were important for derivation of Eq. (2), while the mathematical ones are important for its solutions.

The first mathematical approximation that we explain is a continuum approximation $u_n(t) \rightarrow u(x,t)$, which allows a series expansion of the terms $u_{n\pm1}$, that is:

$$u_{n\pm1} \rightarrow u \pm \frac{\partial u}{\partial x} l + \frac{1}{2} \frac{\partial^2 u}{\partial x^2} l^2 \tag{3}$$

which straightforwardly brings about the following continuum dynamical equation of motion:

$$m \frac{\partial^2 u}{\partial t^2} - kl^2 \frac{\partial^2 u}{\partial x^2} - qE - Au + Bu^3 + \gamma \frac{\partial u}{\partial t} = 0 \tag{4}$$

The last term is coming from the introduced viscosity force $F_v = -\gamma \mathrm{d}u/\mathrm{d}t$, where γ is a viscosity coefficient.[21]

The remaining mathematical approximation is a semi-discrete one.[25,28,29] We assume small oscillations:

$$u_n(t) = \varepsilon \, \Phi_n(t) \, , \, \varepsilon << 1 \tag{5}$$

and look for wave solution which is a modulated wave. Its envelope is continual, while its carrier component is discrete. Such solution can be written as:

$$\Phi_n(t) = F(\xi) e^{i\theta_n} + \varepsilon \, F_0(\xi) + \varepsilon \, F_2(\xi) e^{i2\theta_n} + cc + \mathrm{O}(\varepsilon^2) \tag{6}$$

where $\xi = (\varepsilon nl, \varepsilon t)$, $\theta_n = nql - \omega t$, ω is the optical frequency of the linear approximation, $q = 2\pi/\lambda > 0$ is the wave number, *cc* represents complex conjugate terms and the function F_0 is real. The dimers length l, mentioned above, is nothing but a period of one dimensional crystal lattice. Obviously, the continuous function F represents an envelope, while $\exp(i\theta_n)$, including discreteness, is a carrier component. The first term in the expansion (6) is a leading one, while the remaining ones, multiplied by ε, are higher harmonics, representing a certain correction. Notice that the parameter ε exists in the function F but does not in $\exp(i\theta_n)$. This is so because the frequency of the carrier wave is much higher than the frequency of the envelope and we need two time scales, t and εt, for those two functions. Of course, the same holds for the coordinate scales.

This method is very tedious and we do not go through all the derivations. The complete procedure and important explanations can be found in literature.[30]

The point is that the functions $F_0(\xi)$ and $F_2(\xi)$, existing in Eq. (6), can be expressed through $F(\xi)$. In this particular case they turned out to be constants.[25] Hence, we only need the equation for the function $F(\xi)$ and this is a well-known solvable nonlinear Schrödinger equation (NLSE):

$$iF_\tau + P F_{SS} + Q \left|F\right|^2 F = 0 \tag{7}$$

where the dispersion coefficient P and the coefficient of nonlinearity Q, as well as the coordinates τ and S, are explained elsewhere.[25]

Therefore, the crucial Eq. (2), describing nonlinear dynamics of MTs, has been transformed into Eqs. (4) and (7). The final step is the solutions of these two equations. This is a topic of the next section.

SOLITARY WAVES IN MICROTUBULES

The very first observation of solitary waves, or solitons for short, was made in 1834 by the hydrodynamic engineer John Scott Russel.[29] He was riding his horse, while a pair of horses drew a boat along a narrow channel. When the boat was suddenly stopped he noticed an interesting wave moving along the channel. That was a smooth and well defined heap of water, which moved along the channel without change of form or diminution of speed.[29] The wave was so stable that the engineer followed it about one or two miles. He called this phenomenon the wave of translation.

Understanding this interesting observation is nothing but a derivation of an equation whose solution is the observed wave. This equation is now called as KdV equation according to the initials of its authors Korteweg and de Vries, who derived it in 1895.[31] More than 20 years earlier this equation existed in an implicit form in research of Boussinesq.[32]

Nonlinear equations and solitons are nowadays very common in many branches of sciences.[33,34] Being a non-linear, it became fashionable. The most interesting characteristic of solitons is their stability in sense that these waves can pass through one another without annihilation. This was experimentally observed in neurons.[35]

Now we return to nonlinear biophysics, *i.e.*, to Eqs. (4) and (7). The former one is a partial differential equation (PDE). Generally, PDEs cannot be easily solved. Hopefully, Eq. (4) can be transformed into an ordinary differential equation (ODE). Namely, it is well known that, for a given wave equation, a travelling wave $u(\xi)$ is a solution which depends upon x and t only through a unified variable ξ:

$$\xi \equiv \kappa x - \omega t \tag{8}$$

where κ and ω are constants. Introducing a dimensionless function ψ through the relation:

$$u = \sqrt{\frac{A}{B}}\psi \tag{9}$$

we straightforwardly obtain the following ODE

$$\alpha\psi'' - \rho\psi' - \psi + \psi^3 - \sigma = 0 \tag{10}$$

where

$$\alpha = \frac{m\omega^2 - kl^2\kappa^2}{A},\ \sigma = \frac{qE}{A\sqrt{A/B}},\ \rho = \frac{\gamma\omega}{A},\ u' \equiv \frac{du}{d\xi} \tag{11}$$

Notice that ρ and σ are proportional to the viscosity coefficients and electric field, respectively.

It was pointed out that the first nonlinear model of MT was introduced in 1993.[21] If we compared Eq. (10) with the appropriate one in literature[21] we would see that they match for $\alpha = -1$. Hence, this approach is more general and this is what we have called as *u*-model.[24,25] The key point is that α can be determined.

Equation (10) has been solved using a couple of mathematical procedures such as standard procedure,[21] modified extended tanh-function method,[24] procedure based on Jacobian elliptic functions,[36] method of factorization[37] and the simplest equation method (SEM). Beside a couple of diverging functions all these procedures bring about the same solutions having physical sense. These are three kink solitons, shown in Fig. 5. Of course, the function $\psi(\xi)$ is the solution of Eq. (10). These solitons are kink-solitons or kinks (ψ_3) and antikink-solitons (ψ_1 and ψ_2). It is common to call both of them as kinks for short. If we look at any of them we see that the kinks represent transition between two asymptotic states ($\xi \to \pm\infty$). In other words, orientation of the dimers is changed. Regarding the present figure the transition occurs in the approximate interval of $\xi \in$ (–6,+6). This interval is moving along MT.

The most general method SEM brings about infinitely many parallel lines corresponding to all the three functions in Fig. 5.[38] Of course, this is of mathematical interest but all those functions have the same physical meaning. A real advantage of SEM method over the remaining ones is a completely new solution.[38] This is a bell-type soliton, shown in Fig. 6. This solution of Eq. (10) can be obtained only for $\rho = 0$, *i.e.*, when viscosity is neglected.

Therefore, two completely different solutions of Eq. (10) have been derived. A final step is derivation of Eq. (7). Even though this is PDE its solution exists.[29,30] Hence, we know *F*, the functions F_0 and F_2, existing in Eq. (6), can be expressed through *F* and all this brings about the final expression for *u*. This interesting solution is:

$$u_n(t) = A_0 \mathrm{sech}\left(\frac{nl - V_e t}{L}\right) \cos(\Theta nl - \Omega t) - \frac{C}{A} \quad (12)$$

where the expressions for all the parameters can be found in elsewhere.[25] The hyperbolic function represents the envelope, while the cosine represents the carrier wave. This is shown in Fig. 7. Obviously, this is a localized modulated wave usually called as breather. We see that its width is about 200nm, which means that it covers about 25 dimers.

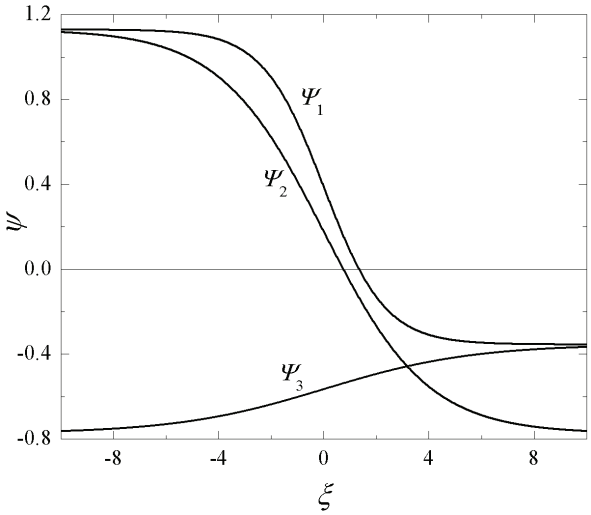

Fig. 5. The functions $\psi(\xi)$ for $\rho = 2$ and $\sigma = 0.31$.

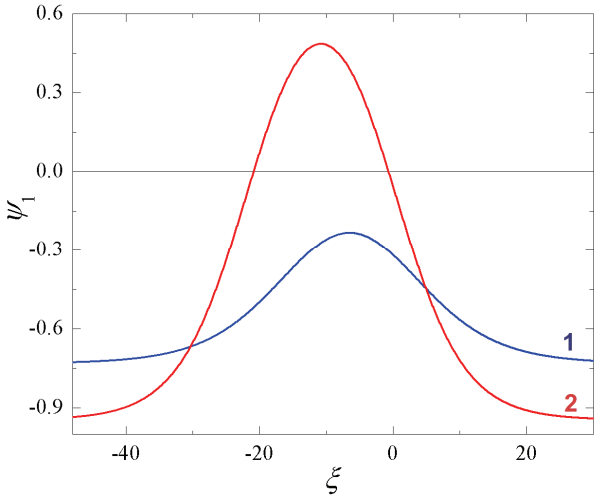

Fig. 6. A bell-type soliton for $\sigma = 0.34$ (1) and $\sigma = 0.1$ (2).

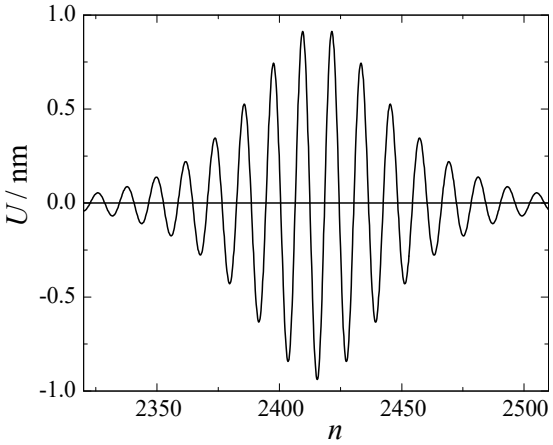

Fig. 7. A localized modulated soliton (breather).

As a conclusion we can say that all the three known kinds of solitary waves have been found in MTs. All these analytical results have been numerically supported.

CONCLUSION AND FUTURE RESEARCH

The three different solitons have been predicted as possible candidates for information carriers along MTs. They are shown in Figs. 5–7. A crucial question is their stability, which is very important task that should be performed soon.

A weak point in the *u*-model is the last term in Eq. (1). The φ-model was an attempt to overcome the problem. A better potential energy:

$$U(\varphi) = -\vec{p} \cdot \vec{E} = QdE\cos\varphi$$

was introduced instead but the *W*-potential has been lost.[27] Hence, research in progress has been carried out with a goal to create a general model which will include both $U(\varphi)$ and *W*-potential.

Let us return to Eq. (1) and Fig. 4. According to the latter, one would conclude that all the dimers are positioned in the direction of PFs. Of course, this is a simplified picture. The last three terms in Hamiltonian given by Eq. (1) represent the nonsymmetrical *W*-potential. The graph of this function has two minima. This means that there are two possible orientations of the dimers, *i.e.*, two possible angles between them and PFs. According to the dimensions of the dimers we expect that it should be possible to measure these angles. Such experiments would prove or disapprove the theoretical expectation regarding *W*-potential. In case that the used potential has been a good choice the measured angles would improve theory a lot.

Therefore, stability analysis, the general model and the experimental verifications are new tasks that should be performed in near future.

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ИЗВОД

МИКРОТУБУЛЕ: ПУТЕВИ ЗА СОЛИТОНСКЕ ТАЛАСЕ

У овом раду се бавимо нелинеарном динамиком микротубула. Објашњени су састав и улога микротубула у ћелијама као и један од модела који описује њихову динамику. Рјешења најважније нелинеарне диференцијалне једначине зависе од коришћених математичких поступака. Објашњена су два често коришћена поступка. То су континуална и семидискретна апроксимација. Поменута рјешења су солитонски таласи који се често зову кинк солитони, бродери и звонасти солитони.

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