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Electric field generated by longitudinal axial microtubule vibration modes with high spatial resolution microtubule model

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Abstract. Microtubules are electrically polar structures fulfilling prerequisites for generation of oscillatory electric field in the kHz to GHz region. Energy supply for excitation of elasto-electrical vibrations in microtubules may be provided from GTP-hydrolysis; motor protein-microtubule interactions; and energy efflux from mitochondria. It recently was determined from anisotropic elastic network modeling of entire microtubules that the frequencies of microtubule longitudinal axial eigenmodes lie in the region of tens of GHz for the physiologically common microtubule lengths. We calculated electric field generated by axial longitudinal vibration modes of microtubule, which model is based on subnanometer precision of charge distribution. Due to elastoelectric nature of the vibrations, the vibration wavelength is million-fold shorter than that of the electromagnetic field in free space and the electric field around the microtubule manifests rich spatial structure with multiple minima. The dielectrophoretic force exerted by electric field on the surrounding molecules will influence the kinetics of reactions via change in the probability of the transport of charge and mass particles. The electric field generated by vibrations of electrically polar cellular structures is expected to play a role in biological self-organization.

1. Introduction

Several experimental works have reported the electrical oscillations of living cells in the frequency region kHz-GHz [1–3]. These works have been motivated by the theoretical analyses indicating that the electrodynamic field is generated by the living cells and that it can have role in organization of intracellular processes [4,5] and interaction between the cells [6,7]. The proposed mechanisms for the organizational role of cellular electrodynamic field lies in the influence of the electrodynamic field force on the probability of the spatial distribution of biomolecules and organelles [4, 5, 8].

2. Microtubule

The fundamental question is which cellular structures are capable of generation of electrodynamic field. Such structures must fulfil following necessary conditions:

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- have sufficient energy supply
- have an ability to convert the input energy to electrodynamic field (either by elastoelectric vibrations or by electronic conduction)
- sufficiently low damping of process which generates the electrodynamic field

Currently, microtubules seem to be the cellular structures which fulfil above mentioned conditions [9]. Microtubules are dynamic structures present in every eukaryotic cell.

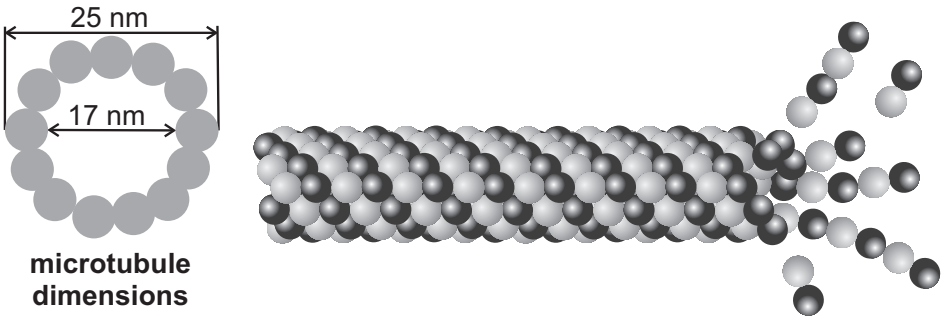


Figure 1. (a) Cross section of microtubule. (b) Detail of chemical plus end of a microtubule undergoing dynamic instability.

Energy may be provided to microtubules from three major sources [1, 8, 9]:

- Energy released from mitochondria as "wasted" energy in the course of citric acid cycle may be the most significant energy source for excitations of MT vibrations.
- Energy released from hydrolysis of guanosine triphosphate (GTP) in processes of dynamic instability of MTs is the energy supply dependent on internal MT process.
- Energy transferred from moving of motor proteins and their interaction with MTs may also contribute to excitation of vibrations in MTs

Once the energy is supplied to microtubule, amplitude of microtubule vibration modes is increased. The problem of the energy spectral distribution (dissipation or condensation) will not be treated here, we refer interested reader to [10, 11]. Here we assume underdamped eigenmode vibrations of the microtubule.

Microtubule is electrically polar structure due to the polarity of its subunits, tubulin heterodimer proteins. Due to the intrinsic electric polarity of microtubules, vibrations of the microtubule lattice will be accompanied by oscillatory electric fields due to the displacement of charges. Vibrations and accompanying oscillatory electric fields are of the same frequency in the first approximation. These type of vibrations can be viewed upon as elastoelectric (electroelastic), acoustoelectric (electroacoustic) [12] or elasto-polarization [13, 14] waves.

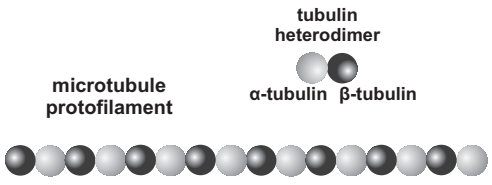


Figure 2. Structural subunits of microtubules: protofilament composed of tubulin heterodimers

Microtubules, treated as tube like orthotropic structures, are able to oscillate from kHz - GHz region [15, 16]. 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 [17].

Hypothetically, electric oscillations could be generated by microtubule also in case of charge oscillations based on charge conduction. Special frequency dependent type of ballistic-like electric conduction at specific frequencies in MHz region has been demonstrated in microtubules only very recently [18]. However, it is not described in details yet in any known publication. We will not include possible microtubule charge conduction properties in our model since we describe different frequency region.

In this paper we provide preliminary study of electrodynamic field generated by electrically polar longitudinal axial vibrational modes of microtubules based on the subnanometer resolution of microtubule charge distribution.

3. Materials and Methods

3.1. Subnanometer microtubule charge distribution

Model of microtubule lattice with subnanometer resolution is based on crystallography data of tubulin heterodimers from Nogales et al. [19] (1TUB on RCSB Protein DataBank) and on refined crystallography data of tubulin from Löwe et al. [20] (1JFF on RCSB Protein DataBank). Tubulin heterodimers with subnanometer resolution have been assembled to the 13:3 B-microtubule lattice. Model of microtubule with the length of 1200 nm has been created. This length corresponds to 150 tubulin heterodimers in every microtubule protofilament. Microtubule structure has been refined in order to obtain physiologically realistic lattice. Details of the optimization and refinement procedure of microtubule lattice can be found in [21]. Each atomic group with its coordinates in microtubule has been assigned a charge using Gromos 53a6 force field.

3.2. Dispersion relation

Dispersion relation of stretching (longitudinal axial) mode is based on data from normal mode analysis of coarse grained elastic network model of microtubules published in [21]. The dispersion relation is depicted in Figure 3a.

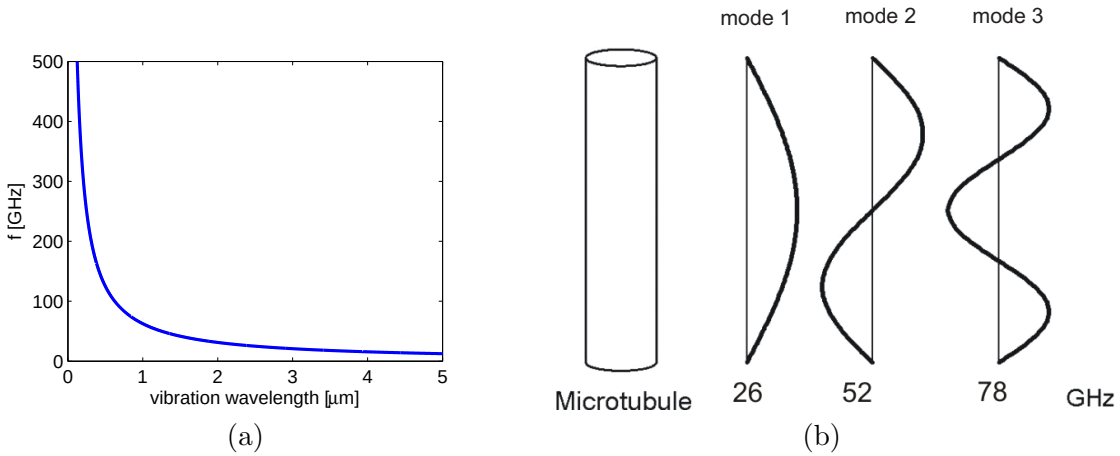


Figure 3. (a) Dispersion relation of longitudinal axial (stretching) vibration modes of microtubules (b) Distribution of vibrational amplitude along the microtubule axis for first three longitudinal axial vibration modes

3.3. Microtubule vibrations and dipole representation

We consider harmonic longitudinal vibrations of microtubules with fixed ends, i.e. vibration amplitude of the first and the last heterodimer is zero. Direction of the vector of the oscillations of the individual charges is parallel to the axis of microtubule. Amplitude of the charge oscillatory motion is same in the cutting plane perpendicular to the microtubule axis and is given by the shape of the longitudinal eigenmode, see e.g. Figure 3b. Electric field generated by the oscillatory motion of every charge is approximated by the electric field of the dipole with the same frequency as microtubule vibrations. Total field is calculated as vector sum of contributions from all dipole fields.

4. Results

Figure 4 and 5 shows microtubule in the coordinate system and depiction of the planes where the electric field has been calculated in following figures.

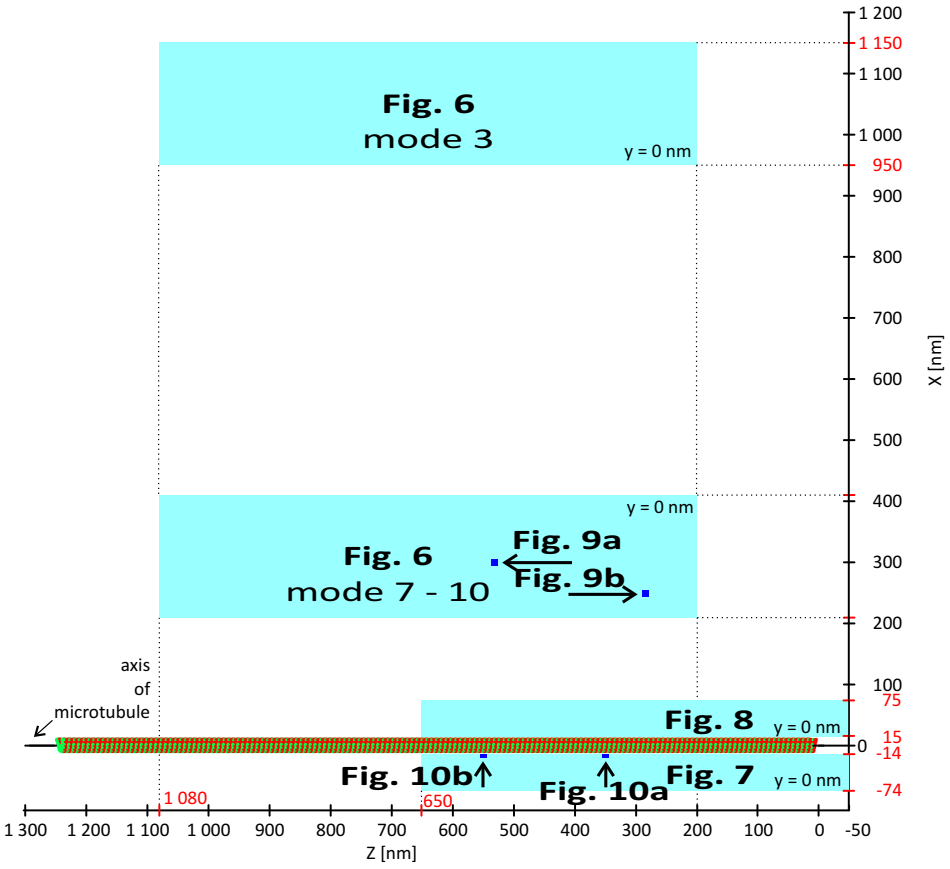


Figure 4. Microtubule in the coordinate system and depiction of the planes where the electric field has been calculated

5. Discussion and conclusion

We calculated electric field generated by collective longitudinal axial vibration modes of microtubule. Every charge involved in the vibrations generates dipole field. Total field is given by the vector sum of fields form all dipoles. We see that electric field of microtubule exhibits

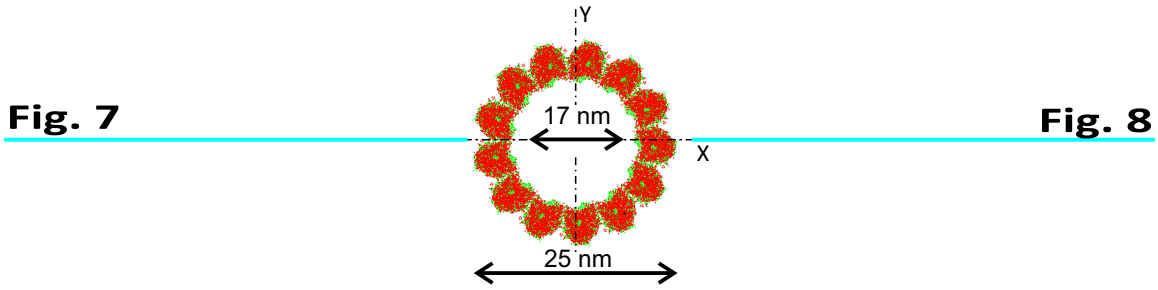


Figure 5. Microtubule in the coordinate system and depiction of angular position of the planes where the electric field has been calculated

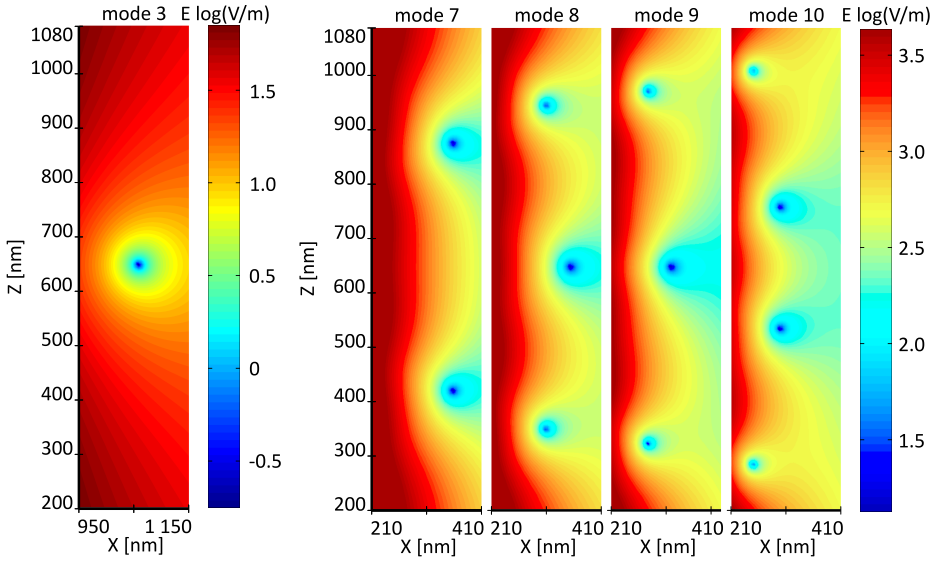


Figure 6. Electric field generated by several microtubule vibrations modes

rich spatial pattern. We can distinguish several levels of the field patterns. First, we can identify local minima of electric field in Figure 6. High resolution calculations in the region of selected field minima generated by the mode 10 are in the Figure 9.

The higher is the mode number, the more local minima occur in the field. These local field minima are caused by the dipole-like fields created by vibrational half-wavelengths as is described in following text. There is one dipole-like field per vibrational half-wavelength created. One can see the dipole-like fields in the Figures 7 and 8. There is high intensity of the electric field at the poles of these dipole-like fields. Neighbour dipole-like fields oscillate with opposite phase and the fields of opposite orientation compensate in certain distance and create local minimum of electric field. Those minima are visible in Figures 6 and 9. Distance of the field minima from the microtubule wall is related to the vibration wavelength. The shorter is the vibrational wavelength (i.e. the higher is the mode number), the closer are located the field minima to the surface of the microtubule wall. It should be emphasized here that this kind of field structure with minima located several tens to several hundreds nanometers from each other is possible

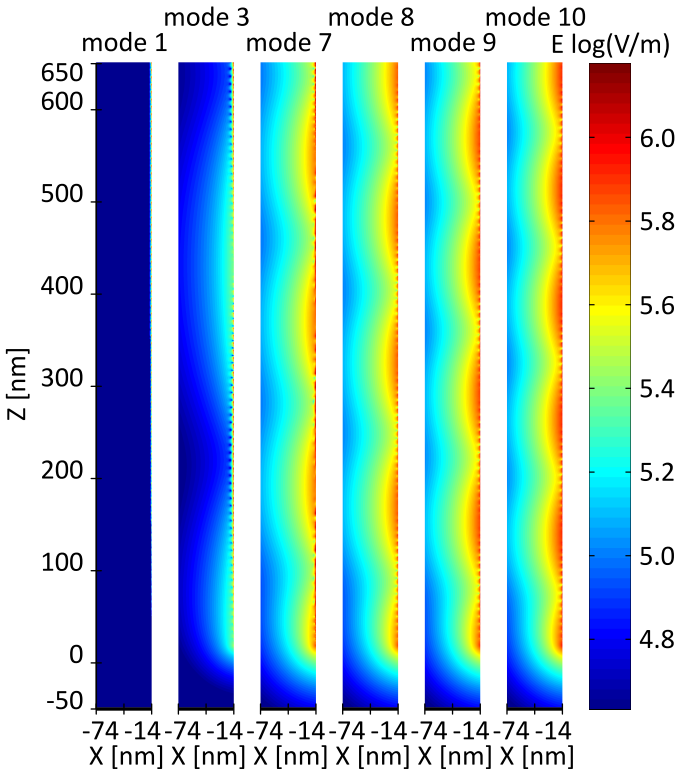


Figure 7. Electric field structure very near to the microtubule surface on the one side of microtubule

due to the elastoelectric nature of the oscillations at this frequency range. Elastic component of the microtubule vibrations propagates approximately with the sound velocity. In the frequency range of longitudinal vibrations of microtubules (tens and hundreds of GHz), wavelength of vibrations will be of the order of hundreds or tens of nanometers.

In the case of multiple microtubules in mutual vicinity (common case within the cell) the generated fields will interfere and create further local maxima and minima of the field. One can easily imagine that the field of the whole microtubule network will have rich three dimensional structure. This kind of field structure seems to be capable of creating field minima and maxima with sufficient spatial resolution (tens of nanometers) to contribute to the organization of biological intracellular processes.

One of the possible mechanisms of action of the cellular field on its internal processes may be dielectrophoresis. Dielectrophoresis [22] is a phenomenon in which nonuniform electric field acts on neutral particle by force via polarization effects. The physical mechanism is following: electric field of an external source acting on a dielectric particle induces separation of charges and exerts forces on them. The forces have opposite directions and in a nonuniform electric field they have also different magnitudes resulting in a non-zero force acting in the direction of the gradient of the intensity of the electric field. Additional force effect on the particle is exerted by the electric field generated by the surrounding polarized medium. The final effect, i.e. motion of the particle depends on the superposed electric fields. The particle is pulled to the region of the highest intensity of the electric field if the polarizability (which depends on permittivity) of the particle is greater than that of the surrounding medium and vice versa in the opposite case.

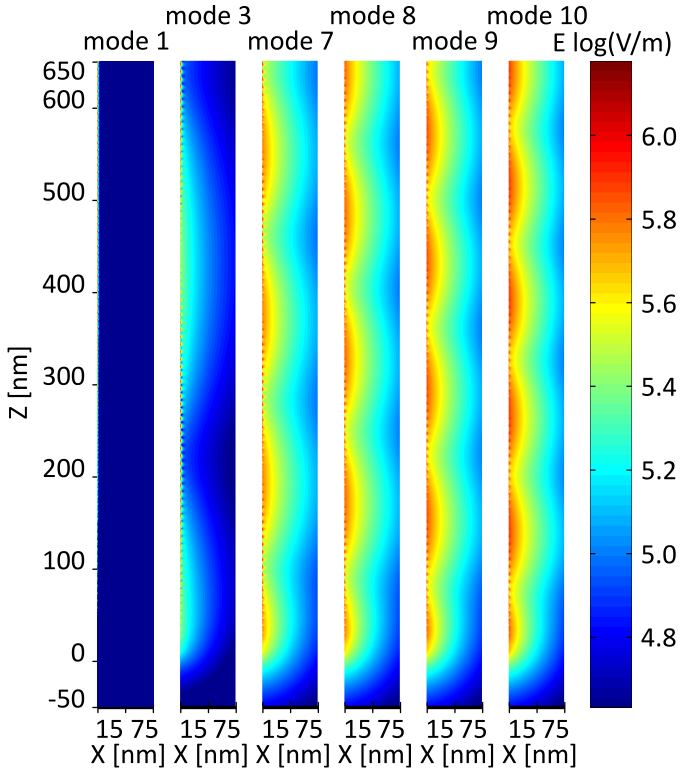


Figure 8. Electric field structure very near to the microtubule surface on the side of microtubule opposite to the that in Figure 7

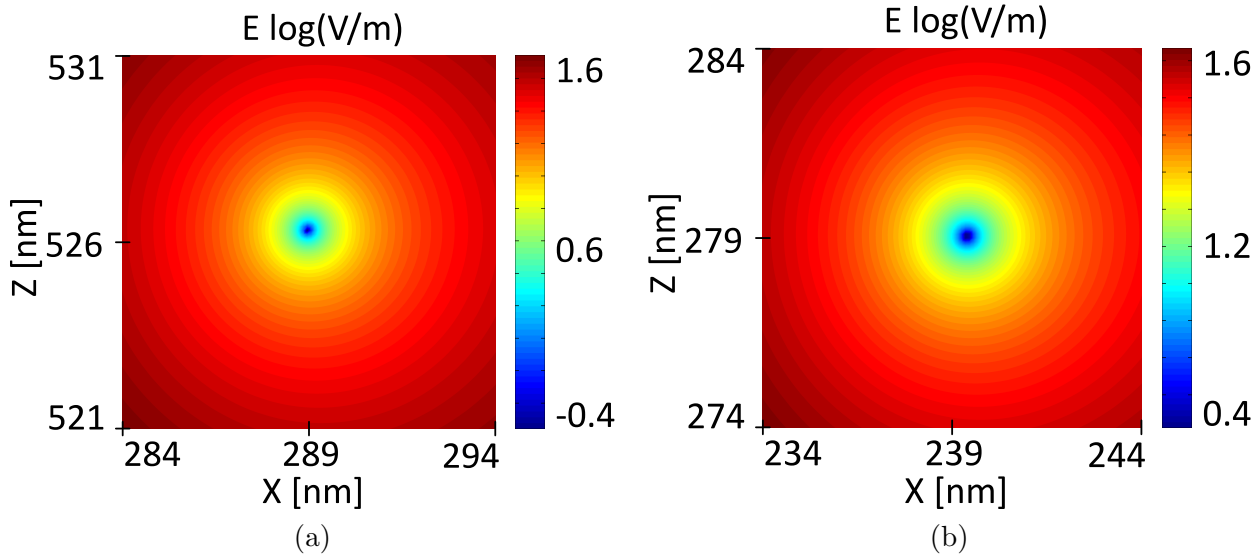
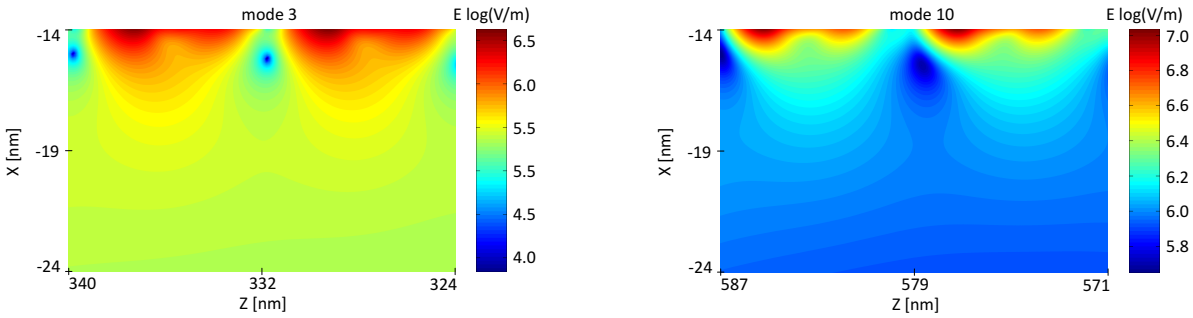


Figure 9. Local electric field minima of mode 10 calculated with 0.1 nm resolution

Underlying physical principle is the same as that of an optical tweezer.

Thus, even neutral particles and molecules can be acted upon by the dielectrophoretic force



(a) (b)

Figure 10. Local electric field minima calculated with 0.1 nm resolution near the microtubule wall

of the non-uniform electric field generated by elastoelectric vibrations of cellular polar structures such as microtubules. The force can influence the probability of the position of the molecules and organelles and influence the chemical kinetics in this manner.

We can conclude that the electric field generated by vibrations of electrically polar cellular structures is expected to play a role in biological self-organization. To what extent needs to be verified by the direct measurement of the electric oscillations of the cells which still remains a technical challenge.

Acknowledgements

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