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Effects of External Electric Field on the Thermodynamic Properties of Microtubules During Dynamic Instability

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Abstract We investigate the dynamics of microtubules (MTs) under the influence of the electric field using the Ising model. The mean-field theory is used to compute the thermodynamic properties of the model such as polarization, critical temperature, and free energy in the absence and presence of the external electric field. The results show that the magnitude of the external electric field plays a critical role in symmetry breaking in MTs. However, when the magnitude of the external electric field is weak and the environmental temperature is below the critical value, the system adopts a favorable configuration where the transmission process occurs.

Keywords Microtubules, Thermodynamic properties, Electric field, Mean-field theory, Symmetry breaking, The electric field

1. Introduction

Electronic microscopy imaging shows three major types of constituents in the cytoskeleton such as microtubules (MTs) [1,2], intermediate filaments, and actin microfilaments. Microtubules, major elements of the cytoskeleton are responsible for maintaining the shape of the cell, supposed to be the center of cellular organization and information processing. In fact, they play an important role in intracellular transport where they serve as road-rail for motors proteins, essential during cell division and cell motility [3,4,5]. X-ray crystallography shows that an MT is a hollow cylindrical tube about 25 nm in outer diameter and 14 nm in inner diameter [6,7,8]. The interior of the cylinder is likely to be filled with ordered water, which implies the existence of electric dipoles and an electric field. In fact, MT wall is an assembly of 13 protofilaments, each of which may be a series of subunit proteins referred to as tubulin dimers [9,10,11], capable of bonding GTP (guanosine triphosphate), but GTP bonded to β tubulin is a smaller amount stable than GTP bonded to α tubulin. After incorporating the dimer on the protofilament, β tubulin will hydrolyze its GTP to GDP (guanosine diphosphate). The hydrolyzed GDP will detach from the microtubule and therefore the latter is going to be liable for the dynamic instability. The dynamic instability of the MT is that the transition between the polymerization and depolymerization processes. The dynamic instability phenomenon was highly investigated during these last decades because its understanding reveals peculiar processes within cells. In 2013, Xin Li et al. [12], investigated a theoretical model of microtubule dynamics supported discrete-state stochastic models to elucidate the MTs dynamics accounting hydrolysis rate of GTP. They reported that the strong cooperatively in hydrolysis suppress dynamic instability while weak cooperatively in hydrolysis care the dynamics instability. Consistent with the role of MTs during chromosomes spindle Schwietert et al. [13], recently reported that cooperative stochastic microtubule depolymerization bistable force-velocity exhibited stochastic chromosome oscillations with reduced amplitude and a phase shift between sisters kinetochore. As MTs are road-rail for motor cargoes, Swaminathan et al. [14], in 2011, studied MTs self-organization by modeling MTs as polar rods and shown that originally disordered systems of interacting rods exhibit an orientational instability leading to spontaneous ordering. In fact, the tubulins dimers consist to β tubulin, positively charged, and α tubulin, negatively charged. These two tubulins form an electric dipole where the electron can be localized in α or β tubulin. Therefore the electric dipole is considered as a pseudo spin where the electron can be in spin-up or spin-down [15,16]. In that way, microtubule is ferroelectric, which is a characteristic of certain materials to have a spontaneous electric polarization that can be reversed by the application of an external electric field [17,18,19].

Many works on ferroelectric systems have been carried out using the Ising model in which collective effects are

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produced by local interactions between two-state particles [20-26] particularly microtubules because, of their intrinsic properties and by the way that they obey to collective interactions [11,27,28].

The piezoelectric properties of the microtubule were first discovered by Athenstadt et al. [29], He was looking for piezoelectric effects in living systems. The measurement of its piezoelectric properties and the subsequent classification as a piezoelectric polymer declared the existence of a permanent electric dipole on the microtubule. In 1999, Brown et al. [30], re-examined the ferroelectric model of microtubules by showing the condition that the ferroelectric properties are important for the microtubule dynamics, and that microtubule can be affected by the transient endogenous electric fields of living cells. Pokorny et al. [31] 2004, showed that the vibrations produced in the cell can generate an external electric field that influences certain proteins of the cell such as microtubules. In 2011, Cifra et al. [32], measured the electric field generated by the modes of longitudinal vibration of axial microtubules in the dynamics. In 2017, Satelice et al. [33], showed that electrolytic solutions containing microtubules are small signal alternating current conductors. Also, the microtubules in an electrolyte diluted 20 times increase the conductance of the solution by 23% at 100 kHz. From the abovementioned, it is clear that the external electric field plays a significant role in MT dynamics. But, in 2004, Chen Ying et al. [11], approach MTs as a one-dimensional ferroelectric system and described the nonlinear dynamics of electric dipoles of dimers in a protofilament of the microtubule by virtue of the double-well potential, where they study MTs in the absence of the external electric field. They showed that the ferroelectric (FE) to paraelectric (PE) transition in the system occurs through temperature.

Thus, we propose to give a theoretical look at external electric field effects on the ferroelectric character of MT dimers. In fact, in the ferroelectric phase, MT network orders their electrical dipoles in the same direction and allows efficient transportation of materials along with the network. While, in the paraelectric phase, electric dipoles are in disorder state where dimers are disorganized and the transport along the network is disturbed. These two phases are described by an order parameter which is polarization. The system is in the ferroelectric or ordered state when the polarization is different to zero and go to paraelectric state or disorder when the polarization is canceled, at a particular temperature usually call critical temperature or Curie Weiss temperature [34]. In this study, we aim to study the external electric field effects on MT's properties using the mean-field theory (MFT) in order to bring a theoretical clear explanation of how to control the dynamical critical temperature and the information direction. The paper is organized as follows: section 2 describes MT's system in terms of Hamiltonian and presents the mean-field approximation. Section 3 derives thermodynamic parameters and section 4 concludes.

2. Model and the Hamiltonian of the System

2.1. Model

In the present paper, we assume that MT consisting of a nonlinear ferroelectric [10] chain of N sites of pseudo-spin capable to undergo various phases transitions. The total energy of MT ferroelectric chain can be more powerful describe by the Ising model.

The Hamiltonian of the system is given by:

$$H = -\Omega\sum_{i=1}^{N} S_i^2 - J\sum_{\prec i,j\succ}^{N} S_i S_j - \varepsilon E\sum_{i=1}^{N} S_i \qquad (1)$$

The first term represents anisotropic interaction energy, where Ω is the anisotropic coefficient [35,36], N is the total number of tubulin dimers. S_i And S_j represents the pseudo-spin respectively in site i and site j with $S = \pm\frac{1}{2}$. The second term characterizes the nearest-neighbor exchange interaction energy between the spin of site i and the spin of site j, with an interaction coupling $J > 0$. The notation $< i, j >$ stands to the sum restricted to nearest-neighbor pair of pseudo-spin, each pair being counted only once [37]. The last term represents electric energy since E an external electric field and ε denotes the electric dipole moment.

Let's find the effective Hamiltonian of the system using mean-field theory (MFT) in order to derive MT's properties.

2.2. Effective Hamiltonian of the System and Mean-field Theory

MT is a many-body system consisting of a chain of N sites of pseudo-spin. Therefore, it is complicated to explore the general behavior of the system without approximation. Thus, in order to simplify the system, certain aspects can be neglect. Many works on the Ising model use the mean-field theory (MFT) which assumes that thermal fluctuations are relatively small and therefore can be neglected. We assume that all tubulins in the system represented by a spin only interact with the mean-field, supposing that the effect of interaction between tubulins are considered weak and can be neglect during the approximation. Then the behavior of the whole system is captured by the average behavior of spin around [38]. To decouple the Ising Hamiltonian using MFT, let's express the interaction terms $S_i S_j$ in the form:

$$S_i S_j = < S_i >< S_j > + < S_j > \delta S_i + < S_i > \delta S_j + \delta S_i \delta S_j \qquad (2)$$

$$\text{Since } S_i = < S_i > + \delta S_i \qquad (3)$$

By the assumption that fluctuations are very small, the quadratic term of Eq.(2) can be neglected:

$$\delta S_i \delta S_j = 0 \qquad (4)$$

Then $S_i S_j$ become:

$$S_iS_j = < S_i > \left[\left(S_i + S_j \right) - < S_i > \right] \quad (5)$$

According to the fact that the MT's system is considered translational invariant, the expectation value S_i of any given site is independent of the site, so we can, therefore, weigh the average total spin by a specific number seen as order parameter which best describe, MT's system. Then polarization is powerful to describe the whole behavior of the system:

$$< S_i >= p \quad (6)$$

Eq.(6) into Eq.(5) allows expressing S_iS_j as:

$$S_iS_j = p\left(S_i + S_j \right) - p^2 \quad (7)$$

The Ising Hamiltonian can now be written as:

$$H_{MF} = -\Omega \sum_{i=1}^{N} S_i^2 - Jp \sum_{\prec i,j \succ}^{N} \left(\left(S_i + S_j \right) - p \right) - \varepsilon E \sum_{i=1}^{N} S_i \quad (8)$$

According to the sum over nearest neighbors defined as:

$$\sum_{\prec i,j \succ} \rightarrow \frac{1}{2} \sum_{i=1}^{N} \sum_{j \in nn(i)} \quad (9)$$

Where the factor of $\frac{1}{2}$ is to avoid double counting pairs of sites and $nn(i)$ denotes nearest neighbors of i. Since there is no explicit j dependence inside the summation, this inner sum is simply and

$$\sum_{j \in nn(i)} = q \quad (10)$$

Where the coordination number q is equal to the number of neighbors of any given site, Eq.(10) into Eq.(9) give:

$$\sum_{\prec i,j \succ} \rightarrow \frac{q}{2} \sum_{i=1}^{N} \quad (11)$$

The value of q depends to the dimension of the system, for example, for a 1D lattice, $q = 2$; for a 2D triangular lattice, $q = 3$; for a 3D square lattice, $q = 4$ …

$$H_{MF} = \left(\frac{qJ}{2} + \Omega \right) Np^2 - h_{eff} \sum_{i=1}^{N} S_i \quad (12)$$

With

$$h_{eff} = \left(\left(qJ + 2\Omega \right) p + \varepsilon E \right) \quad (13)$$

3. The Thermodynamics Parameters of the System

3.1. The Partition Function

The partition function is one of the best tools which can allow us to derive the properties of a given system. Starting by definition, the partition function can be expressed as:

$$Z_{MF} = Tr\left(e^{-\beta H_{MF}} \right) = \prod_{i=1}^{N} \left(\sum_{S_i = \pm 1/2} e^{-\beta H_{MF}} \right) \quad (14)$$

After a trivial calculation on Eq.(14) and replacing H_{MF} and S_i by their values, the partition function becomes:

$$Z_{MF} = e^{-\beta \left(\frac{qJ}{2} + \Omega \right) Np^2} \left[2\cosh\left(\frac{1}{2} \beta h_{eff} \right) \right]^N \quad (15)$$

Let's compute the thermodynamics parameters relate to MT's system.

3.2. Total Polarization of System

According to Eq.(6), the total polarization of MT's system can be expressed as:

$$p \equiv \frac{1}{N} \sum_{i=1}^{N} < S_i > \quad (16)$$

Where p is the average polarization of the system.

Knowing that the average value of the pseudo-spin is given by:

$$< S_i >= \frac{Tr\left(S_i e^{-\beta H_{MF}} \right)}{Z_{MF}} \quad (17)$$

Eq.(17) into Eq.(16) gives the final value of the polarization:

$$p = \tanh\left[\frac{1}{2} \beta \left(\left(qJ + 2\Omega \right) p + \varepsilon E \right) \right] \quad (18)$$

For the rest of our work we will let

$$G = \frac{1}{2} \beta \left(qJ + 2\Omega \right) \quad (19)$$

Eq.(18) is a polarization self-consistent equation in the presence of an external electric field. Let's solve this self-consistent equation numerically with $f = \tanh\left(Gp \right) - p$, In the absence of external field, the solutions are showed in Fig 1.

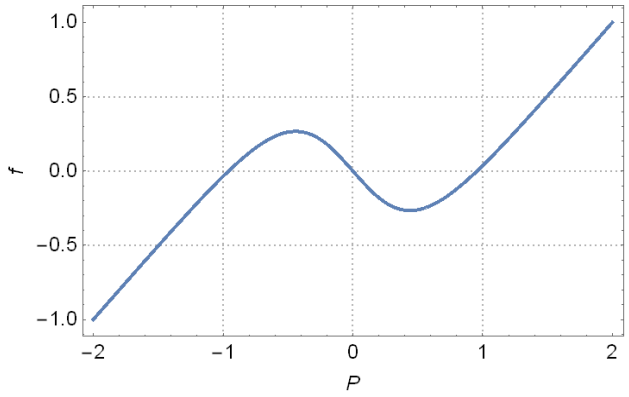
3.3. Critical Temperature of the System and Phase Transition without the External Electric Field

In this subsection, we going to use the non-zero and the zero polarization to characterize the state of the system as we previously mentioned in the introduction. We need to keep in mind that the non-zero polarization stands to the ferroelectric state; the zero-polarization stands to the paraelectric phase.

In **Fig.(1a),** f has three solutions: $p = 0$; $p \approx 0,9$ and $p \approx -0,9$ and $G > 1$ meaning that $0.5\left(qJ + 2\Omega \right) p > K_B T$. As the system has a non-zero polarization, we conclude that the system is in the

ferroelectric phase where $T < T_c$. This result suggests that the tubulin dimers are aligned in the best configuration which promotes the polymerization and organelle's transport along with the network of the microtubule.

In **Fig.(1b),** f has one solution: $p = 0$ and $G < 1$ meaning that $0.5(qJ + 2\Omega)\, p < K_B T$. As the system has a zero polarization, we conclude that the system is in the paraelectric phase where $T > T_c$. Here the tubulin dimers are disordered, state that promotes depolymerization and deregulates the intracellular traffic.



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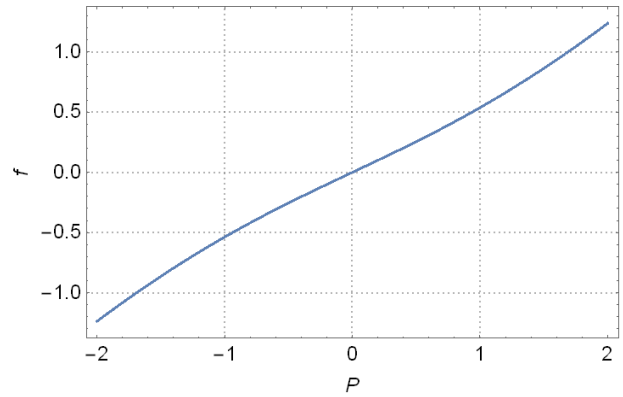

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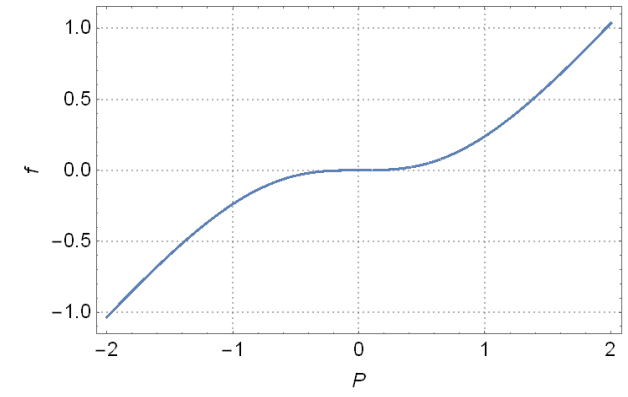

c

Figure 1. Polarization's self-consistent equation in the absence of an external electric field. These graphs show the behavior of polarization for different fix values of G. For a): $G = 1.8$; For b): $G = 0.3$; For c): $G = 1$

In **Fig.(1c)**, we observed an ensemble of value range and $G = 1$ meaning $0.5(qJ + 2\Omega) = K_B T$. We can be approved that, this phase corresponds to the transition from order to a disorder where $T = T_c$, and the critical temperature T_c is derived by the following expression:

$$K_B T_c = \frac{1}{2}(qJ + 2\Omega) \tag{20}$$

3.4. Polarization in Microtubules as a Function of Temperature

In this subsection, the polarization behavior dependence on temperature will be studied in the absence and presence of the external electric field.

- For $E = 0$, and assuming that p is very small near the critical temperature, let expand Eq.(18) as shown in Eq.(21).

$$p = \frac{1}{2}\beta(qJ + 2\Omega)\, p - \frac{\left(\frac{1}{2}\beta(qJ + 2\Omega)\, p\right)^3}{3} \tag{21}$$

Using Eq.(20) and performing calculations, the polarization dependence on temperature is given by:

$$\begin{cases} p(T) = \pm\sqrt{3\left(\frac{T_c}{T}\right)^2\left(\frac{T_c - T}{T_c}\right)}, T \to T_c^- \\ p = 0, T \to T_c^+ \end{cases} \tag{23}$$

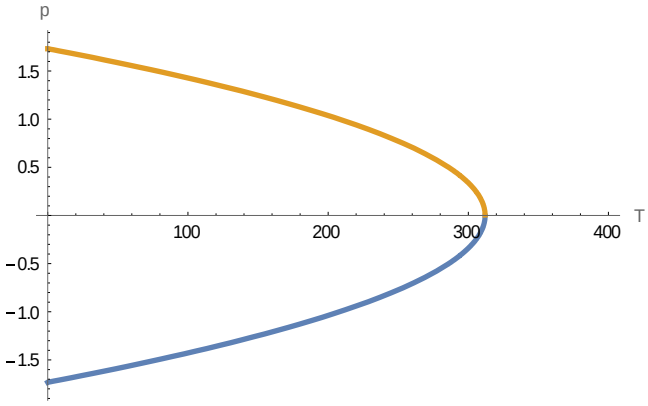

Figure 2. Behavior of the polarization $p(T)$ as a function of temperature

Fig.2 shows that below $T_c = 312$ the system is in the ferroelectric phase and above T_c the system is in the paraelectric phase where the polarization vanishes after the critical temperature $T_c = 312$. The result confirms that the MT has a spontaneous polarization in absence of electric field and collapses after the physiological temperature of the human body [39].

- For $E \neq 0$ and assuming the same assumption previously used, we computed the polarization as:

$$p(T)=-\frac{\varepsilon E}{K_B T_c}-\frac{2^{1/3}\left(9\left(\frac{T_c}{T}\right)^3-9\left(\frac{T_c}{T}\right)^4\right)}{3\left(\frac{T_c}{T}\right)^3\left(81\frac{\varepsilon E}{K_B T}\left(\frac{T_c}{T}\right)^5+\sqrt{6561\left(\frac{\varepsilon E}{K_B T}\right)^2\left(\frac{T_c}{T}\right)^{10}+4\left(9\left(\frac{T_c}{T}\right)^3-9\left(\frac{T_c}{T}\right)^4\right)^3}\right)^{1/3}}+\frac{\left(81\frac{\varepsilon E}{K_B T}\left(\frac{T_c}{T}\right)^5+\sqrt{6561\left(\frac{\varepsilon E}{K_B T}\right)^2\left(\frac{T_c}{T}\right)^{10}+4\left(9\left(\frac{T_c}{T}\right)^3-9\left(\frac{T_c}{T}\right)^4\right)^3}\right)^{1/3}}{3\times 2^{1/3}\times\left(\frac{T_c}{T}\right)^3} \quad (24)$$

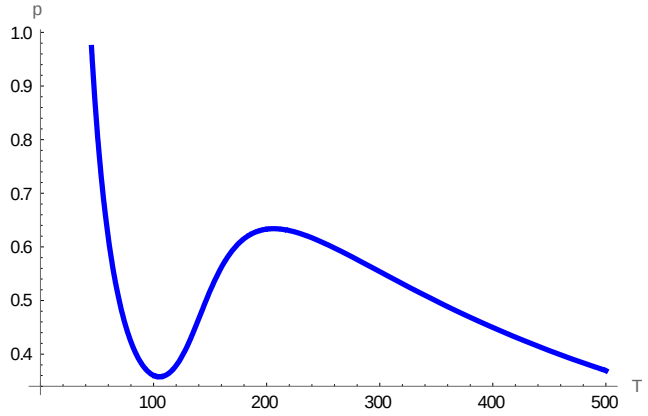

Figure 3. Polarization versus temperature, with $K_B = 8,62\times10^{-5}$, $\varepsilon = 10$, $T_c = 150$, $E = 8,62\times10^{-5}$

In Fig.3, It is shown that the polarization no longer vanishes when the temperature changes. The result put forward the contribution of the external electric field to promote the ferroelectric phase and control MT at high temperatures. The system exhibits two transitions during the ferroelectric phase, especially around 100K and 220K.

3.5. Free Energy

We can also gain some useful insight into the physics of this system by looking at its (Helmholtz) free energy. Free energy is a mathematical function quantifying the work provided by a closed thermodynamic system during a reversible transformation at a constant temperature. The free energy of a system is minimal in the state of thermodynamic equilibrium. In microtubules, the energy given by the system comes from the hydrolysis process and thermal fluctuations at a high temperature which is an energy that promotes the depolymerization of microtubules. The microtubule is more stable if free energy is minimal. This energy is defined by:

$$F_{MF} = U - TS = -K_B T \ln Z_{MF} \quad (25)$$

In the neighborhood of the transition temperature T_c, p is small. We can so do a limited develop on F like and replace equation (15) in (25) we get:

$$F_{MF} = \frac{1}{2}(qJ+2\Omega)Np^2 - K_B TN\ln 2 - K_B TN\ln\left[\frac{(\frac{1}{2}\beta h_{eff})^2}{2}-\frac{(\frac{1}{2}\beta h_{eff})^4}{12}+0\left((\frac{1}{2}\beta h_{eff})\right)^6\right] \quad (26)$$

According to equation (13) and (20) in (26), free energy given by:

$$F_{MF} = -K_B T\ln 2-\frac{N(\varepsilon E)^2}{8K_B T}+\frac{N(\varepsilon E)^4}{192K_B^3T^3} + \left[\frac{N(\varepsilon E)^2 T_c}{24K_B^2T^3}-\frac{N(\varepsilon E)T_c}{2T}\right]P + \left[NK_B T_c+\frac{N(\varepsilon E)T_c^2}{8T^3}-\frac{NK_B T_c^2}{2T}\right]P^2 + \frac{N(\varepsilon E)T_c^3}{6T^3}P^3+\frac{NK_B T_c^4}{12T^3}P^4 \quad (27)$$

For this energy which depends on the external electric field E, we will discuss the stability of the microtubule by considering two cases: $E=0$ and $E\neq 0$

- For $E=0$ the free energy of this system is:

$$F_{MF} = -K_B NT\ln 2+\frac{NK_B T_c}{2T}(2T-T_c)p^2+\frac{NK_B T_c^4}{12T^3}P^4 \quad (28)$$

Eq.(27) gives an interpretation of the Ferroelectricity of the system, the equilibrium state is observed in for $2T = T_c$. The system control parameter is $2T - T_c$. If the latter is negative $(2T < T_c)$ the system is in ferroelectric phase, positive, $(2T > T_c)$ paraelectric phase. The 2 on the command, parameter comes from the anisotropy interaction

considered in the system. For the Ising model without anisotropy interaction the control parameter is $T - T_c$. From these results, we can conclude that anisotropy plays an important role in phase transitions.

We plot F for p in Fig.4 for $E = 0$, we observe that: In the disordered phase $(T > T_c)$ of the system, we have a single minimum p = 0. But in the ordered phase $(T < T_c)$, energy becomes negative and we observe the appearance of two minima at values $p = \pm 0.5$ that they represent the points of stability of the system and a maximum $p = 0$ which is an instability point. Free energy in the ordered phase is smaller than in the disordered phase. From these results, we can conclude that: at low temperature $(T > T_c)$, the microtubules pass between the points of stability and dynamic instability. At high $(T < T_c)$ temperature the microtubules are unstable.

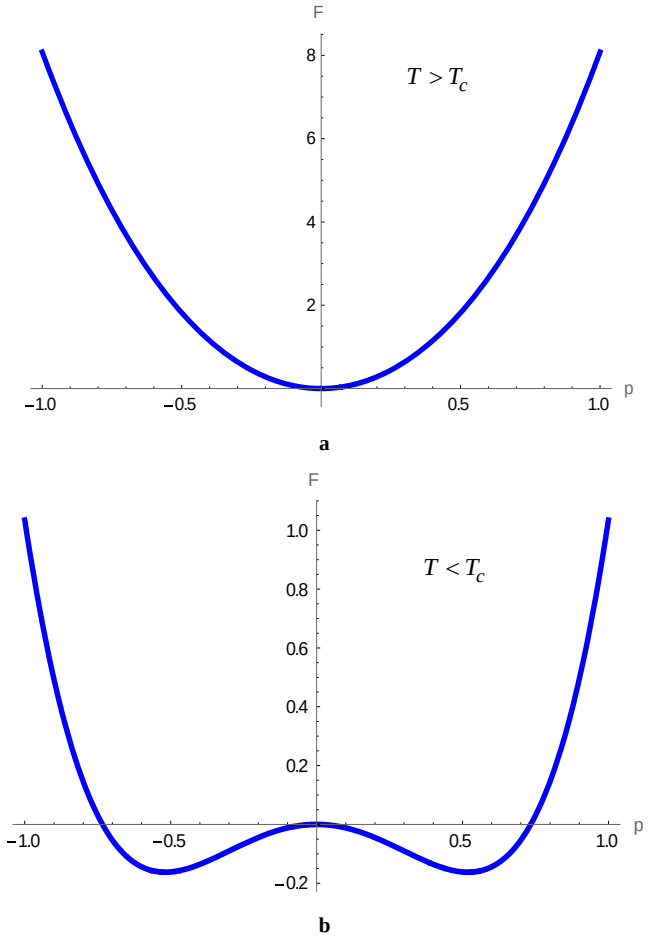

Figure 4. Free energy a as function of mean polarization for $N = 125$, $K_B = 8,62 \times 10^{-5} ev$, (a) $T > T_c$, (b) $T < T_c$

- For $E \neq 0$, the free energy of this system is:

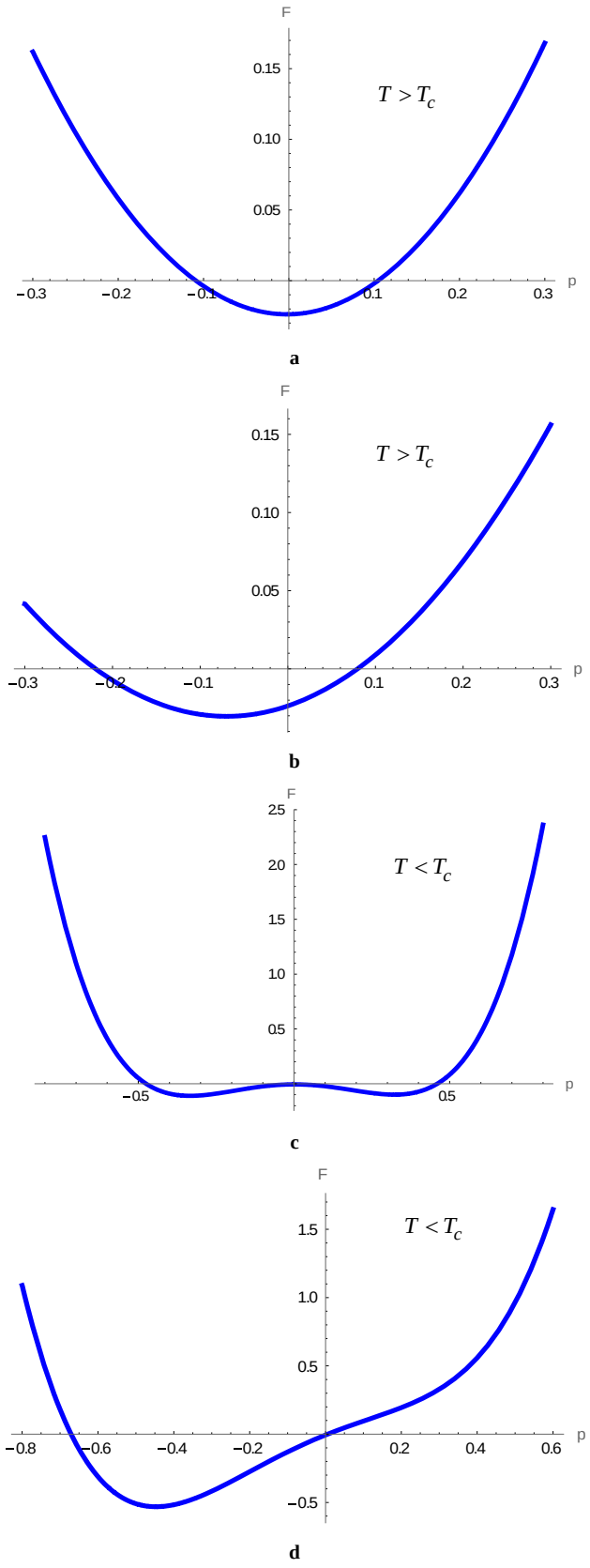

Figure 5. Free energy a as function of mean polarization for $N = 125$, $K_B = 8,62 \times 10^{-5}$, a) $E = 18,62 \times 10^{-5}$, b) $E = 0.0011$, c) $E = 18,62 \times 10^{-5}$, d) $E = 0.0011$

In Fig.5, we Plot free energy F as a function of polarization p, In the presence of the electric field, we find that the free energy decreases when $T > T_C$ and $T < T_C$. In fig a, when $T > T_C$, the unstable solution $p = 0$ becomes a metastable solution. In Fig b, the increase in the electric field forces the metastable solution to orient in the direction of the field. We can conclude that: at high temperatures, the external electric field can stabilize the microtubules and orient them in the direction of the field. In figure c, for higher T_C the electric field breaks symmetry with the disappearance of the point of instability $p = 0$ and directs the system towards single minimum energy. Thus, by applying an external electric field, we forced the system to choose one of the two solutions.

4. Conclusions

In this work, we have studied the thermodynamic properties of microtubule that is developing in the absence and presence of an external electric field using the mean-field theory (MFT). We found the same parameters without the electric field and with the electric field in order to prove the effect of the external electric field on the microtubule dynamics. Numerical results obtain put forward the dynamic instability phenomenon which occurs in microtubule by the self-organization process. It is clearly shown that the breaking symmetry of the system strongly depends on the magnitude of the external electric field and the value of temperature. So the study of MT in the presence of external field exhibits phase transitions from the ferroelectric phase to paraelectric one and sometimes the metastable phase where both coexist in solution. We have just shown that: at low temperatures, the electric field increases the stability of microtubules; at high temperatures, this field increases the critical temperature which allows the transition from the ordered state of the dipoles to the disordered state of the electric dipoles. We also show that the increase in the field makes it possible to direct the electric dipoles in the direction of the field. Then this electric field can also be used to control the direction of the microtubule which will be very important in the transport of information in the cells.

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