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A pseudo-spin model for the wall of cytoskeletal microtubule*

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A pseudo-spin model is intended to describe the physical dynamics of unbound electrons in the wall of cytoskeletal microtubule (MT). Due to the inherent symmetry of the structure and the electric properties in the MT, one may treat it as a one-dimensional ferroelectric system, and describe the nonlinear dynamics of dimer electric dipoles in one protofilament of the MT by virtue of the double-well potential. Consequently, the physical problem has been mapped onto the pseudo-spin system, and the mean-field approximation has been taken to get some physical results.

Keywords: cell microtubule, double-well potential, pseudo-spin hamiltonian, mean-field approximation

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1. Introduction

For a biological system, due to its macroscopic nature and usually living near room temperature, one may naively suspect that the rule of quantum theory would not be applicable. However, for some special biological systems under certain conditions, they may have macroscopic quantum coherent states that are maintained for some time.[1] The macroscopic quantum coherent state is defined as a quantum state governed by a macroscopic wavefunction, shared by multiple particles. It is typically related to the space–time organization of the multi-particle system.

Years ago, based on the quantum theory, Fröhlich[2] studied the energy transfer and storage in biological cells and predicted the long-range coherent dipolar propagating waves. He then further developed[3] a basic physical idea concerning the nature of biological order. In addition, by using the quantum coherent state theory, Davydov[4] investigated the migration of energy and electrons in biological systems, and paid attention to the protein molecules. Inspired by applications of the quantum theory to biological systems initiated by Fröhlich in the 1960s and Davydov in the 1970s, a number of scientists began to study biological matter and brain functioning based on the quantum theory over the decades of the 1980s and 1990s. Several groups[5–7] focused especially on networks of filamentous proteins which dynamically organize the interiors of living cells. These networks are referred to as the well-known cytoskeleton. Microtubules (MTs) are the important components and function units in cytoskeletons as well as cellular organization and information processing.

MTs are ubiquitous through the entire biology, especially enriched in brain tissue.[8] From x-ray crystallography,[5] one already knows that a MT is a hollow cylindrical tube about 25nm outer diameter and 14nm inner diameter. The interior of the cylinder is likely to be filled with ordered water which implies the existence of electric dipoles and an electric field. The MT wall is an assembly of 13 protofilaments, each of which is a series of subunit proteins known as tubulin dimers. Measurements by electron crystallography[9] have further demonstrated the structure of the tubulin subunit. Each tubulin subunit is a peanut-shaped dipolar, 8nm dimer consisting of alpha and beta 4-nm monomers, called the α- and β-tubulin, respectively. The electric dipolar character

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of the $\alpha\beta$-tubulin dimer originates from 18 Ca ions bound within each β-monomer and an equal number of unpaired electrons localized near the neighbouring α-monomer. Therefore, MTs are oriented assemblies of electric dipoles and can be identified as electret substance with ferroelectric properties. There is an unbound mobile electron on each tubulin dimer, which can be localized either more toward the α-monomer or more toward the β-monomer.

It has been shown that the GTP→GDP hydrolysis releases approximately 0.42eV/molecule accompanied by a conformational change according to the unbound mobile electron's localization (closer to the α-monomer or β-monomer). Thus the tubulin dimer protein has only two basic states $|\alpha\rangle$ and $|\beta\rangle$. When the mobile electron is in the β-state, there is a 29° distortion of the electric dipole moment compared with that in the α-state.

Some models for the MT dynamics have been presented.[10−14] For the tubulin dimer dipoles in one protofilament of a MT, some authors[12] have taken the well-known double-well potential model to describe its nonlinear dynamic behaviour. This model is very successful in the descriptions of bistable molecular systems,[15] dipolar excitations in ferroelectrics[16] and other relevant fields. In this paper, we study the nonlinear dynamic behaviour of dimer–electric dipoles in one protofilament of a MT, and utilize the double-well potential to represent each $\alpha\beta$–dimer. But according to the quantum character of mobile electrons and a matter worth noting: the quantum tunnelling effects penetrating the barrier, we further take the pseudo-spin model to describe the system.

2. The physical model and the Hamiltonian of the system

We utilize the double-well potential to represent each $\alpha\beta$-tubulin dimer in one protofilament of a MT.[12] The single mobile electron on each $\alpha\beta$-tubulin dimer can be localized in the site of the α-monomer or the site of the β-monomer. Correspondingly, this mobile electron can be localized in either well of this double-well potential. Under certain conditions, the electron which is even in the ground state may go from a well into the other by quantum tunnelling penetration. The ground state of the electron in each potential well is a doublet state. The tunnelling penetration effect may eliminate this degeneracy, and hence crucially influence the dynamic properties of the system. It is possible that the electron may occupy the higher excitation states. But here, we prefer to assume that the energy differences between these excited states and the ground state are quite large compared with the energy splitting of the doublet state. And then we neglect the contributions from the excited states, considering only the doublet state. Based on the quantum characters of mobile electrons and the spin wave theory developed in the solid state physics[17] and ferroelectrics,[18] each such double-well may be represented by one pseudo-spin. The two possible orientations of the pseudo-spin, up and down, correspond to the two possible localized positions of the mobile electron, the site of α-well and the site of β-well. Using the pseudo-spin wave of the system, we can describe the distribution and the dynamic behaviour of mobile electrons on the protofilament.

The Hamiltonian operator $\hat{H}$ for the system of the electrons consists of three parts: the kinetic energy of the electrons, the effective potential energy related to the double-well potential in the one-dimensional chain of tubulin dimers, and the Coulomb interaction energy between the electrons (note that the Coulomb interaction energy makes by far the greatest contribution of all the interaction energies between the electrons). Eventually, it may be divided into two parts: one part describing the one-body problem (movement) and the second part describing the two-body electron–electron Coulomb interaction.

In the framework of quantum field theory,[17] the explicit form of $\hat{H}$ mentioned above is as follows:

$$\hat{H} = \int \psi^+(x)\left(-\frac{\hbar^2}{2m}\nabla^2 + V_{\text{eff}}(x)\right)\psi(x)\mathrm{d}x + \frac{1}{2}\iint \psi^+(x)\psi^+(x')\frac{e^2}{\varepsilon|x-x'|}\psi(x')\psi(x)\mathrm{d}x\mathrm{d}x', \tag{1}$$

where $\psi^+(x)$ and $\psi(x)$ are particle field operators satisfying the Fermi commutation relations, and can be expanded in terms of Wannier functions in the form

$$\psi^+(x) = \sum_{i\lambda} a^+_{i\lambda} W^*_\lambda(x-i),$$
$$\psi(x) = \sum_{i\lambda} a_{i\lambda} W_\lambda(x-i). \tag{2}$$

Here $W_\lambda(x-i)$ and $W^*_\lambda(x-i)$ represent the Wannier function and its conjugate, respectively. And they describe the localization of an electron in the vicinity of the site i for a distance of about one "lattice" length (∼8nm) and are orthogonal to each other for being localized at different sites i, j, or belonging to different

energy states λ, v:

$$\int W_\lambda^*(x-i)W_v(x-j)\mathrm{d}^3x = \delta_{\lambda v}\delta_{ij}. \tag{3}$$

They construct a complete set of orthonormal functions. And we distinguish the separate electrons from one another by the subscript i and the two separate energy states by the subscript λ. $a_{i\lambda}^+$ is the Fermion's creation operator, which creates an electron i in the quantum state λ at the site i in the chain of tubulin dimers, while its conjugate operator $a_{i\lambda}$ with the same subscripts annihilates this electron. In addition, $a_{i\lambda}^+$ ($\lambda = \pm$) may be constructed by the linear combinations of Fermi operators $a_{i\alpha}^+$ and $a_{i\beta}^+$ as follows:

$$\begin{aligned} a_{i+}^+ &= \frac{1}{\sqrt{2}}(a_{i\alpha}^+ + a_{i\beta}^+), \\ a_{i-}^+ &= \frac{1}{\sqrt{2}}(a_{i\alpha}^+ - a_{i\beta}^+). \end{aligned} \tag{4}$$

Here $a_{i\alpha}^+$ creates an electron at the site i in the equilibrium position of the α-well of the double-well, and $a_{i\beta}^+$ in the equilibrium position of the β-well. For the annihilation operators $a_{i\lambda}$, there are two similar relation expressions, which just replace all the creation operators in Eq.(4) by the corresponding conjugate operators. These Fermi operators $a_{i\lambda}^+$ and $a_{i\lambda}$, as well as $a_{i\alpha}^+$ and $a_{i\beta}^+$, $a_{i\alpha}$ and $a_{i\beta}$, satisfy the anti-commutators $[a_{i\lambda}, a_{jv}^+]_+ = \delta_{ij}\delta_{\lambda v}$, $[a_{i\lambda}^+, a_{jv}^+]_+ = [a_{i\lambda}, a_{jv}] = 0$, and the normalized condition $\sum_\lambda a_{i\lambda}^+ a_{i\lambda} = 1$.

In this case, one may have the following explicit form of the Hamiltonian $\hat{H}$ for the two-level quantum system:

$$\hat{H} = \sum_i H_0(i) + \frac{1}{2}\sum_{i\neq j} H_{int}(i,j), \tag{5}$$

with

$$H_0(i) = \sum_\lambda E_\lambda a_{i\lambda}^+ a_{i\lambda}. \tag{6}$$

$$H_{\mathrm{int}}(i,j) = \sum_{\lambda v\gamma\delta} v_{\lambda v\gamma\delta}(i,j) a_{i\lambda}^+ a_{iv} a_{j\gamma}^+ a_{j\delta}. \tag{7}$$

Here $v_{\lambda v\gamma\delta}(i,j)$ represent the coupling between the two tubulin dimers at the site i and site j, which depend on the distance between the two sites, and also the quantum states λ, v, γ and δ. Omitting the slight overlapping of the Wannier functions, the expression for the $v_{\lambda v\gamma\delta}$ is the following:

$$\begin{aligned} v_{\lambda v\gamma\delta} = &\iint w_\lambda^*(x-i) w_v(x-i) \frac{e^2}{\varepsilon|x-x'|} \\ &\times w_\gamma^*(x'-j) w_\delta(x'-j)\mathrm{d}x\mathrm{d}x' \\ &- \iint w_\lambda^*(x-i) w_v(x-j) \frac{e^2}{\varepsilon|x-x'|} \\ &\times w_\gamma^*(x'-j) w_\delta(x'-i)\mathrm{d}x\mathrm{d}x' \\ \cong &\iint w_\lambda^*(x-i) w_v(x-i) \frac{e^2}{\varepsilon|x-x'|} \\ &\times w_\gamma^*(x'-j) w_\delta(x'-j)\mathrm{d}x\mathrm{d}x'. \end{aligned} \tag{8}$$

The corresponding Schrödinger equation for the system is

$$\hat{H}|\Phi\rangle = E|\Phi\rangle, \tag{9}$$

where $|\Phi\rangle$ is the many-body quantized state (wave-function).

In the quasi-particle model, it can be decomposed into the form

$$|\Phi\rangle = \sum_{i\lambda} c_{i\lambda} a_{i\lambda}^+ |\Phi_g\rangle, \quad i = 1, 2, \ldots, N; \lambda = \pm, \tag{10}$$

where $|\Phi_g\rangle$ represents a state vector describing the electrons occupying the valence band.

In the following, we map the physical problem of the two-level quantum system onto the pseudo-spin system. First of all note that there are equivalence relations between the Fermi operators $(a_{i\alpha(\beta)}^+, a_{i\alpha(\beta)})$ mentioned above and the spin operators:[18]

$$\begin{aligned} &a_\alpha^+ a_\beta = S^{(+)} = S_x + \mathrm{i}S_y, a_\beta^+ a_\alpha = S^{(-)} = S_x - \mathrm{i}S_y, \\ &a_\alpha^+ a_\alpha = S_z + \frac{1}{2}, \quad a_\beta^+ a_\beta = \frac{1}{2} - S_z. \end{aligned} \tag{11}$$

From the relations (11), one may have the alternative relations

$$\begin{aligned} S_x &= \frac{1}{2}(a_\alpha^+ a_\beta + a_\beta^+ a_\alpha), \\ S_y &= \frac{1}{2\mathrm{i}}(a_\alpha^+ a_\beta - a_\beta^+ a_\alpha), \\ S_z &= \frac{1}{2}(a_\alpha^+ a_\alpha - a_\beta^+ a_\beta). \end{aligned} \tag{12}$$

In addition, using the transformation relations (4) for the creation operators and similar relations for the annihilation operators, one can arrive at the following relations:

$$\begin{aligned} S_x &= \frac{1}{2}(a_+^+ a_+ - a_-^+ a_-), \\ S_y &= \frac{1}{2\mathrm{i}}(a_-^+ a_+ - a_+^+ a_-), \\ S_z &= \frac{1}{2}(a_-^+ a_+ + a_+^+ a_-). \end{aligned} \tag{13}$$

From Eqs.(6) and (13), we have

$$\begin{aligned} H_0(i) =& E_+ + (E_- - E_+)a_{i-}^+ a_{i-} \\ =& \frac{1}{2}(E_- + E_+) - (E_- - E_+)S_x(i). \end{aligned} \quad (14)$$

Noting the normalized condition and substituting Eq.(13) into Eq.(7), we can obtain, by a fairly elementary calculation and omitting the constant term and some trivial terms, an expression for $H_{\rm int}(i,j)$ of the form

$$\begin{aligned} H_{\rm int}(i,j) =& -[v_{----}(i,j) - v_{++++}(i,j)]S_x(i) \\ & - [2v_{++--}(i,j) - (v_{++++}(i,j) \\ & + v_{----}(i,j))]S_x(i)S_x(j) \\ & + 2[v_{-+++}(i,j) + v_{-+--}(i,j)]S_z(i) \\ & + 4v_{+-+-}(i,j)S_z(i)S_z(j). \end{aligned} \quad (15)$$

From Eqs.(5), (14) and (15), we finally obtain the expression for the total Hamiltonian $\hat{H}$ in the pseudo-spin system,

$$\begin{aligned} \hat{H} =& -\sum_i \Omega S_x(i) - \sum_i A_i S_z(i) \\ & - \frac{1}{2}\sum_{i\neq j} J_{ij} S_z(i)S_z(j) \\ & - \frac{1}{2}\sum_{i\neq j} B_{ij} S_x(i)S_x(j), \end{aligned} \quad (16)$$

where

$$\begin{aligned} \Omega =& (E_- - E_+) + \frac{1}{2}\sum_j (v_{----}(i,j) - v_{++++}(i,j)) \\ \cong& E_- - E_+, \\ J_{ij} =& -4v_{+-+-}(i,j), \\ B_{ij} =& 2v_{++--}(i,j) - [v_{++++}(i,j) + v_{----}(i,j)], \\ A_i =& -\sum_j (v_{-+++}(i,j) + v_{-+--}(i,j). \end{aligned}$$

In addition, the term $B_{ij}S_x(i)S_x(j)$ is quite small, compared with the term $\Omega S_x(i)$, and thus it may usually be neglected.

From Eq.(11) (or Eq.(12)) one can see the expectation value $\langle S_z\rangle$ of the operator S_z, which may be defined as the order parameter of the phase transition for the α-conformation $\rightarrow\beta$-conformation, measuring the difference of the occupation numbers between the two equilibrium positions of the double-well. For the paraelectric phase, $\langle S_z\rangle$=0; therefore, one can omit the contribution from the term $\sum_i S_z(i)$ in Eq.(16), while for the MTs with ferroelectric properties ($\langle S_z\rangle \neq 0$), we should in general retain this term.

3. The mean-field approximation

In Section 2, we have given the Hamiltonian $\hat{H}$ in pseudo-spin representation. To simplify the problems, an approach is to take the mean-field approximation. Substituting the average values (thermodynamic expectation values) $\langle S_z(j)\rangle$ for the operators $S_z(j)$ in the interaction terms $\sum_{ij} J_{ij}S_z(i)S_z(j)$, the problems are simplified to the movement of a single particle i, interacting with the mean-field induced by $\langle S_z(j)\rangle$. In this case, one may assume that the density matrix ρ of the many-body system is equal to the product of the single-particle density matrices $\rho_i, \rho = \prod_i \rho_i$, here ρ_i may be expressed as

$$\rho_i = (z_i)^{-1}\exp(\beta \boldsymbol{w}_i \cdot \boldsymbol{S}(i)). \quad (17)$$

Here $\boldsymbol{S}(i) = (S_x(i),\ S_y(i),\ S_z(i))$ is a vector whose components are three Pauli matrices of spin 1/2,

$$\begin{aligned} \beta =& (kT)^{-1}, \\ z_i =& {\rm Tr}\exp(\beta \boldsymbol{w}_i \cdot \boldsymbol{S}(i)) \\ =& \exp\left(\frac{1}{2}\beta \boldsymbol{w}_i\right) + \exp\left(-\frac{1}{2}\beta \boldsymbol{w}_i\right) \\ =& 2{\rm ch}\left(\frac{1}{2}\beta \boldsymbol{w}_i\right), \end{aligned} \quad (18)$$

where w_i denotes the effective field exerting on the $\boldsymbol{S}(i)$. By taking the Helmholtz free energy F of the system as an extremum value, one can determine the form for $\boldsymbol{w}_i$

$$F(\rho) = U(\rho) - TS(\rho) = {\rm Tr}(\rho\hat{H} + kT\rho\ \ln\rho), \quad (19)$$

due to $\delta F(\rho) = 0$, one has

$$\boldsymbol{w}_i = -\frac{\partial\langle\hat{H}\rangle}{\partial\langle \boldsymbol{S}(i)\rangle}. \quad (20)$$

Here $\langle\hat{H}\rangle$ is the thermodynamic expectation value of the Hamiltonian $\hat{H}$ (16) but in the mean field approximation. $\langle \boldsymbol{S}(i)\rangle$ is the expectation value for the pseudo-spin $\boldsymbol{S}(i)$. And $\boldsymbol{w}_i = (w_x, w_y, w_z) = (\Omega, 0, \sum_j J_{ij}\langle S_z(j)\rangle)$. Consequently, the effective Hamiltonian for the single particle is as follows:

$$H_{\rm MFA}(i) = \frac{\partial\langle\hat{H}\rangle}{\partial\langle S(i)\rangle}\cdot \boldsymbol{S}(i) = -\boldsymbol{w}_i \cdot \boldsymbol{S}(i). \quad (21)$$

By using the effective Hamiltonian in the mean field approximation $H_{\rm MFA}(i)$ (21) and Eq.(18) for z_i, the

thermodynamic expectation value of the pseudo-spin $\boldsymbol{S}(i)$ can be calculated as follows:

$$\langle \boldsymbol{S}(i)\rangle = \frac{\mathrm{Tr}\boldsymbol{S}(i)\exp(-\beta H_{\mathrm{MFA}}(i))}{\mathrm{Tr}\,\exp(-\beta H_{\mathrm{MFA}}(i))} = \frac{\mathrm{d}\ln z_i}{\mathrm{d}(\beta \boldsymbol{w}_i)}. \quad (22)$$

Noting

$$z_i = 2\mathrm{ch}\left(\frac{1}{2}\beta \boldsymbol{w}_i\right) = 2\mathrm{ch}\left(\frac{1}{2}\beta \boldsymbol{w}_i^{-1}\boldsymbol{w}_i \cdot \boldsymbol{w}_i\right), \quad (23)$$

$$\boldsymbol{w}_i = \left[\Omega^2 + \left(\sum_j J_{ij}\langle S_z(j)\rangle\right)^2\right]^{1/2}, \quad (24)$$

one has

$$\begin{aligned}\langle \boldsymbol{S}(i)\rangle =& \frac{\mathrm{d}}{2\mathrm{d}\left(\frac{\beta}{2}\boldsymbol{w}_i\right)}\left[\ln 2 + \ln \mathrm{ch}\left(\frac{1}{2}\beta \boldsymbol{w}_i\right)\right] \\ =& \frac{\boldsymbol{w}_i}{2\boldsymbol{w}_i}\mathrm{th}\left(\frac{1}{2}\beta \boldsymbol{w}_i\right). \end{aligned} \quad (25)$$

From Eqs.(24) and (25), it is easy to obtain the following $3N$ equations for the expectation values of the pseudo-spin components:

$$\begin{aligned}\langle \boldsymbol{S}_x(i)\rangle =& \frac{1}{2}w_i^{-1}\Omega \mathrm{th}\left(\frac{1}{2}\beta \boldsymbol{w}_i\right), \\ \langle \boldsymbol{S}_y(i)\rangle =& 0, \\ \langle \boldsymbol{S}_z(i)\rangle =& \frac{1}{2}w_i^{-1}\sum_j J_{ij}\langle S_z(j)\rangle \mathrm{th}\left(\frac{1}{2}\beta \boldsymbol{w}_i\right), \\ & i = 1, 2, 3, \ldots, N. \end{aligned} \quad (26)$$

For the paraelectric phase, one has $\langle S_z(i)\rangle = 0$, and therefore only one component is retained:

$$\langle \boldsymbol{S}_x(i)\rangle = \frac{1}{2}\mathrm{th}\left(\frac{1}{2}\beta\Omega\right). \quad (27)$$

For the ferroelectric phase, one has $\langle S_z(i)\rangle \neq 0$. In this case, for the soft mode of the pseudo-spin wave, its wavevector $q \to 0$, and one may have $\langle S_z(i)\rangle = \langle S_z(j)\rangle = \langle S_z\rangle$, $w_i = w_j = w$. Therefore, the spontaneous polarization P_{s} takes $P_{\mathrm{s}} = 2N\mu\langle S_z\rangle$, where μ denotes the single electric dipole. With Eq.(26), we now have the following relations for the system (ferroelectric):

$$\begin{aligned}&\langle S_x(i)\rangle = \frac{1}{2}w^{-1}\Omega \mathrm{th}\left(\frac{1}{2}\beta w\right), \\ &\langle S_y(i)\rangle = 0, \\ &2w = J_0 \mathrm{th}\left(\frac{1}{2}\beta w\right), \end{aligned} \quad (28)$$

where $J_0 = \sum_j J_{ij}$.

When the temperature T arrives at the phase transition temperature of the system (from ferroelectric to paraelectric phase), $\langle S_z(i)\rangle = 0$, hence $w = \Omega$; and then from Eq.(28), one has the following relation for the phase transition temperature T_{c}:

$$\frac{2\Omega}{J_0} = \mathrm{th}\left(\frac{\Omega}{2kT_{\mathrm{c}}}\right). \quad (29)$$

From Eq.(29) we can see that, if $J_0 > 2\Omega$, then $T_{\mathrm{c}} > 0$. This means that at a certain temperature the ferroelectric phase may exist in the system, while if $J_0 < 2\Omega$, T_{c} becomes an imaginary number, and the system is in the paraelectric phase.

We can roughly estimate the values of Ω and J_0. Taking two harmonic potentials to simulate the double-well potential mentioned above, we may approximately obtain the values of Ω ($\Omega \approx 1.4 \times 10^{-3}$[eV] and J_{12}($J_{12} \approx 0.2\frac{1}{\varepsilon}$[eV]), where J_{12} is the coupling strength between the two neighbouring dimers at the site i=1 and site j=2, with ε the dielectric constant of the medium. Using $J_0 = \sum_j J_{ij}$ and $J_{12} \approx 0.2\frac{1}{\varepsilon}$[eV], taking ε=10 as an example, for a moderately long MT consisting of 125 dimers (i.e. N=125) with a length L=1μm, we can estimate the value of J_0, $J_0 \approx 0.11$[eV] In this case, using Eq.(29) we eventually obtain the phase transition temperature $T_{\mathrm{c}} \approx 312$K. It is of interest to note that the estimated value of the phase-transition temperature T_{c} is very close to the physiological temperature ~310K. As the MT is responsible for numerous cellular activities and even suitable for dynamic information processing, the above results certainly make some sense.

4. Summary

In this paper, a pseudo-spin model is presented, which is intended to describe the physical dynamics of unbound mobile electrons in the wall of cytoskeletal microtubule. Due to the inherent symmetry structures and the electric properties in the MT, we treat it as a one-dimensional ferroelectric system, and describe the nonlinear dynamics of dimer electric dipoles in one protofilament of the MT by virtue of the double-well potential. Then, the physical problem is mapped onto a pseudo-spin system, and the mean-field approximation has been taken to gain some physical results, such as the equations of motion for the expectation values of the pseudo-spin, and the relation among the ordered-disordered phase transition tem-

perature T_c, the coupling strength J_0 and the quantum tunnelling parameter Ω. In addition, we have estimated the phase transition temperature, and obtained $T_c \approx 312$K. This value of T_c indicates that it is reasonable to expect an interesting phase behaviour in the physiological temperature range around 310K for the feasible model parameters.

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