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Mechanical properties of an adsorbed elastic polymer in contact with a rigid membrane

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A static and a dynamical model are introduced to study the physical properties of an elastic polymer adsorbed on a rigid membrane. We analyze the detailed microscopic model for the adhesion problem and show that in the force ensemble a critical force is expected. Forces smaller than the critical value are not able to peel off the filament, while larger forces will cause the filament to completely desorb from the membrane. To demonstrate the nonequilibrium properties of the moving states for forces larger than the critical value, we present the linear response of the system in the form of a force-velocity relation. In addition, we use a very simple short-range static model and obtain the equilibrium phases of the system in different cases where either a fixed force or a fixed height can be applied at the end. For the fixed force the equilibrium phases arising from the static model are in agreement with dynamical model. Forces smaller than the critical value are not able to peel off the filament while the larger forces will cause the filament to completely desorb as in the dynamical model.

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I. INTRODUCTION

Development of atomic force microscope (AFM), optical tweezers, and other experimental techniques has opened a new era in investigation of the mechanical properties of long macromolecules [1,2]. Such experiments, which vary from measuring the thermal fluctuations of biological charged macromolecules to the adhesion or desorption properties of polyelectrolytes, are able to give a clear picture of what is happening at the microscopic level [3–8]. Adhesion of long elastic macromolecules to membranes plays an important role in understanding many problems in biophysics as well as material science. There is also much experimental and theoretical work studying the adhesion of vesicles in contact with substrates [9]. Such investigations are important both for applications and from fundamental point of view [10,11]. Microtubules, actin filaments, and DNA double strands are examples of adhering filaments which can adhere on either cell cortex or synthetic substrates for *in vitro* experiments [12]. Examination of the response of such adhering filaments to forces of the order of piconewtons is a problem with physical realization both *in vivo* and *in vitro*. These forces can be exerted by an AFM tip or molecular motor proteins, which are present inside living cells.

There are theoretical models based on the interaction between microtubules and cell cortex. Such interactions are essential in describing the mechanics of cell division [12]. Since the early studies of the adhesion problem, several authors have devoted many contributions to this field [13]. Bell was the first to define and use the adhesion mechanism to study cell-cell interaction [14]. He proposed a detailed theoretical framework for the analysis of adhesion between two cells or cells and surfaces. His model is based on an attachment-detachment mechanism for the ligand and receptor molecules on the cell surface.

Here we study a detailed microscopic model for polymer adhesion in contact with a rigid membrane. We show that the competition between filament elasticity and the adhering forces will lead the system to different stationary states. The resulting stationary states can be static or moving. In the moving state the filament is detached with nonzero rupture velocity. For this moving state, we calculate the linear response function of the system.

The rest of the paper is organized as follows. In the next section we present a detailed microscopic model for an individual elastic polymer interacting with a rigid membrane. Then we present the numerical solution of rupture dynamics. In the equilibrium part we study the static limit with short-range interactions. A summary and concluding remarks are presented at the end.

II. MODEL

Figure 1 shows a schematic view of a semiflexible polymer in the vicinity of a rigid membrane. Atomic bonds between the monomers of the polymer and molecular ligands on the substrate are responsible for mediating the interaction

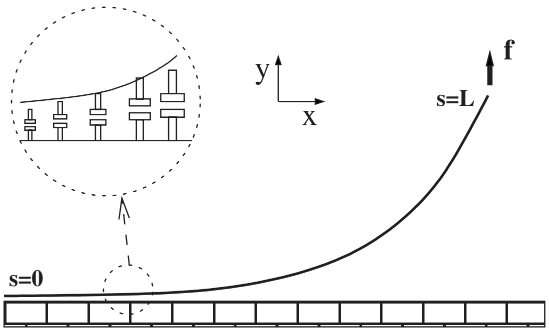

FIG. 1. Schematic view of an elastic semiflexible rod attracted by a rigid membrane. The rod is submitted to a vertical force at the end. Inset shows the microscopic origin of the attraction.

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at the atomic level. An external force is applied to one end of the polymer while the other end is fixed to prevent any motion at that end. We assume that the persistence length of the polymer is much larger than its total length. This assumption allows us to neglect the thermal fluctuations of the polymer.

We use the position vector $\mathbf{R}(s,t)$, of the sth monomer to show the parametric configuration of the polymer in space and time. This polymer has total length denoted by L. For the relevant time and length scales and water viscosity in a typical biophysical experiment, the Reynolds number is very low. For this reason we can neglect any inertial effect in the polymer dynamics [15]. To write the dynamical equation of the filament we can go ahead and neglect the long-range hydrodynamic interaction between different parts of the filament. In this case the overall dynamics of the polymer is given by

$$\frac{\partial}{\partial t}\mathbf{R}(s,t)=\left(\frac{1}{\xi_{\|}}\hat{\mathbf{t}}\hat{\mathbf{t}}+\frac{1}{\xi_{\perp}}\hat{\mathbf{n}}\hat{\mathbf{n}}\right)\cdot\left(-\frac{\delta\mathcal{G}}{\delta\mathbf{R}}+\mathbf{f}^{a}(s,t)+\mathbf{f}^{e}(s,t)\right),\tag{1}$$

where $\mathcal{G}$ is the elastic free energy density of the filament, $\mathbf{f}^{a}(s,t)$ is the adsorbing force density due to the interaction with the substrate, and $\mathbf{f}^{e}(s,t)$ denotes any other external force. The friction coefficients for motion in the transverse and tangential directions are given, respectively, by $\xi_{\perp}$ and $\xi_{\|}$. The fact that the friction coefficients in the transverse and tangential directions are different is a result of solving the hydrodynamic equations for a cylinder motion with no-slip boundary conditions [15]. Here, to simplify the calculations we use a two-dimensional modeling where the polymer geometry is confined to a plane. We use a single bending modulus κ and write the total elastic free energy as

$$G=\frac{\kappa}{2}\int_{0}^{L}ds\,C^{2}(s,t)+\frac{1}{2}\int_{0}^{L}ds\,\lambda(s,t)[\mathbf{t}(s,t)\cdot\mathbf{t}(s,t)-1],\tag{2}$$

where $C(s,t)=|\partial^{2}\mathbf{R}(s,t)/\partial s^{2}|$ is the local curvature of the filament and $\mathbf{t}(s)$ is a unit vector that is locally tangential to the filament. The condition of nonextensibility of the polymer is imposed by the Lagrange multiplier $\lambda(s)$. The functional derivative of the bending free energy gives the elastic forces. By defining the energy density by $G=\int_{0}^{L}\mathcal{G}\,ds$, we arrive at the following equation:

$$\frac{\delta\mathcal{G}}{\delta\mathbf{R}}=-[\kappa C(s)\dot{C}(s)+\dot{\tau}(s)]\hat{\mathbf{t}}+[\kappa\ddot{C}(s)-C(s)\tau(s)]\hat{\mathbf{n}},\tag{3}$$

where the overdot indicates the derivative with respect to s and the tension profile is defined through $\tau(s)=\lambda(s)+\kappa C^{2}(s)$.

To determine the adsorbing forces, we choose a molecular picture and introduce the molecular forces through the direct interaction between monomers and the molecules on the surface. These molecules could bind together and enforce the polymer to adhere to the membrane. In this manner any monomer could be in a bound or unbound state. Considering the typical binding energy of molecules, which is comparable with the thermal energy, thermal fluctuations are present in bond formation. We can define the probability to find a monomer in the bound state. Due to thermal fluctuations, any attached monomer could detach at some rate [16–18]. Denoting the probability of finding the sth monomer in the bound state with $n_{b}(s,t)$ and the corresponding probability to be in the unbound state with $n_{u}(s,t)=1-n_{b}(s,t)$, we can write the following deterministic dynamical equation for these probabilities:

$$\frac{\partial}{\partial t}n_{b}(s,t)=\omega_{\mathrm{on}}n_{u}(s,t)-\omega_{\mathrm{off}}n_{b}(s,t),\tag{4}$$

where ω_{on} and ω_{off} stand for the attachment and detachment rates. Following Kramer's theory the transition rates are modified in the presence of external forces. Such modifications are due to the fact that the mechanical energy, which depends on the external force, enters the probabilities of the different states through a Boltzmann factor [19,20]. Now the force-dependent detachment rate is given by

$$\omega_{\mathrm{off}}=\omega_{\mathrm{off}}(0)\exp\left(\frac{f_{b}\gamma}{k_{B}T}\right),\tag{5}$$

where $k_{B}T$ is the thermal energy and γ is a microscopic length scale representing the distance between the bound state and the energy barrier separating bound and unbound states. When a molecule goes to the bound state, there is a force $f_{b}(s)$ between two attached molecules. The force between attached molecules depends on the relative configurations of the molecules. For simplicity, we consider the case where the binding forces are modeled as perpendicular springs: $f_{b}(s,t)=-k_{b}\hat{\mathbf{y}}\cdot\mathbf{R}(s,t)$. Here we assume that the spring constant for the harmonic interactions between attached molecules, k_{b}, is uniform along the whole polymer length. Collecting all the descriptions above we can write the adhesion forces as

$$\mathbf{f}^{a}(s,t)=n_{b}(s,t)f_{b}(s,t)\hat{\mathbf{y}}.\tag{6}$$

By simultaneous solution of Eqs. (1) and (4) with suitable boundary conditions, we can determine the whole dynamics of the polymer that is subjected to the external boundary forces given by $\mathbf{f}^{e}(s,t)$.

In the rest of this paper we concentrate on the stationary as well as equilibrium states of a polymer that is subjected to as external force at its end, namely, $\mathbf{f}^{e}(s,t)=f\delta(s-L)\hat{\mathbf{y}}$.

III. NUMERICAL SOLUTION

So far we have formulated the problem of an adhering filament subjected to an external force at its end. Here we consider the dynamical response of this system. Equations (1) and (4) govern the dynamical equation of this system. A numerical solution of these equations reveals the filament dynamics.

Defining a microscopic molecular length scale a and using a microscopic time scale $a^{3}\xi_{\perp}/\kappa$, we go to nondimensional equations. For this purpose we use κ/a^{2} to make nondimensional forces. To estimate numerical values, we consider a microtubule which is interacting with the cell membrane. Such microtubules can form a spindlelike struc-

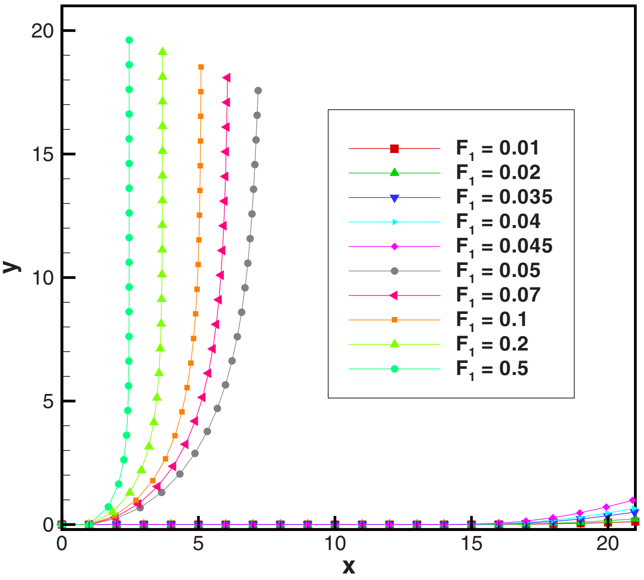

FIG. 2. (Color online) Equilibrium shape of the filament, for different values of the external force. We have chosen $\omega_{\mathrm{on}} = \omega_{\mathrm{off}}(0) = 1\ \mathrm{s}^{-1}$. It can be seen that there is a critical force, below which the whole of the rod is attached and beyond which the rod completely peels off from the substrate.

ture which is responsible for the cell division. In this case we choose $a = 1\ \mu\mathrm{m}$, $\kappa = 10^{-22}\ \mathrm{N\,m}^2$, $\omega_{\mathrm{on}} = \omega_{\mathrm{off}}(0) = 1\ \mathrm{s}^{-1}$, $k_b = 10^{-6}\ \mathrm{N\,m}^{-1}$, $\gamma = 1\ \mathrm{nm}$, $T = 300\ \mathrm{K}$, $\xi_\perp = 2\xi_\parallel = 4\pi\mu/\ln(a/d) = 10^{-2}\ \mathrm{N\,s/m}$ with $\mu = 10^{-3}\ \mathrm{N\,s/m}^2$, and d is the diameter of the filament [12].

By applying a constant force of the order of piconewtons at one end of a completely horizontal rod, we study the dynamics of an adhering polymer. Letting the polymer reach the equilibrium state, we see that there is a critical force as shown in Fig. 2; for forces smaller than the critical value the polymer cannot be peeled off. For this case the equilibrium state is a completely attached filament. As the external force goes beyond this critical value, there is a tendency to peel off from the surface with a certain peeling velocity. The critical force depends on different parameters, such as bond strengths and rates. We will present a very simple description for the critical force.

By applying a very small force deviation from the critical value we can investigate the dynamical behavior of the system. To demonstrate the nonequilibrium properties of the moving states for forces larger than the critical value, we present the linear response of the system in the form of a force-velocity relation. To avoid numerical errors related to the boundary effects of the polymer, we choose a long polymer and investigate the peeling velocity at intermediate lengths.

Figure 3 shows the numerical results for the peeling velocity in terms of the small force deviation from the corresponding critical values for different attachment rates. As we can see, change of the attachment rate causes a change of the response. For constant force deviations small attachment rates correspond to small peeling velocities. This is a result of the fact that the critical force also depends on the attachment rate. The inset of Fig. 3 shows that large attachment rates correspond to large critical forces.

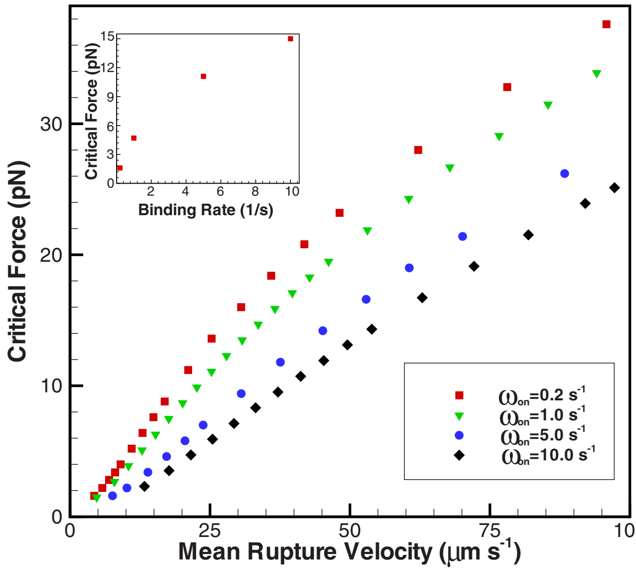

FIG. 3. (Color online) Linear response of an adhering polymer to small force deviation from the critical value represented by plotting the rupture velocity in terms of the external force. Inset: the behavior of the critical force in terms of the attachment rate.

IV. EQUILIBRIUM STATES

Let us consider the equilibrium state of a polymer interacting with a solid membrane and subjected to different boundary conditions at its end. Many theoretical works are devoted to analysis of the stationary states of this system [21]. We distinguish two general different classes of the problem: height and force ensembles. In the height ensemble we keep one end of the polymer at a constant height while in the force ensemble a constant vertical force is applied to one end of the polymer. In both cases the other end of the polymer is fixed and attached to the membrane to prevent any motion. Each case corresponds to different accessible experimental situations.

In each category we use a simplified energy method to investigate the equilibrium phases of the system. Actually, by assuming a very short-range nature for the interaction with the membrane, we can define a critical point along the polymer that is the border line separating the attached and detached parts of the polymer; we call this point the *attachment point*. Now we can assign an adhesion energy proportional to the length of the attached part of the polymer. There is a competition between the external force that makes the polymer bend and the adhesion energy that increases the adhesion length. Analysis of the details of this competition will reveal the different equilibrium states of the system.

A. Height ensemble

Here we study the equilibrium behavior of a semiflexible polymer constrained by a fixed height at its end. Representing the angle between the local tangent to the polymer and x axis with $\theta(s)$ and introducing a Lagrange multiplier Υ to enforce a constant height h at the end, we can write the free energy functional of an elastic filament as

$$E=\frac{\kappa}{2}\int_{s_0}^{1}\dot{\theta}^2 ds - w s_0 - \Upsilon\left(\int_{s_0}^{1}\sin(\theta)ds - h\right), \tag{7}$$

where the first term is the bending energy and the second term stands for the adhesion contribution, representing the short-range interaction with the substrate. Here w is the macroscopic adhesion energy per unit length of the polymer and s is the arclength along the rod. s_0 is the length of polymer that is attached to the membrane. The partial derivative with respect to s is shown by an overdot. Physically, Υ is the corresponding constraint force which makes a constant height at the end.

For the next calculations we use dimensionless quantities denoted by an overbar. The polymer length L, characteristic force κ/L^2, and energy scale κ/L are used to make nondimensional quantities.

As one can see from Eq. (7), the energy is a functional of the $\theta(\bar{s})$ and $\bar{s}_0$ variables. To determine the equilibrium shape we should study the variation of this energy functional with respect to these variables. Calculating the variation with respect to $\bar{s}_0$, we get an equation that is actually a boundary condition for the torque at the adhesion point, namely, $\dot{\theta}(\bar{s}_0)=\sqrt{2\bar{w}}$ [20]. At the other hand, by calculating the variations with respect to $\theta(\bar{s})$, we arrive at a differential equation for the polymer profile:

$$\ddot{\theta}+\bar{\Upsilon}\cos(\theta)=0. \tag{8}$$

We use the boundary conditions $\dot{\theta}(\bar{s}_0)=\sqrt{2\bar{w}}$, $\theta(\bar{s}_0)=0$, and choose a particular value for the external torque at the end ($\bar{s}=1$) to solve the above differential equation and find the equilibrium position of $\bar{s}_0$ and equilibrium profile for the filament, $\theta(\bar{s})$.

We need to investigate whether the derived equilibrium states are stable or not. To answer the question of stability of the equilibrium solutions we use another equivalent method. First we assume that $\bar{s}_0$ is given, then, by using the boundary conditions $\theta(\bar{s}_0)=0$, $\dot{\theta}(1)=0$ (zero torque at the end) and noting that $\int_{\bar{s}_0}^{1}d\bar{s}=1-\bar{s}_0$, we can find the polymer profile in terms of $\bar{s}_0$. Using this solution we can eliminate $\theta(s)$ from the free energy and express the energy in terms of $\bar{s}_0$:

$$\bar{E}(\bar{s}_0)=\int_0^{\theta(1)}\frac{c+w-\bar{\Upsilon}\sin(\theta)}{\sqrt{2c-\bar{\Upsilon}\sin(\theta)}}d\theta. \tag{9}$$

In order to find the unknown coefficients we apply the conditions of constant height and constant filament length in the detached part:

$$\int_0^{\theta(1)}\frac{1}{\sqrt{2[c-\bar{\Upsilon}\sin(\theta)]}}d\theta=1-\bar{s}_0, \tag{10}$$

$$\int_0^{\theta(1)}\frac{\sin(\theta)}{\sqrt{2[c-\bar{\Upsilon}\sin(\theta)]}}d\theta=\bar{h}. \tag{11}$$

Now using the condition of zero torque at the end we see that the angle at the end, $\theta(1)$, is related to the Lagrange multiplier by $c=\bar{\Upsilon}\sin[\theta(1)]$.

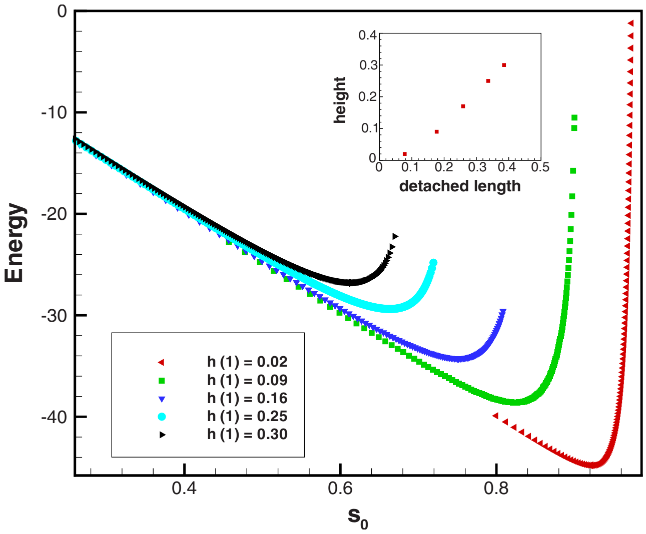

FIG. 4. (Color online) Total dimensionless energy of the filament versus the attached length of the filament, taking $w=50.0$ and $L=1$. The graphs are plotted for different values of heights at the end. Inset: height versus the equilibrium value of the length of the detached part of polymer.

Figure 4 shows the energy of the filament [Eq. (9)] in terms of the attached length s_0 for different values of the filament height at its end. We can see that for each value of the height there is an equilibrium state with a well-defined attached length. Regarding the energy landscape, this equilibrium state is obviously stable. Increasing the height at the end will decrease the equilibrium value of the attached length. The inset of the graph shows the behavior of the height versus the equilibrium value for the detached length of the polymer.

B. Force ensemble

In addition to the height ensemble here, we consider the case where a constant vertical force is applied at the end of polymer. We use the same method of the previous section to investigate the stationary states of this constant force case. The total dimensionless energy of the filament can be written as

$$\bar{E}=\frac{1}{2}\int_{\bar{s}_0}^{L}ds\,\dot{\theta}^2-\bar{w}\bar{s}_0-\bar{f}\bar{y}(1). \tag{12}$$

To incorporate the effects of the external force f, we have inserted it through the mechanical work that is necessary to displace the end point of the polymer from zero height to an equilibrium height denoted by $y(L)$.

Minimizing this free energy with respect to the filament profile, we arrive at the same differential equation given by Eq. (8) in which Υ is replaced by f. We solve this equation with required boundary (zero torque at the end) conditions and eliminate the θ field to obtain the energy as a function of s_0. Figure 5 shows the energy as a function of s_0. As this figure shows, our system does not have stable equilibrium states with finite adhesion length. The energy profile has a local extremum which is not a minimum. This equilibrium

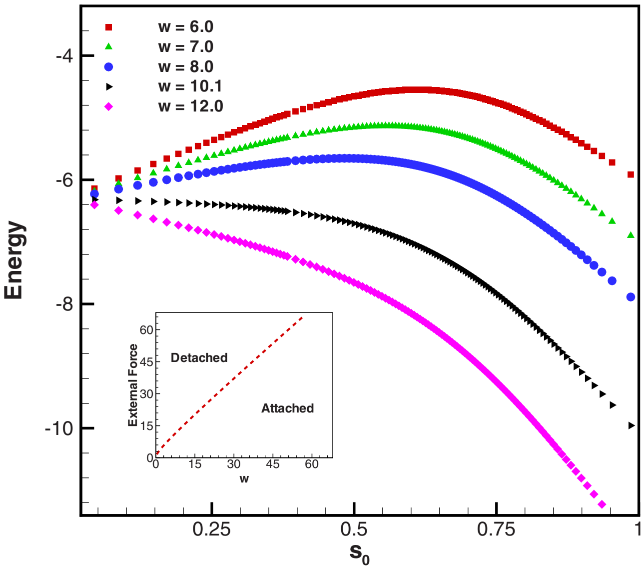

FIG. 5. (Color online) Total dimensionless energy of the filament versus the attached length of the filament, taking $f=10.0$ and $L=1$. The graphs are plotted for different values of adhesion energy. There is a local extremum in the energy landscape which is not a minimum. As one can see, $w=f$ is the border between two different phases. For $w<f$ the equilibrium position is given by $s_0=0$ while for large w the equilibrium state is given by $s_0=L$. Inset: Equilibrium phase diagram for an elastic polymer. Border line separates the completely adsorbed and completely detached polymers.

point is not stable and the system will go to a global minimum that critically depends on the force value. For forces less than a critical value, the stable state corresponds to a case where the whole of the filament is attached to the membrane (we call it complete adhesion) while for forces beyond it the stable equilibrium state will be a detached state with divergent detached length. This state corresponds to a completely peeled-off filament. In the previous section we investigated this moving stationary state in more detail.

These two ensembles are equivalent in the sense that the thermodynamic free energies Eqs. (7) and (12) are connected through a Legendre transformation. This means that a simple mathematical transformation could also be used to obtain the results for height ensembles directly from those of the force ensemble.

Instead of applying zero torque at the end, we can consider a fixed angle at the end. Following the same procedure as described above, we can solve the differential equation for the polymer profile and eliminate corresponding degrees of freedom in free energy. The energy functional, which is not reported here, shows that for $f\sin[\theta(1)]<w$ the energy plot shows a stable equilibrium state with a finite length of the detached part. For forces greater than this critical force, the polymer will eventually go to the completely peeled-off state.

V. CRITICAL FORCE

The physics of the critical force which usually appears in problems with a stochastic nature is a challenging issue [22].

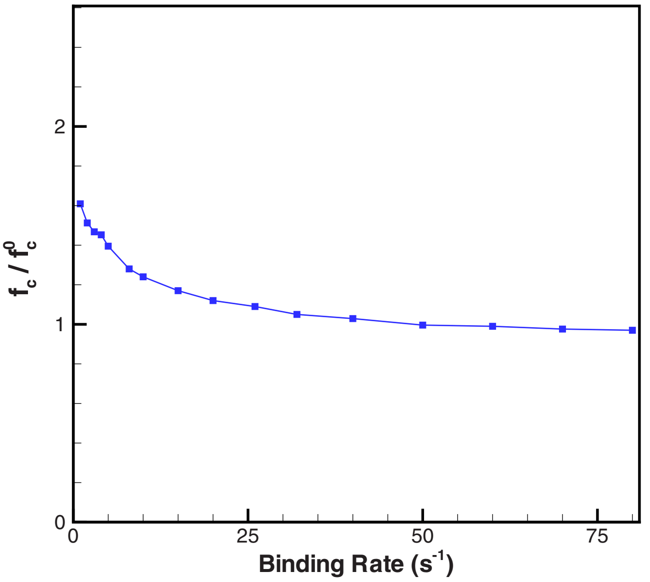

FIG. 6. (Color online) Critical force normalized by f_c^0 in terms of attachment rate.

Here in our model, inspired by the results of the equilibrium calculations, we saw that the adhesion energy w is a measure of the critical force (content of Fig. 5). Here we try to understand the microscopic origin of the adhesion energy. In terms of the microscopic parameters, the adhesion energy can be approximated by the amount of mechanical work that is necessary to peel off a connected bond. So we expect a relation like

$$f_c^0=\frac{1}{a}\int_0^\infty dy\, k_b y \frac{\omega_{\rm on}}{\omega_{\rm off}+\omega_{\rm on}}. \qquad (13)$$

We have assumed that the stationary value of the binding probability appears in the mechanical work as a weight function. Here a is the microscopic length scale representing the distance between adjacent bonds on the membrane. This length scale can have a value about the same as the microscopic length scale defined by γ.

Defining the dimensionless quantity $\epsilon=\omega_{\rm on}/\omega_{\rm off}(0)$, we can express the result of the above integral in terms of a polylogarithmic function as $f_c^0=-[(k_BT)^2/k_b a\gamma^2]\text{polylog}[2,-\epsilon]$. For small attachment rates we can expand this result to reach $f_c^0=-[(k_BT)^2/k_b a\gamma^2][\epsilon-\frac{1}{4}\epsilon^2+O(\epsilon^3)]$. It is expected that the critical force is a characteristic of the equilibrium phase diagram of the system and does not depend on dynamic properties of the system. Here the critical force depends on ϵ, which is an equilibrium parameter.

However, we use the result of this simplified picture just as a reference value for the critical force. Figure 6 shows the critical force divided by this f_c^0 versus the attachment rate. As one can see for large attachment rates the above simple picture makes a better theoretical framework for the critical force.

VI. SUMMARY AND CONCLUDING REMARKS

We have presented a dynamical approach to study the behavior of an elastic filament interacting with a rigid membrane. We investigated the properties of the filament for two different general categories, namely, force and height ensembles. The general aspects of filament dynamics in the force ensemble are investigated numerically. The simulation results shows that a critical force is expected. For forces smaller than the critical value, the system reaches an equilibrium state where the polymer is completely attached to the substrate. When the strength of the external force is increased, the system goes to a stationary state with a peeling velocity. For large forces the equilibrium state is a completely peeled-off filament. To demonstrate the nonequilibrium properties of this moving state, we have presented the linear response function of the system, in the form of a force-velocity relation for very small force deviation from critical force. Because of the equivalence of these ensembles, which was mentioned before, the physical observations in the dynamic part are not sensitive to the nature of the external force.

With a static phenomenological description we investigated the equilibrium states of the filament. For the force ensemble we found two different subclasses for the equilibrium phases: (a) For the case with zero torque at the end, competition between the external force and the adhesion energy determines the equilibrium states. Small forces correspond to complete adhesion while large forces correspond to complete rupture; the critical force is the border between these two states. (b) In the case with nonzero torque or fixed angle at the end, the equilibrium state is a phase with a finite equilibrium adhered length for the polymer. The results of case (a) are in agreement with the dynamical model. For the height ensemble, where the end point is fixed at a constant height, the polymer will reach a stable equilibrium state with finite attached length for the polymer.

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