# Moving interfaces in rod-like macromolecules

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**Abstract.** - We present a model that describes mechanical unfolding behavior in rod-like macromolecules. We propose that the unfolding occurs via the motion of a folded/unfolded interface along the molecule. We predict the speed of this interface as a function of the pulling velocity such that the resulting force-extension curve replicates the overstretching transition typical of coiled-coils and DNA. We model the molecules as one-dimensional continua capable of existing in two metastable states under an applied tension. The interface separates these two metastable states and represents a jump in stretch, which is related to applied force by the worm-like-chain relation. The Abeyaratne-Knowles theory of phase transitions in continua governs the mechanics of the interface.

**Introduction.** – Single-molecule experiments have been performed using atomic force microscopy and optical tweezers [1–4], in which long molecules are stretched between rigid and semi-rigid supports in a fluid flow. In a constant velocity setup, for example, one end of the molecule is attached to an AFM tip, which is held stationary. The other end is attached to a cover slip which is moved at a fixed speed. Similarly, in a constant force setup, the cover slip is moved in such a way that the force experienced at the AFM remains close to a fixed value. Both kinds of experiments yield different insights regarding the forced unfolding process. However, all experiments have shown that molecules, such as DNA and myosin coiled-coils undergo massive structural changes (often called 'overstretching transitions'), initiated by the achievement of a certain force threshold at a point in the molecule. The force threshold varies with the type of molecule being examined and the solution conditions [2] and temperature [5]. The structural change is accompanied by absorption of energy due to the breaking of bonds and is characterized by force-extension curves that have a force plateau bookended by two steep rises in the force. The plateau region of the curve corresponds to the gradual unfolding of the molecule as it undergoes the structural transition. The steeply rising parts of the curve have been shown to be well fit by the Worm-Like Chain (WLC) model of polymer elasticity [13].

This transition has largely been studied through the perspective of the force-extension curves obtained. However, the mechanism by which the transition occurs had only been speculated about till now. In the absence of experimental evidence, a number of theories attempted to explain this phenomenon. These include characterizing the transition as a conversion of the native state of DNA, B-DNA to a new state termed S-DNA [6,8,19], and overstretching as a force-induced melting to single-stranded DNA [5, 11, 12]. These developments are summarized, among others, in Williams et al [10] and in Whitelam et al [7].

In this paper, we propose a mechanism for this process by employing the Abeyaratne-Knowles Theory of phase transitions [22]. We propose that the unfolding occurs via the motion of a folded/unfolded interface along the length of the molecule. Such interfaces have been shown to exist in the recent experiments of van Mameren *et al.* [9]. This is probably the first instance in which a continuum theory of phase transitions with a moving interface is used to describe an evolving structural transition in a biopolymer. This is also the first attempt to make predictions for the speed of the interface as a function of the mechanical properties of the folded and unfolded phases and boundary conditions. We first introduce a one-dimensional model for a molecule which is in the completely folded state and state the force balance and constitutive relations. Next, we de-
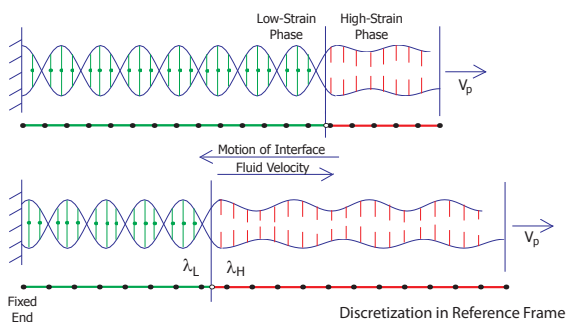
Fig. 1: The molecule is represented as a one-dimensional continuum (lines underneath the cartoon of the partially unfolded molecule) with an interface separating two metastable phases. Black circles on the lines indicate nodes used in the numerical scheme. Open circles indicate position of the interface. One end of the molecule is fixed while the other is pulled at a constant velocity.

scribe the two-phase model and the modified constitutive equation which allows for the presence of discontinuities in stretch. We then give the force and kinematic jump conditions at the discontinuities and introduce the concept of the thermodynamic driving force. Finally, we discuss the computation scheme and obtained results.

**Elements of rod-like molecule model.** – A schematic diagram of the model is presented in fig. 1. The molecule is assumed to exist, at any given time, as a mixture of two metastable states – a folded native state (low strain phase) and an unfolded state with broken bonds (high strain phase). Prior to the achievement of the force threshold, the molecule remains exclusively in the folded state, and can undergo stretching and relaxation. Following the achievement of the force threshold, we propose that overstretching occurs via the propagation of a folded/unfolded interface (or 'phase boundary' in phase transitions terminology) moving through the molecule. As it moves, the interface progressively converts the folded region into the unfolded state, till the molecule is completely unfolded. The speed of the interface depends on the force applied at the end of the molecule through a kinetic relation. In this paper, we have considered only unidirectional motion of the interface, i.e. only unfolding has been explored and not subsequent refolding. At the interface, tension, strain and particle velocities are determined by jump conditions obtained from the governing equations.

We begin our description of the model by first considering the situation where the applied forces are small enough that the entire molecule is in a single phase. The molecule is conceptualised as a slender rod, in which there is a single position parameter, namely the arc length $s$, with $0 \leq s \leq L$ in a reference configuration. The position of material point $s$ in the deformed configuration at time $t$

is $z(s,t)$. The balance of forces on the rod is expressed as

$$\frac{\partial f}{\partial s} = d_w \left( v - v_f \right), \tag{1}$$

where $f$ is the internal axial force in the rod, $d_w$ is the axial drag coefficient due to the surrounding fluid and $v(s,t) = \frac{\partial z}{\partial t}$ is the velocity of the segment of the molecule at reference position $s$. $v_f$ is the fluid velocity, which is non-zero in experiments in which a fluid flow is used to stretch the molecules in the place of optical tweezers or AFM. The axial drag coefficient $d_w$ is calculated from slender body theory for low Reynolds number flow [18], viz., $d_w = \frac{2\pi\mu}{\log\left(\frac{2l}{a}\right)+c}$ where $\mu$ is the fluid viscosity, $2l$ is the length of the body, $a$ is the radius of gyration of the body and $c$ is a constant that depends upon the shape of the body. The rod is assumed to follow the worm-like chain constitutive law [20, 21], i.e.

$$f = \frac{1}{4\beta^2 K_b \left(1 - \lambda\right)^2} \tag{2}$$

where $\lambda = \frac{\partial z}{\partial s}$ is the position- and time-dependent stretch of the molecule. $K_b = \xi_p k_B T$ is the bending modulus of the molecule, where $\xi_p$ is the persistence length, and $\beta = 1/k_B T$ where $k_B$ is the Boltzmann constant and $T$ is the absolute temperature. We have assumed here that the persistence length $\xi_p$ is much shorter than the contour length of the rod and that the process of pulling the molecule is quasistatic so that the worm-like-chain relation derived using equilibrium statistical mechanics is valid. (1) together with (2) can be numerically integrated for appropriate boundary and initial conditions by a finite difference scheme to predict the relaxation behaviour of stretched DNA.

We have confirmed that a single drag coefficient gives excellent fits to the relaxation data of Perkins *et al.* [16] for $\lambda > 0.6$. These experiments were modeled by imposing zero fluid velocity and comparing the decrease in length as a function of time. Furthermore, we looked at the special case in which a stretched molecule has reached steady state in a uniform flow. For this case, an explicit solution is easily found by putting $\frac{\partial z}{\partial t}$ equal to zero. For this case, we have confirmed that the error in the computed results (obtained by letting the system evolve to steady state) with respect to the analytical solution decreases as we increase the number of nodes in the finite difference scheme. We can predict the stretching behavior of the molecule in any fluid velocity field by specifying it on the right hand side of (1). The stationary fluid is a special case of the same.

**The folded/unfolded interface.** – Having ascertained that the model is sound in its handling of a single folded state system, we now add to this description, the proposition that the molecule be considered as a one-dimensional continuum that is capable of undergoing phase transitions between two stable phases, i.e. a

folded and an unfolded phase. These phases are separated by an interface that is modeled as a phase boundary between the low-strain (folded) and high-strain (unfolded) phases. The motion of this phase boundary is assumed to be governed by the Abeyaratne-Knowles theory of phase transitions [14, 22].

The Abeyaratne-Knowles theory in one dimension deals with solid-solid transitions in tensile bars. The origins of the theory go back to Ericksen [15] who showed that solids with two metastable states or phases can be described by a nonmonotonic (up-down-up) stress-strain relation. Thus, for a given range of stress, the one-dimensional continuum may exist in a configuration in which the stress is constant throughout, while the strain is only piecewise constant. Such a state is termed as a phase mixture, and the points at which there are discontinuities in strain are called phase boundaries. In pulling experiments with macromolecules, similar conditions have been shown to exist [9]. Hence, the motivation to employ this theory.

The presence of a discontinuity in the continuum necessitates the consideration of the behavior of quantities at the interface. The equation of motion (1) still holds, but the constitutive description of the rod changes. The expressions for tension in the low-strain and high-strain phases become

$$ f = \begin{cases} \dfrac{1}{4\beta^2 K_{b_L}\left(1 - \frac{\lambda}{r}\right)^2} & \text{for low-strain phase} \\[3mm] \dfrac{1}{4\beta^2 K_{b_H}(1-\lambda)^2} & \text{for high-strain phase} \end{cases} \qquad (3) $$

where $K_{b_L}$ and $K_{b_H}$ are the bending moduli for the low- and high-strain phases respectively. $\lambda$ is the stretch with respect to the reference (fully stretched state in the completely unfolded phase) configuration. The parameter $r$ is the ratio of inter-basepair distances in the folded and unfolded states. For simplicity, we have not included the intrinsic stretching modulus of the molecule in this constitutive law since our focus is on moving interfaces.

At interfaces such as the ones considered by the Abeyaratne-Knowles theory, quantities, such as, particle velocity, stretch and energy density can be discontinuous, but balance laws constrain these jumps in a non-trivial way. In particular, continuity of the deformed configuration, i.e. no breaks in the material, gives a kinematic jump condition,

$$ [|v|] + \dot{x}\,[|\lambda|] = 0 \qquad (4) $$

where $[|y|] = y(x^+, t) - y(x^-, t)$ is the jump in $y(s,t)$ across an interface located at $s = x(t)$ in the reference configuration. Similarly, the balance of forces gives a force jump condition,

$$ [|f|] = 0, \qquad (5) $$

since inertial effects are negligible. This says that the tension is continuous across the interface.

We now turn our attention to the interface itself. We assume that at any given time, there can be at most one interface propagating through the molecule. The presence of a single interface is consistent with recent observations of van Mameren *et al.* [9] though their interfaces were static. The Abeyaratne-Knowles theory specifies two fundamental conditions for the existence and propagation of this interface. The first of these is a nucleation criterion. We have predicated the formation of the boundary on the achievement of a critical force at any point along the molecule. As the molecule is stretched, the force experienced at different points along the molecule varies with time. In particular, this force can be shown to be maximum at the end which is being pulled, and decreasing monotonically along the molecule (for an experiment in which one end is kept fixed and the other end is pulled away at constant velocity). Clearly then, the critical force will be achieved first at the end being pulled, and the nucleation criterion states that this is the point where the interface or phase boundary is formed. This again is consistent with the experiments of van Mameren *et al.* [9]. This phase boundary then proceeds along the molecule as an unfolding front in accordance with the second required condition, which is the kinetic relation.

The kinetic relation specifies the way in which the velocity of the phase boundary varies with the thermodynamic driving force (which is, in general, different from the mechanical force felt at the interface) across it, i.e. $\dot{x} = \dot{x}(f_{driv})$. Alternatively, $f_{driv}$ is the jump in the free energy across the interface and is responsible for driving the interface. The Abeyaratne-Knowles theory provides an expression for this driving force in terms of the jump in stored energy per unit reference length and the jump in strain across the phase boundary. It is given by

$$ f_{driv} = [|W|] - f_x\,[|\lambda|], \qquad (6) $$

where $W$ is the stored energy per unit length, $f_x$ is the tension in the molecule at the phase boundary (same on either side) and $\lambda$ is the stretch. $W$ is calculated using $W = \int_{\lambda_{min}}^{\lambda} f(\lambda')d\lambda'$, where $f(\lambda)$ is obtained from (3). For the high-strain phase, in addition to the integral above we include the average energy per unit length $W_B$ required to make the transition from the low-strain to the high-strain phase. We choose $\lambda_{min}$ to be the lower limit of the stretch at which the WLC formula for the force-extension behavior of the polymer can be applied and $\lambda$ is the current stretch which is equal to $\lambda_L$ in the low-strain phase and $\lambda_H$ in the high-strain phase. It is noteworthy that the strains $\lambda_L$ and $\lambda_H$ are functions of the tension at the interface (as given by (3)), and hence, the driving force is a function of only the tension at the interface.

**Computation.** – We now explain how we reproduce the plateau in the force-stretch response of the molecules. We integrate (1) together with the force-stretch relation (3), allowing for one phase boundary whose position in the reference configuration is $x(t)$ and is governed by jump
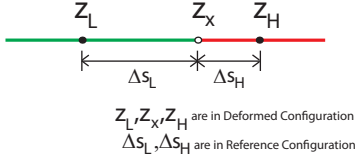
Fig. 2: Nodes represented by $z_L$ and $z_H$ are fixed in the reference configuration, while the extra node for the interface, represented by $z_x$, is a moving node. Also shown are the variable length sub-elements, $\Delta s_L$ and $\Delta s_H$, which are such that $0 \le \Delta s_L, \Delta s_H \le \Delta s$.

conditions (4) and (5), and by the boundary conditions

$$\left(\frac{\partial z}{\partial t}\right)_{s=L} = v_P, \qquad z(0,t) = 0, \qquad (7)$$

where $v_P$ is a pulling velocity imposed at one end of the molecule. At $t = 0$, the entire molecule is assumed to be in the low-strain phase. For the experiments we have sought to model, the fluid velocity is zero, and the molecule is pulled at the end $s = L$ at a constant velocity $v_p$. As a result, as long as the force in the molecule has not equilibrated, it will be a maximum at $s = L$. A phase boundary is nucleated at $s = L$ when the tension there reaches a threshold. Its subsequent motion is governed by another condition, which is a kinetic relation in a general phase transition. However, in the case at hand, its function is performed by the condition that the force at the interface should remain constant for the duration of the unfolding process. This is discussed later in the paper.

We modify our finite difference numerical scheme to account for the presence of the moving phase boundary by adding a mobile node to our existing discretization [23]. In the neighborhood of the phase boundary, the jump conditions are imposed. Assuming that the molecule on both sides of the phase boundary is governed by the worm-like chain constitutive law (3), the force jump condition (5) reduces to

$$\left(1 - \frac{\lambda_L}{r}\right) = \sqrt{\frac{K_{b_H}}{K_{b_L}}}\left(1 - \lambda_H\right), \qquad (8)$$

where $\lambda_L$ and $\lambda_H$ are the stretches in the low- and high-strain phases respectively. In our finite difference scheme the stretches $\lambda_L$ and $\lambda_H$ can be expressed in terms of the position of the discontinuity $z_x$ (in the deformed configuration) and the higher and lower nodes, $z_H$ and $z_L$ respectively, as (see fig. 2)

$$\frac{\lambda_L}{r} = \frac{z_x - z_L}{r\Delta s_L} \quad \text{and} \quad \lambda_H = \frac{z_H - z_x}{\Delta s_H}, \qquad (9)$$

where $\Delta s_L + \Delta s_H = \Delta s$ is the distance separating two nodes bracketing the node representing the moving phase boundary in the reference configuration. From the perspective of obtaining a numerical solution, the quantities

available to us at each time step are the fixed node positions. The position of the interface, however, is not known. Thus, it is convenient to formulate the stretches in terms of the positions of the fixed nodes. Eliminating $z_x$ between (8) and (9), we obtain expressions for the strains in terms of node positions.

$$\lambda_L = \frac{\sqrt{K_{b_H}}(z_H - z_L) + \Delta s_H(\sqrt{K_{b_L}} - \sqrt{K_{b_H}})}{(\sqrt{K_{b_H}} r\Delta s_L + \sqrt{K_{b_L}}\Delta s_H)} \qquad (10)$$

$$\lambda_H = \frac{\sqrt{K_{b_L}}(z_H - z_L) + r\Delta s_L(\sqrt{K_{b_H}} - \sqrt{K_{b_L}})}{(\sqrt{K_{b_H}} r\Delta s_L + \sqrt{K_{b_L}}\Delta s_H)} \qquad (11)$$

Note that we assume $z(x^+(t), t) = z(x^-(t), t) = z_x$ is continuous, hence the kinematic jump condition is automatically satisfied.

At this point, we introduce another quantity, which is the rate of dissipation associated with the motion of a phase boundary across a material. It is defined as the product of the thermodynamic driving force with the interface velocity, both appropriately signed ($\dot{x}$ is positive if it moves from smaller to larger values of arc length $s$). The second law of thermodynamics requires that the dissipation be non-negative at all times during the motion of the phase boundary. Hence, we must have

$$D = f_{driv}\dot{x} \ge 0 \qquad (12)$$

In other words, if the rate of dissipation is negative, the motion is aphysical and cannot occur. A check for this criterion is applied at each time step of our computation.

**Results.** – In order to determine the interface speed, and hence describe the motion of the phase boundary $x(t)$, that produces the overstretching plateau, we assume in our computation that the tension at the interface $f_x$ is a given constant which determines $\lambda_L$ and $\lambda_H$. This is equivalent to specifying a kinetic relation since (9) and the condition that $\Delta s_L + \Delta s_H = \Delta s$ allows us to determine $\Delta s_L$ and $\Delta s_H$ at each time step from which $\dot{x}$ follows automatically. Starting from a completely folded configuration, and with the constant force condition imposed, we computed the variation of $\dot{x}$. The results are shown in fig. 3. This exercise reveals the remarkable result that for a given plateau force and pulling velocity, the speed at which the phase boundary moves is constant for the duration of the unfolding, and is uniquely determined. We have made predictions for four different pulling velocities (0.3 $\mu$m/s, 0.7 $\mu$m/s, 1.5 $\mu$m/s and 3.0 $\mu$m/s) and for four different plateau forces. $\dot{x}$ is a constant independent of time but a function of the plateau force and the pulling velocity. Further, we find that the ratio $\frac{\dot{x}}{v_p}$ remains constant for a given plateau force. This ratio decreases as the plateau force increases (see fig. 3 inset).

Building upon this result, we find the force-stretch response for several different values of the tension $f_x$ with pulling velocity $v_P = 3\mu$m/s. In each of these cases, we
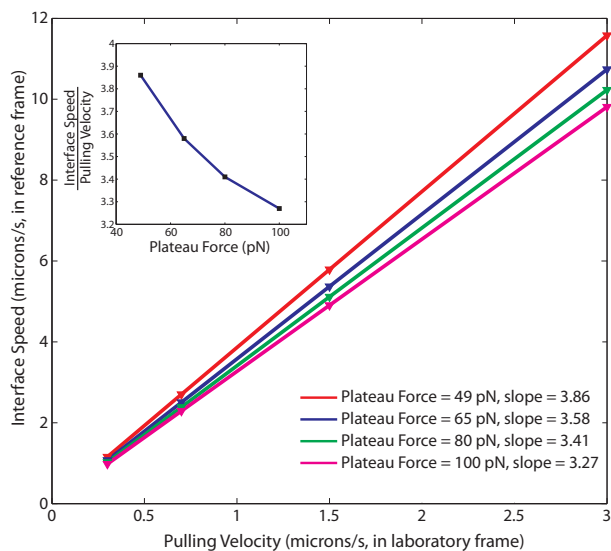
Fig. 3: Prediction for interface speed for given plateau force and pulling velocity. Note that each plateau forces corresponds to a unique ratio $\frac{\dot{x}}{v_p}$ which is given by the slope of the lines. Inset: Variation of $\dot{x}/v_p$ with plateau force. The calculations have been performed assuming $\frac{K_{b_L}}{k_B T} = 50$nm, $\frac{K_{b_H}}{k_B T} = 0.75$nm, and $r = 0.586$, with $k_B T$=4.1 pN-nm at room temperature.
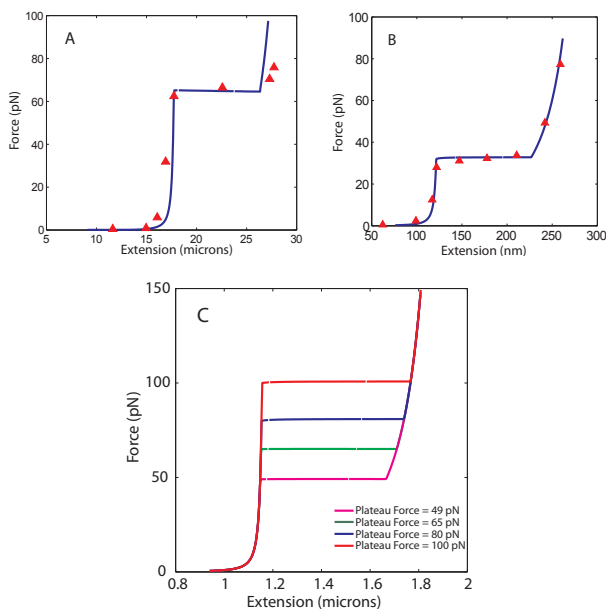


Fig. 4: A: Comparison of the force-extension curve for DNA obtained from the model with experimental data of Smith *et al* [9]. B: Comparison of curve obtained for Myosin II with data of Schwaiger *et al* [1]. C: Force-extension curves produced by the model for different plateau forces. The interface propagation model is able to reproduce all parts of the force-extension curve. The parameters in panel C are $K_{b_L}$=50 nm.$k_B T$ and $K_{b_H}$=0.75 nm.$k_B T$.

employ a different, but constant $\dot{x}$, in accordance with the predicted value in fig. 2. We note that this phase-transition based model handles extremely well all the parts of the force-stretch curve (see fig. 4), including the early pliability, the stiffening at high extensions, and the structural transition.

We have found that both the thermodynamic driving force $f_{driv}$, and the phase boundary speed $\dot{x}$, are constant while the molecule is undergoing the structural transition. The obvious inference from these results is that their product, the dissipation, as defined in (12), is also a constant for a given plateau force $f_x$, i.e. $D = f_{driv}\dot{x} = D_S$.

We also compared the value of dissipation with that of the rate of work done on the molecule at the boundary $s = L$ and found that it is negligible in comparison to the rate of work done at this boundary. According to the Abeyaratne-Knowles theory [14, 22], the thermodynamic driving force $f_{driv}$ should be equal to zero in a reversible process. Since the interface speed $\dot{x}$ is non-zero, zero driving force implies a zero dissipation, or a reversible process. Our computation uses Rouzina and Bloomfield's estimate for the Gibbs free energy of DNA melting [5] to calculate the difference in strain energy densities across the interface. We assume that it is the average of the energies for the two limiting cases considered by them. Negligible dissipation in our computation is consistent with the idea that most of the work is stored as elastic energy in the molecule. We point out that though the force plotted in the force-extension curve is the force experienced at the end of the molecule, not the force at the interface, these two forces are so close to each other in value for fluid viscosities used in our computations, that, they can be used interchangeably.

The physical parameters used above for the folded and unfolded parts are those of DNA. The persistence lengths for the two phases are $\xi_{P_H}$=0.75 nm and $\xi_{P_L}$=50 nm. The folded-to-unfolded length ratio $r$ is 0.586. The contour length in the folded configuration is 30.5 $\mu$m for the experimental comparison, and 2 $\mu$m for other results for DNA in fig. 4. The transition free energy per unit length, $W_B$ is 2.95 $k_B T$/nm. Of the four plateau forces used for our computations (see fig. 4), namely 49 pN, 65 pN, 80 pN and 100 pN, the 65 pN plateau is most commonly associated with the overstretching transition in DNA. It has been shown that the plateau force may be varied by modifying the solution conditions. In our computations, we find that while the nature of the transition remains the same at different plateau forces, the interface speed is different (for the same pulling velocity). Our model successfully reproduces the force-extension behavior for myosin II as well, the physical parameters for which, are $\xi_{P_H}$=0.4 nm and $\xi_{P_L}$=25 nm. The folded-to-unfolded length ratio $r$ is 0.4. The contour length in the folded configuration is 150 nm. Thus, the model succeeds in modeling unfolding behavior at length scales separated by two orders of magnitude.

If the interface speed is increased or decreased around the value that yields a plateau, we expect that in these sce-
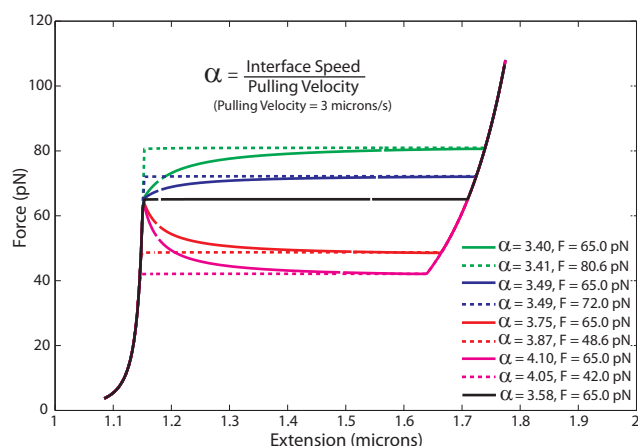
Fig. 5: Force-extension behavior in DNA for non-plateau-generating interface speeds. Solid lines correspond to interface nucleation at 65 pN. Dashed lines are plateau force-extension curves for the same $\frac{\dot{x}}{v_p}$ as the corresponding solid lines. For example, the green solid line has been generated by nucleating the discontinuity at 65 pN and $\frac{\dot{x}}{v_p}$=3.40, while the green dotted line is produced with parameters 80.6 pN and $\frac{\dot{x}}{v_p}$=3.41.

narios, we should not see plateaus being formed. That is indeed the case. However, even though the force-extension curve does not remain flat for the entire duration of the unfolding, there is an unambiguous tendency to approach a constant force as the unfolding proceeds (see fig. 5). The remarkable result from this observation is that the $\frac{\dot{x}}{v_p}$ value that produces this behavior (while nucleation occurs at 65 pN) , is almost equal to the $\frac{\dot{x}}{v_p}$ value that would produce a complete plateau at the same force. For example, the green solid line has been generated by nucleating the discontinuity at 65 pN and with $\frac{\dot{x}}{v_p}$=3.40, while the green dotted line is produced with parameters 80.6 pN and $\frac{\dot{x}}{v_p}$=3.41. This suggests that the initial part of the force-extension curve is much more sensitive to the interface speed chosen than the later part. Also, it strongly indicates a link between $\frac{\dot{x}}{v_p}$ and the plateau force.

**Summary.** – We have developed a model for moving interfaces in rod-like macromolecules and shown that it can reproduce the force-stretch response seen during the overstretching transition in DNA and coiled-coil molecules like myosin II. Our model can predict unfolding behavior for a variety of bending moduli, plateau forces and pulling velocities. We have shown that a special ratio of interface speed to pulling velocity produces plateaus in the force-stretch response and that this special ratio is a function of the value of the plateau force. Finally, our model shows that the force-stretch response has some unique features if we impose a different ratio than the one dictated by a plateau force. Our predictions suggest that experiments such as those of van Mameren *et al.* [9] could be extended or modified to verify these results. The plateau forces

could be changed by varying the ionic conditions or temperature. Average values of $\dot{x}$ could be determined by measuring the time taken for the transition to complete.

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