Stretching-force–dependent transitions in single stranded DNA

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Abstract – Mechanical properties of DNA, in particular its stretch-dependent extension and loop formation properties, have been recognized as effective probes for understanding possible biochemical roles played by them in a living cell. Single stranded DNA (ssDNA), which till recently was presumed to be a simple flexible polymer continues to spring surprises. Synthetic ssDNA, like polydA (polydeoxyadenosines) have revealed an intriguing force-extension (FX) behavior exhibiting two plateaus, which is absent in polydT (polydeoxythymidines). Loop closing time in polydA had also been found to scale exponentially within inverse temperature, unexpected from generic models of homopolymers. Here we present a new model for polydA which incorporates both a helix-coil transition and an overstretching transition, accounting for the two plateaus. Using transfer matrix calculation and Monte Carlo simulation we show that the model reproduces different sets of experimental observations, namely FX characteristics and looping behavior, quantitatively. It also predicts a weak, nonmonotonic behavior in the temperature-extension characteristic of polydA.

In order to understand how the mechanical properties of DNA and RNA influence biological processes like transcription and translation in living cells and viruses, these biopolymers are stretched in vitro to study their nonlinear elasticity and their internal structure. ssDNA, despite receiving less attention compared to double stranded DNA (dsDNA) [1,2], has recently attracted a lot of interest. Smith et al. [3] showed that the FX diagram for the wild-type λ-phase ssDNA can be described by the freely jointed chain (FJC) model only at low force (<10 pN). To explain the behavior at higher force they used a modified freely jointed chain (mFJC) model [1,3] with stretch-dependent Kuhn length. Subsequently, it was discovered that synthetic ssDNA has interesting sequence-dependent properties. For example, polydA was found to have a higher bending rigidity than polydT and consequently polydA takes a longer time to form a loop [4]. Furthermore, the loop formation time varies exponentially with inverse temperature which can neither be explained by FJC nor by worm-like chain (WLC) models, which are generic models for flexible and semi-flexible polymers, respectively. This behavior was attributed to the strong stacking interaction among pyrimidine bases in polydA [4–6]. Subsequently, FX characteristics of polydA revealed that it undergoes two successive transitions under external stretching [7,8], generating two distinct plateaus in the force-extension (FX) curve. The first one at ~23 pN force was proposed to be a helix-to-coil transition in which the inter-base stackings are broken and helical polydA segments transform to a polydA coil. The second transition at ~114 pN force was attributed to the overstretching of the constituent bases. It was conjectured [3,7] that overstretching results from the conformational change of the sugar molecules from C3’-endo to C2’-endo pucker conformation.

The Zimm-Bragg model [9,10], which was originally proposed to explain the temperature-driven helix-coil transition in polypeptides, has been used to study the force-driven helix-coil transition in homo-polypeptides [11] and in polydA [12,13]. Theoretical models have used the exact evaluation of partition function [11] and mean field approximation [12,13] to explain the plateaus experimentally seen in the FX diagrams of homo-polypeptides and DNA. Specifically, the 1st plateau of polydA at low force (< 60 pN), was addressed in ref. [14] using the mean field theory. But the second plateau of polydA [7,8] involving the overstretching transition, is beyond the scope of these models.
Overstretching data from ssDNA [3] and RNA [15] have been analysed by modified FJC and modified WLC models, respectively. These models were adequate for describing continuous overstretching with force. On the contrary, polydA exhibits an abrupt overstretching at a threshold force. This begs for a new quantitative model with a distinct transition, which we propose here. Originally, such abrupt overstretching behavior was reported for wild-type dsDNA [3] at approximately 65 pN force and was subsequently studied using Ising-like two-state models by various groups [16,17].

Here we propose a unified model which quantitatively reproduces both the force-driven behavior (including both the transitions at high and low forces), as well as zero-force conformational fluctuations like the loop formation time, as observed experimentally. The double-plateau behavior in FX curves has also been addressed before [18,19], theoretically, albeit using a lattice model. But lattice models generically underestimate entropic effects. Furthermore, a quantitative comparison to experiments could not be made using this lattice model. The results were at best qualitatively similar to the experimental observations.

Model. — We model polydA as a chain of connected segments, each representing a nucleotide. The length of a segment (bond) represents the phosphate-to-phosphate distance in a dsDNA backbone. The bond length can be \( l_b, l_c \) or \( l_s \) depending on whether the segment is in the helix \((l_b = 0.37 \text{ nm})[14]\), coil \((l_c = 0.59 \text{ nm})[2]\), or overstretched-coil state \((l_s = 0.7 \text{ nm})[7]\). While the value of \( l_c \) has been well documented [2] in the literature, \( l_b \) is determined [14] by noticing the 1.6 times increase in the contour length of polydA upon helix-to-coil transition. Here \( l_b \) is the projected length of the helical contour on the central axis of the helix. Furthermore, \( l_s = 0.7 \text{ nm} \) has been inferred from the maximum extension reached by the polydA chain under very high force (\(~600 \text{ pN}\)) in refs [7,8]. Incidentally, \( l_s = 0.7 \text{ nm} \) also matches with the distance between the deoxyribofuranose ring in the C2'-endo pucker conformation. In our model, the state of a segment is characterized by \((\mu, S)\), where \( \mu \) can take values 0 or 1, corresponding to the coil or helix state, respectively. Once in the coil state \( \mu = 0 \), there are two possible states: the normal coil or the overstretched coil, corresponding to bonds lengths \( l_b \) and \( l_s \). These two states are represented by \( S = -1 \) and \( S = +1 \), respectively. Hence, there are only three possible states \((1, -1), (0, -1)\) and \((0, 1)\), corresponding to helix, coil and overstretched coil. The Hamiltonian of this three-state model of polydA (omitting the external force) is

\[
H_0 = \sum_{i=1}^{N} (2(1 - \mu_i)\mu_{i+1}\Delta w + \mu_{i+1}\Delta f - JS_i S_{i+1}(1 - \mu_i)(1 - \mu_{i+1}) + h S_i (1 - \mu_i)).
\]  

(1)

This Hamiltonian incorporates two transitions, actually cross-overs, since the model is one dimensional. The first part of the Hamiltonian involving \( \Delta w \) and \( \Delta f \) is the simpler version of the original Zimm-Bragg model [9,10], forwarded by the authors themselves and later used by Tamashiro et al. [11] in the context of force extension of polypeptides. The weight of the configurations \( cc, hc, ch, hh \), in this model, are given by \( 1, 1, \sigma s \) and \( s, \) respectively. Here \( \sigma = e^{-2\Delta w/k_B T} \) and \( s = e^{-\Delta f/k_B T} \), where \( 2\Delta w \) is the interfacial energy between the helical and the coil domains and \( \Delta f \) is the difference of the energy between the helix and the coil state. The second part of the Hamiltonian is an Ising Hamiltonian, which will be invoked, when the segments are in the coil or overstretched-coil state i.e., when \( \mu = 0 \). \( J \) measures the correlation energy between an adjacent coil and an overstretched-coil state. \( 2h \) is the energy difference between the coil and the overstretched-coil state. In the literature, the parameters \( \sigma \) and \( J \) are called the cooperativity parameters of the respective transitions.

The helix-coil transition in polyA and that in polyG have so far been theoretically modeled [11,14] by assuming their helical parts to be rigid rods (i.e., having persistence length, \( a_h = \infty \)) and the coil parts to be FJC segments. On the contrary, the experiments by Mills et al. [20] reported \( a_h \sim 8 \text{ nm} \) for polyA and Smith et al. [3] reported the persistence length of the wild-type \( \lambda \)-phase ssDNA coil to be \( a_h \sim 1.5 \text{ nm} \). Furthermore, Seo et al. [15] estimated \( a_h \sim 1 \text{ nm} \) for polyU from their experimental data. In our model we therefore consider the ssDNA chain to be semi-flexible, in which the helical, coil and overstretched-coil domains have realistic persistence lengths. \( a_h, a_c \) and \( a_s \) are the respective persistence lengths. The discretized worm-like chain Hamiltonian for the system is

\[
\beta H_{\text{bend}} = \sum_{i=1}^{N-1} \left\{ \frac{a_h}{2} \mu_i (\mu_i+1) (1 - \mu_i)(1 - \mu_{i+1}) \right. \\
\left. \times \left( \frac{a_c}{8} (1 - S_i)(1 - S_{i+1}) + \frac{a_s}{8} (1 + S_i)(1 + S_{i+1}) \right) \right\} (1 - \cos \theta_{i,i+1}).
\]

(2)

Here, \( \theta_{i,i+1} \) is the angle between the bond vectors \( \vec{t}_i \) and \( \vec{t}_{i+1} \), where \( \vec{t}_i = R_{i+1} - R_i \), and \( R_i \) is the position vector of the \( i \)-th monomer. The Hamiltonian has been constructed in a way such that different bending rigidities are invoked when the neighboring bonds are of the same type, i.e., \( hh, cc \) or \( ss \).

For the purpose of the calculation, we substitute the inter-bond angles in terms of bond vectors: \( \frac{1}{2}(1 - \cos \theta_{i,i+1}) = \frac{1}{2}(l_{i+1} - l_i)^2 \). Finally, including the external stretch \( F \), the total Hamiltonian is

\[
H_{\text{total}} = H_0 + \beta H_{\text{bend}} - F \cdot (R_N - R_0) = \sum_{i=1}^{N-1} H_{i,i+1}^{i+1}. \]

(3)

The force-dependent term above can be expressed as \( F \cdot \sum_{i=1}^{N} l_b \vec{t}_i \) in terms of the bond vectors and their respective lengths \( l_i \), where \( l_i \) could be \( l_b, l_c \) or \( l_s \) depending on the internal state \((\mu, S)\) of the bond.
Finally, the partition function is $Z(F) = \int \prod_{i=1}^{N} d\hat{t}_i \sum_{\{\mu_i, S_i\}} \exp[-\beta(H_0 + H_{\text{bend}} - FR_x)]$, where $R_x = (R_N - R_0) \hat{x}$ is the projection of the end-to-end distance along the force $F = FR_x$. Using the transfer matrix technique we can write $Z(F)$ for the stretched chain as

$$Z = \sum_{\mu_1, S_1, \hat{t}_1, N, S_N, \hat{t}_N} \langle \mu_1, S_1, \hat{t}_1|T^{N-1}|\mu_N, S_N, \hat{t}_N \rangle. \quad (4)$$

Here $T$ is the transfer matrix with elements

$$\langle \mu_i, S_i, \hat{t}_i|T|\mu_{i+1}, S_{i+1}, \hat{t}_{i+1} \rangle = \exp(-\beta H_{\text{total}}^{i+1}). \quad (5)$$

While for a simple 2-state Ising chain, $T$ would be a $2 \times 2$ matrix corresponding to the states $(1, 0)$, $(0, 1)$, here $T$ is a $3M \times 3M$ dimensional matrix corresponding to the state space $(\mu_i, S_i)$ $\otimes$ $\hat{t}_i$. The dimension $3M$ arises because the internal state space $(\mu_i, S_i)$ is three-dimensional, corresponding to the states $(1, -1), (0, -1), (0, 1)$, and the orientation space $\hat{t}_i(\phi, \theta)$ is discretized into $M$ subdivisions. In particular, we divide $\phi$ and $\theta$ spaces into $m$ and $n$ bins, respectively, and therefore, $M = m \times n$. In most applications of the transfer matrix method, where periodic boundary conditions can be used, one obtains $Z(F)$ as $\lambda_{\text{max}}^N$, where $\lambda_{\text{max}}$ is the largest eigenvalue of $T$. But here the polymer has one of its ends ($\hat{t}_1$) fixed and the other end ($\hat{t}_N$) stretched by a force. Therefore we cannot use periodic boundary conditions, instead $Z(F)$ is obtained in eq. (4) as a sum over all the elements of $T^{N-1}$. In the case of the simple Ising chain, eq. (4) would read $Z = \sum_{s_1, s_N} \langle s_1|T^{N-1}|s_N \rangle$ which would amount to summing over all the four elements of the $T^{N-1}$ matrix. One additional complication in our present case is that while the $(\mu_i, S_i)$ space is discrete, the orientation space $\hat{t}_i$ is continuous. So all our discrete sums over $\hat{t}_i$, which are actually surrogates for $\int d\hat{t}_i$, have to take care of weighing factors $d\hat{t}_i = \sin \theta d\theta d\phi$. The details of this calculation are similar to those in ref. [21]. After calculating $Z(F)$ we can finally compute the average extension $X \equiv \langle R_x \rangle$ as a function of the force using $\langle R_x \rangle = \frac{1}{2} \frac{\partial}{\partial \beta} \frac{\partial}{\partial F} Z$. We have also performed a Monte Carlo (MC) simulation of the model (using the same parameters as in our transfer matrix calculations) to compute the fractions of bonds in the helix, coil and overstretched-coil configurations at any given force. Our MC simulation uses crankshaft moves to rotate the bonds.

**Force-extension behavior.** – In general the stretching force tends to align the chain along the force ($\hat{x}$), at the cost of entropy. It would also favor the individual bonds to have their highest possible bond lengths, i.e., 0.7 nm, in order to maximize the $FR_x$ term. This is achieved only at very high force when the other terms in the Hamiltonian give in to the force term. But at low and intermediate force the other terms compete. Although helical segments are favored over coil segments (due to $s$), at low force and at room temperature, entropy has a substantial contribution. As a result, all the segments are not aligned along the force. That is why the extension per base, at very low force is about 0.2 nm and not 0.37 nm (see fig. 1). But bending of the helical domain is disfavored by its large persistence length. Therefore, at low force, the entropy-induced bends help some helical segments to convert to coil, which have higher internal energy but lower bending energy compared to helical segments. As the force rises, the $FR_x$ term enforces alignment as well as stretching of the bonds, leading to a stacking-unstacking transition which adds extra length (that was previously curled up in helix) to $R_x$. The abrupt nature of the helix-coil transition results from cooperativity, $\sigma = e^{-2\Delta \phi/k_B T}$, where $2\Delta \phi$ is the strength of the coupling term $\mu_1 \mu_{i+1}$ in the Hamiltonian.

In fig. 1 we compare our numerical results with the FX curve in ref. [8] (in particular their L-pathway) which is very close to that in ref. [7], except that in ref. [8] it has a kink at the onset of the second plateau. In ref. [8] two pulling speeds were used during stretching, which resulted in two different pathways, namely, $H$ and $L$; but relaxation always occurred through the $L$-pathway. The $L$-pathway presumably shows a quasi-equilibrium behavior since, a) it was obtained at low speed, b) the relaxation always occurred through the $L$-pathway, and c) it matched with ref. [7]. The $H$-pathway, which shows kinetic effects, is beyond the scope of our equilibrium methods. We used three different chain lengths $N = 17, 33$ and 65, to check the $N$-independence of our FX curve in fig. 1.

For all our figures, the parameters used are $a_h = 12\text{ nm}$, $a_s = a_c = 1.5\text{ nm}$, $\Delta f = -4.9k_B T$, $\sigma = 1.8 \times 10^{-3}$, $J = 0.44k_B T$, $h = 1.5k_B T$, where $T$ is the room temperature. To estimate these parameters it is useful to note
that the free-energy change ($\Delta A$) for the transitions can be obtained from the experimental FX curve as $\Delta A = \int F \cdot dx$. As a check, we integrate the experimental FX curve from $X = 0$ to $X = 0.52$ nm, which is approximately the end of the first plateau (the corresponding force is about 40 pN). We get $\Delta A = \int F \cdot dx \sim 1.2$ kT. This is consistent with the reported values of the stacking free energy 1.1 kT, obtained from calorimetric measurements [22]. Continuing this analysis the threshold force for the first transition can be estimated. Integrating the FX curve from 0.37 nm to 0.52 nm (i.e., over the width of the first plateau, $\Delta X = 0.15$ nm), one gets $\Delta A = 3.45$ pm nm. This area being an approximate rectangle we can estimate the threshold force (area/height) to be 3.45 pm nm/$\Delta X \sim 23$ pN.

The estimation of some of the parameters used for the FX curve were helped by having the two plateaus well separated in force, $h$ and $J$ are determined by the height and the sharpness of the second plateau. Furthermore, for the range 0.59–0.7 nm, the free-energy change, $\Delta A = \int F \cdot dx \sim 3$ kT, is approximately equal to the enthalpy change $\Delta H$, since at that high force (>100 pN) the polymer is almost straight and has very little entropy. From our model Hamiltonian $\Delta H = 2h$, and hence $h = 1.5$ kT. For the remaining parameters $a_h$, $\Delta f$ and $\sigma$ we explored the ranges $a_h = 6–14$ nm, $\Delta f = 4–6$ kT and the cooperativity $\sigma = 10^{-4}–10^{-3}$ (note than what appears in the Hamiltonian is the log of $\sigma$). These ranges were motivated, as mentioned earlier, by the experimental estimate for $a_h$ which is 8 nm [20] and by refs. [11–13] which have explored an even broader range of $\sigma$ values. Good fits to the FX and the loop closing data (as shown in the figures) were achieved for the values mentioned above.

From our model and the chosen parameters we estimate the enthalpy change for the $h \rightarrow c$ conversion to be $\Delta H = \Delta f - J - h \sim 3$ kT, and for the $c \rightarrow s$ conversion to be $\Delta H = 2h = 3$ kT. Thus, the stacking enthalpy is about 3 kT in our model. We note that the stacking enthalpy estimated by different groups vary widely, namely, between 5 kT to 13.3 kT (see [5,6] and references in [6]). Furthermore, these estimates are model dependent. Attempting to estimate the stacking energy from the total area under the FX curve [7] is also not appropriate, since firstly, it is the free energy (not enthalpy) and secondly, it includes contribution from the overstretching transition as well. On the other hand, as discussed earlier, estimates of the stacking free energy of polydA are more dependable, as both calorimetric data [22] and experimental FX data agree on a value of about 1.1 kT. For the $h \rightarrow c$ transition our model suggests $\Delta A = 3$ kT · $T(S_c - S_h)$. Since the entropy of the coil is greater than that of the helix ($S_c - S_h > 0$), we expect $\Delta A(h \rightarrow c) > 3$ kT, which is consistent with experimental data.

Given that polydT and polyU do not have any significant stacking interaction, they might be expected to follow the $\Delta f = \Delta w = 0$ limit of our model. But polydT and polyU also have a qualitatively different overstretching behavior than polydA: they overstretch slowly with force (unlike the abrupt transition in polydA). The FX behavior of polyU has already been explained by a modified WLC model [15] and we checked that the same modified WLC model [15] can also explain the FX behavior of polydT but with different parameters.

**Loop formation kinetics.** Now we discuss the zero-force conformational fluctuations resulting from our model. We focus on the observations made by Goddard et al. [4] on loop formation properties of short ($N = 8–30$ bases) polydA and polydT chains. They attached the complementary base sequences TTGCC and AACGG at the two ends of a polydA/polydT strand and fluorophore (F) and quencher (Q) molecules at the ends. This design aimed to detect the formation of hairpin loops by zipping complementary base-pairs at the ends. Such a process resulted in a quenching of fluorescent intensity of $F$ by $Q$.

They found that, for a given chain length, a polydA chain took longer time than a polydT chain to form a loop. This indicates a greater bending stiffness for polydA chains, resulting from the stacking interaction between adenine bases. More intriguing was the result that the loop closing time $\text{ln}(\tau_c) \propto \beta$ for polydA and that there was a nearly flat temperature dependence for polydT.

A simple model made of stacked and unstacked bonds (rods and coils) was proposed in ref [6] to explain the Arrhenius-type temperature dependence of the loop closing time. Here we apply a similar analysis to our present model which is more realistic. The polymer conformations can be approximately described by a two-state system: an open chain ($o$) and a chain forming a closed loop ($c$). At equilibrium, the interconversion $o \leftrightarrow c$ obeys a detailed balance condition: $\rho_c k_{c \rightarrow o} = \rho_o k_{o \rightarrow c}$ [6], where $\rho_c/o$ are the equilibrium densities and $k_{c \rightarrow o}$, $k_{o \rightarrow c}$ are the conversion rates. Loop closing and opening times, $\tau_o$ and $\tau_c$, are inverses of the respective rates. Assuming a small interaction radius $a$ between the chain ends, approximately $\rho_c = \frac{4\pi}{3} a^3 P_N(\tilde{R} = 0)$, where $P_N(\tilde{R})$ is the probability of finding the chain ends at a separation $\tilde{R}$. But since the possible number of open configurations far outweighs the number of closed configurations i.e., $\rho_o \gg \rho_c$, we can approximate $\rho_o = 1 - \rho_c \approx 1$ [6]. This is elaborated in fig. 2. Furthermore, $\tau_o$ is determined by the high-energy barrier of the five-bases long zipping strand, which is independent of the chain length $N$, and hence is a constant. Thus, we arrive at $\tau_c \propto \rho_c^{-3/2}$, which we can compute from our model, as a function of the chain length ($N$) and temperature, at zero force. In fig. 3 we plot $\tau_c/N^{3/2}$ vs. the inverse temperature obtained from our model and compare it with the experimental data of Goddard et al. [4]. The rationale for rescaling $\tau_c$ by $N^{3/2}$ is to partially nullify the strong $N$-dependence in $\tau_c$. Although $\rho_c \propto N^{-3/2}$ only for an FJC model (at large $N$) and not for a WLC model, it turns out to be useful in approximately collapsing both our simulation data and Goddard et al.’s experimental data for large $N(\geq 16)$, near the room temperature.
Temperature dependence of extension. – The change of extension with temperature has been demonstrated to show an interesting behavior for wild-type ssDNA [23]. Figure 4 shows the analogous property resulting from our model of polydA, at fixed force, computed using the transfer matrix method. In the absence of any transitions polymer extension is expected to decrease with temperature because of entropic elasticity, as it happens in rubber, for example. In the case of wild-type ssDNA hairpin loops can form which modifies the extension-temperature behavior in nontrivial ways. For polydA, although loops cannot form in the absence of complementary bases, the existence of two transitions (helix-coil and overstretching) makes it behave in an interesting way (see fig. 4(A)), to the extent that a weak, nonmonotonic, re-entrant behavior can be observed (fig. 4(B), (C)). These can be understood qualitatively. Two important points to remember here are: a) the helix-coil transition can also be affected by raising temperature, and b) entropic fluctuations are enhanced at high temperatures which smoothen the force-driven transitions (data not shown). Figure 4A shows that at a very low force like 5 pN, indeed extension weakly decreases with temperature, but when force rises (10 pN onwards) as we move close to the helix-coil transition, it is easier to affect the transition by raising the temperature and the helix-coil transition leads to a rise in the extension. However at forces just beyond the helix-coil transition (30 pN onwards but much below 100 pN) the ssDNA cannot access the overstretched bond lengths solely by means of thermal fluctuations and it looses out to entropic elasticity thus showing a decrease in the extension with temperature. As the force approaches
100 pN, due to its vicinity to the overstretching transition, the extension again increases, first, but eventually loosens out to entropic elasticity at higher temperature, giving rise to a re-entrant behavior. Beyond the overstretching transition extension again decreases weakly with temperature due to entropic elasticity; weakly because at such high force not much entropy is left in the chain, which is almost straight.

**Conclusion.** – We have proposed a new model for polydA that incorporates two transitions and quantitatively reproduces both force-extension characteristics and loop closing statistics of such homopolymers. Our model also predicts a weak nonmonotonic behavior in the temperature-extension diagram of polydA. In principle, our model can be extended to describe the phenomenology of heterogeneous ssDNA, provided that sequence-dependent stacking and consequent bending properties are included in the model. Furthermore, the possibility of hairpin loop formation in such heterogeneous sequences has to be accounted for by including base-pairing interaction strengths [24].

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