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REVIEW ARTICLE

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Relaxation of a Worm-Like Chain

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MICROTUBULE MECHANICS DEPART FROM THE WORMLIKE CHAIN MODEL

Microtubules are cytoskeletal protein filaments that play an essential role in a multitude of cell functions in all eucaryotes. While specialized structures such as cilia, fla- gella, and axons require microtubule lengths of up to several hundred micrometers, fundamental tasks like cell division and intracellular transport involve microtubules with lengths that are comparable to or smaller than typical eucaryotic cell sizes (10-20 μm). In solution, microtubules undergo strong thermal shape fluctuations but, due to their rigidity, maintain an average direction and are therefore referred to as semiflexible. The standard model for semiflexible polymers is the wormlike chain which envisions a homogeneous, isotropic, continuously flexible rod characterized by its bending stiffness, κ.

Recently, evidence has accumulated suggesting that the wormlike chain as the standard model for semiflexible polymers may constitute an oversimplification in the case of microtubules due to their highly anisotropic molecular architecture. Microtubules consist of strings of α- and β-tubulin heterodimers, so-called protofilaments, that are arranged in parallel forming a hollow tube of 25 nm external diameter. Neighboring protofilaments are shifted relative to each other, giving rise to helicity. Both the rise per turn and the number of protofilaments may vary; however, 3 monomers per turn and 13 constituent filaments are most common *in vivo*. This protofilament architecture makes microtubules a model system for the generalized theory of wormlike bundles. which in addition to various other biological examples also describes the mechanics of carbon nanotube bundles.

Few studies have addressed the dynamics of thermal shape fluctuations of microtubules even though the time scales of these fluctuations affect the time scales on which biological functions occur. Caspi *et al* examined the transverse mean square displacement of microtubules in networks, finding a power law behavior $t^{3/4}$. Janson and Dogterom extracted autocorrelation times for several modes from a shape analysis of growing grafted microtubules. while Brangwynne *et at.* [II] applied this procedure to stabilized fluorescent microtubules. For technical reasons, all of these studies restricted themselves to lengths of several tens of micrometers, while microtubule lengths relevant to cell functions such as cell division are much shorter. In a study of equilibrium position distributions, he most significant systematic deviations from the wormlike chain model were found for microtubules shorter than — 20 μm which coincides with the length regime most crucial to cell division and intracellular transport. This suggests that, in this length regime, corresponding deviations should exist for dynamical parameters such as the relaxation time.

In this Letter, we present an analysis of first mode relaxation times for microtubules of length 2-30 μm. Microtubules are grafted to a substrate at one end and data are extracted from the mean square displacement of the transverse coordinate. Capturing dynamics for microtubules that are only several /*m long is challenging since the corresponding spatial and temporal scales become increasingly small. We overcome these difficulties by using small fluorescent beads attached to the microtubules as tracer particles. Their position can be tracked at frame rates of up to 30 Hz using a high quantum efficiency CCD camera. In contrast to shape analysis techniques that provide low resolution (tens of nanometers position data for the whole filament, the use of the tracer bead yields spatial information with a precision of a few nanometers for one specific point on the filament's contour. Standard semiflexible polymer models are then used to infer relaxation times, bending stiffnesses, and drag coefficients.

MONOMER DYNAMICS OF A WORMLIKE CHAIN

Many of the instruments ready to a trial biophysicist test either the variances of scmiflexible polymers or their reaction to outside powers. This incorporates dynamic light diffusing, animated and latent microrheology of polymer systems or cells, attractive bead winding cytometry, DNA relaxation and extending, single-atom power spectroscopy and electron exchange systems. From a speculative outlook, these routines uncover distinctive parts of the wormlike chain (WLC) model. It gives an insignificant portrayal of scmiflexible polymer material science as far as an inextensible, thermally fluctuating flexible shaft, and has discovered wide

acknowledgement on the grounds of its brilliant concurrence with test information.

Distortions of the polymer shape animate a wide range of curving modes with broadly different relaxation times, hence bringing about peculiar, subdiffusive dynamics. In the straight administration, good for harmony fluctuations or minor outside strengths transverse to the polymer spine, the dynamic mean-square uprooting of a tagged(but mechanically unaltered) monomer obeys $\widetilde{\mathrm{MSD}}_{\perp}(t) \propto t^{3/4}$. For variances parallel to the polymer hub, the supplemental longitudinal dissolvable friction impels tension drives which, in turn, solidify the polymer and give ascent to an alternate scaling conduct, $\mathrm{MSD}_{\parallel}(t) \propto t^{7/8}$. Tension additionally rules the reaction to solid indicate powers and remotely infringed dissolvable streams; the coming about mathematical statements of movement are exceedingly nonlinear and can produce an incalculable number of distinctive dynamical administrations even in the process of a solitary analysis.

In numerous maneuvers of pragmatic investment, a full assessment of the dynamics might be unnecessarily confounded and wasteful, since trial control and information securing are firmly localised, say, to a joined tracer molecule, or a tagged monomer, in the accompanying basically implied as "the tracer". More remote parts of the polymer matter just insofar as they donate to the energy on the tracer. It can then be ideal to combine out the polymeric degrees of opportunity already and subsume them under an effective mathematical statement of movement depicting the tracer arrange just. This diminished portrayal is, for instance, known for the critical unique instance of a tracer subjected to a remotely endorsed deterministic drive methodology. It can't, on the other hand, effectively be expanded to oblige for the fluctuating strengths pushed onto the tracer by a remotely regulated restriction potential. Down to earth illustrations that include this potential are given by different single-atom control systems (consider. e.g., of an actin fiber labelled with a gold nanoparticle that is trapped by optical tweezers). The examination of heightened recurrence shape changes of globular proteins, as measured by electron exchange methods gives a different imperative sample. In reality, the WLC has been proposed as one conceivable model of protein vacillations, yet to date just numerical assessments of the corresponding clamor and contact capacities are ready inside a mean-field close estimation to the WLC.

TUNING RHEOCHAOS BY SIMPLY TEMPERATURE INSIDE WORMLIKE MICELLES

Woimlike micelles are long semiflexible round and hollow totals of surfactant monomers, typically $\approx 1\ \mu\mathrm{m}$ long and about $\approx 3-4$ nm in breadth and can unwind stretch through two instruments: reptation. practically equivalent to polymers, and breaking and recombination. The last procedure of unwinding push, not discovered in polymeric frameworks, prompts a plenty of novel stream conduct under unassuming outer shear. One angle in the nonlinear stream conduct of wormlike micelles that has pulled in much consideration as of late is shear banding. For shear-thinning frameworks, above a discriminating shear rate, the anxiety declines with further build in the shear rate, and this stream is mechanically precarious. The framework along these lines parts into towering and level shear rate groups that coincide at a normal push. For shear-thickening frameworks, the opposite happens, and there exists elevated and level stretch groups at a regular shear rate.

This marvel termed shear banding shows itself as a level in the measured stream bend. Shear banding with a stable shear band interface was initially expected by Gates et al. for shear-thinning wormlike micelles. In any case, there is surmounting exploratory confirmation indicating the above picture to be lacking. In numerous frameworks, shear banding is went with by aperiodic variety in the anxiety or shear rate in relaxation estimations. This marvel termed rheochaos happens at basically zero Reynolds number and emerges from the inherent nonhnearities in the viscoelastic comparisons. Hie phenomenon was initially watched tentatively by Bandyopadhyay et al. in anxiety relaxation estimations for shear thinning wormlike micelles of surfactant cetyltnmethylammomum tosylate (CTAT).

A careful nonlinear time arrangement examination of the anxiety vs time information uncovered the being of deterministic disorderly dynamics. Since then rheochaos has been watched in a wide assortment of different frameworks incorporating shear-thickening wormlike micelles, lamellar and onion stages of surfactants, and thick colloidal suspensions. Later exploratory methods such as Nmr velocimetry and optical estimations consolidated with tried and true rheology to test the shear band dynamics have demonstrated that the band interface in fact shows complex spatio-temporal changes, and this is went with by stress/shear rate vacillations.

In speculative models for rheochaos spatial heterogeneity is a nexus part. C'liakrabarti et al. have considered the spatio-temporal advancement of the traceless symmetric request parameter for a nematogenic liquid and have discovered bedlam in a certain locale of parameter space and the track to this confusion is by means of a regmie of spatio-temporal intemnttency. Doors et al. have proposed a phenomenological model for a shear-thickening liquid with memory and a tendency to structure shear grouped streams with one level of opportunity: shear stress. They have additionally examined a spatially inhomogeneous enlargement of this model, with spatial variety in the vorticity heading and find rich

spatio-temporal conduct. The speculative model of significance to shear-thinning wonnlike micelles is because of Fielding and Olmsted which considers the coupling of stream to the mean micellar length. By tuning the quality of this coupling, stable, mtermittent. also disorderly shear joined states were seen.

In all shear rate/stress relaxation analyses reported thus far. the stress/shear rate is the control parameter and the temperature is held settled. Shear stream can impact the framework in two ways: (i) it can either upgrade breaking of the micelles or (ii) the finish to-end arrangement of the micelles under stream can accelerate lengthening. The model by Fieldmg and Olmsted16 collects the previous. We might include that tentatively it is not clear which of the above happens. As of late. Ganapathy et al. have demonstrated that the track to confusion is by means of sort Ii irregularity in anxiety relaxation estimations and sort in irregularity in shear rate relaxation estimations for the shear thinning wormlike micellar arrangement of CTAT 2 wt % in the vicinity of salt sodium chloride (NaCl) which indicates solid coupling of stream to focus changes. A critical thing to note is that the speculative model by Fieldmg and Olmsted predicts a Hopf bifurcation in anxiety relaxation fundamental for watching the Type-Ii discontinuity track to bedlam. Given the solid likenesses between speculative forecasts and test perceptions, it is common to ask the pretended by the coupling of stream to the micellar length in a trial framework. It is well-realized that the mean micellar length is to a great degree touchy to temperature and diminishes with expansion in temperature. In this study, we have done anxiety's shear rate relaxation estimations at a settled shear rate/stress with temperature as the control parameter and along these lines control the micellar length. We discover that shear accelerates prolongation of micelles throughout the track to rheochaos.

A MIXED WORMLIKE-CHAIN AND ALSO BEAD MODEL FOR ACTIVE SIMULATIONS ASSOCIATED WITH LONG LINEAR DNA

The large-scale dynamic motions of double helical DNA are important for many biological processes, from protein/ DNA interactions to higher-order DNA folding and recombination. Several approaches have been developed during the past decade to model DNA dynamics on the basis of low-resolution models. Such approaches allow simulation of slow motions in long DNA molecules that are not possible to capture with standard all-atom simulations, unfortunately limited to several dozen residues. However, modeling slow motions in large DNA molecules remains a challenge. In particular, it is difficult to simulate slow processes in double-stranded supercoiled DNA where torsional rotation of the chain segments is important. This is a broad objective of the simulation protocol developed here. In this study, we focus on linear DNA. In a second work we continue to treat closed circular DNA, where additional terms are required, and to study biological questions. In particular, our goals here are to verify the model parameters and protocols with respect to all relevant experimental data and equilibrium simulations, to choose the most efficient algorithms, and to test different approximations to increase the speed of the computations.

Our model is based on the classical discrete wormlike chain and is close to the approach introduced by Allison and McCammon. It combines the wormlike chain features with those of a bead model, which has been used extensively for polymer hydrodynamics. The working model accounts for two essential features of the double helix: the bending potential and the electrostatic interaction between chain segments. Electrostatic interactions are not standard components of Brownian simulations. Electrostatic contributions are significant for the conformational properties of long DNA molecules, especially in compact topologically constrained circular DNA. An explicit electrostatic potential also offers a computational advantage over a simple excluded-volume term since its smoothness allows the use of larger integration timesteps without force-discontinuity artifacts. An electrostatic potential has recently been added to the DNA model of Chirico and Langowski. but details are lacking in that work, as well as a description of how different salt concentrations are modeled. Our model also contains a stretching potential to facilitate dynamic simula-tions. The effect of the stretching rigidity constant on obtained dynamic properties of the model is also closely examined in this work.

Details of our computational procedure are presented, along with discussions of parameter choices. Model details are assessed through comparisons of results to equilibrium simulations for the same model, as well as to available experimental data (translational diffusion coefficients). Excellent agreement is obtained for all equilibrium and dynamic properties examined (e.g., end-to-end distance, bending distributions, persistence length, and translational diffusion coefficients).

For generation of molecular trajectories, we rely on the theoretical framework of the generalized Langevin equation used previously in the simplest form by Schlick *et al.* Here, we use the Brownian dynamics (diffusive) regime to study the long-time motion of large-scale DNA systems.

We emphasize that our focus in this work is a careful and detailed development of a macroscopic computational model for dynamic simulations, addressing all issues of potential functions, chain representation, and propagation algorithms. Such issues must be satisfactorily completed to ensure that

there are no artifacts in later results. The excellent agreement obtained with respect to available Monte Carlo, theoretical, and experimental data establishes a reliable and efficient protocol for dynamic simulations of long DNA. Extensions to circular DNA and to site-juxtaposition studies have already been described in the Ph.D. thesis of Jian, and will be published separately.

CALCULATING THE PERSEVERANCE LENGTH OF A NEW WORM-LIKE CHAIN MOLECULE THROUGH FORCE-EXTENSION DIMENSIONS

Stretching individual bio-molecules is now achieved by a variety of techniques including flow stress (Smith et al., 1992), AFM (Rief et al., 1997), micro-needles (Cluzel et al., 1996), optical tweezers (Wang et al., 1997), and magnetic tweezers (Strick et al., 1996) that allow measurement of forces from 10 femtonewtons to hundreds of piconewtons. Different biological molecules have now been analyzed (Kellermayer et al., 1997) and the accuracy of these techniques has sufficiently improved so that the theoretical models used to analyze force-extension curves must be refined. In particular, Bustamante et al. (1994) have shown that the force-extension diagram of a DNA molecule is well described by a worm-like chain (WLC) model. In this note, we present a simple derivation of the WLC model whose solution can easily be implemented on a personal computer.

Furthermore, we propose an improvement to the Marko and Siggia (Bustamante et al., 1994) interpolation formula with a relative error in force of 0.01% for any given extension. This new interpolation scheme is easy to introduce into fitting algorithms and allows for accurate estimation of the persistence length. We propose and discuss the possibility of taking into account the enthalpic elasticity contribution that is observed experimentally in force-extension curves.

A BREATHING WORMLIKE CHAIN MODEL ON DNA DENATURATION AND BUBBLE

Dna is an adaptable biopolymer which shows different compliances to viably keep and convey its hereditary information for natural capacities. At physiological conditions, it regularly structures Watson-Crick's twofold strand structure through hydrogen-holding between correlative bases and stacking communications around bases." The twofold strand structure, in vivo, is opened by atomic apparatuses for example Rna polymerase to read Dna arrangements throughout transcription and replication forms. Without this enzymatic action, the structural disturbances can additionally be impelled by thermal vigor. Upon warming at around 350 K, a twofold stranded Dna (dsdna) totally denatures into two single-stranded Dnas (ssdna). Liquefying bends got from Uv ingestion uncover that the denaturation happens in a sharp way and shows essentially multisteps for heterogeneous in length arrangements. At physiological temperatures, it could be provincially opened to permit transient bubbles, whose relaxation times were assessed to normally a few several microseconds by fluorescence association spectroscopy (Fcs) measurement/' Thermal denaturation. viewed as a novel illustration of one-dimensional stage move, has been since a long time ago concentrated on. As of late, as biotechnology developments in a level to control single biomolecule, comprehension the thermal security of Dna is additionally significant to plan stable Dna architectures and Dna cloning examination utilizing polymer chain response.

Stacking cooperations are intricate noncovalent interactions coming up from Van der Waals, hydrophobic, electrostatic connections, and so forth., which make two neighboring bases lean toward entially shape the eye to eye structure. Their hefty vigor costs (1-2 kcal/mol) (Ref. 14) for destackings make it difficult to disturb the duplex structure at physiological conditions. Momentously, an investigation demonstrates that the base stacking gives extraordinarily to Dna inflexibility contrasted with the phosphate spine; meroduplexes, which have a hole loaded with bases without the phosphate spines at their middles, have determination lengths whose qualities are about 90% of the aforementioned of standard dsdna. As a rule, the stacking face to face times are tremendously improved when two reciprocal strands tie together on the grounds that bases are permitted to communicate not just with neighboring intrabases and yet with proximal interbases." accordingly, a dsdna turns into a firm chain of tirelessness lengths of in the vicinity of 50 nm, which is a request of size bigger than two times that (1-4 nm) (Ref. 17) of a ssdna. The stacking-prompted constancy length distinction can schematically be delineated as a capacity of the base detachment, as indicated in this Figure.

It has been demonstrated that the stacking collaborations and the stacking-incited chain solidness distinction are vital factors to acknowledge in comprehension thermal openings of dsd-Nas, i.e., denaturation and bubble creations. The experimentally acquired liquefying profiles could be quantitatively overall clarified bv denaturation models which acknowledge the base stacking. The Peyrard-Bishop-Dauxois (Pbd) model, which has a term portraying the stacking-impelled chain flexibility distinction, demonstrated that the irregular multistep move happens just when the stacking term was incorporated." The sharp move was additionally anticipated in the summed up Poland-Scheraga (Ps) model which unequivocally incorporates the level of flexibility for the stacking."" Recently, re-enactments through the Pbd model indicated that translation beginning locales have a tendency to shape thermal meanders of something like ten base combines more effortlessly than different destinations." Intriguingly,

this behav¬ior might be gotten just in the vicinity of the stacking term.

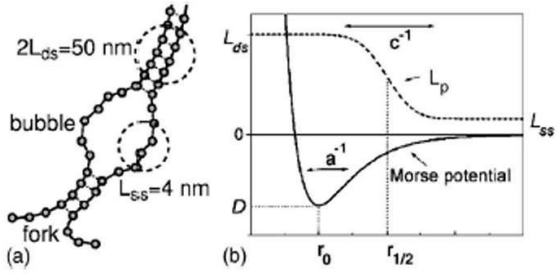

FIGURE : (a) Schcmatic of dsDNA which, due to thermal fluctuation, shows locally denatured structures, a "bubble" which has two closed ends, and a "fork" which has one closed end. In the dsDNA. the persistence length is $50\ \text{nm}=2L_{ds}$ for the double strands and $4\ \text{nm}=L_{ss}$ for the single strands, (b) Illustration showing the variance of L_p for bp distance r in comparison with the Morse potential *U(r).* When base pairs are locally dislocated from the potential minimum r_0, L_p for the local sites is smoothly lowered to L_{ss} from L_{ds}. It is also conjectured that the long relaxation time of thermal bubbles observed by the FCS (Ref. 6) is due to the destackings of bases in the bubbles, which hinder the closings of the bubbles.

These studies proved quantitatively significant roles of the stacking interactions on the thermal opening phenomena. Yet, understanding and prediction on the observed results by simple argument or theory are difficult because most results were obtained at situations where other relevant factors, e.g., sequence correlation, play also a crucial role. For this reason, recently, an efficient approach based on the PBD model to predict the probability for the occurrences of thermal bubbles was developed."" Also, the PS-type distribution of bubble sizes, which is simple to understand and analytically derivable, was used to successfully explain the bubble size distribution for real sequences.

The main purpose of this study is to elucidate clearly how the stacking-induced chain flexibility difference affects the thermal denaturation and bubble formations in dsDNAs. To this end. we generalize our previous DNA model, where a dsDNA is described simply as two wormlike chains (WLC) interacting each other via a pairing potential," to capture the flexibility difference. In our new model, the persistence lengths of the WLC duplex are presumed to increase when they are in proximity due to the stacking and. otherwise, have the values of a ssDNA. We perform the Langevin dynamics simulation and compare the results with those of the previous model without the stacking interactions at same conditions. Surprisingly, we find that large bubbles can be more easily formed in the presence of the stacking interactions which overall suppresses the occurrences of bubbles to stabilize the duplex structure.

This separation-dependent flexibility resembles that of the PBD model. An important advantage of our model is that via WLC incorporating the bending energy, it can be brought into contact with the real DNA characterized by a persistence length, which the PBD model, incorporating the stretching energy, cannot. Recently, a theoretical work using an idea similar to ours was used to calculate the denaturation transition profile and the persistence length of a dsDNA as a function of temperature" and showed the importance of different bending rigidities between a double- and single-stranded DNAs on conformational changes of dsDNA.

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