Helices at interfaces

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Abstract – Helically coiled filaments are a frequent motif in nature. In situations commonly encountered in experiments coiled helices are squeezed flat onto two-dimensional surfaces. Under such 2-d confinement helices form “squeelices” —peculiar squeezed conformations often resembling looped waves, spirals or circles. Using theory and Monte Carlo simulations we investigate the mechanics and the unusual statistical mechanics of confined helices and show that their fluctuations can be understood in terms of moving and interacting discrete particle-like entities —the “twist kinks”. We show that confined filaments can thermally switch between discrete topological twist quantized states, with some of the states exhibiting dramatically enhanced cyclisation probability while others displaying surprising hyperflexibility.

Introduction. – Helically coiled filaments are found everywhere in living nature. The list of examples is close to innumerable with the most prominent ones: FtsZ [1], Mrb [2], bacterial flagella [3,4], tropomyosin [5] and intermediate filament vimentin ([6], see figs. 5, 10 therein). More recently, microtubules were suggested to spontaneously form large-scale superhelices [7,8]. Even whole microorganisms exhibit helicity inherited from their constituent filaments [9]. The superhelicity of filaments is sometimes of strong evolutionary benefit, as in the example of swimming bacteria utilizing the rotational motion of their helical flagellar filament for propulsion [10] and tropomyosin’s helical “Gestalt-binding” around actin [5]. In other cases, such as microtubules, the purpose of superhelicity remains, so far, unknown [8]. Paralleling biological evolution, artificial, man-made helically coiled structures have been created including coiled carbon nanotubes [11], DNA nanotubes [12] and coiled helical organic micelles [13].

As happens often in experiments, our justified desire to simplify observation conditions by confining filaments to a surface (coinciding with the focal plane) changes the physical properties of the underlying objects in an initially unanticipated but physically rather interesting manner. With filament helices being such a ubiquitous structure, it is the purpose of this work to investigate the rich physics emerging when they become confined. As we will show, the confinement produces dramatic changes in the shape, as well as in the statistical mechanics of the confined helix generating several notable and surprising effects: a) enhancement of cyclisation probability, b) enhancement of end-to-end fluctuations and c) generation of conformational multistability (despite apparent linearity of constitutive relations). We will see that the conformational dynamics of confined helices is most naturally described in terms of discrete particle-like entities —the “twist kinks”, cf. fig. 1. We show that these “twist kinks” are completely analogous to overdamped sine-Gordon kinks from soliton physics [14] as well as loops in stretched elastic filaments [15]. These analogies will help us to develop an intuitive phenomenological understanding of the underlying physics.

The phenomenology of squeezed helices. – Confined biofilaments throughout the literature exhibit often abnormal, undulating, spiral, and circular shapes that appear not be rationalized by the conventional Worm-Like Chain (WLC) model. This riddle of peculiar filament shapes is the starting point of our investigation. In this letter, we propose a new augmented model of confined intrinsically curved and twisted chains that leads to a variety of 2-d shapes matching experimental observa-

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Phenomenologically (as detailed further below), the main effect of confinement is to introduce narrow regions where the twist is highly concentrated and the curvature flips, cf. fig. 1. These curvature flip points we will call “twist kinks” in reference to the concept of kinks in soliton physics [14]. In contrast to 3-d where, a helical shape can satisfy both the preferred twist and curvature everywhere along the contour, in 2-d some frustration cannot be avoided. If we match the preferred twist, there is a bending energy cost $\propto B\omega_2^2$, if we match the preferred curvature with a circular shape, there is a twist energy cost $\propto C\omega_3^2$. The control parameter $\gamma \sim \frac{B\omega_2^2}{C\omega_3^2}$ measures the ratio of these two costs. Depending on $\gamma$ two regimes can be distinguished:

i) $\gamma > 1$: Twist kinks having a positive self-energy are essentially expelled and can only be thermally activated.

ii) $\gamma < 1$: Twist kinks have a negative self-energy and the ground state involves a finite density of twist kinks.

In both cases the generic shape motif is a circular arc section, or, in special cases, closed circles. If present, twist kinks separate arcs of opposite curvature orientations, resulting in a wavy undulatory 2-d shape (cf. fig. 1). For a squelix with $\gamma > 1$, the absence of twist kinks results in a circular-arc-shaped ground state—a feature that can favor the occurrence of closed filaments, which are less exciting as effects like circularization and hyperflexibility will be absent. For this reason, we will entirely focus in this very first study on the more illuminating and surprising case $\gamma > 1$.

The squeezed helical chain model. – The variety of squelical shapes in figs. 1 and 4 can be understood by simple energy considerations. The elastic energy of a helical WLC can be written as a function of the local curvatures $\Omega_1,2$ and twist $\Omega_3$ as:

$$ E = \frac{1}{2} \int B \left[ (\Omega_1 - \omega_1)^2 + \Omega_2^2 \right] + C (\Omega_3 - \omega_3)^2 ds, $$

where the integration goes over the filament contour length $s \in [0, L]$. The 3-d ground state is a helix of radius $R = \frac{\omega_1}{\sqrt{\omega_1^2 + \omega_2^2}}$ and pitch $H = \frac{2\pi \omega_2}{\sqrt{\omega_1^2 + \omega_2^2}}$ satisfying the preferred curvature and twist everywhere. To proceed, it is convenient to express the $\Omega_i$ through the Euler angles $\Omega_1 = \phi' \sin \theta \sin \psi + \theta' \cos \psi$, $\Omega_2 = \phi' \sin \theta \cos \psi - \theta' \sin \psi$ and $\Omega_3 = \phi' \cos \theta + \psi'$, where $(\cdot)'$ denotes the derivative with respect to the arc length parameter $s$. The twist $\Omega_3$ is the sum of the centerline torsion and the intrinsic twist $\psi'$. We constrain the chain to a plane by imposing $\theta = \pi/2$. The elastic energy of such a confined squelix can be recast as

$$ E = \frac{B}{2} \int \left( \phi'^2 - 2\omega_1 \phi' \sin \psi + \omega_1^2 + c(\phi' - \omega_3)^2 \right) ds, $$

where $c = C/B$. Now, $\phi'^2 = \Omega_1^2 + \Omega_2^2 \equiv \kappa^2$ gives the local curvature of the chain in the plane and $\phi' = \Omega_3$ is its local twist. Interestingly, it is seen from eq. (2) that the curvature and the twist are now coupled through $\omega_1$—which turns out to lie at the heart of most phenomena discussed here. The ground state satisfies the Euler-Lagrange equations:

$$ \phi' = \omega_1 \sin \psi, $$

$$ \psi'' + \frac{\omega_1^2}{2c} \sin 2\psi = 0. $$

If no external torque is applied on the chain, the twist must satisfy the boundary conditions $\psi'(-L/2) = \psi'(L/2) = \omega_3$.

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One possible representation of the helix in terms of the Euler angles defined below is: $\psi = \pi/2, \tan \theta = \omega_1/\omega_3, \phi' = \omega_3/\cos \theta$.
A quick glance at eq. (4) reveals that $\psi(s)$ is the solution of a pendulum equation and thus is a Jacobi elliptic function. Equation (3) shows that under confinement the curvature becomes “slaved” to the twist. This obviously is at the origin of the localization of twist. For the sake of simplicity, instead of solving eqs. (3), (4) directly, we will gain more physical insight by rewriting eq. (2) in terms of a WLC under tension (WLC-T) for which it is easy to develop intuition. For this, we insert eq. (3) into the energy, eq. (2), and introduce the new angle $\vartheta = 2\psi - \pi$ to get

$$E(\vartheta) = \int \left( \frac{1}{2} \ddot{\vartheta}^2 + \tilde{F} (1 - \cos \vartheta) \right) \, ds - \frac{1}{2} M [ \vartheta(L) - \vartheta(0) ],$$

up to an inessential constant term. Here, we introduced $\tilde{A} = C/4$ as the effective bending modulus of the WLC-T and $\tilde{F} = B \omega_0^2/4$ as the effective external force acting on it. The integral term is precisely the WLC-T energy. The last term with $M = \omega_0 C$ represents the torque exerted on both ends of the chain. If large enough, this term enforces $n$ extra trapped turns/loops $\vartheta(L) - \vartheta(0) = 2\pi n$ or in the $\psi$ representation, $n$ twist kinks along the squelax.

The phenomenology of the stretched chain is common knowledge [15], which makes the mapping attractive. The decay length of any localized distortion $\lambda$ is the size of an optimal loop grown against the tension $F$ (in the loop picture) or the spatial extension of a kink (in the twist-kink picture):

$$\lambda = \sqrt{\tilde{A} / \tilde{F}} = \omega_1^{-1} \sqrt{C / B}.$$  

The WLC-T loop stores a typical energy $\sim \lambda \tilde{F}$. If the work of the external torques $2nM$ per loop reduces sufficiently the loop energy, loops form spontaneously, otherwise they can be thermally activated. We hence conclude that the ground state is wavy for $M \gtrsim \lambda \tilde{F}$, which translates into $1 \gtrsim \frac{B \omega_0^2}{C \lambda^2}$ in the cHWLC language, and circular otherwise.

An overestimate of the energy stored in the loop $2\sqrt{2\pi} \sqrt{\tilde{A} \tilde{F}}$ is obtained assuming a circular loop. The WLC-T featuring loops in the long chain limit has been studied in detail in ref. [15] from which we borrow the more precise expression $E_{\text{loop}} = 8\sqrt{\tilde{A} \tilde{F}}$. After subtracting the work of the torques, we arrive at the effective self-energy of a single twist kink:

$$E_{1, \text{kink}} = (\sqrt{7} - 1)\pi C \omega_3^3,$$

where

$$\gamma = \frac{4B \omega_0^2}{\pi^2 C \omega_3^3}$$

is the twist-kink expulsion parameter introduced previously. The shape of an isolated twist kink is easily obtained upon integrating eq. (4), for a twist kink localized around $s = 0$:

$$\sin \psi(s) = \tanh \left( s / \lambda \right) \quad \text{and} \quad \phi'(s) = \omega_1 \tanh(s / \lambda),$$

a result we could also have transposed from [15]. From eq. (9) it is clear that, provided $L \gg \lambda$, the twist kink is localized and separates two curvature flipped regions of almost constant curvature $\approx \omega_1$ (see footnote 3).

Let us now turn to the main focus of this paper, the case of twist expulsion ($\gamma > 1$), which maps to the ground state to a WLC-T without loops. In a consistent thermodynamic picture, the twist-kink density should be calculated including shape fluctuations, in particular the coupling of the twist kink to small thermal deformations. These linear fluctuations, which in the soliton picture are often referred to as “phonons” [14], are expected to only moderately renormalize the kink’s free energy (by $\sim k_B T$ per kink). Fortunately, intuitive reasoning and simple geometry allow us to calculate the filament’s shape fluctuations associated with the free sliding motion of the narrow twist kink along the filament in the excited state. The associated soft mode (the kink’s position) is at the origin of the surprisingly large fluctuations in the excited state reported in simulations below.

The opposite regime, $\gamma < 1$, where the squelax shapes become undulatory, can be described along similar lines, with the twist-kink density being limited by mutual kink-kink repulsion. Generally speaking, for $\gamma < 1$, the gas of twist kinks ceases to be ideal, giving rise to reduced compressibility and, in turn, weaker extension fluctuations of the squelax. It can be shown that the pair repulsion between twist kinks decreases with their distance $d$ as $U_{\text{int}} \sim \pi C \omega_1 \sqrt{f(d/\lambda)}$ with $f(x) \sim 1/x$ for $x \ll 1$ and $f(x) \sim e^{-x^2}$ for $x \gg 1$. The dense twist-kink regime deserves special consideration, a more detailed description involving Jacobi functions will be given elsewhere.

A note for the experimentalist seems appropriate here. What could be measured? Simplest to assess is the preferred curvature $\omega_1$ which is obeyed but at twist kinks and close to the ends. End effects give direct access to both $\gamma$ and $\lambda$, provided ends are free and do not couple to twist kinks (see footnote 3). Alternatively $\lambda$ can be obtained from the shape of a twist kink in the dilute twist-kink regime, eq. (9). The preferred curvature being known, $\lambda$ determines the ratio $B/C$ via eq. (8). The knowledge of $\gamma$ then allows to estimate $\omega_1$ via eq. (8). A complementary information, like the self-energy of a twist kink, eq. (7),

3Note that a complete twist expulsion at the chain’s ends is formally incompatible with the zero torque boundary condition, giving rise to small boundary layers close to the filament’s edges. For small deviations, eq. (5) implies $\phi''(s) - \phi(s)/\lambda^2 = 0$ supplemented by the boundary conditions $d\phi/ds|_{s=0} = -2w_0$ and $\lim_{s \to \infty} \phi = 0$. Solving for the twist of the cHWLC gives $\psi(s) - \pi/2 = \frac{2}{\pi \omega_1} \exp(-s/\lambda)$. The width of the thin boundary layer is again given by the kink-size $\lambda$ — the only characteristic scale in the problem. The small deflection hypothesis is satisfied provided that $\gamma > 1$, i.e., deeply in the twist expulsion regime.

2The solution is $\psi(s) = \arctan(\sqrt{2} (s - s_0) \omega_1^2 / a)$ (elliptic amplitude function) where the constants of integration $a$ and $s_0$ are determined by the boundary conditions.
would enable to determine $B$ and $C$ separately. To summarize it should be worthwhile to measure the curvature away from twist kinks, end effects, twist-kink shapes and distributions, large overall shape fluctuations (linked to twist-kink dynamics). We anticipate that a lot of information can get lost if averages over several filaments with different structure or defects are performed [18]. Global thermal averages miss important information. As much as possible, the excited state, which can have an appreciable lifetime, should be studied separately. In some experiments filaments are forced onto the substrate by strong adsorption, unless the interface is fluid (like a phospholipid bilayer) and the 2-d shape may be unable to equilibrate. On the other hand, there are many situations where filaments are confined to a hard non-adsorbing walls by depletion interactions [19] or between hard non-adsorbing walls or to non-adsorbing micro channels [20].

Simulation. – Equipped with this intuitive picture of a squeezed chain as a collection of weakly interacting 1-d “particles” (twist kinks), whose positions along the contour relate to chain’s deformations in simple manner (eq. (9)), we move on to investigate the formulated hypotheses with a Wang-Landau–type Monte Carlo simulation [16]. We model the system as a discrete helical WLC consisting of $N$-monomers [21] subjected to a discrete version of the Hamiltonian given in eq. (1). The chain is further confined by a harmonic potential, so that each monomer located at distance $z$ away from the $z = 0$ surface experiences potential $E_{\text{conf}} = K z^2$ with $K = 25 k_B T / b^2$, and the bond length set as $b = 1$. For $K = 0$ the confinement vanishes and we recover the free-chain statistics in 3-d.

The main output of the simulation is the density of states (DOS) [16]. The equilibrium conformational statistics can be obtained from the DOS after Boltzmann weighting according to the Hamiltonian. In addition to the energy $E$, the joint DOS, $g(E, D, n)$, was sampled with respect to the end-to-end distance $D$ and to the “number of kinks” $n$, where $n = \pi^{-1} \sum_i H_i 2 \Omega_{1,i}$. The latter is indeed a statistical analogue of the discrete twist-kink number in the theoretical consideration above. Sampling of two-dimensional or higher histograms is often computationally more demanding than one-dimensional histograms. For efficient sampling, we used the global update method introduced by ref. [22]. The simulations were performed for several chain lengths, $N = 16, 32, 64$ and with fixed mechanical parameters $B = 50, C = 25 k_B T$ throughout. The essential information on the confined chWLC gained from our simulations are summarized in free-energy maps $F(n, D)$ (see fig. 4(a)).

Figure 2 demonstrates the typical changes of chain’s conformation triggered by confinement. For values $\gamma > 1$, the confined helix assumes an approximately circular shape as shown in fig. 2(a’). The binormal vectors pointing all in the same direction (in red) indicate that twist is expelled from the chain. The normal vectors are in-plane and point to the center of the circle (in blue). For $\gamma < 1$, the other hand, the chain assumes a stretched and twisted undulatory shape, as seen in fig. 2(b’). This wavy shape consists of a discrete number of localized twist kinks, as anticipated from theory. At the location of twist kinks, the in-plane normal vectors and the in-plane curvature $\phi$ flip their signs. The curvature between the twist kinks is approximately constant $\approx \omega_1$, as expected from the theoretical shape of single twist kinks, eq. (9).

Hypercyclisation. The phenomenological theoretical arguments above predict that a significant circularization enhancement should be observable for a twist-expelling chain $(\gamma > 1)$. We subject this hypothesis to a simulation test. For the geometric parameters $\omega_1 N = 4.8$ and $\omega_2 N = 3.2$ and elastic constant ratio $B/C = 2$, the twist expulsion parameter is well over unity, with $\gamma = 1.82$. In the absence of confinement, a chain with these parameters assumes a helical shape with a radius given by $R = 0.14 N b$ and a pitch $H = 0.62 N b$. When, on the other hand, such a chain becomes strongly confined to 2-d, it morphs into a slightly open but approximately circular shape with an end-to-end distance approximately given by $D_{\text{cap}} \approx \frac{2}{\omega_1 N} \sin \left( \frac{\omega_1 N}{2} \right) = 0.28$. In such a case, the newly formed ground state under confinement seems to promote circularization. To quantify the circularization enhancement, we define the circularization probability $P_{\text{cap}}^D$ $(D_{\text{cap}})$ given by the likelihood to find both chain ends within a fixed (small) capture distance $D_{\text{cap}}$ as $P_{\text{cap}}^D (D_{\text{cap}}) = D_{\text{cap}} (D_{\text{cap}}) = \int [g(E, D, n) e^{-E/k_B T} dEdnD]$, where $p_1 (D) = Z^{-1} \int g(E, D, n) \rho_0 (D) dD$, $Z = \int \int g(E, D, n) e^{-E/k_B T} dEdnD$ is the radial probability density for a given end-to-end distance $D$ and the index $d = 2$ or 3 stands for the dimensionality of the chain embedding (confined in 2-d or free in 3-d). Figure 3 shows the radial distribution functions $p_2 (D) \ (2-d)$ and $p_3 (D) \ (3-d)$ at various temperatures. The maximum of
The peak of the observable helical pitch. In contrast, the largest \( \gamma \) fluctuations.

the end-to-end distribution broadens due to the thermal correspondence to the expected 2-d circular ground state. At

\[ N_{\text{cap}}(a) = \text{2-d and (b) 3-d (free chain’s free energy) } \]

the temperature with applied to the density of states, which amounts to changing the temperature with \( C/B \) kept constant. (c) The enhancement of circularization probability upon confinement \( f^C = P_2^C(D_{\text{cap}})/P_3^C(D_{\text{cap}}) \) as a function of the normalized chain length \( Nb/l_p \) with capture distance \( D_{\text{cap}} = 0.5b \).

\[ p_3(D) \] (blue line) is located at about \( D = 0.55Nb \), close to the expected helical pitch. In contrast, the largest population of the confined chains is located around the peak of \( p_2(D) \) (blue line) at \( D_0/Nb \approx 0.28 \) which corresponds to the expected 2-d circular ground state. At higher temperature, the chain becomes more flexible and the end-to-end distribution broadens due to the thermal fluctuations.

From \( P_2^C(D_{\text{cap}}) \) we can estimate the cyclization enhancement factor \( f^C = P_2^C(D_{\text{cap}})/P_3^C(D_{\text{cap}}) \), when the chain is squeezed to 2-d as a function of the chains bending persistence length \( l_p = B/k_BT \). As suggested on theoretical grounds, the closing probability is greatly enhanced due to the confinement at lower temperatures (or increased chain stiffness) — with \( f^C \) well in excess of 1000 (fig. 3(c)).

**Multistability and hyperflexibility.** The theoretical considerations of multi-kink solutions presented above indicate that confining a helical chain should generate a complex energy landscape with many coexisting discrete states. Some of these states, in particular those comprising only a few kinks, should exhibit anomalous hyperflexible behavior due to the energetically cheap displacement of kinks. For instance, the motion of a single kink on a chain of length \( L = Nb \) and curvature \( \omega_1 \) satisfying a “close-to-resonance” condition \( \omega_1 \approx 2\pi k/L \) \((k = 1, 2, \ldots)\) should give rise to most dramatic end fluctuation effects.

To test this, we calculate the joint DOS of three variables \( g(E, D, n) \) and the free-energy landscape given by \( \beta F(D, n) = - \ln \left[ \sum_E g(E, D, n) e^{-\beta E} \right] \) (fig. 4(a), (b)). For parameters \( \omega_1 = 0.26b^{-1} \) and \( \omega_3 = 0.1b^{-1} \), in 3-d (confinement free case), we would obtain a helix with helical radius \( R = 8.09b \) and pitch \( H = 3.35b \). As expected from the large twist expulsion parameter \( \gamma = 5.47 \), the chain’s 2-d ground-state shape under confinement becomes a coiled double circle with roughly two turns. Besides the ground state, the free energy as a function of \( n \) indicates the existence of further (“excited”) low-energy states with \( n = 1, 2, \ldots \) (fig. 4). These states with distinct \( n \) are separated by small free-energy barriers. The first excited state \( n = 1 \), for instance, has a free-energy difference of only \( \Delta G_{1\text{kink}} \approx 4k_BT \), a figure that is not far from the theoretical estimate of the kink free energy \( \Delta G_{1\text{kink}} = E_{1\text{kink}} - k_BT \ln N \approx 6.6k_BT \), where the \( \ln N \) \((N = 48)\) term accounts for kinks positional entropy gain along the discrete positions of the chain.

The \( n = 1 \) state (cf. fig. 4(c)) exhibits an enhanced end-to-end distance fluctuation \( \langle (\delta D)^2 \rangle \), in phenomenological agreement with the mobile kink interpretation. For the given length \( (L = 48b) \), and curvature we expect an almost flat free-energy landscape as a function of the end-to-end distance \( D \) in the range \( D \in [0, D_{\text{max}}] \). Here, \( D_{\text{max}} \approx 4\omega_1^{-1} = 15.4b \) is the maximal extension for the \( n = 1 \) state, which is reached when the twist kink is located at a position \( \approx L/4 \) from any of the borders, as seen from simple geometric reasoning. The standard deviation expected in this case, \( \langle (\delta D)^2 \rangle_{n=1} \approx 28b^2 \), compares well with the simulation result \( \langle (\delta D)^2 \rangle_{n=1} \approx 26b^2 \).

The higher states \( n \geq 2 \) display again lower fluctuations. This is in agreement with the interpretation that,

\[^4\text{In contrast, the corresponding 3-d (free chain’s) free energy appears rather tame and featureless, displaying no multiple local minima or barriers and lacking the complexity of its 2-d, confined chain counterpart (data not shown).}\]
with growing kink density, their repulsion and eventually mutual confinement become important.

**Conclusion.** – We have shown that the conceptually simple procedure of planar confinement transforms a simple mundane object—a helically coiled filament—into a complex multistable, anomalously fluctuating filament. The statistical mechanics of this exotic object—the “squeelix”—can be qualitatively understood in terms of the motion of discrete particle-like entities corresponding to sharp curvature inversion points—called “twist kinks”. At low twist-kink concentrations, they move almost freely along the chain and induce anomalously strong conformational fluctuations—notably deviating from WLC behavior. The “squeelical” shapes formed under confinement are just the tip of an iceberg and that the “squeelix” phenomenology laid out here will serve us as a “dictionary” to decode these remarkable observations in forthcoming works.

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