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Rapid Note

Local writhing dynamics

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Abstract. We present an alternative local definition of the writhe of a self-avoiding closed loop which differs from the traditional non-local definition by an integer. When studying dynamics this difference is immaterial. We employ a formula due to Aldinger, Klapper and Tabor for the change in writhe and propose a set of local, link preserving dynamics in an attempt to unravel some puzzles about actin.

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Fuller's ubiquitously used relation between the link, twist, and writhe of a closed ribbon [1] has played a role in a great deal of work on the equilibrium statistical mechanics of DNA [2–4]. While the traditional definition of writhe unambiguously depends on the shape of the DNA backbone, it suffers from being non-local — it depends on the *entire* conformation. This non-locality is merely a technical complication for equilibrium physics but is a severe limitation for the study of dynamics. In this letter we present an alternative, local expression for writhe which differs from the usual expression for writhe only by an integer. Since continuous dynamical evolution cannot smoothly change an integer, from the point of view of dynamics this new local expression is adequate. We will, in addition, propose a local, dynamical link conservation law for a closed curve. Though we will not derive this conservation law from first principles dynamics, using arguments based only on the locality of interactions along a twist-storing polymer such as DNA, we will argue that at some scale it is appropriate.

The classic result relates the linking number Lk of the two sugar-phosphate backbones of DNA to two quantities, the twist Tw, which is a measure of the rate at which one backbone twists around the other, and the writhe Wr, which is a measure of how twisted in space the average backbone is. These three quantities are related by

$$\mathrm{Lk} = \mathrm{Tw} + \mathrm{Wr}. \tag{1}$$

The double helix may be described by the average backbone curve $\mathbf{R}(s)$ with unit tangent vector $\mathbf{T}(s)$ and by a unit vector $\mathbf{U}(s)$ perpendicular to $\mathbf{T}(s)$ which points from the $\mathbf{R}(s)$ to one of the two backbones. In this case twist and writhe are

$$\mathrm{Tw} \equiv \oint \mathrm{d}s\; \mathbf{T}(s) \times \mathbf{U}(s) \cdot \dot{\mathbf{U}}(s) \tag{2}$$

and

$$\mathrm{Wr} \equiv \frac{1}{4\pi} \oint \mathrm{d}s \oint \mathrm{d}s' \,\frac{[\mathbf{R}(s) - \mathbf{R}(s')] \cdot \dot{\mathbf{R}}(s) \times \dot{\mathbf{R}}(s')}{\left|\mathbf{R}(s) - \mathbf{R}(s')\right|^3}, \tag{3}$$

where $\dot{X}(s) \equiv \mathrm{d}X/\mathrm{d}s$ [5] and s measures the arc-length along the curve. We will first suggest a different *local* expression for writhe $\widetilde{\mathrm{Wr}}$ which we will then show differs from the usual definition of writhe Wr by an integer. The locality of the expressions comes at a price: the introduction of some new degrees of freedom, not unlike the introduction of a gauge field to change a non-local coulomb interaction into a local interaction between matter and the gauge field. As we shall show, however, the dynamics can be formulated without reference to these new variables. While there is no new mathematics in this derivation it is useful to have a local expression which captures much of the information of writhe. A similar resulting expression was first used in the context of Fermi-Bose transmutation by Polyakov [6].

We consider a closed curve Γ parameterized by $\mathbf{R}(s)$ with unit tangent vector $\mathbf{T}(s)$ and choose $\mathbf{e}_1(s)$ and $\mathbf{e}_2(s)$ along the curve to form an orthonormal triad with $\mathbf{T}(s)$: $\{\mathbf{e}_1(s), \mathbf{e}_2(s), \mathbf{T}(s)\}$. Parameterizing the "difference direction" $\mathbf{U}(s)$ in terms of $\mathbf{e}_1$ and $\mathbf{e}_2$ we have

$$\mathbf{U}(s) = \cos\theta_U(s)\; \mathbf{e}_1(s) + \sin\theta_U(s)\; \mathbf{e}_2(s). \tag{4}$$

The total twist as defined in (2) is the integral of a local "twist density" which we can compute in terms of θ_U

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and $\mathbf{e}_i$:

$$\mathrm{Tw} = \int \mathrm{d}s\, \mathcal{T}\mathrm{w} \equiv \oint \mathrm{d}s\, \mathbf{T}\times\mathbf{U}\cdot\dot{\mathbf{U}} = \oint \mathrm{d}s\, \{\partial_s\theta_U - e_1^\alpha\partial_s e_2^\alpha\}\,. \quad (5)$$

The first term on the right hand side of (5) is necessarily 2π times an integer. What about the second term? If we imagine that $\mathbf{e}_i(s)=\mathbf{e}_i\big(\mathbf{R}(s)\big)$ are defined everywhere in space then we define:

$$2\pi\widetilde{\mathrm{Wr}} \equiv \oint \mathrm{d}s\, e_1^\alpha\partial_s e_2^\alpha = \oint_\Gamma \mathrm{d}R_i\, e_1^\alpha\partial_i e_2^\alpha. \quad (6)$$

Since $\mathbf{e}_i$ are only defined on the curve, derivatives in space $\partial_i\mathbf{e}_2$ are not necessarily well-defined. However, since we are only interested in this derivative along the curve, we can make sense of (6). This expression appears to be a *local* expression for something which we would like, considering (5), to interpret as writhe (times 2π). At first glance adding the orthonormal triad appears similar to the "generalized Frenet-Serret" frame introduced by Goriely and Tabor [7]. In the following, we will propose a dynamics that makes *no reference* to the additional vectors $\mathbf{e}_1$ and $\mathbf{e}_2$.

Suppose the curve Γ is the boundary of a surface M (we can find such a surface for an unknotted closed curve). Since $\mathbf{T}\in \mathrm{S}^2$ and $\pi_1(\mathrm{S}^2)=0$ we can find a continuous unit vector field $\widetilde{\mathbf{T}}\in\mathrm{S}^2$ on M which is equal to unit tangent vector $\mathbf{T}$ on the boundary Γ [8]. We note that the vector field $\widetilde{\mathbf{T}}$ is defined at every point of M but does not necessarily lie in the tangent plane to M. This field is introduced so that the line integral in (6) can be converted into a surface integral in the following. In Figure 1 we summarize the geometry and notation. Using Stoke's theorem we then have

$$\oint_\Gamma \mathrm{d}R_i\; e_1^\alpha\partial_i e_2^\alpha = \int_{\mathrm{M}} \mathrm{d}S_i\;\left[\nabla\times e_1^\alpha\nabla e_2^\alpha\right]_i. \quad (7)$$

As an aside, we note that the integrand appearing in the integral over M has significance in both two and three dimensions. If $\mathbf{e}_1$ and $\mathbf{e}_2$ are local tangent vectors to a two-dimensional surface embedded in three dimensions, then the curl of the "connection" $\omega\equiv e_1^\alpha\nabla e_2^\alpha$ is the Gaussian curvature of the surface [9] while in three dimensions if $\mathbf{e}_1$ and $\mathbf{e}_2$ are perpendicular to, for instance, the nuclear spin in ^{3}He or the long nematic director in a biaxial nematic then the curl of ω is the geometric realization of a topological fact: in a biaxial nematic +1 disclinations *cannot* escape into the third dimension as in uniaxial nematics [10]. Returning to the problem at hand, the curl of ω is

$$\epsilon_{ijk}\partial_j\omega_k = \left[\nabla\times e_1^\alpha\nabla e_2^\alpha\right]_i = \frac{1}{2}\epsilon_{ijk}\epsilon_{\alpha\beta\gamma}\widetilde{T}^\alpha\partial_j\widetilde{T}^\beta\partial_k\widetilde{T}^\gamma, \quad (8)$$

the famed Mermin-Ho relation [11]. In the following we will show that there is a relation between our proposed expression for writhe and the more traditional expression (3). While we may not be able to define $\mathbf{e}_1$ and $\mathbf{e}_2$ inside the manifold M, the curl of ω is well defined since we can extend $\mathbf{T}$ *via* $\widetilde{\mathbf{T}}$.

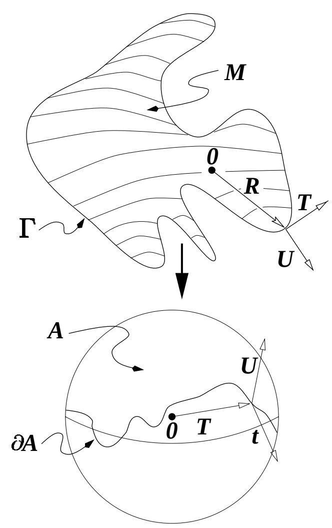

Fig. 1. Summary of geometry and notation used. The curve of interest is Γ with capping surface M. The unit tangent vector $\mathbf{T}$ to the curve can be mapped to the surface of the unit sphere. The area swept out by the tangent vector on the tangent spherical map is A, while $\mathbf{t}$ is the tangent vector to the curve (the tangent indicatrix) lying on the surface of the sphere.

Nearly twenty years ago [12] Fuller showed that the writhe Wr of a curve differed by an integer from the signed area swept out by the unit tangent vector $\mathbf{T}$ on the unit sphere. For completeness we review that result here. As before, let $\mathbf{T}(s)$ be the unit tangent vector to the curve $\mathbf{R}(s)$ and $\mathbf{U}(s)$ be the vector pointing along the ribbon with $\mathbf{U}(s)\cdot\mathbf{T}(s)=0$. $\mathbf{T}(s)$ traces out a curve on the unit sphere (the so-called "tangent indicatrix"). Let the tangent to this curve be $\mathbf{t}(s)$. Since $\mathbf{U}(s)$ is perpendicular to $\mathbf{T}(s)$, it lies in the tangent plane of the unit sphere at $\mathbf{T}(s)$. Applying the Gauss-Bonnet theorem [13] to the region A enclosed by the curve on the unit sphere gives

$$\int_{\mathrm{A}} \mathrm{d}^2\sigma\, K + \int_{\partial\mathrm{A}} \mathrm{d}s\,\kappa_{\mathrm{g}} = 2\pi \quad (9)$$

where K is the Gaussian curvature and κ_{g} is the geodesic curvature, defined as the rate of change of $\mathbf{t}(s)$ in the tangent plane of the sphere. Locally parameterizing A by the orthonormal vectors $\mathbf{e}_1(\sigma_1,\sigma_2)$ and $\mathbf{e}_2(\sigma_1,\sigma_2)$ (with $\mathbf{e}_1(\boldsymbol{\sigma})\times\mathbf{e}_2(\boldsymbol{\sigma})=\mathbf{n}(\boldsymbol{\sigma}_1)$, where $\mathbf{n}$ is the surface normal), we may write the unit vectors $\mathbf{t}$ and $\mathbf{U}$ as

$$\mathbf{t}(s) = \cos\theta_t(s)\;\mathbf{e}_1(s) + \sin\theta_t(s)\;\mathbf{e}_2(s)$$
$$\mathbf{U}(s) = \cos\theta_U(s)\;\mathbf{e}_1(s) + \sin\theta_U(s)\;\mathbf{e}_2(s) \quad (10)$$

where $\mathbf{e}_i(s)=\mathbf{e}_i(\tilde\sigma(s))$ and $\tilde\sigma(s)$ is the parameterization of the boundary in terms of the surface coordinates $\boldsymbol{\sigma}$. Since on ∂A the surface normal is $\mathbf{T}(s)$, the geodesic curvature is $\kappa_{\mathrm{g}}=\mathbf{T}\times\mathbf{t}\cdot\dot{\mathbf{t}}$ while the twist density $\mathcal{T}\mathrm{w}$ is defined as $2\pi\mathcal{T}\mathrm{w}=\mathbf{T}\times\mathbf{U}\cdot\dot{\mathbf{U}}$. Using the orthonormality of $\{\mathbf{e}_1,\mathbf{e}_2,\mathbf{T}\}$

we have

$$\kappa_{\rm g} = \partial_s\theta_t(s) - e_1^\alpha\partial_s e_2^\alpha, \tag{11}$$

and

$$2\pi\mathcal{T}{\rm w} = \partial_s\theta_U(s) - e_1^\alpha\partial_s e_2^\alpha. \tag{12}$$

Since the difference is $2\pi\mathcal{T}{\rm w} - \kappa_{\rm g} = \partial_s(\theta_U - \theta_t)$ after one circuit about the curve the integral of the difference changes by an integer multiple of 2π. Using (9) and the fact that the Gaussian curvature of the unit sphere is $K = 1$, Fuller found that

$$\frac{A}{2\pi} + {\rm Tw} \equiv 0 \mod 1, \tag{13}$$

where A is the signed area of the region enclosed by $\mathbf{T}(s)$ on the unit sphere and ${\rm Tw} \equiv \int {\rm d}s\,\mathcal{T}{\rm w}$. Comparing this to ${\rm Lk} = {\rm Tw} + {\rm Wr}$, we see that

$${\rm Wr} \equiv \frac{A}{2\pi} \mod 1, \tag{14}$$

which establishes Fuller's result. Upon using Stoke's theorem and the Mermin-Ho relation we have:

$$2\pi\widetilde{\rm Wr} = \oint {\rm d}s\, e_1^\alpha\partial_s e_2^\alpha = \frac{1}{2}\int_M {\rm d}S_i\,\epsilon_{ijk}\epsilon_{\alpha\beta\gamma}\widetilde{T}^\alpha\partial_j\widetilde{T}^\beta\partial_k\widetilde{T}^\gamma \tag{15}$$

which is *precisely* the area swept out by the curve $\mathbf{T}$ on the unit sphere! Thus we see that

$${\rm Wr} \equiv \widetilde{\rm Wr} \mod 1. \tag{16}$$

While the total amount of writhe including the integral part is important for calculating ground states of a particular twisted ribbon [2,4,3] when considering changes in writhe the integer is less important. In particular to study dynamics a local "writhe density" is probably essential.

To this end, a useful result [14] for the change in writhe of a curve as a function of some deformation λ

$$\partial_\lambda{\rm Wr}(\lambda) = \frac{1}{2\pi}\oint {\rm d}s\,\mathbf{T}(s,\lambda)\cdot\left[\partial_\lambda\mathbf{T}(s,\lambda)\times\partial_s\mathbf{T}(s,\lambda)\right], \tag{17}$$

can be used. Note that this result follows from the preceding discussion: (17) (multiplied by ${\rm d}\lambda$) is the differential in the area swept out by the tangents of two closed curves with tangent vectors $\mathbf{T}(s,0)$ and $\mathbf{T}(s,{\rm d}\lambda)$. We now consider distortions in time (t) so that ${\rm d}\lambda = {\rm d}t$. Since the twist is really the local torsional strain of the polymer, we denote it as $\Omega(s,t)$ and then we have

$$\partial_t{\rm Lk} = \oint {\rm d}s\,\left\{\partial_t\Omega + \partial_t\mathbf{T}\cdot[\partial_s\mathbf{T}\times\mathbf{T}]\right\} + \partial_t n \tag{18}$$

where n is the integer difference between Wr and $\widetilde{\rm Wr}$. Since continuous evolution cannot lead to discontinuous changes in the integer n and since link is conserved we have

$$0 = \oint {\rm d}s\,\left\{\partial_t\Omega + \partial_t\mathbf{T}\cdot[\partial_s\mathbf{T}\times\mathbf{T}]\right\}. \tag{19}$$

This conservation law need not be satisfied locally: the curve can twist in one place and writhe at some distant location to satisfy (19). In addition, the integer can change if the curve develops cusps and evolves in a non-smooth way. While mathematically consistent this is not a physically plausible effect. We expect that the linking number is conserved *locally* and only changes through the diffusion of some "link current" j. With this assumption we can suppose a local conservation law

$$\partial_s j = \partial_t\Omega + \partial_t\mathbf{T}\cdot[\partial_s\mathbf{T}\times\mathbf{T}], \tag{20}$$

which satisfies (19). This conservation law enforces total link conservation since $\oint {\rm d}s\,\partial_s j \equiv 0$, yet allows for *local* deviations in the twist and writhe. Note that although we introduced the framing vectors $\mathbf{e}_i$ they do not appear in the conservation law. The invariance of $\widetilde{\rm Wr}$ with respect to the choice of $\mathbf{e}_i$ only holds for a closed curve. Nonetheless the form of (20) suggests that for dynamics we may apply the conservation law to *open curves*. We might also comment on the change of the link mod 1: when the link changes there must be a "kink" in the link density current j. Again, one would expect that this kink would start locally and spread out. This would correspond to the physical situation in which, after a critical amount of excess link is forced into a filament, it will buckle from a state with a relatively uniform twist into a configuration with a small closed loop which contributes a compensating amount of writhe [3].

We consider now the relaxational Rouse dynamics of a closed, twist-storing polymer with a free energy

$$F = \frac{1}{2}\int {\rm d}s\,\left\{A\left(\partial_s\mathbf{T}\right)^2 + C\Omega^2 - \lambda\left(\mathbf{T}^2 - 1\right)\right\} \tag{21}$$

where A and C are the bend and twist elastic constants, respectively, and λ is the Lagrange multiplier which enforces the constraint that $\mathbf{T}$ be a unit vector [15]. The dynamical equations for $\mathbf{T}$ and Ω are

$$\partial_t\Omega = -\Gamma_\Omega\frac{\delta F}{\delta\Omega} = -C\Gamma_\Omega\Omega \tag{22a}$$

$$\partial_t\mathbf{T} = -\Gamma_T\frac{\delta F}{\delta\mathbf{T}} = A\Gamma_T\partial_s^2\mathbf{T} + \Gamma_T\lambda\mathbf{T} \tag{22b}$$

$$0 = \mathbf{T}^2 - 1, \tag{22c}$$

where Γ_Ω and Γ_T are dissipation constants. Using (22) we may rewrite (20) as [16]

$$\partial_s j = -C\Gamma_\Omega\Omega - A\Gamma_T\mathbf{T}\cdot\left[\partial_s\mathbf{T}\times\partial_s^2\mathbf{T}\right]. \tag{23}$$

We recognize the second term on the right-hand side of (23) as $\kappa^2(s)\tau(s)$ where $\kappa(s)$ is the curvature of the curve and $\tau(s)$ is the torsion. Note that while usually the torsion is ill-defined for a curve with zero curvature, there is no problem here because of the explicit factor of κ^2. This formulation differs from the work in [17] by the introduction of a link density current which allows a local constraint. Thus we see that the "link current" obeys

$$\partial_s j = -C\Gamma_\Omega\Omega - A\Gamma_T\kappa^2\tau. \tag{24}$$

This form of the link current allows us to locally understand how link moves: link moves when there is a twist and when the curve is non-planar (*i.e.* $\tau \neq 0$). Assuming a Fick's law form for the current $j = -D\partial_s \mathcal{L}\mathrm{k}$ in terms of the link density $\mathcal{L}\mathrm{k}$, we finally have

$$D\partial_s^2 \mathcal{L}\mathrm{k} = C\Gamma_\Omega \Omega + A\Gamma_T \kappa^2 \tau. \quad (25)$$

Note that Fick's law implies that if the link is uniformly spread along the polymer then the current is constant.

As a simple application of (20) we can consider a closed ribbon of radius $r = \kappa^{-1}$ lying in the xy-plane. If we consider relaxational dynamics around the curved ground state we see that in this case (25) will depend *linearly* on $\mathbf{T}$ through the torsion τ (as opposed to quadratically if κ were 0). We can consider the dynamics of the ribbon in extreme cases. The diffusion constant D can be large (infinite) or small (zero). Additionally the twist modulus C can be large (infinite) or small (zero). If the diffusion constant is infinite then (20) is not much of a constraint: any writhe or twist deformation can be quickly compensated for by small local link deformations. This is the limit in which dynamics is non-local and in which the only constraint is (19).

The case of zero diffusion is more interesting and corresponds to "ultra-local" dynamics in which link is conserved point by point. In this case we have $j = 0$ and so

$$C\Gamma_\Omega \Omega = -A\Gamma_T \kappa^2 \tau. \quad (26)$$

If the twist modulus is 0 or small then it is easy to change Ω and this is hardly a constraint. However, if the twist modulus is large or infinite then (26) implies that if the curve starts planar then *it remains planar* since $\tau = 0$ and $\kappa \neq 0$. This is, of course, only true if the polymer has an everywhere non-zero curvature. We note that this observation may explain some puzzling experiments on actin, another double-helical polymer [18,19]. Though $\mathrm{Lk} = \mathrm{Tw} + \mathrm{Wr}$ applies only to closed curves, we would expect the local dynamics of closed twist-storing polymers to be the same as that for similar open polymers. In those experiments on open actin strands there were two surprising observations. The first was that in [18], at long wavelengths, the persistence length seems to grow from around 2 μm to roughly 10 μm though it remained uniform at 2 μm until some crossover wavenumber q_c. The experiment was done by observing actin filaments oscillating in a sample volume. In order to distinguish in-plane motion from out of plane-motion, an actin filament which did not completely remain in focus for the duration of the sampling was not used in the data analysis. It is rather surprising that a polymer would remain in a single plane for an extended period [20]. In the light of (26) a possible explanation emerges: if an actin filament has zero average curvature, then, on average, (20) is not a linear constraint since $\kappa = 0$. However if the longest wavelength undulation modes have not equilibrated then it is possible for $\langle\kappa\rangle \neq 0$. This could explain *both* effects. The long wavelength modes do not have good statistics which is why they appear to have an anomalous persistence length and, at the same time, the non-equilibration of these modes forces the torsionally stiff actin filament to remain in the plane for some time until link can diffuse in from the ends.

As a mathematical aside for the *cogniscenti* we note that when continuing $\mathbf{T}$ into the region M there is an ambiguity since $\pi_2(\mathrm{S}^2) = \mathcal{Z}$. However, the integrand in (15) is the skyrmion density [21], which, when integrated over the entire region can differ by 2π times an integer for interior continuations which are homotopically distinct. This is not a problem since there is already a mod 1 ambiguity between Wr and $A/(2\pi)$. Finally, we might consider the case of a knotted curve. In this case the curve can be unknotted by adding to the curve small loops. It can be shown in this case that the addition of a small segment of curve will change $\widetilde{\mathrm{Wr}}$ by an integer, which is therefore unimportant for dynamics.

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