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Terminal Twist Induced Continuous Writhe of A Circular Rod with Intrinsic Curvature

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Abstract

It is well known that a large linking number induces an abrupt writhing of a circular rod with zero intrinsic curvature, i.e., the stress-free state of the rod is straight. We show here that for any rod with a uniform natural curvature, no matter how small the intrinsic curvature is, a twist will induce a continuous writhing from the circular configuration and the abrupt writhing is only the limiting case when the intrinsic curvature is absolutely zero. The implication of this result on elastic models of circular DNA is discussed.

Introduction

Closed loops of DNA of several hundred base pairs, whether those formed as simple closed mini-circles or those formed by protein binding, play an important role in many biological functionings of DNA, for example in the control of gene expression. To understand the geometric conformations these loops assume under stress, there has been much recent research in modeling such DNA as an elastic isotropic rod and studying the conformations of minimum elastic energy. It has been shown that if such DNA have sequences that contain intrinsic bends in their unstressed state the resulting geometric shapes under stress are considerably different than those that have no intrinsic curvature. In particular, it is well known that, if an unstressed straight DNA is closed into a planar circle and then subjected to a change in linking number due to terminal twist, conformations assumed are fundamentally different from those with even the slightest original intrinsic curvature. This has been suggested (1,2) and shown in detail using finite element analysis and numerical techniques to solve the partial differential equations that arise (1,3). In this paper, using linear analysis, we give a direct analytic proof of the fact that an isotropic elastic rod with any intrinsic curvature, no matter how small, uniformly distributed along the rod becomes non - planar under the slightest change, even a partial change, in linking number. This contrasts with the well-known result of Le Bret (4) and Benham (5) that for an originally straight isotropic rod with Poisson ratio ν, which has been closed into a planar circle, any change of linking number up to $\sqrt{3}(1+\nu)$ does not alter the configuration from a plane circle.

The Le Bret-Benham's result is known as buckling phenomenon in the classical mechanic. A large twist i.e., imposing a large linking number, induces an abrupt bending (buckling) in a naturally straight, elastic thin rod. The rod keeps its straight configuration under a mild terminal twist until the buckling due to an elastic instability which breaks the axial symmetry in the rod (6,7). Similarly, when twisting a planar circle formed by a naturally straight rod, an abrupt writhing occurs (8). However, the earlier results of Bauer et al. (1,3) and Tobias and Olson (2) suggested that there is no elastic instability for naturally curved rods.

In our analysis, the (induced) curvature of the circle is κ^o and the intrinsic curvature of the rod is κ^*. κ^o, which is directly related to the length of the rod L ($\kappa^o = 2\pi/L$), is not necessarily the same as κ^*. A local coordinate system along the relaxed planar circle can be defined: let's use ℓ as the arc length of the rod. At each point ℓ ($0 \le \ell \le L$) along the central-line (line of centroids) of the rod, $\hat{\zeta}$ is a unit vector in the tangential direction, $\hat{\eta}$ is a unit vector directed along the rotational axis of the intrinsic bending, i.e., perpendicular to the plane. Unit vector $\hat{\xi}$ is in the centripetal direction perpendicular to the rod but in the plane. The three unit vectors form a right-hand local coordinate system (*body-fixed frame*): $\hat{\zeta} = \hat{\xi} \times \hat{\eta}$ (Figure 1).

The configuration of the rod is characterized by an infinitesimal rotation $\overrightarrow{\Omega}(\ell)$ along the axis of the rod ($\hat{\zeta}$). $\overrightarrow{\Omega}$ is defined through the continuous rotation of the body-fixed frame (*bff*) in the laboratory-fixed frame (*lff*):

$$\frac{d\hat{e}}{d\ell} = \overrightarrow{\Omega} \times \hat{e}, \qquad \hat{e} = \hat{\xi}, \hat{\eta}, \hat{\zeta}$$

It can be written in terms of bending ($d\hat{\zeta}/d\ell$) and twisting ($tw = \Omega_\zeta$):

$$\overrightarrow{\Omega} = \hat{\zeta} \times \frac{d\hat{\zeta}}{d\ell} + (tw)\hat{\zeta}$$

with the local curvature of the central axis being:

$$\kappa = \left| \frac{d\hat{\zeta}}{d\ell} \right| = \sqrt{\Omega_\xi^2 + \Omega_\eta^2}$$

Elastic Energy and Equations for Equilibrium State

The elastic energy due to mechanical bending and twisting, including the stored energy of the internal strain and potential energy of external force acting on the terminal ends of the rod, is usually given as (9-11):

$$U[\overrightarrow{\Omega}(\ell)] = \frac{1}{2}\int_0^L \left\{ A(\Omega_\xi - \Omega_\xi^o)^2 + A(\Omega_\eta - \Omega_\eta^o)^2 + C(\Omega_\zeta - \Omega_\zeta^o)^2 \right\} d\ell - \int_0^L \left\{ \overrightarrow{F} \cdot \hat{\zeta} \right\} d\ell \qquad (1)$$

where $\overrightarrow{\Omega^o}$ is the intrinsic bending and twisting in the relaxed state of the rod, A and C are the elastic moduli for bending and twisting, respectively. $(A - C)/C = \nu$ will be the Poisson ratio). For our present study, we choose $\Omega_\eta^o = \kappa^*$, and $\Omega_\xi^o = \Omega_\zeta^o = 0$. Eqn. [1] indicates that the energy for a rod with bending and twisting is a quadratic function of deformation, and the unique minimal energy configuration is in its relaxed state. $\overrightarrow{F}$ is an external force on the terminals of the rod, which is constant in the *lff*. The presence of this terminal shear force, in addition to torques, is essential for the rod to be a closed loop (10). The shear force has zero contribution to the energy U if the rod is a closed loop. This is a mathematical idealization because we have assumed that the rod is unshearable.

Interesting mechanics occur when the thin rod is subject to end-to-end, also known as face-to-face rotation (3) at its two joining terminals. These constraints serve as the boundary conditions for a set of differential equations which govern the equilibrium state of the rod. The set of differential equations is readily obtained from $U[\overrightarrow{\Omega}(\ell)]$ by the Euler-Lagrange variational calculus (9,10,12):

$$A\Omega'_\xi - (A - C)\Omega_\eta\Omega_\zeta + A\kappa^*\Omega_\zeta = \hat{\eta} \cdot \overrightarrow{F} \tag{2}$$

$$A\Omega'_\eta - (C - A)\Omega_\zeta\Omega_\xi = -\hat{\xi} \cdot \overrightarrow{F} \tag{3}$$

$$C\Omega'_\zeta - A\kappa^*\Omega_\xi = 0 \tag{4}$$

where $'$ is the derivative with respect to ℓ and $\cdot$ is the dot product of vectors. Eqn. [2]-[4] is a set of nonlinear differential equations (7).

Coordinate Transformations

Our analysis is based on linearizing the nonlinear Eqn. [2]-[4] around the planar circular configuration. We proceed by expressing the $\overrightarrow{\Omega}$ in the cylindrical coordinate system in *lff*: (R, Θ, Z).

Any vector can have its coordinates in two different coordinate systems, the *body-fixed frame (bff)* and the *laboratory-fixed frame (lff)*. These two coordinate systems are related through the Euler angle (ϕ, θ, ψ) with the transformation matrix from *lff* to *bff* (12):

$$\mathbf{T} = \begin{pmatrix} cos\psi cos\phi - cos\theta sin\phi sin\psi & cos\psi sin\phi + cos\theta cos\phi sin\psi & sin\psi sin\theta \\ -sin\psi cos\phi - cos\theta sin\phi cos\psi & -sin\psi sin\phi + cos\theta cos\phi cos\psi & cos\psi sin\theta \\ sin\theta sin\phi & -sin\theta cos\phi & cos\theta \end{pmatrix} \tag{5}$$

The unit tangent vector ζ in these two coordinate systems are

$$(\zeta_\xi, \zeta_\eta, \zeta_\zeta) = (0, 0, 1) \quad \text{and} \quad (\zeta_x, \zeta_y, \zeta_z) = (sin\theta sin\phi, -sin\theta cos\phi, cos\theta), \tag{6}$$

respectively. One can verify that by

$$(\zeta_x, \zeta_y, \zeta_z) = (\zeta_\xi, \zeta_\eta, \zeta_\zeta)\mathbf{T}$$

In the *lff* we have:

$$\frac{d\hat{\zeta}}{d\ell} = -\hat{\zeta} \times \overrightarrow{\Omega} \tag{7}$$

which defines the infinitesimal rotational vector $\overrightarrow{\Omega}$:

$$(\Omega_\xi, \Omega_\eta, \Omega_\zeta) = (\phi' sin\theta sin\psi + \theta' cos\psi, \phi' sin\theta cos\psi - \theta' sin\psi, \phi' cos\theta + \psi') \qquad (in\ \ bff) \quad (8)$$

and

$$(\Omega_x, \Omega_y, \Omega_z) = (\psi' sin\theta sin\phi + \theta' cos\phi, -\psi' sin\theta cos\phi + \theta' sin\phi, \phi' + \psi' cos\theta) \qquad (in\ \ lff) \quad (9)$$

$\overrightarrow{\Omega}$ can be obtained by taking derivative of (5) with respect to ℓ:

$$\frac{d\mathbf{T}}{d\ell} = \mathbf{T} \begin{pmatrix} 0 & \Omega_z & -\Omega_y \\ -\Omega_z & 0 & \Omega_x \\ \Omega_y & -\Omega_x & 0 \end{pmatrix} \tag{10}$$

In the cylindrical coordinate system in *lff*, we have:

$$(\zeta_x, \zeta_y, \zeta_z) = \frac{(R' cos\Theta - R\Theta' sin\Theta, R' sin\Theta + R\Theta' cos\Theta, Z')}{I} \tag{11}$$

where

$$I^2 = (R')^2 + R^2(\Theta')^2 + (Z')^2$$

Combining Eqn. [6] with Eqn. [11] and eliminating the ζ's, we have the cylindrical coordinates (R, Θ, Z) for the central-line in terms of the Euler angles (ϕ, θ, ψ):

$$\frac{(R')^2 + R^2(\Theta')^2}{I^2} = sin^2\theta, \qquad \frac{R\Theta' sin\Theta - R' cos\Theta}{R\Theta' cos\Theta + R' sin\Theta} = tan\phi, \qquad \frac{Z'}{I} = cos\theta \tag{12}$$

Therefore,

$$\phi = \Theta - tan^{-1}\left(\frac{R'}{R\Theta'}\right) \tag{13}$$

The infinitesimal rotation is related to the Euler angles as shown in Eqn. [8]. Using Eqn. [8], [12], and [13] and eliminating the Euler angles, we have:

$$\Omega_\xi = \phi' \frac{\sqrt{(R')^2 + R^2(\Theta')^2}}{I} sin\psi - \frac{IZ'' - I'Z'}{I\sqrt{(R')^2 + R^2(\Theta')^2}} cos\psi \tag{14}$$

$$\Omega_\eta = \phi' \frac{\sqrt{(R')^2 + R^2(\Theta')^2}}{I} cos\psi + \frac{IZ'' - I'Z'}{I\sqrt{(R')^2 + R^2(\Theta')^2}} sin\psi \tag{15}$$

$$\Omega_\zeta = \phi' \frac{Z'}{I} + \psi' \tag{16}$$

where

$$\phi' = \Theta' - \frac{(RR'' - (R')^2)\Theta' - RR'\Theta''}{(R')^2 + R^2(\Theta')^2}$$

Without a terminal twist, the rod is a planar circle with curvature κ^o. For small deviation from the planar circular configuration in cylindrical coordinates, we use r, Z, and δ to represent the deviations from the circle, the plane, and the untwisted configuration, respectively. Hence, $R = 1/\kappa^o + r$, $\Theta' = 1/R \approx \kappa^o(1 - \kappa^o r)$, $\psi = \delta$, where r, δ, Z are small. Substituting these into Eqn. [14]-[16] and neglecting the higher order terms:

$$\Omega_\xi = -Z'' + \kappa^o\delta, \quad \Omega_\eta = \kappa^o - (\kappa^o)^2 r - r'', \quad \Omega_\zeta = \kappa^o Z' + \delta' \tag{17}$$

Linearized Equation for Twisted Circle

With the transformation given in Eqn. [17], we can linearize differential Eqns. [2]-[4] in the cylindrical coordinate system by Eqn. [17] into Eqn. [2]-[4] and keep only the therms with zeroth and first order of r, Z, and δ:

$$r''' + (\kappa^o)^2 r' = 0 \tag{18}$$

$$AZ''' + [(A-C)\kappa^o - A\kappa^*]\kappa^o Z' - (C\kappa^o + A\kappa^*)\delta' = -F \tag{19}$$

$$C\delta'' + (C\kappa^o + A\kappa^*)Z'' - A\kappa^*\kappa^o\delta = 0 \tag{20}$$

where F is the $\hat{z}$ component of the terminal force. The deformation in r is naturally separated from the Z and δ. The two equations for Z and δ have five eigenvalues as the roots of the characteristic polynomial

$$\lambda(\lambda^2 + \kappa^{o2})[C\lambda^2 + \kappa^*(C\kappa^o - A\kappa^o + A\kappa^*)] = 0 \tag{21}$$

two of the five roots are always imaginary: $\pm i\kappa^o$. Another two changes from imaginary to real when κ^* decreases: $\pm i\sqrt{\kappa^*(C\kappa^o - A\kappa^o + A\kappa^*)/C}$. They are real for $\kappa^* = 0$ and imaginary for $\kappa^* = \kappa^o$. From now on we will denote $\sqrt{\kappa^*(C\kappa^o - A\kappa^o + A\kappa^*)/C}$ by λ. The general solution for the inhomogeneous differential Eqn. [19] and [20] is:

$$\begin{pmatrix} Z \\ \delta \end{pmatrix} = a_0 \begin{pmatrix} 1 \\ 0 \end{pmatrix} + (a_1 sin\kappa^o\ell + a_2 cos\kappa^o\ell) \begin{pmatrix} 1 \\ -\kappa^o \end{pmatrix} + (a_3 sin\lambda\ell + a_4 cos\lambda\ell) \begin{pmatrix} -1 \\ \frac{\lambda^2}{\kappa^*} \end{pmatrix} + \begin{pmatrix} \frac{\kappa^* F\ell}{C\kappa^o\lambda^2} \\ 0 \end{pmatrix} \tag{22}$$

where a's are the constants of integration. They have to be determined by applying the boundary conditions. Note that if λ is imaginary, we replace $cos(\lambda\ell)$ by $cosh(\lambda\ell)$ and $sin(\lambda\ell)/\lambda$ by $sinh(\lambda\ell)/\lambda$ in Eqn. [22].

Boundary Conditions

The five a's and F have to be determined based on appropriate boundary conditions. In particular, the terminal shear force F is determined according to loop closure condition $Z(0) = Z(L)$ ($L = 2\pi/\kappa^o$).

It is interesting to note that constant δ is not a solution for the equations. This is easy to understand: if we introduce boundary conditions $\delta(0) = \delta(L) = \delta_0$, then the whole planar circular rod will have a pure rotation without any intrinsic twist and writhe. And even though the rod is still a planar circle, it is not in the $Z = 0$ plane, rather it is in a plane which has a angle δ_0 with the $Z = 0$ plane. The pure rotation solution is:

$$Z(\ell) = \frac{\delta_0}{\kappa^o}(1 - cos\kappa^o\ell)$$

which corresponds to $-a_2(1 - cos\kappa^o\ell)$ in the Eqn. [22].

The boundary conditions are:

$$Z(0) = Z(L) = 0, \quad Z'(0) = Z'(L) = 0, \quad \delta(0) = -\beta\Psi, \quad \delta(L) = (1-\beta)\Psi \quad 0 < \alpha, \beta < 1 \tag{23}$$

where is the first two equations follow the fact that the terminal ends of the rod are jointed smoothly and lie in the xy plane. And where Ψ is the face-to-face rotation at the joining ends due to rotating the two terminal faces ith respect to each other; while the parameter β indicates the twist of each end with respect to the untwisted state. The concept of end-to-end rotation is motivated by the concept of linking number which plays a central role in circular DNA (13). Substituting Eqn [23] into [22] leads to the terminal force:

$$F = C\kappa^o\Psi/L = C\kappa^{o2}\Psi/2\pi \tag{24}$$

Thus we can see that the force is independent of β, only the net end-to-end rotation. The boundary conditions (Eqn. [23]) lead to:

$$a_0 = \frac{\kappa^*\kappa^o - \lambda^2}{\kappa^*\kappa^o}a_4 - \frac{\beta\Psi}{\kappa^o}, \quad a_1 = \frac{\lambda}{\kappa^o}a_3 - \frac{\kappa^*\Psi}{2\pi\lambda^2}, \quad a_2 = \frac{\lambda^2}{\kappa^*\kappa^o}a_4 + \frac{\beta\Psi}{\kappa^o}$$
$$a_3 = \frac{\kappa^*\Psi + \lambda^2(1 - cos(2\pi\lambda/\kappa^o))a_4}{\lambda^2 sin(2\pi\lambda/\kappa^o)}, \quad a_4 = -\frac{\kappa^*\Psi}{2\lambda^2} \tag{25}$$

The condition $Z'(0) = Z'(L)$ ensures a smooth closure. a_2 determines the pure rotational component due to the twist. We see that apart of the pure rotation, the solution is independent of β. In other words, the relative twist, i.e., the end-to-end rotation Ψ determines the solution. The pure rotation angle is $(\frac{1}{2} - \beta)\Psi$ which is simply $\frac{\delta(0)+\delta(L)}{2}$.

The final solution is:

$$\begin{pmatrix} Z \\ \delta \end{pmatrix} = \frac{\kappa^*\Psi}{2\lambda^2}\left(\frac{2\ell - L}{L}\right)\begin{pmatrix} 1 \\ 0 \end{pmatrix} - \frac{\kappa^*\Psi}{2\pi\lambda^2}\left[1 - \frac{\lambda L}{2} ctg\left(\frac{\lambda L}{2}\right)\right] sin(\kappa^o\ell)\begin{pmatrix} 1 \\ -\kappa^o \end{pmatrix}$$
$$+\frac{\kappa^*\Psi}{2\lambda^2}\left(\frac{sin(\lambda L/2 - \lambda\ell)}{sin(\lambda L/2)}\right)\begin{pmatrix} -1 \\ \frac{\lambda^2}{\kappa^*} \end{pmatrix} \tag{26}$$

Figure 2 shows the out-of-plane component and the twist of rod with different intrinsic curvature. For nonzero κ^*, the equilibrium configuration is not planar under twist. The central result of the present study is that for nonzero Φ, Z is not zero. That is to say, there is a writhing (out-of-plane component) for any nonzero twist. An intrinsically curved rod can not resist the terminal twist and keep its planar configuration. The twist and the writhe is directly linked in the intrinsically curved rod.

In the limit of $\kappa^* = 0$, the twisted planar circle is an equilibrium configuration. For naturally straight rod ($\kappa^* = 0$), bending and twisting leads to a helical configuration; a terminal force on the $\hat{z}$ direction is necessary for the rod to form a closed loop with bending (κ^o) and twisting (tw). When $\kappa^* = 0$, Eqn. [24] is reduced to the well known $F = C\kappa^o(tw)$ (10). The rod keeps in its planar circular configuration under mild twist. There is no out-of-plane (writhe) with small twist $tw = \Psi/L$. With increasing twist, eventually an abrupt writhing occurs when $tw = \sqrt{3}A\kappa^o/C$ (4,5,8).

For a very small κ^*, we have asymptotics for the solution:

$$Z(\ell) \approx \frac{\pi^2\kappa^*\Psi}{3\kappa^{o2}}\left[\frac{\kappa^o\ell}{2\pi} - 3\left(\frac{\kappa^o\ell}{2\pi}\right)^2 + 2\left(\frac{\kappa^o\ell}{2\pi}\right)^3 - \frac{sin\kappa^o\ell}{2\pi}\right] \tag{27}$$

$$\Omega_\zeta \approx \frac{\kappa^o\Psi}{2\pi} + \frac{\pi A\kappa^*\Psi}{6C}\left[1 - 6\left(\frac{\kappa^o\ell}{2\pi}\right) + 6\left(\frac{\kappa^o\ell}{2\pi}\right)^2\right] \tag{28}$$

Discussion

One of the important questions in the modern molecular biology is how twisting of a DNA modulates its bending (looping) which plays a central role in biological processes such as transcription activation (14;15). Growing biochemical evidence suggests that DNA molecules have intrinsic curvature in their stress-free state (16,17). In a recent paper, the contribution of intrinsic bending to the flexibility of long DNA molecules has been studied in conjunction with random polymer theory (18). The present work provides the first rigorous analysis on the contribution of intrinsic bending to the elastic behavior of short circular DNAs which are usually dominated by elasticity. It is shown that the face-to-face rotation of a circular DNA molecule is likely to immediately cause writhe (supercoiling) without elastic instability.

The linear solution of the problem enables us to identify two different modes for rods under terminal twist and bend, a damped regime ($\kappa^*/\kappa^o < \frac{A-C}{C} = \nu$) and an oscillatory regime ($\kappa^*/\kappa^o > \frac{A-C}{C} = \nu$), where A and C are bending and twisting constants of the rod, ν is the Poisson ratio, and κ^* and κ^o are intrinsic and induced curvatures of the rod, respectively.

In a paper on the dynamics of circular rod with intrinsic curvature just published independently, Tobias et al. (19) have shown that the sufficient and necessary condition for a circular rod with intrinsic curvature being at equilibrium is zero twist.

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Figure Captions

Figure 1 A schematics for the local coordinate system (*bff*) along a planar circle.

Figure 2 The out-of-plane component and the twist ($\Omega_\zeta = \kappa^o Z' + \delta'$) of a circular rod under twist. The Poisson ratio $(A - C)/C = 0.25$, $\kappa^o = 2\pi$ so that $L = 1$. Different curves are for rods with different intrinsic curvatures κ^*/κ^o listed by the symbols. $\kappa^* = 0$ represents the naturally straight rod. $\kappa^*/\kappa^o = 1$ represents the O-ring of Bauer et al. (1993). The boundary conditions are such that the two terminals joint smoothly: $Z(0) = Z(L)$ and $Z'(0) = Z'(L)$. All curves are proportional to Ψ because they are the linearized solutions.

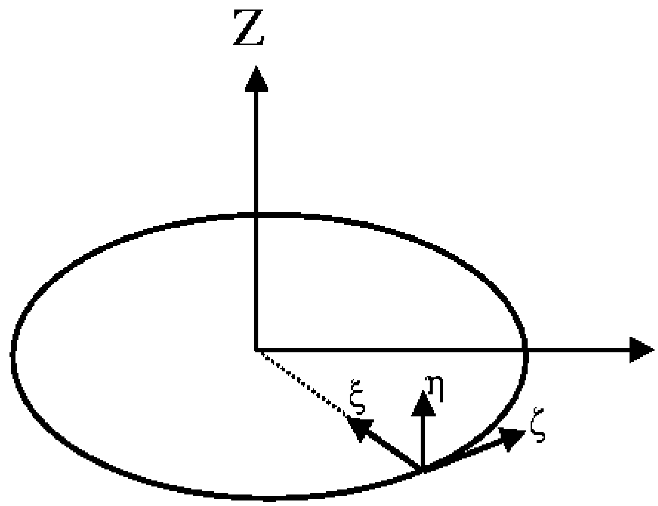
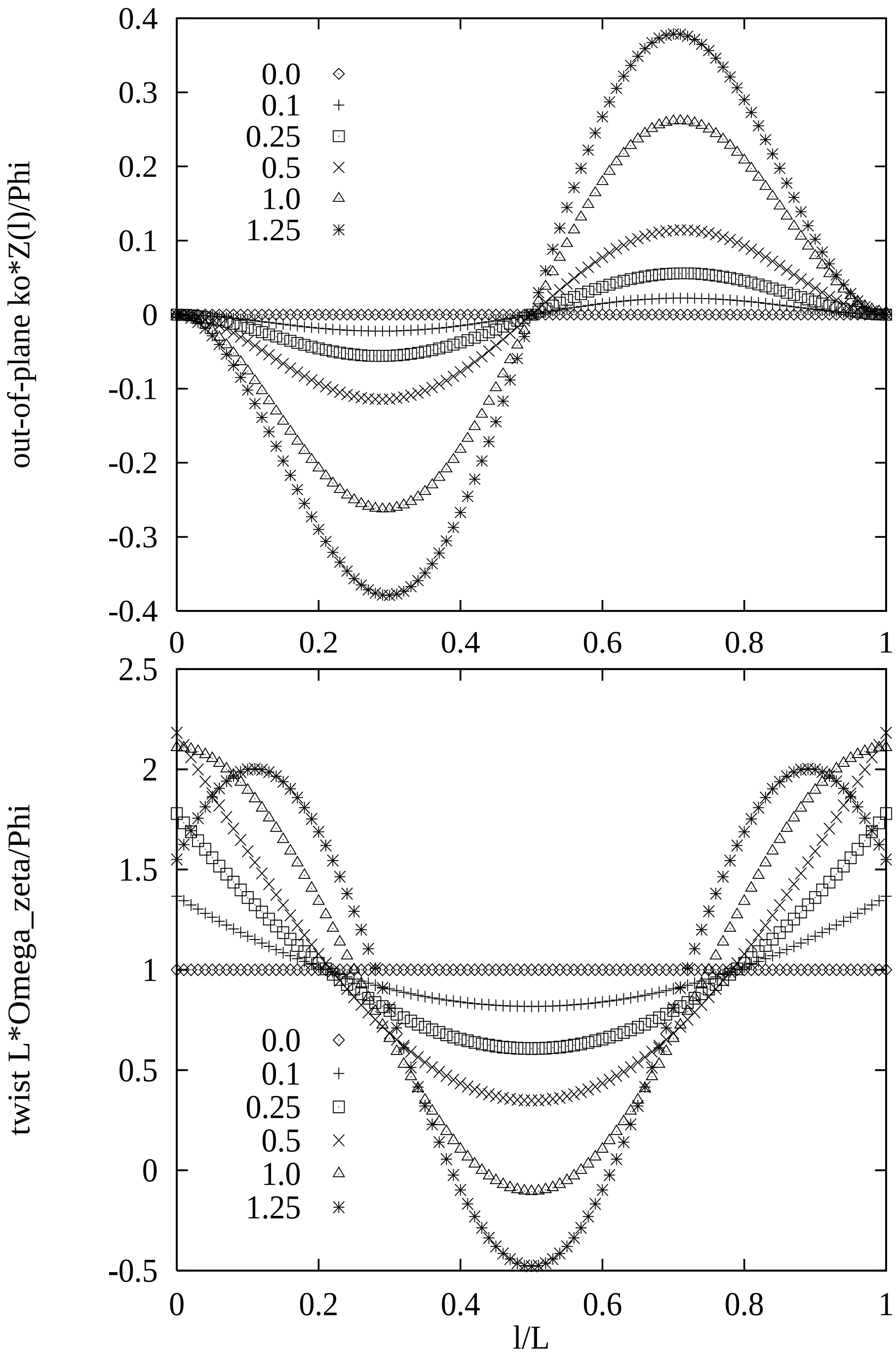


Figure 1:



out-of-plane ko*Z(l)/Phi
0.0
0.1
0.25
0.5
1.0
1.25
twist L*Omega_zeta/Phi
l/L

Figure 2: