General investigation of elastic thin rods as subject to a terminal twist

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The recent development of DNA structure, brought by the elastic rod model, revives the study of the so-called Michell-Zajac instability for isotropic naturally straight elastic rings. The instability states that when subjected to a terminal twist, a manipulation which cuts, rotates, and then seals closed rods, an elastic ring does not writhe until the amount of rotation exceeds a rod-dependent threshold. From the data generated by a finite element method, Bauer, Lund, and White [Proc. Natl. Acad. Sci. USA. **90**, 833 (1993)] concluded that the instability becomes extreme for isotropic naturally singly bent, doubly bent, and *O*-ring elastic rings since they writhe immediately as subject to a terminal twist. This paper continues their study for other closed rods. In order to understand DNA structure in DNA-protein interactions, this paper also extends the study to open rods with clamped ends; for such rods, a terminal twist is a manipulation which releases, rotates, and then reclamps one end of the rods. Moreover, the rods under consideration need not be isotropic or may violate Kirchhoff-Clebsch conservation law of total energy. By linearizing the Euler-Lagrange equations which govern equilibrium rods and analyzing the linearized equations, this paper establishes an inequality such that if the initial values of the bending curvatures, their first derivatives, and the twisting density of an equilibrium rod satisfy the inequality, the rod axis deforms immediately as the rod is subject to a terminal twist. Since the initial data dissatisfying the inequality form a hypersurface in the five-dimensional Euclidean space, this paper asserts that a terminal twist makes the axis deformed instantly for almost every equilibrium rod.

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I. INTRODUCTION

Since diverse conformations observed up to date suggest that a single DNA molecule is semiflexible, one may consider the molecule an isotropic elastic thin rod when one investigates structural properties of DNA. For example, Bauer, Lund, and White studied protein-DNA loops of hundreds to thousands of base pairs with a small deficiency in the linking number [1] (a rather extensive study was presented in Ref. [2]). More circumstantially, they considered four closed circular relaxed DNA rods which are naturally straight, singly bent, doubly bent, and *O* ring. Their significant numerical results demonstrate that all but the naturally straight rod writhe once the deficiency is initiated; the naturally straight rod does not writhe until the deficiency is about 1.8 turns which agrees with the instability found by Michell (see the review article [3] which includes Michell's original paper) and independently by Zajac [4].

From the viewpoint of the elastic rod model for DNA structure, a closed circular DNA rod with a linking number change may result from cutting the rod perpendicular to its axis, rotating one of the cut faces about the local tangent to the axis as the other is fixed, and then sealing the cut [1]. The type I topoisomerase (Ref. [5], Chap. 5) uses an equivalent mechanism to relax negatively supercoiled DNA in prokaryotes and both positively and negatively supercoiled DNA in eukaryotes, to introduce positive supercoils into DNA in thermophilic archaea, and to help DNA replication elongate by removing precatenanes behind the replication fork [6]. (In the preceding statement, by negatively supercoiled DNA we mean DNA with a linking number deficiency and by positively supercoiled DNA we mean the contrary.) After being subject to a terminal twist, namely, undergoing the aforementioned cut-rotate-seal manipulation, the resulting DNA structure may promote protein-DNA loops formation since the proteins need not expend binding free energy on the entropy cost of bringing separate DNA sites together (Ref. [5], Chap. 6). Loops are widely observed in repression of DNA transcription in prokaryotes as in the case of the *ara*, *gal*, and *lac* operons [7–12], as well as inactivation of transcription as in the interaction between NtrC and the σ^{54} RNA polymerase holoenzyme in *E. coli* [13]. The negatively supercoiled DNA structure is thought to stimulate homologous recombination as RecA, which catalyzes DNA synapsis in *E. coli*, is known to unwind duplex DNA (Ref. [5], Chap. 6). It has also been demonstrated that DNA supercoiling has a profound effect on the site-specific recombination; in the example of λ integration reaction, which integrates the bacteriophage λ DNA into the *E. coli* chromosome by λ Int protein, the only effective substrates are negatively supercoiled closed circular DNAs bearing the *att*P site [14].

Since open DNA rods might have domains whose structural properties are similar to closed circular DNAs', we shall also study these so-called topological domains as subject to a terminal twist. We thus have to clarify the notion of such domains being subject to a terminal twist. But, first note that a domain, such as the domains between two consecutive sites anchored to a nuclear matrix [15,16], may be treated as a clamped-end rod because the ends of the domain are bound to proteins so that they neither move nor rotate freely. We say that a clamped-end rod is subject to a terminal twist if one of its ends is released and then reclamped after a rotation. Thus, we can consider all closed rods as a special case of clamped-end rods, particularly when the rods are subject to a terminal twist.

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One may linearize the governing equations, about an equilibrium rod and then solves the linearized equations. This approach has been widely employed to establish Michell-Zajac instability for naturally straight equilibrium rods: when subjected to a terminal twist, such a rod does not writhe until its total twist γ satisfies $|\gamma|>2\pi\rho/\tilde{\rho}$ if the rod is linear [17,18], $|\gamma|>2\sqrt{3}\pi\rho/\tilde{\rho}$ if the rod is closed circular [3,4,18–21], $|\gamma|>(2\pi\rho/\tilde{\rho})\sqrt{j^2-(\kappa l/2\pi)^2}$ if the rod is a planar arch [18], where $\rho,\tilde{\rho},\kappa$, and l are the bending stiffness, twisting stiffness, axis curvature, and axis length of the rod, respectively, and j is the smallest positive integer whose square is larger than $(\kappa l/2\pi)^2$. The approach was also employed to verify that the naturally O-ring elastic ring writhes immediately when subjected to a terminal twist [21] (the authors called a writhe of this fashion a "continuous writhe" and the one described previously an "abrupt writhe"). However, if the governing equations have no general closed-form solutions, for example, the equations for the naturally O-ring equilibrium rods, then the approach becomes ineffective. Therefore, we should look for a new one which ideally makes no use of techniques of solving ordinary differential equations or as little use as possible.

Aside from the aforementioned approach, there is a different one. In Ref. [22], the authors showed a unique naturally O-ring elastic ring by solving the governing equations; this uniqueness can be used to verify that the naturally O-ring elastic ring writhes instantly when subjected to a terminal twist since if not, there should be two distinct rings. Using this approach, I was able to show that any naturally straight equilibrium rod which is not linear, circular, or helical [23], and some naturally O-ring equilibrium rods which are linear, circular, and helical [24] writhe immediately when subjected to a terminal twist.

Although the approach of Ref. [22] is based on an innovatory idea, it involves solving ordinary differential equations. So in Ref. [25] I developed an argument to study general naturally O-ring equilibrium rods. The argument goes as follows. First, we construct a mapping defined on a product space of some function spaces so that its zeros represent naturally O-ring equilibrium rods. Next, for an arbitrarily given zero we consider the curves passing through the zero that realize terminal twists exerting on the equilibrium rod represented by the zero. Finally, we calculate the tangent vector to the image of each of the curves under the mapping. If all such vectors are not zero, then the equilibrium rod has no neighboring equilibrium rods with the same axis. Therefore, the rod axis shall deform immediately as the rod is subject to a terminal twist. This argument can be considered the infinitesimal version of the one of Ref. [22]. While the argument of Ref. [22] attempts to show that the space of all equilibrium rods with a specific axis is a singleton, mine intends to prove that the space is discrete.

In fact, my argument also works for anisotropic rods and rods which disobey the Kirchhoff-Clebsch conservation law of total energy [17]. Therefore, in this paper I intend to demonstrate the following result which generalizes the result shown in Ref. [25].

For almost every equilibrium rod, the axis deforms immediately as the rod is subject to a terminal twist. More precisely, let $\mathcal{R}$ be an equilibrium rod with bending curvatures u_1,u_2, and twisting density u_3, and let κ_1 and κ_2 be the bending curvatures of the undeformed state of $\mathcal{R}$. Let x,y,z,u,v, respectively, denote the value of $u_1,u_2,u_3,\dot{u}_1,\dot{u}_2$ at the point on the rod axis that also belongs to the fixed end while $\mathcal{R}$ being subject to a terminal twist, and let $\beta_1,\beta_2,\dot{\beta}_1,\dot{\beta}_2$, respectively, denote the value of $\kappa_1,\kappa_2,\dot{\kappa}_1,\dot{\kappa}_2$ at the same point. If

$$4(\rho_1-\rho_2)xyz+[2(\rho_1-\rho_2)-\rho_3]xu-[2(\rho_1-\rho_2)+\rho_3]yv + 2\rho_2\beta_2xz-2\rho_1\beta_1yz-2\rho_1\dot{\beta}_1x-2\rho_2\dot{\beta}_2y\neq 0, \quad (1)$$

then the axis of $\mathcal{R}$ deforms instantly as $\mathcal{R}$ is subject to a terminal twist, where ρ_1 and ρ_2 are the bending stiffnesses, and ρ_3 is the twisting stiffness of $\mathcal{R}$.

This paper is organized as follows. The next section presents a brief review of Kirchhoff's elasticity theory of thin rods. Section III gives the so-called dynamic equations which describe the null tangent vector mentioned in the last paragraph but one. It also shows that there is no nontrivial solution to the dynamic equations for any equilibrium rod satisfying the inequality (1). Section IV recovers the main result presented in Ref. [23]. The last section concludes this paper by asserting that for almost every equilibrium rod, the axis deforms immediately as the rod is subject to a terminal twist. It also discusses the exceptional rods for which the dynamic equations might have non-trivial solutions, and compares the White's formula [26] with the result of this paper.

II. THE EULER-LAGRANGE EQUATIONS

All elastic rods studied in this paper are supposed to have the following features. First, they are cylindrical and slender. Second, the configuration of each rod is completely determined by an immersed curve, called the axis, and a preferred unit normal vector field defined along the curve, called the material direction. Finally, there is a rod $\mathcal{R}_u$ considered the undeformed state of all the rods, moreover, any rod other than $\mathcal{R}_u$ results from $\mathcal{R}_u$ through some inextensible and unshearable deformation.

The inextensibility condition implies that all the rods have the same length, call it l, and thus the same arc length parameter, call it s. As a rod is subject to a terminal twist, we always assume that the parameter s takes the value l at the point on the rod axis that also belongs to the normal cross section on which the twist exerts.

Because the rigid body motions of $\mathbb{R}^3$ do not change the physical properties of a rod, we may assume that the rod axis passes through the origin of $\mathbb{R}^3$ in a way that at the point the unit tangent vector to the rod axis and the material direction of the rod are the unit vectors in the direction of the positive x axis and y axis, respectively. Moreover, we always assume that the parameter s takes the value 0 at the origin when studying the twist-induced deformation of the rod axis.

For an elastic rod $\mathcal{R}$, let $\boldsymbol{d}_3$ be the unit tangent vector field to the rod axis, $\boldsymbol{d}_1$ the material direction, and $\boldsymbol{d}_2=\boldsymbol{d}_3\times\boldsymbol{d}_1$. Let $\boldsymbol{u}$ be a vector field satisfying

$$\frac{d\boldsymbol{d}_i}{ds} = \boldsymbol{u} \times \boldsymbol{d}_i$$

for $i=1,2,3$. Since $\{\boldsymbol{d}_1,\boldsymbol{d}_2,\boldsymbol{d}_3\}$ forms an ordered orthonormal basis of $\mathbb{R}^3$ at each point on the rod axis of $\mathcal{R}$, we write $\boldsymbol{u}$ as $\boldsymbol{u}=u_1\boldsymbol{d}_1+u_2\boldsymbol{d}_2+u_3\boldsymbol{d}_3$. Here, u_1,u_2 are called the bending curvatures and u_3 is called the twisting density; particularly for the undeformed state $\mathcal{R}_u$ they are also denoted as κ_1,κ_2, and κ_3, respectively. The elastic energy of $\mathcal{R}$ is defined by

$$\frac{1}{2}\int_0^l \rho_1(u_1-\kappa_1)^2+\rho_2(u_2-\kappa_2)^2+\rho_3(u_3-\kappa_3)^2 ds,$$

where the positive constants ρ_i's denote the stiffnesses of the rod.

$\mathcal{R}$ is called an equilibrium rod if it satisfies the following Euler-Lagrange equations [27]:

$$\rho_1\dot{u}_1+(\rho_3-\rho_2)u_2u_3 = \boldsymbol{\lambda}\cdot\boldsymbol{d}_2+\rho_1\dot{\kappa}_1+\rho_3\kappa_3u_2-\rho_2\kappa_2u_3, \tag{2}$$

$$\rho_2\dot{u}_2+(\rho_1-\rho_3)u_1u_3 = -\boldsymbol{\lambda}\cdot\boldsymbol{d}_1+\rho_2\dot{\kappa}_2-\rho_3\kappa_3u_1+\rho_1\kappa_1u_3, \tag{3}$$

$$\rho_3\dot{u}_3+(\rho_2-\rho_1)u_1u_2 = \rho_3\dot{\kappa}_3+\rho_2\kappa_2u_1-\rho_1\kappa_1u_2, \tag{4}$$

where $\boldsymbol{\lambda}$ is some constant vector, and the dot between $\boldsymbol{\lambda}$ and $\boldsymbol{d}_i$ is the standard inner product of $\mathbb{R}^3$.

Remark. The reader may consult Ref. [27] for more details on Eqs. (2)–(4), but first notice that the vector fields e_1,e_2, and e_3 there are $\boldsymbol{d}_3$, $\boldsymbol{d}_1$, and $\boldsymbol{d}_2$ here, respectively. The reason for such a difference is because in the field of submanifolds geometry, tangent vectors to a submanifold are used to being named first. Derived from the definitions for ω_i's of Ref. [27] and u_i's of this paper, we have $u_1=-\omega_2, u_2=\omega_1$ and $u_3=\omega_3$. Also, the ρ_1,ρ_2,ρ_3 appearing in Ref. [27] are, respectively, ρ_2,ρ_1,ρ_3 appearing in this paper.

For an equilibrium rod $\mathcal{R}$, write $\boldsymbol{\lambda}$ as $\boldsymbol{\lambda}=-\lambda_1\boldsymbol{d}_1+\lambda_2\boldsymbol{d}_2+\lambda_3\boldsymbol{d}_3$ (so the $\lambda_1,\lambda_2,\lambda_3$ of Ref. [27] are, respectively, $\lambda_3,\lambda_1,-\lambda_2$ of this paper). Because $\boldsymbol{\lambda}$ is constant, $\dot{\boldsymbol{\lambda}}=0$ and it leads to

$$\dot{\lambda}_1+\lambda_2u_3-\lambda_3u_2=0, \tag{5}$$

$$\lambda_1u_3-\dot{\lambda}_2+\lambda_3u_1=0, \tag{6}$$

$$\lambda_1u_2+\lambda_2u_1+\dot{\lambda}_3=0. \tag{7}$$

Equation (7) implies Kirchhoff-Clebsch conservation law of total energy if κ_1,κ_2, and κ_3 are all constant [17]; the law states that the total energy of an equilibrium rod, defined by

$$\frac{1}{2}(\rho_1u_1^2+\rho_2u_2^2+\rho_3u_3^2)+\lambda_3$$

is constant under the assumption.

The Euler-Lagrange equations are complicated because of the following two terms: $\boldsymbol{\lambda}\cdot\boldsymbol{d}_1$ and $\boldsymbol{\lambda}\cdot\boldsymbol{d}_2$. So, to obtain equilibrium rods we shall solve Eqs. (4)–(7) instead, where λ_1 and λ_2 are, respectively, substituted by Eqs. (3) and (2). After rewriting Eqs. (4)–(7) as $\dot{\boldsymbol{x}}=\boldsymbol{F}(\boldsymbol{x})$, where $\boldsymbol{x}$ is the transpose of $(u_1,u_2,u_3,\dot{u}_1,\dot{u}_2,\lambda_3)$, one may easily conclude that if each κ_i is real analytic, then the u_1,u_2,u_3, and λ_3 of an equilibrium rod are also real analytic [28]. Therefore, we assume that each κ_i is real analytic from now on.

III. THE DYNAMIC EQUATIONS AND THEIR SOLUTIONS

For $k=0,1,2$, let $\mathcal{C}^k$ denote the space of all C^k functions defined on $[0,l]$ that is topologized by the usual C^k norm. Define two product spaces $\mathcal{M}=\mathcal{C}^1\times\mathcal{C}^2\times\mathcal{C}^2\times\mathcal{C}^1$ and $\mathcal{N}=\mathcal{C}^0\times\mathcal{C}^0\times\mathcal{C}^0\times\mathcal{C}^0$. Let $S:\mathcal{M}\to\mathcal{N}$ be a map defined by

$$\begin{aligned} S(u_1,u_2,u_3,\lambda_3) = [&\rho_3\dot{u}_3+(\rho_2-\rho_1)u_1u_2-\rho_3\dot{\kappa}_3-\rho_2\kappa_2u_1 \\ &+\rho_1\kappa_1u_2, \dot{\lambda}_1+\lambda_2u_3-\lambda_3u_2, \lambda_1u_3-\dot{\lambda}_2 \\ &+\lambda_3u_1, \lambda_1u_2+\lambda_2u_1+\dot{\lambda}_3],\end{aligned}$$

where

$$\lambda_1 \overset{\text{def}}{=} \rho_2\dot{u}_2+(\rho_1-\rho_3)u_1u_3-\rho_2\dot{\kappa}_2+\rho_3\kappa_3u_1-\rho_1\kappa_1u_3,$$

$$\lambda_2 \overset{\text{def}}{=} \rho_1\dot{u}_1+(\rho_3-\rho_2)u_2u_3-\rho_1\dot{\kappa}_1-\rho_3\kappa_3u_2+\rho_2\kappa_2u_3.$$

So $S^{-1}(\mathbf{0})$ represents the set of all equilibrium rods, where $\mathbf{0}\overset{\text{def}}{=}(0,0,0,0)\in\mathcal{N}$.

Let $p\in\mathcal{M}$ represent an equilibrium rod $\mathcal{R}$. A deformation of $\mathcal{R}$ gives rise to a C^1 curve $\gamma(t)$, where $-1<t<1$, on $\mathcal{M}$ so that $\gamma(0)=p$. Let us write $\dot{\gamma}(0)=(\Omega_1,\Omega_2,\Omega_3,\Lambda)$. If the deformation is induced by a terminal twist, namely, $\mathcal{R}$ has been twisted around its axis by an angle $\Psi=\Psi(s,t)$ satisfying $\Psi(s,0)=0$ for $0\le s\le l$ and $\Psi(0,t)=0$ for $-1<t<1$, then

$$\Omega_1=u_2\psi, \Omega_2=-u_1\psi \quad \text{and} \quad \Omega_3=\dot{\psi},$$

where

$$\psi = \left.\frac{\partial}{\partial t}\right|_{t=0}\Psi.$$

Moreover,

$$\left.\frac{d}{dt}\right|_{t=0} S[\gamma(t)]=0$$

is equivalent to the following equations:

$$\rho_3\ddot{\psi}=[-(\rho_1-\rho_2)(u_1^2-u_2^2)+\rho_1\kappa_1u_1+\rho_2\kappa_2u_2]\psi, \tag{8}$$

$$\begin{aligned}\Lambda u_2 + [&-(\rho_1-\rho_2)(\ddot{u}_1+2\dot{u}_2u_3+u_2\dot{u}_3-u_1u_3^2)+\rho_1\ddot{\kappa}_1 \\ &-2\rho_2\dot{\kappa}_2u_3-\rho_2\kappa_2\dot{u}_3-\rho_1\kappa_1u_3^2]\psi+\{-[2(\rho_1-\rho_2)-\rho_3]\dot{u}_1 \\ &-[2(\rho_1-\rho_2)+\rho_3]u_2u_3+2\rho_1\dot{\kappa}_1-2\rho_2\kappa_2u_3\}\dot{\psi} \\ &+[-(\rho_1-\rho_2-\rho_3)u_1+\rho_1\kappa_1]\ddot{\psi}=0,\end{aligned} \tag{9}$$

$$\Lambda u_1 + [(\rho_1-\rho_2)(-\ddot{u}_2 + 2\dot{u}_1 u_3 + u_1\dot{u}_3 + u_2 u_3^2) - \rho_2\ddot{\kappa}_2 - 2\rho_1\dot{\kappa}_1 u_3 - \rho_1\kappa_1\dot{u}_3 + \rho_2\kappa_2 u_3^2]\psi + \{-[2(\rho_1-\rho_2)+\rho_3]\dot{u}_2 + [2(\rho_1-\rho_2)-\rho_3]u_1u_3 - 2\rho_2\dot{\kappa}_2 - 2\rho_1\kappa_1 u_3\}\dot{\psi} + [-(\rho_1-\rho_2+\rho_3)u_2 - \rho_2\kappa_2]\ddot{\psi} = 0, \quad (10)$$

$$\dot{\Lambda} + \{(\rho_1-\rho_2)[\dot{u}_1 u_2 + u_1\dot{u}_2 - (u_1^2-u_2^2)u_3] + (\rho_1\kappa_1 u_1 + \rho_2\kappa_2 u_2)u_3 + \rho_2\dot{\kappa}_2 u_1 - \rho_1\dot{\kappa}_1 u_2\}\psi + [2(\rho_1-\rho_2)u_1u_2 + \rho_2\kappa_2 u_1 - \rho_1\kappa_1 u_2]\dot{\psi} = 0. \quad (11)$$

Equations (8)–(11) are called the "dynamic equations" in this paper. It is a little unexpected that the dynamic equations do not depend on the twisting density of the undeformed state.

The existence of nontrivial solutions to the dynamic equations implies that within an infinitesimally short time interval, the deformed $\mathcal{R}$ is still in a state of equilibrium. Therefore, the axis of $\mathcal{R}$ must deform instantly when $\mathcal{R}$ is subject to a terminal twist if the corresponding dynamic equations have the trivial solution only.

Since $\Psi(0,t)=0$ for $-1<t<1$, we have $\psi(0)=0$, furthermore, $\ddot{\psi}(0)=0$ due to Eq. (8). Let x,y,z,u, and v denote $u_1(0), u_2(0), u_3(0), \dot{u}_1(0)$, and $\dot{u}_2(0)$, respectively. Then, at $s=0$, Eqs. (9) and (10) can be expressed as

$$A\boldsymbol{x} = \boldsymbol{0},$$

where

$$A = \begin{pmatrix} y & -[2(\rho_1-\rho_2)-\rho_3]u - [2(\rho_1-\rho_2)+\rho_3]yz + 2\rho_1\dot{\kappa}_1(0) - 2\rho_2\kappa_2(0)z \\ x & -[2(\rho_1-\rho_2)+\rho_3]v + [2(\rho_1-\rho_2)-\rho_3]xz - 2\rho_2\dot{\kappa}_2(0) - 2\rho_1\kappa_1(0)z \end{pmatrix},$$

$\boldsymbol{x}$ and $\boldsymbol{0}$ are the transpose of $(\Lambda(0), \dot{\psi}(0))$ and $(0,0)$, respectively. If A is nonsingular, namely, the inequality (1) holds, then the above system of linear equations has only a trivial solution. In particular, $\dot{\psi}(0)=0$. Therefore, as a solution to the following initial value problem:

$$\rho_3\ddot{\psi} = [-(\rho_1-\rho_2)(u_1^2-u_2^2) + \rho_1\kappa_1 u_1 + \rho_2\kappa_2 u_2]\psi,$$

$$\psi(0) = \dot{\psi}(0) = 0,$$

$\psi=0$ on $[0,l]$ since ψ is real analytic and is 0 over a subinterval containing 0 by the uniqueness of solutions of ordinary differential equations [28].

IV. RECOVERY OF A KNOWN RESULT

We consider here the case of isotropic naturally straight rods, namely, $\rho_1=\rho_2$ (hence we write $\rho_1=\rho_2=\rho$ and $\rho_3=\tilde{\rho}$) and $\kappa_1=\kappa_2=\kappa_3=0$. Using the criterion established in the preceding section, the dynamic equations have only the trivial solution for any equilibrium rod whose squared axis curvature has nonzero first derivative at $s=0$. Therefore, the axis of such a rod deforms immediately as the rod is subject to a terminal twist.

Since the dynamic equations are very simple for this case, next we shall directly solve the equations for more details on the twist-induced axis deformation for isotropic naturally straight equilibrium rods. First, Eqs. (8)–(11) are largely simplified as

$$\ddot{\psi} = 0,$$

$$\Lambda u_2 + \tilde{\rho}(\dot{u}_1 - u_2u_3)\dot{\psi} = 0,$$

$$\Lambda u_1 - \tilde{\rho}(\dot{u}_2 + u_1u_3)\dot{\psi} = 0,$$

$$\dot{\Lambda} = 0,$$

respectively. The middle two equations give rise to

$$(\dot{k^2})\dot{\psi} = 0,$$

where k denotes the axis curvature of an equilibrium rod. So, clearly, k being constant is a necessary and sufficient condition for the existence of nontrivial ψ. It was shown in Ref. [23] that the axis of such an equilibrium rod must be a line, a circular arc, or a circular helix. Therefore, the axis of an equilibrium rod deforms instantly as the rod is subject to a terminal twist if it is none of the aforementioned curves.

The preceding conclusion has already appeared in Ref. [23]. In there, it was drawn from a result stating that two distinct equilibrium rods have the same axis if and only if the axis is a line, a circular arc, or a circular helix. This result was obtained by showing that, via the closed-form solutions to Eqs. (4)–(6), the axis of an equilibrium rod sustains only one twisting density if it is not a line, nor a circular arc, nor a circular helix.

V. CONCLUSION AND DISCUSSIONS

For solving Eqs. (4)–(7) for equilibrium rods, we need the initial values of $u_1, u_2, u_3, \dot{u}_1, \dot{u}_2$, and λ_3 (see the last paragraph of Sec. II). If the first five satisfy the inequality (1), then the axis of the associated equilibrium rod deforms immediately as the rod is subject to a terminal twist. Since the initial data which dissatisfy the inequality form a hypersurface in $\mathbb{R}^6$, we may assert that for almost every equilibrium rod, the axis deforms instantly as the rod is subject to a terminal twist.

A rod is called "singular" if it is an equilibrium rod generated by the initial data lying on the hypersurface. It is not certain that the axis of any singular rod must deform abruptly as the rod is subject to a terminal twist. Some of the singular rods indeed have continuous writhe, for example, isotropic naturally *O*-ring equilibrium rods with linear, circular or helical axis [24], and anisotropic naturally straight equilibrium rods with circular or helical axis [29]. To the best of my knowledge, it is not clear if there is an isotropic naturally *O*-ring singular rod which has abrupt axial deformation as subject to a terminal twist, even though this topic has been studied for over a decade. Such a rod, if exists, relates to a solution to a generalized Riccati equation [25].

On the other hand, [30] has witnessed that anisotropic naturally straight linear equilibrium rods, which are also singular, may writhe abruptly as subject to a terminal twist. As a matter of fact, the author took up the so-called second variation formula (Ref. [31] Chap. 1) to study the stability of the rods: such a rod is stable if its total twist γ satisfies $|\gamma| \leq 2\pi\sqrt{\rho_1\rho_2/a}$ when $a=b>0$ or $a>b\geq 0$ or $a>-b>0$ or $b>a\geq 0$, $|\gamma|\leq 2\pi\sqrt{-\rho_1\rho_2/b}$ when $a=b<0$ or $0\geq a>b$ or $-b\geq a>0>b$ or $0\geq b>a$, and there is no restriction on $|\gamma|$ when $a=b=0$ or $a<0<b$, where $a=-(\rho_1-\rho_2+\rho_3)^2+2(\rho_1^2-\rho_2^2+\rho_3^2)$ and $b=(\rho_1-\rho_2-\rho_3)^2+2(\rho_1^2-\rho_2^2-\rho_3^2)$. (The above is not the author's original statement but the correction and expansion presented in Ref. [29].) Therefore, she gave estimates on the critical twist, unfortunately, none of them is known to be optimal. Verifying whether the estimates are optimal or not is in progress [29].

The nature of the writhing instability of an isotropic naturally straight elastic ring is subcritical: the ring suddenly buckles and folds back onto itself by forming a figure-8 stabilized by self-contact. On the other hand, as illustrated by White *et al.* [2], it seems that the writhing instability of an isotropic naturally curved elastic ring is not subcritical since there is always a closed equilibrium rod close to the twisted ring.

The so-called White's formula $Lk=Tw+Wr$ [26] is also helpful to explain how a closed equilibrium rod reacts to a terminal twist since, according to the formula, a change in the linking number Lk converts as a single change of the twisting number Tw, or the writhing number Wr, or both. As demonstrated by Bauer *et al.* [1] and White *et al.* [2], each rod has its own unique conversion from ΔLk to Wr; this suggests that the conversion depends on the geometry of the undeformed state of the rod. Since the formula is invalid for open rods, it is inferred that the twist-induced axial deformation for elastic rods should be resulted from the clamped-end boundary conditions.

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