

# Direct Determination of DNA Twist-Stretch Coupling

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The symmetries of the DNA double helix require a new term in its linear response to stress: the coupling between twist and stretch. Recent experiments with torsionally-constrained single molecules give the first direct measurement of this important material parameter. We extract its value from a recent experiment of Strick *et al.* [Science **271** (1996) 1835] and find rough agreement with an independent experimental estimate recently given by Marko. We also present a very simple microscopic theory predicting a value comparable to the one observed.

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## 1. Introduction

The idea of studying the response of DNA to mechanical stress is as old as the discovery of the double helix structure itself [1]. While many elements of DNA function require detailed understanding of specific chemical bonds (for example the binding of small ligands), still others are quite nonspecific and reflect overall mechanical properties. Moreover, since the helix repeat distance of  $\ell_0 \approx 3.4$  nm involves dozens of atoms, it is reasonable to hope that this length-scale regime would be long enough so that the cooperative response of many atoms would justify the use of a continuum, classical theory, yet short enough that the spatial structure of DNA matters. In this Letter we will argue that this expectation is indeed fulfilled.

Since moreover various important biological processes involve length scales comparable to  $\ell_0$  (notably the winding of DNA onto histones), the details of this elasticity theory should prove important. Yet until recently little was known about the relevant elastic constants. Extensive experimental work yielded fair agreement on the values of the bend and twist persistence lengths, though the former was plagued with uncertainties due to the polyelectrolyte character of DNA [2]. A simple model of DNA as a circular elastic rod gives a reasonable account of many features of its long-scale behavior, for example supercoiling [3][4]. Some authors have sought to justify this model by invoking a shell of structured water around the DNA [3].

Recently, techniques of micromanipulation via optical tweezers and magnetic beads have yielded improved values for the bend stiffness from the phenomenon of thermally-induced entropic elasticity [5][6], as well as the direct measurement of a third elastic constant, the stretch modulus, by exploring the force range 10–50pN [7][8]. Significantly, the relation between bending stiffness, stretch modulus, and the diameter of DNA turned out to be roughly as predicted from the classical theory of beam elasticity [7][8][9], supporting the expectations mentioned above.

Still missing, however, has been any direct measurement of the elastic constants reflecting the *chiral* (*i.e.* helical) character of DNA. One such constant, a twist-bend coupling, was investigated by Marko and Siggia [10], but no direct experimental measurement has yet been devised. In this Letter we introduce a new chiral coupling, the twist-stretch energy. Electrostatic effects do not complicate the analysis of this coupling. We will explain why our term is needed, extract its value from the experiment of Strick *et al.* [11], and compare it to a the prediction of a simple microscopic model to see that its magnitude

is in line with the expectations of classical elasticity theory. J. Marko has independently introduced the same coupling and estimated its value from different experiments[12]; our values are in rough agreement.

## 2. Experiment

DNA differs from simpler polymers in that it can resist twisting, but it is not easy to measure this effect directly due to the difficulty of applying external torques to a single molecule. Early investigations of DNA twist were either limited to passive, fluorescence-depolarization measurements [2], or else to studying global shape changes in circular DNA of varying linkage [3]. The first single-molecule stretching experiments constrained only the locations of the two ends of the DNA strand. The unique feature of the experiment of Strick *et al.* was the added ability to constrain the *orientation* of each end of the molecule.

We will study Fig. 3a of ref. [11]. In this experiment, a constant force of 8pN was applied to the molecule and the end-to-end length  $z_{\text{tot}}$  monitored as the terminal end was rotated through  $\Delta\text{Lk}$  turns from its relaxed state (which has  $\text{Lk}_0$  turns). In this way the helix could be over- or undertwisted by as much as  $\pm 10\%$ . Over this range of imposed linkage  $z_{\text{tot}}$  was found to be a linear function of  $\sigma$ :

$$\varepsilon = \text{const.} - 0.15\sigma \text{ where } \sigma \equiv \Delta\text{Lk}/\text{Lk}_0 \text{ and } \varepsilon \equiv (z_{\text{tot}}/z_{\text{tot},0}) - 1. \quad (2.1)$$

Thus  $\sigma$  is the fractional excess link and  $\varepsilon$  is the extension relative to the relaxed state. Eqn. (2.1) is the experimentally observed twist-stretch coupling.

The existence of a linear term in (2.1) is direct evidence of the chiral character of the molecule, and its sign is as expected on geometrical grounds: untwisting the molecule tends to lengthen it. Still geometry alone cannot explain this result. Consider the outer sugar-phosphate backbones of the DNA. Suppose that the twist-stretch phenomenon were due to the straightening of these helical backbones while they maintained constant length, 0.6 nm per phosphate, and constant distance 0.9 nm from the center of the molecule. Then since each basepair step is  $h = 0.34$  nm high, the circumferential length per step is  $\ell_c = \sqrt{.6^2 - .34^2}$  nm. The corresponding twist angle per step is given by [13]  $\theta = (\ell_c/2)/.9\text{nm} = 32^\circ$ , roughly as observed. Supposing now an extension by  $\Delta h/h = \varepsilon$ , we find an untwisting by  $\sigma = \delta\theta/\theta = \text{const.} - \varepsilon/2.0$ , quite different from what is observed, eqn. (2.1). We must seek an explanation of the experimental result not in terms of a geometrical ball-and-stick model but in the context of an elastic response theory.

### 3. Simple Model

We will begin by neglecting bend fluctuations (see below). A straight rod under tension and torque will stretch and twist. We can describe it by the reduced elastic free energy

$$f_1(\sigma, \varepsilon) \equiv \frac{F_1(\sigma, \varepsilon)}{k_B T z_{\text{tot},0}} = \frac{\omega_0^2}{2} [\bar{C}\sigma^2 + \bar{B}\varepsilon^2 + 2\bar{D}\varepsilon\sigma] - \tau\varepsilon. \quad (3.1)$$

The twist persistence length is  $\bar{C} \approx 75$  nm [2], while the helix parameter  $\omega_0 = 2\pi/\ell_0 = 1.85/\text{nm}$ . We will take<sup>1</sup>  $\bar{B} \approx 1100 \text{ pN}/\omega_0^2 k_B T \approx 78$  nm [8]. In the experiment under study the reduced force is  $\tau = 8 \text{ pN}/k_B T \approx 1.95/\text{nm}$ . For a circular beam made of isotropic material the cross-term  $\bar{D}$  is absent [9], since twisting is odd under spatial inversion while stretching is even. For a helical beam, however, we must expect to find this term.

We now minimize  $f_1$  with respect to  $\varepsilon$ ,  $\sigma$  at fixed tension with an imposed constraint on the overtwist  $\sigma$ . Minimizing at fixed  $\sigma$  and  $\tau$  gives  $\Lambda = \omega_0^2(\bar{D}\varepsilon + \bar{C}\sigma)$  and hence

$$\varepsilon = \varepsilon_{\sigma=0} - (\bar{D}/\bar{B})\sigma. \quad (3.2)$$

Comparing to (2.1), we obtain the desired result:  $\bar{D} = 12$  nm. To compare this to Marko's analysis, we note that his dimensionless  $g$  equals our  $\bar{D}\omega_0$ , so that we get  $g = 22$ . The rough agreement with Marko's result  $g = 35$  [12] indicates that the data show a real material parameter of DNA and not some artifact. We do not expect exact agreement, since Marko studied the nonlinear overstretching transition of [14][7]; our value came from the linear regime of small strains.

### 4. Bend Fluctuations

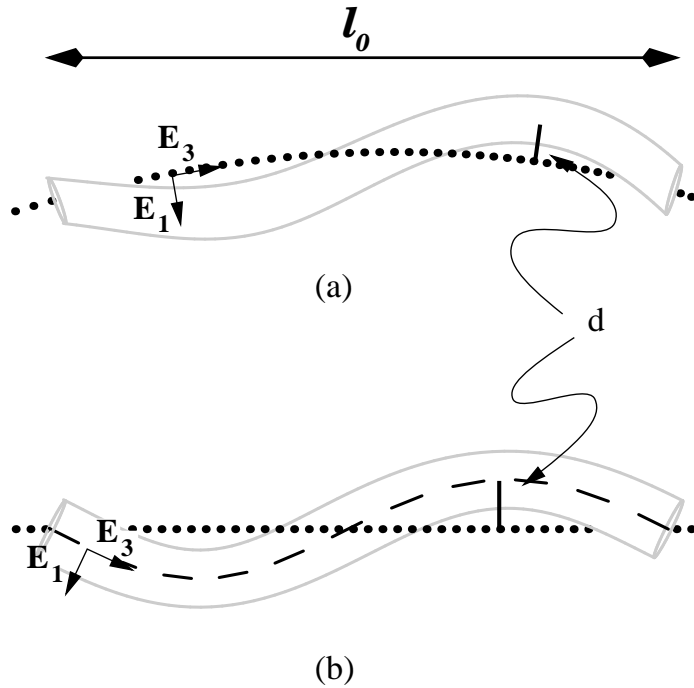
To arrive at (3.1) we listed the variables which were constrained, coupled to external forces, and/or observed in the experiment, namely  $\varepsilon$  and  $\sigma$ , then wrote the most general quadratic function allowed by symmetry. Thus (3.1) is a phenomenological model; its coefficients  $\bar{C}$ ,  $\bar{B}$ ,  $\bar{D}$  reflect both intrinsic elasticity and the effects of thermal fluctuations.

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<sup>1</sup>  $\bar{B}$  reflects the intrinsic stretchiness of DNA, since electrostatic self-repulsion simply shifts the equilibrium length without affecting the spring constant. Indeed experiments show little or no dependence of  $\bar{B}$  on salt, unlike the situation with the effective bend persistence length [8]. We also expect  $\bar{C}$  to reflect intrinsic elasticity, since twisting does not affect the average charge distribution.

Indeed it is well known that thermal bend fluctuations reduce the effective stretch modulus at modest tension via the “entropic elasticity” effect [5][6]. Somewhat inconsistently we arrived at our value of  $\bar{D}$  by using the intrinsic stretch modulus in (3.2). In this section we will justify the procedure by introducing a more elaborate model with bend fluctuations, rederiving the analog of (3.2), and again comparing to (2.1).

We begin by defining local variables (Fig. 1a) (see [10][13]). DNA is a stack of base pairs. We neglect sequence effects and so regard all base pairs as copies of one standard slice. The standard slice contains a reference point with the property that the locus of these is the helix axis, a straight line of length  $L$  in the relaxed state. Through this reference point we next draw a fixed vector; a convenient choice is the “dyad” pointing into the minor groove and perpendicular to the helix axis.



**Fig. 1:** Schematic diagrams defining variables used in the text. The offset from the helix axis has been exaggerated for clarity. a) Notation used in the study of bend fluctuations. We describe the DNA by the helix axis (dotted curve) and the axis  $\hat{E}_1$ , which is a fixed vector in each base pair. b) Notation used in the microscopic model. The helix axis (dotted line) is now supposed straight. We describe the DNA by the dashed curve and the axis  $\hat{E}_1$  as before.

To describe stressed states, we simply specify the locus of reference points as a parameterized curve in space (dotted line in Fig. 1a) and the dyad as a field of vectors  $\hat{E}_1$  normal to this curve. We let  $\hat{E}_3$  be the unit tangent to the axis and complete to an orthonormal triad by defining  $\hat{E}_2 = \hat{E}_3 \times \hat{E}_1$ . Next we introduce a parameter  $s$  to label each slice;  $s$  corresponds to arc length along the original, unstressed helix axis and so always runs from 0 to  $L$ . The actual arc length along the distorted axis will not be  $ds$  but rather  $(1 + \alpha(s))ds$ ;  $\alpha$  is thus the axial strain.

Thus our local variables are  $\hat{E}_i(s)$  and  $\alpha(s)$ . Our program consists of four steps: *i)* Find the strains in terms of the local variables. *ii)* Write the general linear elasticity theory of these strains with a force coupling to the extension  $\varepsilon$  and a torque coupling to the twist  $\sigma$ . *iii)* Compute and minimize the free energy to find the end-to-end length  $\langle z_{\text{tot}} \rangle$  in terms of the constrained  $\sigma$  and the applied force  $\tau$ . (It will prove convenient in this step to convert to new variables  $t_1(s)$ ,  $t_2(s)$ ,  $\varphi(s)$ , and  $\alpha(s)$ .) *iv)* We will then be able to relate the experimental result to intrinsic elastic constants. We will see that our naive calculation of the previous section is justified. Details of this calculation will appear elsewhere.

*Step i:* In the relaxed state each slice bears a constant relation to its predecessor. Thus while  $\hat{E}_{10}$ ,  $\hat{E}_{20}$ , and  $\hat{E}_{30}$  all vary in space, the derivatives with respect to  $s$  are of the form

$$d\hat{E}_{i0}/ds = -\varepsilon^{ijk}\Omega_{j0}\hat{E}_{k0} , \quad (4.1)$$

where  $\Omega_{j0}$  are the constants  $(0, 0, \omega_0)$ . For the deformed state, (4.1) defines the functions  $\Omega_i(s)$ . Our strain variables are then  $\Omega_1(s)$ ,  $\Omega_2(s)$ ,  $\Omega_3(s) - \omega_0$ , and  $\alpha(s)$ .

*Step ii:* Our strain variables have the desirable property that in terms of them the elastic constants are independent of  $s$ . Moreover the end-for-end symmetry of DNA implies that the elastic matrix is unchanged upon changing the sign of  $\Omega_1$  [10]. Thus we generalize the model of [10] to

$$f_2 = \frac{1}{2L} \int_0^L ds \left[ A'\Omega_1^2 + A\Omega_2^2 + C(\Omega_3 - \omega_0)^2 + B\omega_0^2\alpha^2 + 2D\omega_0(\Omega_3 - \omega_0)\alpha + 2G(\Omega_3 - \omega_0)\Omega_2 + 2K\omega_0\Omega_2\alpha \right] . \quad (4.2)$$

Here  $G$  is the twist-bend coupling of [10], while  $K$  is an allowed coupling between stretch and bend.

We will apply a perturbative treatment to (4.2). Such an approximation is valid since in the experiment we are analyzing the applied force is large enough to keep the end-to-end distance over 90% the full relaxed contour length, but not large enough to create large

intrinsic stretch  $\alpha$ . In addition, the applied overtwist  $\sigma$  is at most  $\pm 10\%$  [11]; indeed the slope reported in (2.1) can be found from an even smaller range of  $\sigma$  than this.

*Step iii:* It proves useful to refer the frame  $\{\hat{E}_1, \hat{E}_2, \hat{E}_3\}$  to a reference frame  $\{\hat{e}_1, \hat{e}_2, \hat{z}\}$  rotating at  $\omega_0$ :

$$\hat{e}_1 = \hat{x} \cos(\omega_0 s) + \hat{y} \sin(\omega_0 s) \quad \hat{e}_2 = -\hat{x} \sin(\omega_0 s) + \hat{y} \cos(\omega_0 s) . \quad (4.3)$$

We will then write the deformed frame in terms of three small quantities: two deviations of the tangent vector  $t_{1,2}$  and an angle  $\varphi$ . To first order in these we have

$$\hat{E}_1 = \hat{e}_1 + \varphi \hat{e}_2 - t_1 \hat{z} , \quad \hat{E}_2 = -\varphi \hat{e}_1 + \hat{e}_2 - t_2 \hat{z} , \quad \hat{E}_3 = t_1 \hat{e}_1 + t_2 \hat{e}_2 + \hat{z} . \quad (4.4)$$

Thus  $\hat{E}_1$  is the unit vector perpendicular to the tangent whose projection to the  $xy$  plane makes angle  $\varphi$  with the reference frame. The advantage of these coordinates is now that the excess link is simply the difference  $\varphi(L) - \varphi(0)$ . The relation between Link, Twist, and Writhe will also emerge automatically instead of having to be enforced by hand.

Exercising the definitions we find that in terms of  $t_1, t_2, \varphi$  the strains are  $\Omega_1 = -\dot{t}_2 - \omega_0 t_1, \Omega_2 = \dot{t}_1 - \omega_0 t_2, \Omega_3 = \omega_0 + \dot{\varphi}$ . Substituting into (4.2), adding external tension  $\tau$  and torque  $\Lambda$ , and rearranging gives the free energy

$$\begin{aligned} f_2 = \frac{1}{2L} \int ds & \left[ A'(\dot{t}_2 + \omega_0 t_1)^2 + A\left(\dot{t}_1 - \omega_0 t_2 + \frac{G}{A}\dot{\varphi} + \frac{K\omega_0}{A}\alpha\right)^2 \right. \\ & \left. + \left(C - \frac{G^2}{A}\right)\dot{\varphi}^2 + \omega_0^2\left(B - \frac{K^2}{A}\right)\alpha^2 + 2\omega_0\left(D - \frac{GK}{A}\right)\dot{\varphi}\alpha \right] \\ & - \frac{\tau}{L} \int ds (1 + \alpha)\left(1 - \frac{1}{2}t_1^2 - \frac{1}{2}t_2^2\right) - \frac{\Lambda}{L} \int ds \dot{\varphi} . \end{aligned} \quad (4.5)$$

*Step iv:* Let us first focus only on the linear couplings to the applied forces  $\tau, \Lambda$ . Then eqn. (4.5) shows that the Lagrange multiplier  $\Lambda$  couples only to the constant part of  $\dot{\varphi}$ , which is just the overtwist  $\omega_0 \sigma$ . Also the constant part of  $\alpha$  is the extension  $\varepsilon$ . Thus neglecting the quadratic couplings to  $\tau$  gives that only the constant modes  $\bar{t}_1, \bar{t}_2, \sigma$ , and  $\varepsilon$  respond to  $\tau$  and  $\sigma$ , and they minimize the function

$$\begin{aligned} \frac{\omega_0^2}{2} \left[ A' \bar{t}_1^2 + A\left(\bar{t}_2 - \frac{G}{A}\sigma - \frac{K}{A}\varepsilon\right)^2 + \left(C - \frac{G^2}{A}\right)\sigma^2 + \left(B - \frac{K^2}{A}\right)\varepsilon^2 + 2\left(D - \frac{GK}{A}\right)\sigma\varepsilon \right] \\ - \tau\varepsilon - \Lambda\omega_0\sigma . \end{aligned} \quad (4.6)$$

We see that  $\bar{t}_2$ , which is neither controlled nor observed, adjusts slightly but that the measured twist-stretch coupling  $\bar{D}$  reflects the combination  $D - \frac{GK}{A}$  of intrinsic elastic parameters. Parenthetically we note that  $\bar{C} = C - \frac{G^2}{A}$  is nearly equal to  $C$  because we expect  $G$  to be small, and similarly for  $\bar{B}$ . The corrections are small because they reflect the small deviation of DNA from a straight circular rod.

We are almost done. Normally the linear force terms suffice since the applied force  $\tau/\omega_0^2$  is small compared to the persistence length  $A$ . The only exception to this rule comes from those modes which decouple completely from (4.5) when  $\tau = 0$ : these modes will have large fluctuations, and the nonlinear couplings to  $\tau$  are needed to cut them off. These dangerous modes are the Fourier modes of  $t_1, t_2$  of wavenumber close to  $\omega_0$ , as we see from (4.5). Their thermal fluctuations indeed make a large contribution to  $\langle z_{\text{tot}} \rangle$  at small force. Fortunately, though, this contribution is completely independent of  $\sigma$ , since  $\sigma$  enters linearly in the problem and hence makes no contribution to the fluctuation problem. Thus we can simply absorb this contribution to  $\langle z_{\text{tot}} \rangle$  into the constant term of (2.1).

Thus we have found the interpretation of the experimentally-determined twist-stretch coupling found in section 2: in terms of the intrinsic elasticity of DNA the slope in (2.1) fixes the combination  $(DA - GK)/AB$  to be 22 nm. The low-force stretching experiments give bend stiffness<sup>2</sup>  $A = 40$  nm [8]. Other experiments fix  $B, C$  to the approximate values quoted earlier. The remaining two combinations of the six couplings in (4.5) do not appear to be relevant for existing experiments.

## 5. Microscopic Model

The elastic theory in the previous section was very general, but it gave no indication of the expected magnitudes of the various couplings. To gain further confidence in our result, we will now see how to *estimate* the expected twist-stretch coupling based on the measured values of the other elastic constants and geometrical information about DNA. We will use a simple, intuitive microscopic picture of DNA as a helical rod to show how twist-stretch coupling can arise and get its general scaling with the geometric parameters. While the model is unrealistic it captures the underlying symmetries and shows that the value of  $\bar{D}$  calculated above is reasonable.

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<sup>2</sup> This value for  $A$  is slightly smaller than the traditional one. The authors of ref. [8] eliminated the electrostatic contribution to  $A$  by extrapolating to high concentration of high-valence added salt.



Our picture will be a beam of isotropic elastic material of circular cross-section, initially bent into a helix of pitch  $\ell_0$ , with the beam center slightly displaced from the helix axis by  $d_0 \ll \ell_0$  [15]. Fig. 2b defines notation (for realistic depictions of DNA structure see for example [13]). In this section we will consider only uniform deformations of the helix; in particular the helix axis will always be straight. It proves convenient to define slightly different variables from the previous section: instead of following the helix axis, now our curve follows the centerline of the beam. We again call the tangent to this curve  $\hat{E}_{30}(s)$ , where the arc length  $s$  runs from 0 to  $\tilde{L}$ , but now  $\tilde{L}$  is slightly longer than the end-to-end length of the relaxed beam. Next we draw a second curve, the locus of points farthest from the helix axis. Let  $\hat{E}_{10}(s)$  be the field of vectors perpendicular to the tangent  $\hat{E}_{30}(s)$  and pointing from the first to the second curve. Finally complete  $\hat{E}_{30}$ ,  $\hat{E}_{10}$  to an orthonormal triad by defining  $\hat{E}_{20} = \hat{E}_{30} \times \hat{E}_{10}$ .

The distorted beam will then have its modified frame  $\{\hat{E}_1(s), \hat{E}_2(s), \hat{E}_3(s)\}$ , where now  $s$  is the arc length rescaled by  $(1 + \alpha)^{-1}$  to again run from 0 to  $\tilde{L}$  and  $\alpha$  is the axial strain as before. We also define strain variables  $\Omega_i$  as before; for the uniform deformations considered these are constants independent of  $s$ . For a nearly-straight, circular rod the elastic energy is then [9]

$$f_3 = \frac{1}{2} [A(\Omega_2 - \Omega_{20})^2 + C(\Omega_3 - \Omega_{30})^2 + B\omega_0^2\alpha^2] . \quad (5.1)$$

We have rotated our reference frames about the tangent vector to eliminate  $\Omega_1$ . The constants  $A$ ,  $C$ , and  $B$  can in turn be expressed in terms of the effective Young modulus, shear modulus, and diameter of the rod, but we instead use the measured values quoted earlier.

To use (5.1) we need to find  $\Omega_2$  and  $\Omega_3$  in terms of the helix parameters: helix axis offset  $d$ , end-to-end length  $z_{\text{tot}}$ , and total rotation of the cross-section. The latter quantity plays the role of linking number for open DNA, and so we will call it Lk. To get the required relations it is helpful to use the physical image of a gyroscope rotating at “angular frequency”  $|\vec{\Omega}|$  about an axis parallel to  $\vec{\Omega}$  while moving at constant “speed” along an axis  $\hat{E}_3$  fixed in the body. We take “time” to run from 0 to  $\tilde{L}$ , the original relaxed arc length; to allow for intrinsic stretching we then take the “speed” to be  $1 + \alpha$ . One then finds that

$$d = \Omega_2(1 + \alpha)/|\vec{\Omega}|^2 , \quad z_{\text{tot}} = \tilde{L}\Omega_3(1 + \alpha)/|\vec{\Omega}| , \quad \text{Lk} = \tilde{L}|\vec{\Omega}|/2\pi . \quad (5.2)$$

To fix  $\bar{\Omega}_0$  we impose the values  $\alpha_0 = 0$ ,  $\omega_0 = 2\pi\text{Lk}_0/z_{\text{tot},0} = 1.85/\text{nm}$ , and a helix offset  $d_0$ . We will choose  $d_0$  to get the observed value of  $\bar{D}$  and see that it is reasonable. Working to second order in  $d_0$  (5.2) gives  $\Omega_{30} = \omega_0(1 - d_0^2\omega_0^2)$ ,  $\Omega_{20} = d_0\omega_0^2$ .

We must now minimize (5.1) with the constraint of fixed  $z_{\text{tot}}$  and  $\text{Lk}$ . Let  $z_{\text{tot}} \equiv (1 + \varepsilon)z_{\text{tot},0}$ , so that  $\varepsilon$  again measures changes in end-to-end distance, and  $\text{Lk} = (1 + \sigma)\text{Lk}_0$  as usual. Again using (5.2), one finds

$$\Omega_2 - \Omega_{20} = \beta\omega_0, \quad \Omega_3 - \Omega_{30} = \omega_0\sigma - \omega_0^2d_0\beta, \quad \alpha = \varepsilon + \omega_0d_0\beta - (\omega_0d_0)^2\sigma, \quad (5.3)$$

where  $\beta$  is free. Substituting into (5.1) and minimizing over  $\beta$  reveals a  $\sigma\varepsilon$  coupling corresponding to  $\bar{D} = (\omega_0d_0)^2(C - A)B/A$ . This formula fits our measured value of  $\bar{D}$  if we choose  $d_0 = 0.2 \text{ nm}$ .

The value of  $d_0$  is not known *a priori*, since of course DNA is not really an elastic continuum with circular cross-section. Nevertheless, inspection of the known molecular structure indeed suggests an elastic center offset from the helix axis by a couple of Ångströms [13]. In any case we have shown that the measured value of  $\bar{D}$  is of the order of magnitude expected from simple elasticity theory.<sup>3</sup>

## 6. Conclusion

We have pointed out a strong twist-stretch coupling in torsionally-constrained DNA stretching experiments, evaluated it, argued that it reflects intrinsic elasticity of the DNA duplex, and shown that the value we obtained is consistent with elementary considerations from classical elasticity theory. A greater challenge remains to predict this coupling from the wealth of available crystallographic information on the conformation of short oligomers.

## Acknowledgments

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<sup>3</sup> Actually a helical beam can have a twist-stretch coupling even if its axis is on center,  $d_0 = 0$ , provided its cross-section is not circular [15]. To explain the observed coupling in this way would require a rather large eccentricity of 70%. However for molecules such as actin, for which  $d_0 = 0$ , this second mechanism may be important.

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