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DNA STRUCTURE CHANGES DUE TO COUPLING OF MACROMOLECULE DEFORMATION COMPONENTS

A DNA macromolecule deformation model that includes external and internal deformation components and their coupling is introduced. The external components describe twisting and stretching of the double helix. The internal component is associated with relative displacements of structural elements within base pairs. Coupling of both twist and stretch to the internal component is taken into account. A counterintuitive response is obtained: under tension, the DNA double helix can increase its twist. This anomalous behavior persists up to a critical force, above which the conventional untwisting regime is recovered. The results show that DNA mechanics in the pN force range is strongly affected by coupling between external deformation and internal conformational mobility. The unusual mechanical response is attributed to the influence of the conformational state on deformation through coupling, with the conformational component remaining within a local minimum over the relevant force range.

K e y w o r d s: DNA mechanics, twist–stretch coupling, internal conformation, coupled deformation, force-induced response.

1. Introduction

Understanding how the DNA double helix deforms is a significant step toward fully comprehending the functioning of this essential macromolecule [1–4]. To describe these deformations, established theoretical models, such as the elastic rod model or the worm-like chain (WLC) model, envision the macromolecule as a continuous chain of homogeneous monomer links. Deformation is represented as minor displacements between neighbouring links, often expressed through independent external components such as bending, twisting, and stretching within the framework of the elastic rod model [5, 6].

Because of the helical geometry of DNA, deviations from equilibrium generally involve more than one deformation component. This interdependence can be described as coupling between the external deformation modes. Single-molecule experiments allow for the manipulation of stretch while measuring twist, and vice versa [6–10], validating the existence of twist–stretch coupling. Notably, when the stretching force is below a critical value (approximately 35 pN), stretching provokes the winding of the double helix (positive twist). However, when this critical threshold is exceeded, stretching results in the unwinding of the double helix (negative twist).

This counterintuitive behavior has been modeled by modifying the coupling parameter as a function of

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force [7, 10]. These changes could instead arise from coupling to a component that represents the inherent conformational mobility of the double helix. The method of conformationally induced deformation, developed in [11–14], has been successfully applied to the description of B–A and B–S conformational transitions, as well as transitions between heteronomous states of the TATA-box, within a two-component model of double-helix deformation. In this approach, the first component describes internal structural rearrangements, whereas the second represents the overall deformation of the double helix. Although this method was originally formulated for a single generalized external deformation component linked to changes in the internal conformation of DNA, it has subsequently been extended to describe deformations involving coupling between external components [14].

Notably, molecular dynamics studies of twist–stretch coupling under force show conformational changes resembling B–A transitions [8]. When B-DNA unwinds, the reduced twist is accompanied by base-pair inclination and length reduction, generating similarities with the A-form. Among the known helical conformations, only the A-form is available to dsRNA, whereas both A- and B-forms occur in dsDNA [1]. Recent studies [15, 16] highlight that these specific conformations are responsible for the observed variances in twist–stretch coupling behavior for dsRNA and dsDNA. The proposed model presented here incorporates an internal structural component, reflecting the DNA's ability to undergo conformational transitions. This feature of the model provides a framework for understanding the mechanism of interplay between twist and stretch during DNA deformation.

The present study explores the effect of coupling between elastic components and the internal flexibility of the double helix on twist–stretch coupling. To this end, the elastic description is extended by introducing an internal conformational component representing structural displacements within the DNA links. This makes it possible to analyse the force-dependent mechanical response of DNA in terms of coupled elastic and conformational effects, rather than through empirical assumptions alone.

This allows the mechanical response of DNA to be interpreted in terms of the interplay between external deformation and internal structural mobility. In particular, the observed force-induced change in the sign of coupling between elastic components can be understood as a consequence of their interaction with the internal conformational component. The resulting quantitative estimates are consistent with single-molecule experiments and molecular modelling, and they provide a physical basis for the response of the double helix to applied force.

2. Modeling DNA Deformation

In this section, we introduce a model that provides insights into the mechanical behavior of DNA macromolecules under various deformations. DNA, the molecule that carries genetic information, undergoes various deformations and conformational changes during different biological processes such as replication, transcription, and repair. Understanding how DNA responds to mechanical forces and deformations is crucial for unravelling the physical principles that govern its function and dynamics. The elastic rod model is widely used to describe the deformation of filament structures, including DNA. This model takes into account the three primary modes of deformation that DNA can undergo: bending, twisting, and stretching. While these modes can be studied independently, the coupling between them is essential for a more accurate representation of DNA behavior, especially under large-amplitude deformations. We now turn to the mathematical representation of the model.

2.1. Elastic rod model for DNA

In mechanical analyses of DNA, bending, twisting, and stretching are treated as the primary deformation components contributing to the elastic energy. For small deformations, the energy can be expanded to second order in the deviations from equilibrium, leading to the following quadratic form:

$$E_{\mathrm{WLC}} = \frac{1}{2}\sum_{n=1}^{N}\{C_r(R_{n+1}-R_n)^2 + \\ + C_\varphi(\varphi_{n+1}-\varphi_n)^2 + C_z(Z_{n+1}-Z_n)^2\}, \quad (1)$$

where N represents the number of monomer links within the molecular chain, R_n is the dimensionless displacement of the n-th link as a whole from its equilibrium position (in a direction orthogonal to the helix axis) and describes the bending, φ_n represents the rotation of the n-th link as a whole around the helix

axis, measured in radians, and describes the twisting, Z_n is the dimensionless displacement of the n-th link as a whole along the helix axis of the macromolecular chain, which describes stretching. The parameters C_r, C_φ, C_z, correspond to the bending, twisting, and stretching rigidities of the macromolecular chain, respectively.

Within the worm-like chain (WLC) model, bending, twisting, and stretching are assumed to vary independently [1, 5]. This description can be extended by including coupling between elastic components, which allows their mutual influence to be represented at the mechanical level. Yet even in this form the model does not capture the internal conformational degrees of freedom of the double helix. As a result, coupling between elastic modes alone cannot provide a complete description of DNA deformation [6].

2.2. Incorporating coupling between deformation components

To explore the nature of couplings within the DNA structure, we begin with a simplified model that accounts for the linear coupling between any pair of elastic components. For this analysis, we introduce the variables u and v, which represent pairs of elastic components such as bending, twisting, and stretching (with $u, v = \{R, \varphi, Z\}$). An external force is specifically applied to the component v. The potential energy associated with the deformation of these components is given by the following expression:

$$E = \sum_{n=1}^{N} \Big[C_u (u_{n+1} - u_n)^2 + C_v (v_{n+1} - v_n)^2 + \\ + 2\gamma_{uv} (u_{n+1} - u_n)(v_{n+1} - v_n) - fh(v_{n+1} - v_n) \Big], \quad (2)$$

where C_u and C_v are the rigidity constants of the macromolecule, γ_{uv} (with $\gamma_{uv} = \gamma_{vu}$) represents the coupling parameters between the u and v components, and f is the force applied to induce a change in the v component. The monomer link length, h, acts as a scaling factor, rendering the component v dimensionless.

Let us consider uniform deformation of the macromolecule chain. Assume $u_{n+1} - u_n = u$, $v_{n+1} - v_n = v$. Introducing the variables of the deformation of the chain as uniform, the energy can be split into N separate terms. Taking this into consideration, the energy density expressed in the new variables has the following form:

$$\varepsilon(u, v) = \frac{E(u, v)}{N} = \frac{C_u u^2}{2} + \frac{C_v v^2}{2} + \gamma_{uv} uv - fhv. \quad (3)$$

The energy consists of three parts, $\varepsilon(u, v) = \varepsilon_0(u, v) + \\ + \varepsilon_{\text{corr}}(u, v) - A_f$, where the harmonic part $\varepsilon_0(u, v) = \\ = C_u u^2/2 + C_v v^2/2$, the correlated part $\varepsilon_{\text{corr}}(u, v) = \\ = \gamma_{uv} uv$, and A_f is the energy associated with the applied force, quantifying the work done due to the force-induced changes in component v.

We can determine the minimum of the energy by finding the stationary state equations, as follows:

$$\begin{cases} \dfrac{\partial \varepsilon(u, v)}{\partial u} = C_u u + \gamma_{uv} v = 0, \\ \dfrac{\partial \varepsilon(u, v)}{\partial v} = C_v v + \gamma_{uv} u - fh = 0. \end{cases} \quad (4)$$

Solving the system of linear Eqs. (4) by expressing u from the first equation and substituting it into the second, one obtains

$$\begin{cases} u = -\dfrac{\gamma_{uv} v}{C_u}, \\ v = \dfrac{C_u fh}{(C_u C_v - \gamma_{uv}^2)}. \end{cases} \quad (5)$$

In the case of zero force, the system has a nontrivial solution when the determinant of the coefficient matrix vanishes, i.e., when $\gamma_{uv}^2 = C_u C_v$. In this case, for any deformation $v = v_a$, the corresponding value of u is determined as proportional to v_a, and the solution takes the form

$$u = -\frac{\gamma_{uv} v_a}{C_u}. \quad (6)$$

The system defined by Eqs. (4) has a unique, trivial solution if the determinant of the system is nonzero. This is equivalent to the condition $\gamma_{uv}^2 \neq C_u C_v$. We introduce a deviation coefficient, γ_0, to relate the deviation of γ_{uv} to the other parameters, according to the relation $\gamma_{uv} = \gamma_0 \sqrt{C_u C_v}$.

In a physiological environment, B-form DNA, representing the equilibrium state of this mechanical system, possesses the minimum energy when compared to any deformed state. This is attributed to the optimal balance of molecular interactions in B-DNA, such as hydrogen bonds, base stacking, and electrostatic interactions, under physiological conditions.

Substituting the partial solution from Eq. (5) into the energy density expression given by Eq. (3), and assuming that $\varepsilon(u,v) \geq 0$ for any non-zero u, v, we find that the deviation coefficient γ_0 is constrained to the interval $-1 \leq \gamma_0 \leq 1$. This interval for γ_0 suggests that the energy state reaches a minimum, i.e., all forces acting on the molecule (bending, twisting, and stretching forces) are balanced, when there is no deviation from the equilibrium state. Thus, any deformation from this state results in an increase in the energy of the system.

In the unstressed state, the minimum energy for a system with coupling is the same as for a system without coupling, occurring at $u_0 = 0$, $v_0 = 0$, and $E_0 = \varepsilon(u_0, v_0) = 0$. However, when external forces are applied, the minimum energy shifts. Consequently, a uniformly stressed state of the chain $v = v_f$ has minimum energy at $u_0 = u_{\min} \neq 0$, due to the presence of coupling. Notably, if $\gamma_{uv} > 0$, a positive sign in one of the components is accompanied by a negative one in the other. In contrast, both components exhibit the same sign if $\gamma_{uv} < 0$.

Deviation from the equilibrium state (or static strain) in one of the components leads to a proportional deformation in the other component. In this case, the deformation energy, given by Eq. (3), becomes:

$$\begin{aligned} &\varepsilon(u, v_a) = C_u(u - u_{\min})^2 + \varepsilon_f, \\ &u_{\min}(u) = -\frac{\gamma_{uv} v_f}{C_{uv}}, \\ &\varepsilon_f = \varepsilon(u_{\min}, v_f) = \frac{1}{2}(1 - \gamma_0) C_v v_f^2. \end{aligned} \tag{7}$$

For any fixed $u = u_f$ and $|\gamma_0| < \sqrt{1/2}$, the energy can be written in the form

$$\varepsilon(u) = \frac{1}{2}\left(C_u - \frac{\gamma_{uv}^2}{C_v}\right) u^2. \tag{8}$$

Let us consider a critical deformation value u_c, where the energy of the u-component due to its own deformation equals the energy from its coupling with the v-component. This critical value u_c is determined by the condition $\varepsilon(u_c, 0) = \varepsilon(u_c, v_f)$ and is given by $u_c = -C_v v_f / \gamma_{uv}$. There are three possible behaviors based on the relationship between $u_{\min}$ and u_c:

1. When $|u_{\min}| > |u_c|$, corresponding to $|\gamma_0| > \sqrt{1/2}$, the energy of single-component deformation at $u_{\min}$ exceeds the two-component coupled deformation energy.

2. When $|u_{\min}| = |u_c|$, corresponding to $|\gamma_0| = \sqrt{1/2}$, the energies of single-component and two-component deformations are equal.

3. When $|u_{\min}| < |u_c|$, corresponding to $|\gamma_0| < \sqrt{1/2}$, the single-component deformation energy at $u_{\min}$ is less than the coupled deformation energy.

In the third case, the two-component model with coupling is likely valid only for deformations exceeding u_c.

As a result of the interaction between components, the stiffness in one of the components can be effectively reduced. Although this reduction is small and may not have a noticeable impact on the character of elastic deformation, our study of the influence of conformational rearrangement on chain bending has shown that conformational transitions can be advantageous in deformed molecular chains, such as DNA, when the rigidity of the strained fragment is lower than the average rigidity. Consequently, coupling between components can lead to more likely conformational transformations. These transformations are believed to be a competitive mechanism that influences and connects the elastic components within the DNA chain.

3. Deformations Accompanied by Internal Conformational Changes

3.1. Incorporating conformational component

Let us now consider the deformation of the DNA double helix accompanied by internal structural changes within the monomer links. The double helix is represented as a chain in which each link can undergo both overall displacement and internal rearrangement.

The relative displacement of the internal structural elements of the n-th link is described by the variable r_n, and the corresponding internal energy is described by the function $\Phi(r_n)$. In this way, the model includes both the motion of the link as a whole and its internal structural deformation.

The total potential energy of the chain is given by:

$$\begin{aligned} E_{\text{pot}} = \sum_{n=1}^{N} \Big\{ &C_v(v_{n+1} - v_n)^2 + C_r(r_{n+1} - r_n)^2 + \\ &+ \chi(v_{n+1} - v_{n-1}) F(r_n) + \Phi(r_n) \Big\}, \end{aligned} \tag{9}$$

where the first two terms describe the elastic contributions associated with the external and internal components, respectively, while $\Phi(r_n)$ represents the conformational potential. The coupling

term $\chi(v_{n+1}-v_{n-1})F(r_n)$ accounts for the interaction between external deformation and internal structural displacement, showing how internal rearrangements influence, and are influenced by, the overall motion of the chain.

For uniform movements across all monomers, the energy density simplifies to:

$$\varepsilon(v,r) = \frac{E_{\text{pot}}}{N} = \frac{C_v v^2}{2} + \chi v F(r) + \frac{\Phi(r)}{2}, \tag{10}$$

where uniform movement implies $v_{n+1} - v_n = v$ and $r_{n+1} - r_n = 0$. A stable configuration, indicating minimal energy, is defined by:

$$v(r) = -\frac{\chi F(r)}{C_v}. \tag{11}$$

Notably, external forces or interactions with proteins may localize these movements to specific chain sections.

3.2. Impact of external force

Let us consider a case in which an external force is applied to the DNA stretching the double helix according to experiments in which the ratio between stretching and twist changes sign [8–10].

Thus, we consider a chain of two coupled components and incorporate a relationship between displacement of the internal parts of the links and both the twisting and stretching of the chain.

Besides the impact of directly applied forces through single-molecule manipulation, interactions with proteins during DNA functioning can also influence deformation and conformational changes. These interactions can serve as natural forces affecting the DNA structure.

For instance, proteins binding to the DNA or enzymatic activity can induce strain or conformational changes in the DNA. This underlines the significance of considering not only externally applied forces but also the biological interactions that DNA undergoes in its natural environment.

Let us consider a chain of two coupled components. In addition to v-component, we consider $u_{n+1} - u_n = u$, and coupling of conformational component with both v and u components according to potential functions depending on conformational component r: $\chi_u F_u(r)$ and $\chi_v F_v(r)$. Component u is deformed by the applied force, and both of them are coupled with a generalized conformational component. In this case, the deformation energy takes the form:

$$\varepsilon(u,v,r) = \frac{C_u u^2}{2} + \frac{C_v v^2}{2} + \gamma_{uv} uv - ufh - \\ - \chi_u F_u(r) u - \chi_v F_v(r) v + \Phi(r). \tag{12}$$

To determine the equilibrium state of macromolecule chains with interrelation between components, we find the energy minimum. The partial derivatives of the energy function $\varepsilon(u,v)$ with respect to u and v can be written as:

$$\frac{\partial \varepsilon(u,v,r)}{\partial u} = C_u u + \gamma_{uv} v - fh - \chi_u F_u(r) = 0, \tag{13}$$

$$\frac{\partial \varepsilon(u,v,r)}{\partial v} = C_v v + \gamma_{uv} u - \chi_v F_v(r) = 0. \tag{14}$$

Substituting equations with respect to u and v, we obtain expressions for both components:

$$u = \frac{(fh + \chi_u F_u(r)) C_v - \gamma_{uv} \chi_v F_v(r)}{C_u C_v - \gamma_{uv}^2}, \tag{15}$$

$$v = \frac{\chi_v F_v(r) C_u - \gamma_{uv}(fh + \chi_u F_u(r))}{C_u C_v - \gamma_{uv}^2}. \tag{16}$$

Since both components have the same denominator, their signs are determined by their corresponding numerators. Components of the same sign correspond to an effectively negative coupling, whereas components of opposite signs correspond to an effectively positive one. In the present classical description, the equilibrium state is assumed to be stable, so any deviation from it must increase the deformation energy, which requires that $C_u C_v - \gamma_{uv}^2 > 0$. Under this condition, the sign combinations of the coupled components are determined by the following inequalities:

$$\frac{\gamma_{uv}}{C_u} < \frac{\chi_v F_v(r)}{(fh + \chi_u F_u(r))} < \frac{C_v}{\gamma_{uv}}, \quad \text{if } u > 0, v > 0 \tag{17}$$

$$\frac{\chi_v F_v(r)}{(fh + \chi_u F_u(r))} < \frac{\gamma_{uv}}{C_u} < \frac{C_v}{\gamma_{uv}}, \quad \text{if } u > 0, v < 0 \tag{18}$$

These conditions reveal the relationship between the conformational parameter and the applied force, which in turn determines the signs of the coupled components. The first case corresponds to a solution with the same sign, interpreted as a negative sign of coupling. The second case corresponds to a solution with opposite signs of the coupled components

and is interpreted as an effectively positive coupling. This result agrees with experimental observations, which show that the signs of twist and stretching are the same when the applied force is below a critical value, but have opposite signs for forces above the critical value.

To clarify the relation between the coupling parameters, let us consider the limiting case in which the external force f is absent and $F_v(r) \approx F_u(r)$. In this case, the coupling coefficients can be expressed in terms of the geometric mean of the corresponding rigidity constants: $\gamma_{uv} = \gamma_0\sqrt{C_uC_v}$, $\chi_v = \chi_{0v}\sqrt{\varepsilon C_v}$, and $\chi_u = \chi_{0u}\sqrt{\varepsilon C_u}$, where ε denotes the energy barrier between conformational states.

For $\gamma_0 = 0.5$, the condition determining the sign change of the coupled response takes the form

$$\gamma_0 < \frac{\chi_{0v}}{\chi_{0u}} < \frac{1}{\gamma_0}.$$

Accordingly, χ_{0v} must be larger than one half of χ_{0u} and smaller than twice that value.

These relations characterize the balance between the twist and stretch couplings to the internal conformational component. They therefore specify the parameter range in which the model reproduces the force-dependent deformation response of the DNA double helix.

4. Discussion and Conclusions

The mechanics of DNA deformation are complex and are influenced by various factors including base pair motions and internal structural adjustments. To capture the intricate interplay within the double helix structure, we base our model on a set of parameters derived from experimental data.

In the model, the parameters u and v represent dimensionless measures of elongation and twist deviations per base pair, respectively. Since u is defined per base-pair step, with a step length of 0.34 nm, the ratio u/v can be converted into the experimental units of elongation per turn by expressing the elongation in nanometres and summing over one helical turn. This makes it possible to compare the model results directly with experimental data on twist–stretch coupling in DNA double helices.

Elongation per turn for different coupling constants in theoretical models of DNA deformation and experiment

Ref.	[7, 10]	[8]	[19]	This work
u/v [nm/turn]	0.48–0.5	0.42–0.69	1.06–1.2	0.72–2

To assess the impact of the conformational aspect on twist-stretch coupling, we utilize rigidity parameters derived from experimental data [9]. To facilitate comparisons with stiffness parameters in other models of DNA deformation, we convert the units from erg · cm to $(\text{erg} \cdot \text{cm} \cdot N_a)/h = 42.3 \times 10^{19}$ kcal/mol, while considering that 1 pN · nm^2 $= 10^{-21}$ erg · cm. This gives 1 pN · nm $= 0.145$ kcal/mol.

For the stretching rigidity, $S \cdot h = 50$ kcal/mol, where $S \sim 10^3$ pN represents the stretch modulus of double-stranded DNA. To estimate our model parameters, we refer to the rigidity constants from experimental data [7]: twist rigidity ($C_v = 195$ kcal/mol) and stretching rigidity ($C_u = 56$ kcal/mol).

In the present model, the twist–stretch coupling parameter $|\gamma_{uv}| = \gamma_0\sqrt{C_uC_v} = 52$ kcal/mol is fixed by choosing $\gamma_0 = 0.5$. Even with a constant coupling parameter, the model reproduces the experimentally observed sign change in the ratio u/v. This result is attributed to the coupling of both twisting and stretching to the internal conformational component.

While existing models with linear coupling parameters accurately predict a sign change at a specific force value, they may not fully capture the complex mechanics involved. In contrast, our model, while offering similar interpretations of the observed ratio, also provides a more nuanced explanation. It underscores the inherent complexities and dependencies within the DNA molecule, thereby providing a more accurate description of the molecule's mechanical behavior. This approach enhances our understanding of DNA mechanics, bringing us a step closer to more realistic predictions and interpretations of experimental results.

The Table compares the stretch–twist ratio obtained in different theoretical models and in experiment. The values show qualitative agreement with the trend and critical-force behavior considering $\gamma_0 = 0.5$. Taking into account that the force is applied to u-component, the effect on the conformational component could be slightly higher, with $\chi_{0u} = 0.6$. We can estimate the value $\chi_{0v} = 0.35$, which yields a sign change of the v-component at a force $f \approx 30$ pN. The ratio of equilibrium deviations in stretch and twist is

of the same order of magnitude as the experimentally observed values in the force range around 10 pN [7–10, 19] presented in the Table.

This analysis helps us understand the influence of the conformational component on twist–stretch coupling and how the coupling between different components of the DNA chain can lead to more likely conformational transformations. Further studies may shed light on the specific molecular mechanisms that govern these interactions and how they can be modulated in response to external forces or the presence of proteins and other biomolecules.

This model may be particularly relevant when studying artificial DNA, which has been shown to exhibit both A- and B-form structures [25]. Similar to natural DNA, artificial DNA could display unusual twist–stretch coupling behavior due to its ability to undergo conformational changes during deformation. Investigating the mechanical properties of artificial DNA using our model could provide valuable insights into the structural optimization and adaptability of DNA under various conditions and interactions.

By accounting for both collective base-pair motions and internal structural rearrangements, the model provides a more realistic coarse-grained description of DNA deformation. This framework may also be useful in approaches that relate local rigidity to global flexibility [17, 19], and could help extend such methods to force-dependent conformational processes in DNA.

In conclusion, the proposed model incorporates an internal conformational component into the description of coupled elastic deformation in DNA. The model reproduces the force-induced sign change of the twist–stretch response and provides a physical interpretation of this effect in terms of the coupling between external deformation and internal conformational mobility. These results indicate that internal structural flexibility should be taken into account in theoretical descriptions of DNA mechanics under force.

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СТРУКТУРНІ ЗМІНИ ДНК,
ЗУМОВЛЕНІ ВЗАЄМОЗВ'ЯЗКОМ КОМПОНЕНТ
ДЕФОРМАЦІЇ МАКРОМОЛЕКУЛИ

Запропоновано модель деформації макромолекули ДНК, яка враховує зовнішні та внутрішню компоненти деформації, а також їхній взаємозв'язок. Зовнішні компоненти описують кручення й розтяг подвійної спіралі. Внутрішня компонента пов'язана з відносними зміщеннями структурних елементів у межах пар основ. Враховано зв'язок як кручення, так і розтягу з внутрішньою компонентою. Отримано неочікуваний результат: під дією розтягувальної сили подвійна спіраль ДНК може збільшувати ступінь закручування. Така аномальна поведінка зберігається доки сила не досягне деякої критичної величини, вище якої реалізується звичайний режим розкручування. Показано, що механіка ДНК у діапазоні сил порядку пН істотно визначається взаємозв'язком між зовнішньою деформацією та внутрішньою конформаційною рухливістю. Нетиповий механічний відгук є результатом впливу конформаційного стану на деформацію через зв'язок компонент, причому конформаційна компонента в межах відповідного діапазону сил залишається в локальному мінімумі.

Ключові слова: механіка ДНК, зв'язок кручення–розтяг, внутрішня конформація, пов'язані деформації, силовий відгук.