Himalayan Physics

# Elasticity and flexibility of nucleic acid duplexes: A bio-physical perspective

https://doi.org/10.3126/hp.v13i1.78117

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**Abstract:** The study of DNA, RNA, and PNA (peptide nucleic acid) molecules has various applications in fields such as drug design, nanotechnology, and electronics. Active biological processes like transcription, replication, recombination, protein synthesis, DNA repair, and DNA packaging require nucleic acids to undergo structural changes such as bending, stretching, and twisting under the influence of intercellular forces. To understand these processes, it is important to study their mechanical properties, such as Young's modulus, persistence length, and twisting rigidity. This work reviews the structural and mechanical properties of nucleic acid duplexes—RNA and DNA—including the PNA duplex. We found that the PNA duplex, which is capable of forming stable hybrids with DNA and RNA and has significant applicability in the field of drug design, is highly flexible in bending, stretching, and twisting compared to DNA and RNA duplexes. DNA exhibits greater bending flexibility but higher stretching rigidity than the RNA duplex.

**Keywords:** Nucleic Acid Duplexes • Peptide Nucleic Acids • Young's Modulus • Presistence Length • Twisting Rigidity • Drug Delivery

**Recieved: 2025-04-29** **Revised: 2025-05-30** **Published: 2025-06-02**

## I. Introduction

Deoxyribonucleic acid (DNA) and ribonucleic acid (RNA) are the nucleic acids found in humans and other species. Humans and almost all other species have DNA as their genetic material. Adenine (A), guanine (G), cytosine (C), and thymine (T) are the four chemical bases used to store information in DNA. In RNA, uracil (U) is found in place of T. A and G are termed as purines, which contain one six-membered ring accompanied by another five-membered ring made of carbon and nitrogen. C, T, and U are called pyrimidines, which include only one six-membered carbon-nitrogen ring. T base pairs with an A base and a C base pairs with a G base to generate base-pairs. In RNA, U base pairs with A base instead of T. A-T or A-U base-pair has only two Watson-Crick (WC) hydrogen bonds (H-bonds) while G-C has three H-bonds [1, 2]. This implies that A-T and A-U base-pairs are weaker than G-C base-pair.

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Self-assembly, manipulation, and miniaturization are all components of nanoscience, and biophysics is primarily concerned with self-assembly. As a result, self-assembly provides a common ground for biophysics and nanoscience. Biomedicine is where biophysics and nanoscience meet. DNA, RNA, and PNA have become essential emblems in modern nanoscience and nanotechnology because of their elegant and straight alignment of double-helical structure [3]. When contemplating DNA, RNA, and PNA as prospective options for nucleic acid-based nanobiotechnology, it is critical to understand their material characteristics. In this context, the mechanical properties of various nucleic acid duplexes and their interactions with other biomaterials are the subjects of interest.

In this work, we review the mechanical properties, mainly elastic properties, of different nucleic acid duplexes; namely, deoxyribonucleic acid (DNA) duplex, ribonucleic acid (RNA) duplex, and peptide nucleic acid (PNA) duplex. The elastic properties are associated with the physical properties like bending persistence, stretch modulus, twist rigidity, etc. Whereas DNA and RNA are found in living beings as the natural ingredients of cells, Peptide Nucleic Acids (PNAs) are synthetic compounds in which N-(2-aminoethyl)glycine (simply written as (2-aminoethyl)glycine or AEG) units replace the normal phosphate and sugar backbone of a nucleotide, and the nucleobase is connected to it through methylene-carbonyl linkers [4]. PNA is a potential nucleic acid nanotechnology molecule. PNA's medicinal importance stems mostly from the fact that it is easier to synthesize than other nucleic acids, as well as the fact that it is chemically stable, resistant to hydrolytic or enzymatic cleavage, and does not degrade inside live cells [5].

## II. Structural Aspects

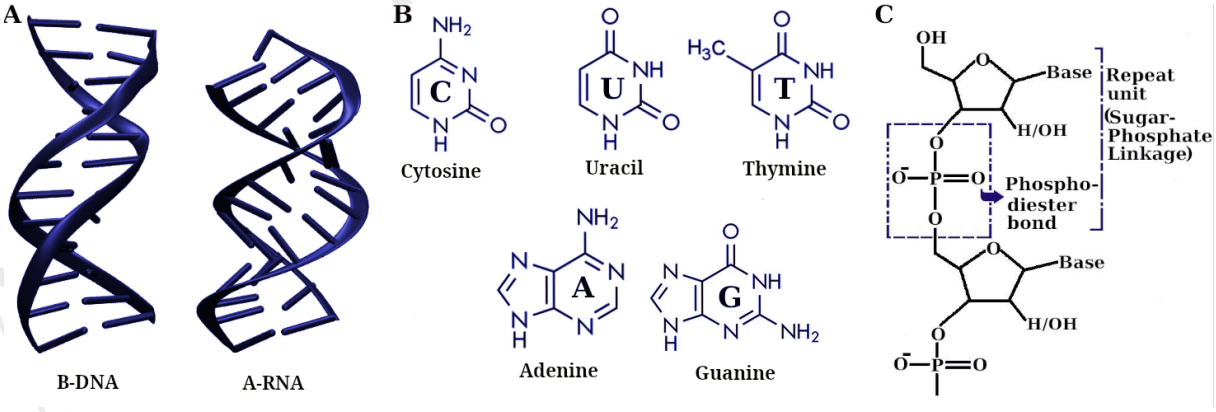


Figure 1. Cartoon representations of DNA (B-form) and RNA (A-form) duplexes (A), molecular structures of different nucleobases (B) and schematic representation of phospho-diester bond (C). The most prominent structure of DNA duplex is its B-form geometry and that of RNA duplex is the A-form geometry. In DNA, the two-carbon nitrogen ring bases (adenine and guanine) are purines, while the one-carbon nitrogen ring bases (thymine and cytosine) are pyrimidines. In RNA, in place of thymine, uracil is present.

DNA is a double-stranded molecule forming a helix, while RNA is typically single-stranded. Both are made up of nucleotides, but DNA contains deoxyribose sugar, while RNA contains ribose sugar.

Furthermore, DNA uses thymine (T) as a base, while RNA uses uracil (U) instead of thymine. While RNA is typically single-stranded, it can also form double-stranded structures, known as double-stranded RNA (RNA duplex) [6]. RNA duplex can trigger RNA interference and activate the innate immune system [7].

Fig. 1(A) shows the cartoon representations of DNA and RNA duplexes and Fig. 1(B) shows molecular structures of nucleobases. Each base additionally has a sugar molecule and a phosphate molecule linked to it. A nucleotide is a combination of a base, sugar, and phosphate. Fig. 1(C) shows the schematic for the backbone of DNA/RNA formed by repetition of nucleotides. Nucleotides are structured in a spiral-shaped double helix, which is made up of two long strands, forming a ladder-like shape. Fig. 2 shows the pairings formed by the nucleobases in DNA/RNA. The base-pairs serve as the ladder's rungs, while the sugar and phosphate molecules serve as the ladder's vertical sidepieces. DNA's ability to replicate, or generate duplicates of itself, is an important property. Each double helix strand of DNA may be used as a template for reproducing the base sequence. In human cells, DNA is generally in coiled form and its extended contour length (backbone) can range from few kilo base-pairs to billion base-pairs. The phosphate residues make the backbones of DNA and RNA electrically negative which robusts their binding efficiency with positively charged histones that makes the long-chains of nucleic acid duplexes capable to form loops and arrange inside the minute dimensions inside nucleus [8, 9].

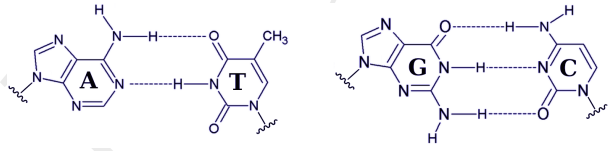


Figure 2. AT and GC Watson-Crick base-pairs in DNA duplex. There are two hydrogen bonds between adenine and thymine bases and three hydrogen bonds between guanine and cytosine bases. In case of RNA duplex, uracil is present in place of thymine. Uracil and thymine only differ by the presence of a methyl group in thymine.

Peptide Nucleic Acids (PNAs) are synthetic compounds in which N-(2-aminoethyl)glycine (simply written as (2-aminoethyl)glycine or AEG) units replace the normal phosphate and sugar backbone of a nucleotide, and the nucleobase is connected to it through methylene-carbonyl linkers [4]. Figs. 3(A) and 3(B) describe the chemical structures of the DNA/RNA backbones and PNA backbone, respectively. In DNA/RNA, the sugar-phosphate linkage is the repetitive unit and the phospho-diester bond connects two repetitive units, whereas, in the PNA, (2-aminoethyl)glycine unit is the repetitive unit and the peptide bond connects two repetitive units. The peptide bond that connects two (2-aminoethyl)glycine units is shown in Fig. 3(C). Unlike the backbones of DNA and RNA, the backbone of PNA is achiral and does not carry any charge. PNA may efficiently target DNA or RNA, functioning as a chemical tool for gene control, since nucleic acid backbone modification and functionalization boost the affinity for a specific sequence, enhancing selectivity [10]. PNA's DNA/RNA recognition properties, as well as its excellent

chemical stability and synthetic flexibility, have attracted researchers from a wide range of disciplines, including molecular biology and medicine [11].

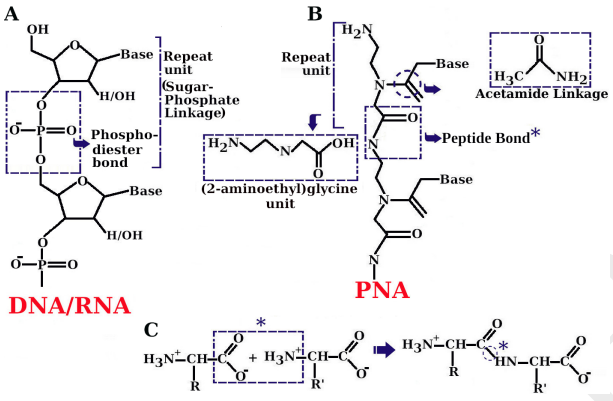


Figure 3. (A) Schematics for backbone of of DNA/RNA which is formed by repetitive sugar phosphate units, linked with phospho-diester bond. (B) Backbone of PNA which is formed by repetitive N-(2-aminoethyl)glycine units, linked with peptide bond (C). (D) The PNA-DNA hybrid duplex.

Despite the fact that PNA is a very different molecule from DNA since the phosphate backbones have been substituted with uncharged pseudo-peptide polymers, it has been demonstrated that PNA can recognize DNA and RNA sequences using the Watson-Crick hydrogen-bonding scheme [5]. PNA hybrid duplexes are thermally stable and have different ionic strength effects [12]. When comparing PNA-DNA recognition to DNA-DNA recognition, it was discovered that sequence discrimination is more robust and efficient on PNA-DNA [13].

## III. Mechanical Aspects

The persistence length ($l_p$) (also known as the tangent-tangent correlation length) is the length over which the direction of the nucleic acid duplex's tangent is maintained. It effectively quantifies the stiffness of the DNA molecule. This means that over a length of $l_p$, the duplex retains its original direction; beyond that, thermal fluctuations cause it to bend. The persistence length of DNA is a key parameter for understanding its conformational properties and interactions with other molecules. Considering the thermal fluctuation of a non-constrained nucleic acid duplex, the $l_p$ can be calculated from it's bending angle distribution. The bending angle distribution of a freely fluctuating nucleic acid can be approximated by a Gaussian, given by [14, 15],

$$P(\theta) = \sqrt{\frac{\beta\kappa}{2\pi L_0}} e^{-\frac{\beta\kappa}{2L_0}\theta^2} \tag{1}$$

For small $\theta$, we can re-write equation 1 as,

$$lnP(\theta) = -\frac{l_p}{L_0}(1 - cos\theta) + \frac{1}{2} ln\Big(\frac{\beta\kappa}{2\pi L_0}\Big) \tag{2}$$

The persistence length can be extracted from the slope of the graph of $lnP(\theta)$ versus $(1 - cos\theta)$ [16, 17]. With this, the bending modulus($\kappa$) is given by [16, 18],

$$\kappa = \frac{l_p}{\beta} = kTl_p \tag{3}$$

where $k$ is the Boltzmann's constant.

The stretch modulus $\gamma$ of a nucleic acid duplex, a measure of its resistance to stretching, quantifies its Young's modulus of elasticity or the stretching elasticity. This value reflects how much force is needed to stretch given nucleic acid duplex to produce a unit longitudinal strain in it. Similar to the bending angle distribution, one can write down the contour length distribution of a freely fluctuating nucleic acid duplex as a Gaussian, given by [16],

$$P(L) = \sqrt{\frac{\beta\gamma_G}{2\pi L_0}} e^{-\frac{\beta\gamma_G}{2L_0}(L-L_0)^2} \tag{4}$$

By taking logarithm, equation 4 can be rewritten as,

$$lnP(L) = -\frac{\beta\gamma_G L_0}{2}\left(\frac{L}{L_0} - 1\right)^2 + \frac{1}{2} ln \frac{\beta\gamma_G}{2\pi L_0} \tag{5}$$

where $L_0$ is the time averaged contour length, $\gamma_G$ is the stretch modulus, and $\beta = 1/kT$ with $T$ being the temperature of equilibrated system and $k$ being the Boltzmann constant. We can extract the stretch modulus $\gamma_G$ of the molecule from the slopes of the fits with the $P(L)$. Equation 5, gives a straight line while plotting $lnP(L)$ versus $\left(\frac{L}{L_0} - 1\right)^2$, and the stretch modulus $\gamma_G$can be extracted from its slope.

The mechanical property of nucleic acid duplex which is associated with the twisting stiffness against torsional deformation is called its torsional rigidity or twist modulus ($C$). The torsional modulus of nucleic acid duplex is given by [19, 20],

$$C = \frac{kTL}{\sigma_\Phi^2} \tag{6}$$

where $L$ is the contour length, $\Phi$ is the total helical twist, and $\sigma_\Phi^2$ is the variance of angle $\Phi$.

The elastic properties like stretch modulus $\gamma_G$ and persistence length ($l_p$) of nucleic acid duplexes can be influenced by factors like temperature, salt concentration, pressure etc [21–23].

Table 1. Persistence length and Stretch Moduli of the nucleic acid duplexes

| Measures | DNA | RNA | PNA | Remarks | Ref. |
|---|---|---|---|---|---|
| Contour Length | 3.40 per bp | 2.60 per bp | — | Exp. | [24] |
| ($L_0$) in Å | $3.25 \pm 0.52$ per bp | $2.75 \pm 0.38$ per bp | $2.58 \pm 0.83$ per bp | MD Sim. | [15] |
| Persistence Length | 45–50 | 60 – 70 | — | Exp. | [25–28] |
| ($l_p$) in nm | $57.58 \pm 1.39$ | $66.99 \pm 1.38$ | $34.52 \pm 1.15$ | MD Sim. | [15] |
| Stretch Modulus | 1000–1500 | 350–600 | — | Exp. | [26, 28–30] |
| ($\gamma_G$) in pN | $1368.60 \pm 49.10$ | $602.83 \pm 27.73$ | $169.11 \pm 14.99$ | MD Sim. | [15] |
| Twist Modulus | $451.48 \pm 16.57$ | $414.20 \pm 8.28$ | — | Exp. | [30] |
| ($C$) in pN.nm$^2$ | $464.02 \pm 10.93$ | $416.78 \pm 13.16$ | $198.41 \pm 17.27$ | MD Sim. | [15] |
| T-S coupling | +ve | -ve | -ve* | Exp./MD Sim* | [30, 31],[15]* |

The persistence length of RNA is generally greater than that of DNA due to its different chemical structure and shape. RNA and DNA differ in their sugar component. RNA uses ribose, which has a 2'-hydroxyl group, while DNA uses deoxyribose, which lacks this group. This 2'-hydroxyl group in RNA is thought to increase its resistance to bending and make it stiffer. The 2'-hydroxyl group in RNA also leads to a slightly different helical structure compared to DNA. RNA typically forms an A-form helix, which is wider and shorter than the B-form helix of DNA (see Fig. 4). This difference in structure contributes to RNA's greater persistence length. The difference in structure and shape also affects the way RNA and DNA interact with their environment, influencing their flexibility and resistance to bending. The persistence length of PNA is found to be smaller than that of DNA and RNA molecules. It implies that the DNA and RNA possess higher bending stiffness than the PNA molecule. As the PNA backbones are charge-neutral, the absence of electrostatic repulsion between the two strands provides more flexibility to the backbone. An increase of negative charge is found to increase the stiffness via electrostatic repulsion in DNA and RNA [32].

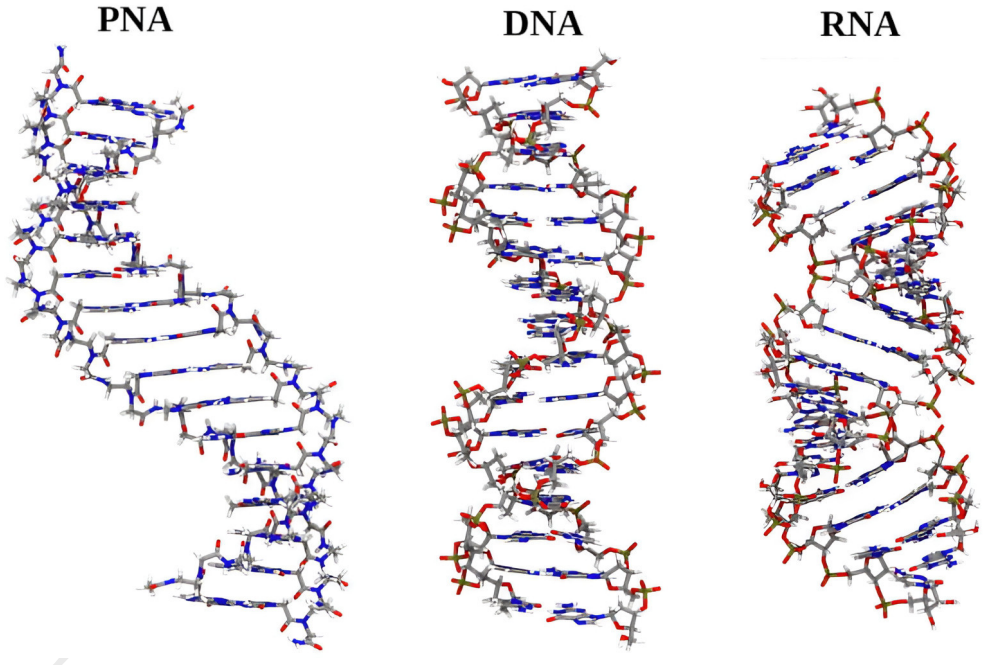


Figure 4. Structures of PNA, DNA and RNA duplexes. The DNA duplex adopts a narrower, more elongated B-form geometry compared to RNA and PNA duplexes, contributing to its robust stretching rigidity. In contrast, RNA typically adopts the A-form geometry, which is wider and more compact, resulting in different mechanical responses under force. While both DNA and RNA duplexes predominantly exhibit right-handed helical structures, PNA (peptide nucleic acid) duplexes have been observed to adopt both right-handed and left-handed conformations with nearly equal probability, reflecting their unique backbone flexibility and base-pairing properties.

The stretch modulus of RNA is smaller than DNA due to differences in their structural flexibility and how they respond to external forces. Specifically, RNA has a more open structure and an opposite negative coupling. Just opposite to RNA, DNA has a more compact structure and a positive twist-stretch coupling. These structural differences result in RNA being more flexible and less resistant to stretching

compared to DNA. Structurally, RNA duplex's base pairs are more inclined than those in DNA (see Fig. 4), leading to a larger base pair inclination and a more open, flexible structure. This allows for more movement and less resistance to stretching. The stretching flexibility of PNA duplex, depicted by smaller stretch modulus, compared to DNA and RNA is again due to its neutral backbone and greater flexibility. The absence of the negatively charged phosphate backbone in DNA and RNA allows PNA to adopt a wider range of conformations, leading to lower stiffness.

The value of twist modulus or or the torsional rigidity (C) for RNA is slightly greater than DNA due to more open shape of RNA compared tmolecules and the hybrid duplexes are found smaller than those of DNA and RNA. The twist modulus of PNA duplexes is smaller than that of DNA and RNA duplexes primarily due to PNA's neutral backbone and its inherent flexibility. PNA's lack of charge and ability to adopt various conformations make it more pliable and less resistant to twisting compared to the more rigid DNA and RNA duplexes.

Twist-stretch coupling refers to the relationship between the twist (helical rotation) and stretch (extension) of the nucleic acid's double helix (duplex) when subjected to external forces. RNA exhibits a negative twist-stretch coupling, meaning that it unwinds (decreases twist) when stretched. In contrast, DNA has a positive twist-stretch coupling, meaning it twists (increases twist) when stretched. Thus, the more open structure and positive twist-stretch coupling of RNA duplex make it more susceptible to being stretched and deformed under force. The opposite behavior in DNA duplex results in it being more resistant to stretching and more stable under force.

The opposite twist-stretch coupling of DNA and RNA molecules indicates that with the increase in a twist, the DNA double helix becomes narrower, reducing the inter-strand distance thereby increasing its helical length. The overtwisting of DNA strands is physically connected with the shrinkage of the average helix diameter [15, 33]. The RNA double helix exhibits the exact opposite behaviour. This means that the RNA molecule can only be elongated by unwinding. So, the overwinding of RNA makes it more compact axially with narrower major grooves, thereby reducing helical extension, whereas DNA becomes laterally compact with narrower minor grooves [28, 34]. The negative values of twist-stretch coupling for RNA and PNA suggest that RNA and PNA backbones show higher stretch flexibility such that their twisting unwinds and makes them wider, unlike that of DNA molecule.

## IV. Conclusion

In this work, we have reviewed and presented a comparative study of the elastic properties, namely persistence length, stretch modulus, and twist-stretch coupling of DNA, RNA and PNA duplexes.

The persistence length, the measure of bending stiffness, of DNA backbones lies between that of RNA and PNA, with RNA backbones having highest stiffness. The PNA molecules are considered to be

more flexible than DNA and RNA because increasing negative charge of the backbones decreases duplex stability and flexibility via electrostatic repulsion [32]. The more open structure of RNA makes it to govern more bending rigidity than DNA, even though both have negatively charged backbones.

The twist moduli for DNA and RNA are more significant than that of PNA duplex. It depicts the higher twisting flexibility of PNA duplex than that of DNA and RNA. RNA duplex possesses more flexibility to twist relative to DNA. The twist-stretch coupling, which shows the correlation between extension and twist of the molecule, is found to be positive for DNA and negative for RNA. The twist-stretch coupling is found to be weakly negative for PNA duplex. Weak twist-stretch coupling of PNA means that the extension and twist are weakly correlated on them. The -ve twist-strech coupling of RNA and PNA implies that the duplexes are unwinded upon twisting and more open in structure that makes them flexible in stretching and compacting axially. The +ve twist-strech coupling of DNA implies that the duplexes are overwinded upon twisting and more constricted in structure that makes them rigid in stretching and compacting axially. Thus the stretch modulus, the measure of stretching rigidity, of PNA and RNA duplexes is smaller compared to DNA.

This review highlighted PNA molecule as the structurally flexible duplex. Studies show that PNA strands are capable of producing stable complexes with DNA and RNA strands easily. Thus, we suggest to the future experimentalists in the engineering of the PNA-DNA and PNA-RNA hybrids for gene-delivery and drug-delivery applications in the field of nano-medicine. The PNA-based antibiotics can be the future clinical alternatives to battle against multidrug-resistant bacteria.

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