The DNA Helix and How It Is Read
By Richard E. Dickerson

DNA encodes for two types of information:
- extrinsic: triplet genetic code that specifies structure of proteins, actual structure of DNA does not matter, information carried via transcription and translation
- intrinsic: actual structure of DNA promotes binding of regulatory proteins (for example, lac and lambda repressors), regions of DNA (the operator) probably form hydrogen bonds with amino acids of regulatory proteins, local structure of DNA important for the identification of these sites

Basic Structure of DNA:
- determined by x-ray diffraction from stretched natural DNA fibers
- double-ringed purines: adenine (A) and guanine (G)
- single-ringed pyrimidines: thymine (T) and cytosine (C)
- base pairs hydrogen bond across double helix: A forms 2 bonds with T, G forms 3 with C
- major and minor grooves since base pairs do not attach directly across from each other (see diagram on p. 96)

Differences between A and B DNA:
- use of DNA oligomers (short strands of 4 to 24 bases) in single-crystal x-ray studies helps to determine smaller local variations
- B helix is probably most common form of DNA in nucleus: it is stabilized by hydrogen bonding with a layer of water around it, there is a "zigzag spine of hydration" in the minor groove due to A-T pairs; C-G pairs break up this spine of hydration
- helix probably changes into A form during transcription
- base inclination: tilt of the bases with respect to helical axis
- helical twist: angle from one base pair to the next (corresponds to base pairs per turn and helix rise per base pair)
- propeller twist: angle between planes of two opposite base pairs (p. 98); helps improve stacking of base pairs
- base roll: orientation of the plane of the base pair about its long axis
<table>
<thead>
<tr>
<th></th>
<th>A DNA</th>
<th>B DNA</th>
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<tbody>
<tr>
<td>relative humidity</td>
<td>75%</td>
<td>92%</td>
</tr>
<tr>
<td>general description</td>
<td>short and fat</td>
<td>slimmer and taller</td>
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<tr>
<td>groove depth</td>
<td>major much deeper</td>
<td>similar depth</td>
</tr>
<tr>
<td>base inclination (°)</td>
<td>13.0 ± 1.9</td>
<td>-2.0 ± 4.6</td>
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<tr>
<td>base pairs per turn</td>
<td>10.9</td>
<td>10.0</td>
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<tr>
<td>helix rise per base pair (Å)</td>
<td>2.92 ± .39</td>
<td>3.36 ± .42</td>
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<tr>
<td>helical twist (°)</td>
<td>33.1 ± 5.9</td>
<td>35.9 ± 4.3</td>
</tr>
<tr>
<td>propeller twist (°)</td>
<td>15.4 ± 6.2</td>
<td>11.7 ± 4.8</td>
</tr>
<tr>
<td>base roll (°)</td>
<td>5.9 ± 4.7</td>
<td>-1.0 ± 5.5</td>
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**Discovery of Z DNA from Single Crystal Studies:**
- synthesized short C-G copolymers
- left-handed helix with zigzag backbone
- quite thin and elongated: 12 base pairs per turn
- deep, narrow minor groove and very shallow major groove
- repeating unit really two base pairs: G-C and then C-G
- alternating syn-anti conformation (in A and B DNA all the conformations are anti); syn: guanine has its sugar ring rotated 180 degrees so that it is in towards the minor groove

**How Code Contributes to Local Structure of DNA:**
- floor of major groove has many nitrogen and oxygen atoms that can hydrogen bind with amino acids (minor groove offers less information)
- A-T pair offers a nitrogen atom (hydrogen acceptor), an NH₂ group (donor), and an oxygen atom (acceptor)
- G-C pair offers a nitrogen atom (acceptor), an oxygen atom (acceptor), and an NH₂ group (donor) [these patterns can also be reversed]
- steric hindrance (especially in the minor groove) between large purine bases contribute to base roll, propeller twist, local helical twist, and other characteristics
- Dickerson’s group has determined way to predict these characteristics based on local sequence (p. 111 shows correlation between the predictions and actual characteristics)
- since local sequence can determine localized variations on the DNA structure, these can intrinsically encode information, such as the binding site for a regulatory protein