Chapter 8
DNA Recognition in Prokaryotes by Helix-Turn-Helix Motifs

1. Helix-turn-helix proteins
2. Zinc finger proteins
3. Leucine zipper proteins
4. Beta-scaffold factors
5. Others
λ-REPRESSOR AND CRO
A molecular mechanism for genetic switch

Bacteriophage λ: A temperate bacteriophage infecting *E. coli*

The phage injects its DNA.

Bacterial chromosome circularizes.

Daughter cell with prophage

Occasionally, a prophage exits the bacterial chromosome, initiating a lytic cycle.

Cell divisions produce population of bacteria infected with the prophage.

The bacterium reproduces, copying the prophage and transmitting it to daughter cells.

Lytic cycle

Lysogenic cycle

Phage DNA integrates into the bacterial chromosome, becoming a prophage.

New phage DNA and proteins are synthesized and assembled into phages.

Lytic cycle is induced or Lysogenic cycle is entered

The cell lyses, releasing phages.

Phage DNA circularizes.

Phage DNA

Phage

Bacteriophage λ

Dimensions: 55 nm x 150 nm x 25 nm

Volume: $9.1 \times 10^{-5} \mu m^3$

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A molecular mechanism for genetic switch
Repressor and Cro proteins operate a prokaryotic genetic switch region

“Turning off synthesis of Cro” or “activator for its own synthesis”
Repressor and Cro proteins operate a prokaryotic genetic switch region

Palindrome: the same forward as it is backward

Examples: RACECAR, OTTO

DNA: read base pairs

Examples: Restriction enzyme recognition sequences
Repressor and Cro proteins operate a prokaryotic genetic switch region

Table 8.1 The nucleotide sequences of the three protein-binding regions OR1, OR2, and OR3 of the operator of bacteriophage lambda

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Palindromic base pairs that are most frequent at the two ends are green, and the pseudo-twofold symmetry axis is indicated by a red dot.

Palindromic sequences: 8 bp per a monomer
Sequence information shows a pseudo 2-fold symmetry
The x-ray structure of the complete lambda Cro protein is known.

**Figure 7.4** The DNA-binding protein Cro from bacteriophage lambda contains 66 amino acid residues that fold into three $\alpha$ helices and three $\beta$ strands. (a) A plot of the C$_{\alpha}$ positions of the first 62 residues of the polypeptide chain. The four C-terminal residues are not visible in the electron density map. (Adapted from Anderson et al., *Nature* 290: 755, 1981.) (b) A schematic diagram of the subunit structure. $\alpha$ helices 2 and 3 that form the helix-turn-helix motif are colored blue and red, respectively. The view is different from that in (a). (Adapted from D. Ohlendorf et al., *J. Mol. Biol.* 169: 757, 1983.)
Dimeric structure of N-terminal domain of lambda repressor

Figure 7.7 The N-terminal domain of lambda repressor, which binds DNA, contains 92 amino acid residues folded into five α helices. Two of these, α2 (blue) and α3 (red) form a helix-turn-helix motif with a very similar structure to that of lambda Cro shown in Figure 7.5. The complete repressor monomer contains in addition a larger C-terminal domain. (Adapted from C. Pabo and M. Lewis, Nature 298: 445, 1982.)

Figure 7.8 The N-terminal domains of lambda repressor form dimers, in spite of the absence of the C-terminal domains, which are mainly responsible for dimer formation in the intact repressor. The dimers are formed by interactions between α helix 5 from each subunit. The different subunits are colored green and brown, except the helix-turn-helix motif, which is colored blue and red as in Figure 7.5. (Adapted from C. Pabo and M. Lewis, Nature 298: 446, 1982.)
Figure 1. Structure of the λ Repressor C-Terminal Domain Dimer

The dimer in the asymmetric unit of the crystal is shown in ribbon representation. The view is perpendicular to the 2-fold axis of symmetry (noncrystallographic). The monomer on the left (gold) is shown with β strands labeled β1-β7, coil and turn regions L1-L6, and the 3_{10}-helix 3_{10}. Lys-192 and Ser-149, shown in blue ball-and-stick, form the active site for RecA-mediated cleavage. Residues shown in brown ball-and-stick (and labeled for the green subunit) are affected by mutations that inhibit dimerization. Notice that these residues map to the dimer interface. Also notice that the C-terminal 3_{10}-helices are “swapped.”

[Bell et al., Cell (2000)]
Lambda repressor C-terminal domain forms tetramers in the crystal

Figure 4. The Dimer-Dimer Association of the λ Repressor CTD that Mediates Cooperative Binding to DNA Is Captured in the Crystal

(A) The structure of the λ repressor CTD dimer is shown in surface representation with one subunit colored gold and the other subunit colored green. Two dimers are shown as they would approach one another to form a complex. The view of the top dimer is roughly from the bottom of Figure 1, and the bottom dimer is related to the top dimer by 180° rotation about an axis perpendicular to the plane of the figure. Residues that are affected by cooperativity mutations cluster into two patches, colored red and blue, in the surface of each monomer (the blue patch is actually comprised of two neighboring but noncontiguous regions). Within the red patch are Arg-196, Asp-197, Ser-198, Gly-199, Phe-202, Gin-204, and Met-212. Within the blue patch are Gly-147, Asn-148, Ser-149, Gin-196, Lys-192, and Tyr-210. (B) Two dimers of the λ repressor CTD associate about a 2-fold crystallographic axis of symmetry. The interactions between the two dimers involve the patches of residues (colored red or blue) that are affected by cooperativity mutations. Specifically, the red patches on the gold subunits dock to the blue patches on the green subunits. Notice that half of the patches (the red patch on each green subunit and the blue patch on each yellow subunit) are exposed to solvent, offering potential sites for further association.

(C) Ribbon representation of the λ repressor CTD tetramer, looking down the crystallographic 2-fold axis of symmetry (same view as (B)). The crystallographic 2-fold axis, shown as a red dot in the center, relates the top dimer to the bottom dimer. The black lines indicate the 2-fold axes (noncrystallographic) that relate the two subunits within each dimer. Residues that are affected by cooperativity mutations are shown in ball-and-stick representation and are colored red or blue, as indicated in (A). Notice that the interactions between the two dimers (indicated by the brown arrows) involve the red cluster of residues on each gold subunit and the blue cluster of residues on each green subunit. Also notice that the β4-β5 hairpin of the gold subunit inserts into a pocket on the green subunit.

(D) Close-up view of the atomic interactions at the dimer-dimer interface. The orientation is the same as in (B) and (C). Ion-pair and hydrogen bonding interactions bridging the dimer-dimer interface (within 3.5 Å) are shown as dotted lines. Notice that the interactions center on the ion pair between Asp-197 and Lys-192.

(E) View of the CTD tetramer looking from the left side of (C). The rotation axis shows the relation of (E) to (C). Notice that the N terminus of each subunit extends to the left side of the tetramer, with the N termini of the “top” dimer pointing up and the N termini of the “bottom” dimer pointing down. This suggests the likely orientation of the CTD tetramer with respect to the DNA, as each of the four N-terminal DNA binding domains would point to the left side.

(F) The dimer-dimer association of the λ repressor C-terminal domain can be repeated to form an octamer. The brown arrows indicate each dimer-dimer interface. Although the outer dimers (bottom left and bottom right) expose potential sites for further association, adding a fifth dimer would result in steric clashes. Notice that the N terminus of each subunit extends to the outside of the octamer, so that the N-terminal DNA binding domains of the intact repressor could fan out without steric hindrance.

[Bell et al., Cell (2000)]
LETTERS

Crystal structure of the λ repressor and a model for pairwise cooperative operator binding

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Bacteriophage λ has for many years been a model system for understanding mechanisms of gene regulation\textsuperscript{1}. A ‘genetic switch’ enables the phage to transition from lysogenic growth to lytic development when triggered by specific environmental conditions. The key component of the switch is the cl repressor, which binds to two sets of three operator sites on the λ chromosome that are separated by about 2,400 base pairs (bp)\textsuperscript{2,3}. A hallmark of the λ system is the pairwise cooperativity of repressor binding\textsuperscript{4}. In the absence of detailed structural information, it has been difficult to understand fully how repressor molecules establish the cooperativity complex. Here we present the X-ray crystal structure of the intact λ cl repressor dimer bound to a DNA operator site. The structure of the repressor, determined by multiple isomorphous replacement methods, reveals an unusual overall architecture that allows it to adopt a conformation that appears to facilitate pairwise cooperative binding to adjacent operator sites.

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Figure 4 | Models of the intact repressor octamer reveal the structural basis for alternate pairwise cooperativity. 

**a**, Interaction of two DNA-bound tetramers. The model, which was created by superimposing two DNA-bound tetramers (see Fig. 3) on a structure of the λ repressor CTD octamer, illustrates why three interacting repressor dimers (shown in dark colour) cannot bind to three adjacent operators (Oₐ₁, Oₐ₂ and Oₐ₃, for example). Each repressor dimer has two potential cooperativity interfaces, allowing it to interact with up to two additional dimers (consider, for example, the dimer at the bottom left, which is shown interacting with both the dimer at the bottom right and the darkly coloured dimer at the top). This superimposition of structures shows that only two of the three interacting dimers (those at the bottom) can be positioned at adjacent sites on the DNA. When the octamer is configured as shown, the third (top dark) and fourth (top pale) dimers are appropriately positioned to bind cooperatively to a distant pair of operator sites; the model thus shows how a pair of repressor dimers bound cooperatively to Oₐ₁ and Oₐ₂ can interact with a second pair bound cooperatively to Oₐ₁ and Oₐ₂, located 2.4 kb away. 

**b**, Alternative configuration for the intact repressor octamer. Because of the inherent asymmetry of the intact repressor dimer, two DNA-bound repressor dimers can be superimposed on the CTD tetramer in two different ways, resulting in two different configurations for the intact tetramer (one of which is depicted at the bottom, the other at the top). The superimposition depicted at the top does not allow for cooperative binding to adjacent operator sites; rather, the NTDs fan out in opposite directions. In this model, as well, however, the configuration of the three interacting dimers (shown in dark colour) is such that only two of the three (those at the bottom) can be positioned at adjacent sites on the DNA. 

**c**, Schematic of Oₐ region that illustrates alternate pairwise cooperativity. A repressor (CI) dimer bound at Oₐ₂ can interact with either another dimer bound at Oₐ₁ or another dimer bound at Oₐ₃, but not both simultaneously. On a wild-type Oₐ region, sites Oₐ₁ and Oₐ₂ are occupied by a cooperatively bound pair of CI dimers (top), whereas when Oₐ₁ is inactivated by mutation, sites Oₐ₂ and Oₐ₃ are occupied by a cooperatively bound pair of CI dimers (bottom).
Both lambda Cro and repressor proteins have a specific DNA-binding motif.
Model building predicts Cro-DNA interactions

34 Å apart between two α3 helices in a dimer → 10 bp apart DNA recognition helix (α3) / stabilizing helix (α2)
Genetic studies agree with the structural model

Altered DNA binding specificity by redesigning recognition helix (by Mark Ptashne's group at Harvard)

- Recognition helix swap between repressor and Cro $\rightarrow$ changes in the binding affinity
- Changes in a single amino acid of repressor between 434 and P22 phage $\rightarrow$ engineered 434 repressor binds to P22 operator, not to 434 operator
Figure 7.12 There are six operator regions (OR1–OR3 and OL1–OL3), each of 14 base pairs in bacteriophage 434. The palindromic base pairs of these regions are marked in green. Crystal structures have been determined of complexes between both 434 Cro and the repressor fragment with synthetic DNA fragments—one 14 base pairs long (a 14 mer), which is completely palindromic, and one 20 base pairs long (a 20 mer), which contains the sequence of OR1 in its middle region.
PROKARYOTIC DNA BINDING PROTEINS
The structures of DNA-binding domain are very similar

(434 Cro vs 434 repressor: 48% sequence identity)
(434 Cro vs lambda repressor: 26% sequence identity)
The proteins impose precise distortions on the B-DNA in the complexes

DNA helix axis bent toward a repressor

Normal B-DNA

Distorted DNA complexed with 434 Cro & repressor
Sequence specific protein-DNA interactions recognize operator regions

Recognition helix ↔ A major groove
- H-bonding / hydrophobic interaction
  (Q28 & Q29 form H-bonds to A1-C2) / (methyl-group on T)
Protein-DNA backbone interactions determine DNA conformation
Main features of the interactions between DNA and the helix-turn-helix motif in DNA binding protein

1. H-bonds between sugar-phosphate backbone and protein help anchor protein to DNA

2. Sequence-specific interaction between DNA and recognition helix allows recognition of OR regions

3. DNA distortion allows close interactions with other regions of Cro and repressor and accounts for differential affinities
DNA binding is regulated by allosteric control

Binding of the small molecules (i.e., allosteric effectors) to the sites quite different from the functional binding sites of repressor or activator causes the conformational changes.

Figure 7.22 The subunit of the trp repressor. The subunit contains 107 amino acid residues that are folded into six α helices. Helices 4 (blue) and 5 (red) form the DNA-binding helix-turn-helix motif. (Adapted from R. Schevitz et al., Nature 317: 782, 1985.)
w/o Trp, repressor is inactive
→ turn on operon for the synthesis of Trp

w Trp, repressor is active
→ turn off operon

Major groove binding of $\alpha_5$ via water-mediated interactions

Structural changes by the binding of Trp into a pocket

Inactive (28-29 Å between two $\alpha_5$ helices) → active (34 Å)

Binding of Trp to the cavity alters the orientation of $\alpha_5$ helices
LAC REPRESSOR
In the absence of lactose, Lac repressor binds to an OR site [RNAP can’t bind to the site, hence operon is off]

In the presence of inducer (lactose or IPTG), repressor-effector complex no longer binds to the OR site [Operon is on]

Four domains in monomer (HTH - hinge helix - core domains -tetramerization domain)
E. coli lac operon: review

- Lactose present
  - Lac repressor cannot bind to operator
  - lac mRNA produced

- NO lactose
  - Lac repressor binds to operator
  - No lac mRNA produced
Inducer of Lac repressor

Lactose
(galactose-\((\beta1->4)\)-glucose)

Allolactose
(galactose-\((\beta1->6)\)-glucose)

IPTG
(isopropyl \(\beta\)-D-1-thiogalactopyranoside)

A molecular mimic of allolactose
Tetrameric Lac repressor binds to both the major and the minor grooves inducing a sharp bend in the DNA.

Each dimer binds to the separated palindromic DNA sequence.
Tetrameric Lac repressor binds to both the major and the minor grooves inducing a sharp bend in the DNA.

- Major (HTH) & minor (hinge helix) groove binding (seq. specific)
- HTH binding as were seen in Cro and repressor in a phage
- Hinge helix: Leu opens up the minor groove and DNA is bent away from the protein
CATABOLITE GENE ACTIVATING PROTEIN
CAP-induced DNA bending could activate transcription

Figure 7.25 Catabolite gene activating protein, CAP, is a DNA-binding protein that assists RNA polymerase to bind more effectively to certain promoters and thereby CAP enhances the rate of initiation of RNA synthesis. A preliminary x-ray structure determination in the laboratory of Tom Steitz, Yale University, of a complex between CAP and a DNA fragment has shown that the CAP dimer induces sharp bends in DNA. In vivo CAP binding might induce a loop in DNA so that regions far from the operator site can interact with RNA polymerase. This might result in tighter binding of the enzyme to the DNA. (Adapted from T.
### Table 7.2
Sequence alignment of presumed helix-turn-helix DNA-binding motifs

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![Diagram of DNA-binding motifs](image)