9 - Transcription

When a gene is activated, the gene is **transcribed**, producing an RNA intermediate. **Structural genes** are genes that are transcribed to produce **messenger RNA (mRNA)** molecules. The mRNA molecule is then **translated** to make a protein product. **Nonstructural genes** are also transcribed to produce RNA molecules; however, the RNA molecule is not translated and instead functions directly in the cell. These functional RNA molecules, called **noncoding RNAs (ncRNAs),** include transfer RNA molecules (tRNAs), ribosomal RNA molecules (rRNAs), and the *Xist* and *Tsix* RNA molecules discussed in Part 2.

Key Questions

- What is the difference between a structural and a nonstructural gene?

A. Transcription in Bacteria

Expression of Structural Genes

What factors determine whether a bacterial structural gene is **expressed**; in other words, the gene is activated to make a mRNA molecule? Gene expression requires the interaction between **transcription factor** proteins and specific DNA sequences near the gene.

The DNA sequences that regulate the expression of a particular structural gene include (see **figure 9.1**):

- **Regulatory DNA sequences.** Regulatory DNA sequences influence how often transcription starts. These DNA sequences are located, in most cases, adjacent to a structural gene.
- **The promoter sequence.** The promoter consists of DNA sequences that determine where transcription starts. The promoter is typically adjacent to the controlled structural gene.
- **The terminator sequence.** The terminator consists of DNA sequences that signal termination of transcription by causing the RNA polymerase to dissociate from the DNA.

Transcription produces an RNA molecule that is complementary to the **template** or **antisense** strand of DNA. The other DNA strand, the one that forms hydrogen bonds with the template DNA strand, is called the **coding** or **sense** DNA strand. The coding DNA strand is identical in sequence to the RNA transcript, except that the RNA molecule contains uracil (U) instead of thymine (T).

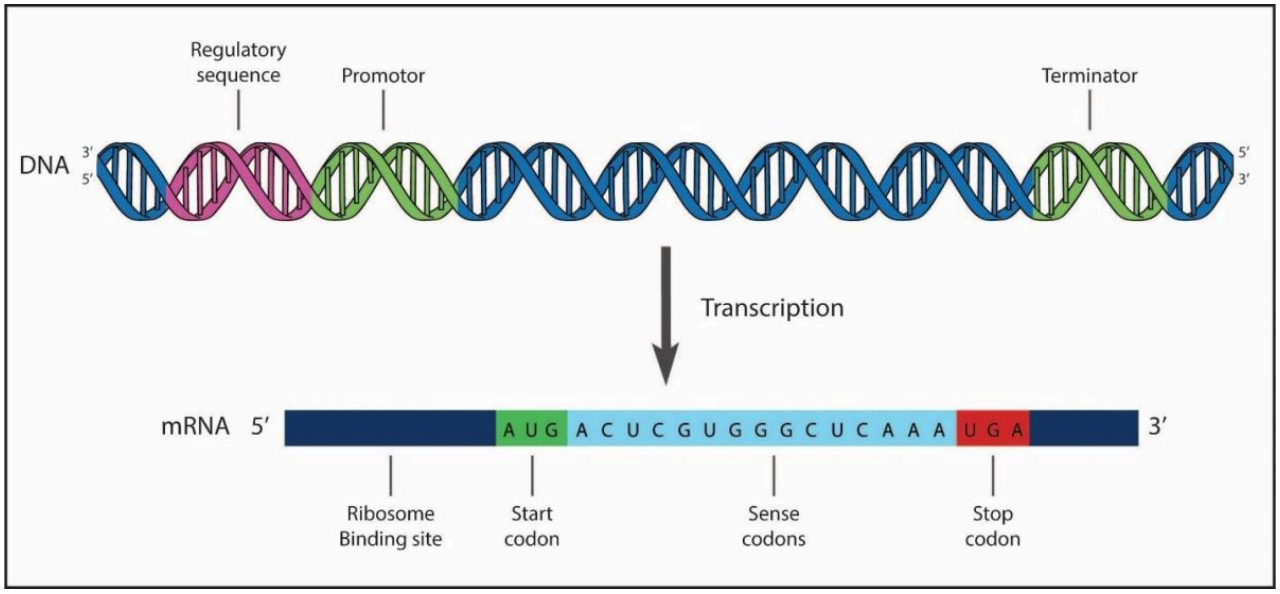


Figure 9.1 ***DNA sequences that control transcription.*** *--- Image created by SL*

Key Questions

- What are the functions of the three DNA sequences that regulate transcription?
- What is the difference between the template and the coding DNA strands?

Transcription Stages

Transcription of structural genes in the bacterium *E. coli* has the following three stages (see **figure 9.2**):

1. **Initiation.** During the initiation stage of transcription in bacteria, a transcription factor protein called **sigma (σ) factor** guides the **RNA polymerase** to the promoter.
2. **Elongation.** During elongation, the RNA polymerase bound to the promoter acts as a DNA helicase, separating the two DNA strands, forming an **open complex.** RNA polymerase then reads the template DNA strand while synthesizing a complementary mRNA transcript.
3. **Termination.** The termination stage of transcription involves the release of the RNA polymerase and the mRNA molecule from the DNA.

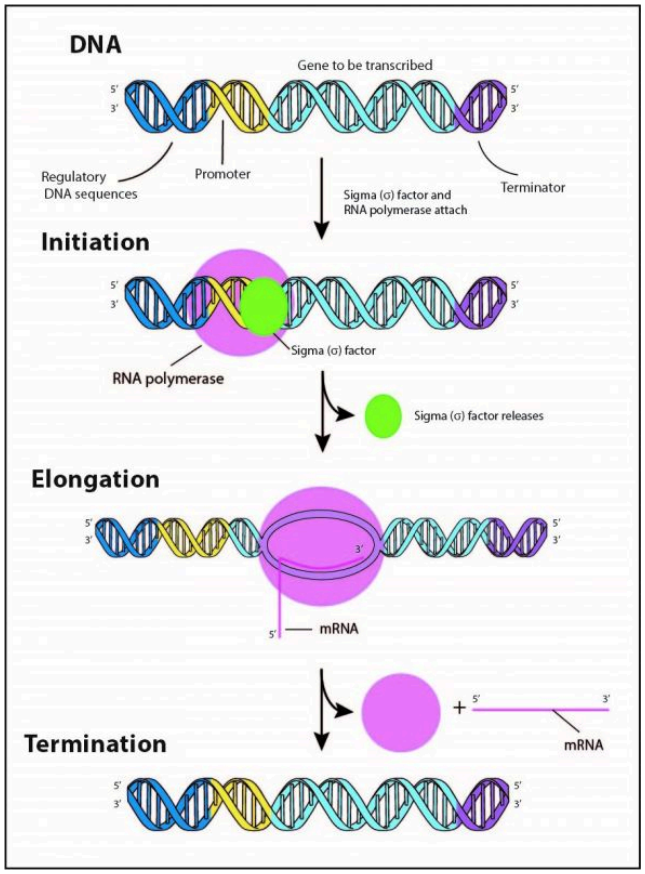


Figure 9.2 ***Transcription Overview*** *--- Image created by SL.*

Key Questions

- What is happening during the three stages of transcription?
- What is the function of sigma factor?

Promoter Structure in Bacteria

The bacterial **promoter** is located **upstream** (typically drawn to the left) of the structural gene to be transcribed and serves as a docking site for the sigma (σ) factor protein and later RNA polymerase. DNA sequence elements within the promoter are numbered relative to the **+1 site**, the first nucleotide in the template DNA strand that is transcribed (see **figure 9.3**). Important DNA sequences within the bacterial promoter include the following:

- **-35 sequence.** The -35 sequence (5'-TTGACA-3' in the coding DNA strand) allows high transcription rates because it serves as part of the binding site for the **sigma (σ) factor** protein. The -35 sequence is located approximately 35 base pairs (bp) upstream of the transcription start site (+1 site).
- **-10 sequence.** The -10 sequence (5'-TATAAT-3' in the coding DNA strand) is essential for transcription in prokaryotes because it serves as the second part of the sigma factor binding site. Moreover, the -10 sequence is AT-rich, promoting the separation of the two DNA strands, a requirement for transcription. The -10 sequence is located approximately 10 bp upstream of the transcription start site (+1 site).
- **+1 site.** The +1 site is the **transcription start site**. The nitrogenous base at the +1 site in the coding DNA strand is usually adenine (A). Since the mRNA and the coding DNA strand have the same sequence, the first nitrogenous base in the mRNA is also adenine (A).

Both the -35 and -10 sequences described above (5'-TTGACA-3' and 5'-TATAAT-3') are **consensus sequences**, meaning that they are the "average" sequences found when the DNA sequences of many *E. coli* promoters are compared. Some bacterial promoters are **strong promoters**, whereas others are **weak promoters**. The difference between strong and weak promoters largely depends on how closely the promoter DNA sequence in question matches the -35 and -10 consensus sequences. Strong promoters initiate transcription frequently, while weak promoters initiate transcription less frequently.

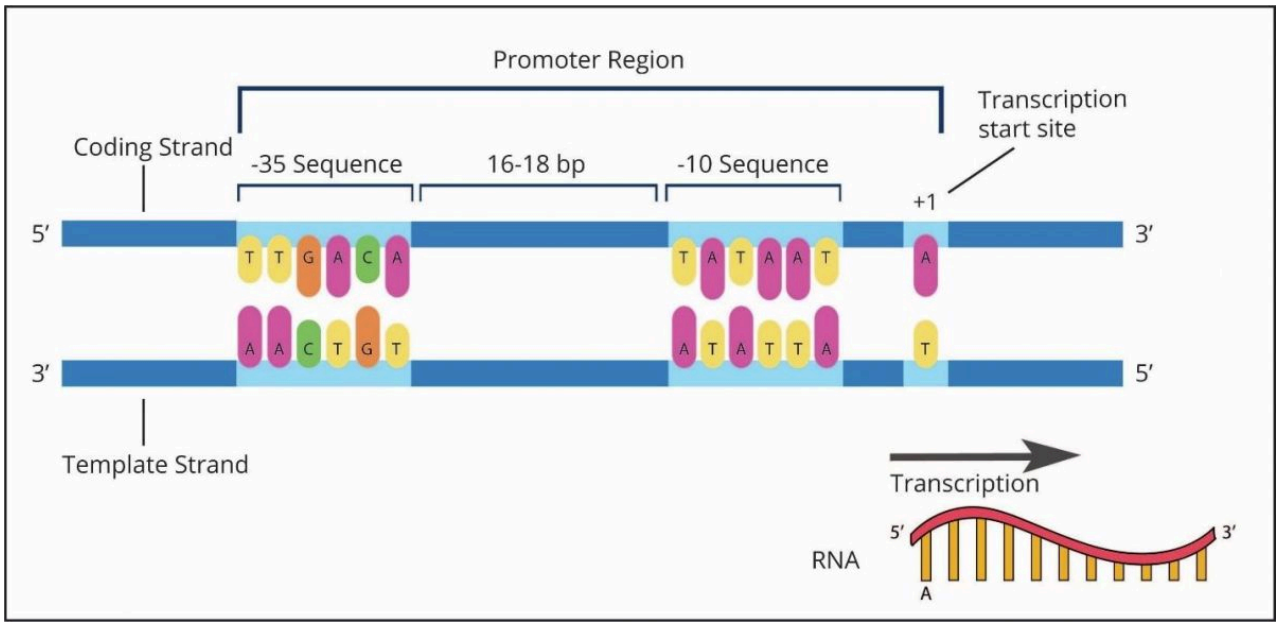


Figure 9.3 ***Bacterial Promoter*** *--- Image created by SL*

Key Questions

- What is the function of the -35 sequence?
- What are the two functions of the -10 sequence?
- What is the function of the +1 site?
- What is the difference between a strong and a weak promoter?

Bacterial RNA Polymerase

In the bacterium *E. coli*, the **RNA polymerase core enzyme** is composed of five protein subunits (α_1, α_2, β, β', and ω) (see **figure 9.4**). The two α subunits and the ω subunit function to assemble the enzyme and bind to the DNA sequence to be transcribed. The RNA molecule is synthesized between the β and β' subunits.

The RNA polymerase core enzyme (α_1, α_2, β, β', and ω subunits) associates with the **sigma (σ) factor** protein to form the **RNA polymerase holoenzyme**. *E. coli* makes at least eight different types of sigma factor proteins, depending on the environmental conditions encountered by the cell. For example, the main sigma factor in *E. coli* is called the **housekeeping sigma factor** or **σ^{70}** protein. The σ^{70} protein functions to guide the RNA polymerase core enzyme to the promoters of structural genes required for the viability of the *E. coli* cell in a typcial environment (e.g., body temperature with plenty of carbon and nitrogen sources). In addition to the σ^{70} protein, there are specialized sigma factor proteins that guide the RNA polymerase core enzyme to survival genes when an *E. coli* cell encounters stressful environments. These specialized sigma factors include a nitrogen starvation sigma factor (σ^{54}), a carbon starvation sigma factor (σ^{38}), and a heat shock sigma factor (σ^{32}). Because the sigma (σ) factor proteins regulate transcription, the sigma (σ) factor proteins are example **transcription factor proteins**

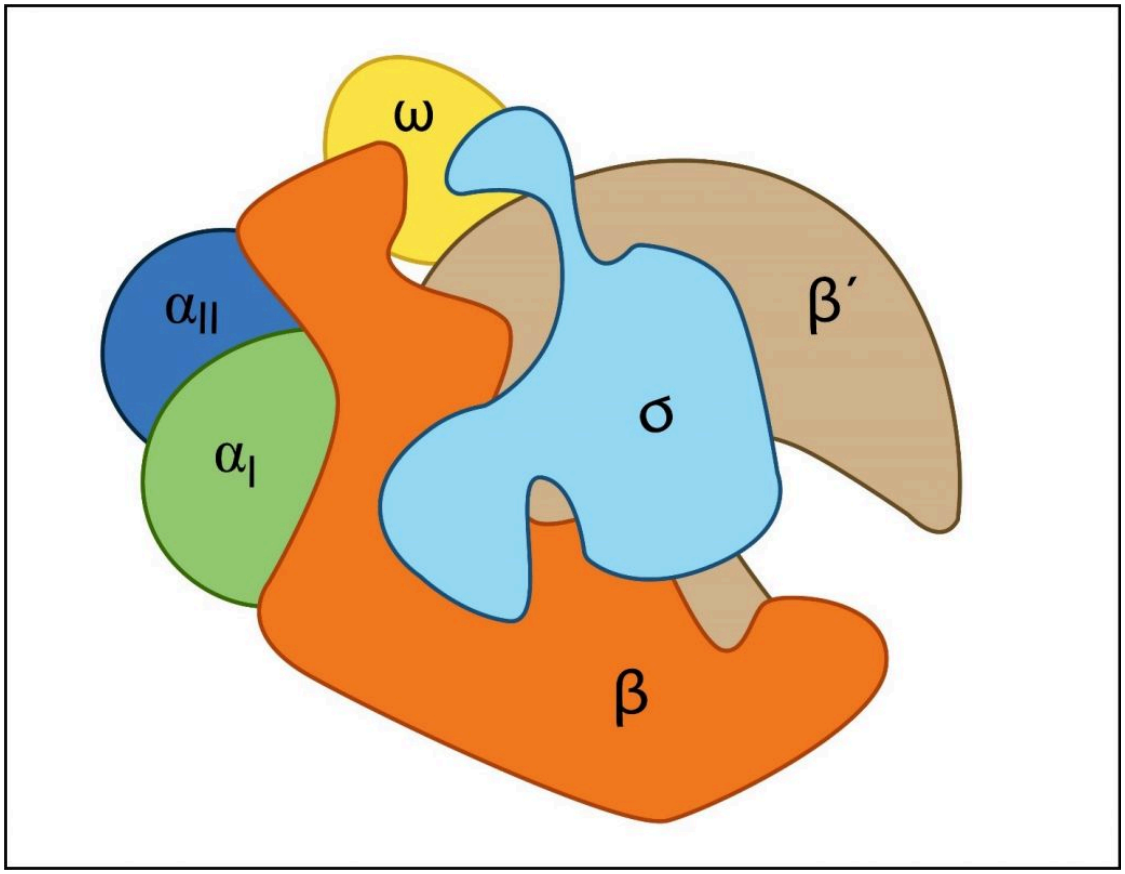


Figure 9.4 ***RNA Polymerase Holoenzyme Subunits*** *--- Image created by SL*

Key Questions

- Why does *E. coli* make several different types of sigma factor proteins?
- What is the difference between the RNA polymerase core enzyme and the RNA polymerase holoenzyme?

Transcription Initiation in Bacteria

Transcription initiation in bacteria (*E. coli*) occurs as follows:

1. The RNA polymerase holoenzyme recognizes the promoter via sigma (σ) factor binding to the -35 and -10 DNA sequences. At this stage, the RNA polymerase holoenzyme:DNA complex is called a **closed complex** because the two DNA strands are still hydrogen bonded together.
2. The AT hydrogen bonds within the -10 sequence are broken forming an **open complex**. The RNA polymerase core enzyme is the DNA helicase that separates the two DNA strands at the -10 sequence.
3. A short RNA molecule is synthesized beginning at the +1 sequence; however, the RNA polymerase core enzyme is still attached to σ factor. Sigma (σ) factor is still bound to the -10 and -35 DNA sequences.
4. The sigma (σ) factor protein is released, freeing the RNA polymerase core enzyme.
5. Once the sigma (σ) factor protein is released, transcription transitions to the elongation phase as the RNA polymerase core enzyme incorporates additional nucleotides at the 3’ end of the RNA transcript.

Key Questions

- Describe the initiation phase of transcription in bacteria.

Elongation in Bacteria

The elongation phase of transcription in bacteria involves RNA synthesis by the RNA polymerase core enzyme (see **figure 9.5**). The *E. coli* RNA polymerase core enzyme has the following features:

- The RNA polymerase core enzyme does not require a primer for RNA synthesis (in other words, no 3'-OH group is required to initiate transcription). Because the RNA polymerase core enzyme has no primer requirement, the first nucleotide incorporated into the mRNA has three phosphate groups attached to the 5' carbon.
- The RNA polymerase core enzyme has DNA helicase activity, separating the two DNA strands during transcription elongation.
- The RNA polymerase core enzyme reads the template DNA strand in the 3' to 5' direction.
- The RNA polymerase core enzyme synthesizes the mRNA in the 5' to 3' direction.
- The RNA polymerase core enzyme catalyzes the formation of a covalent bond between the 3'-OH of the growing RNA strand and the 5' phosphate group on the incoming **nucleoside triphosphate (NTP)**. The NTPs used by the RNA polymerase core enzyme are ATP, UTP, CTP, and GTP. The NTP molecules are cleaved during transcription, releasing pyrophosphate (PP_i) during the RNA synthesis reaction.
- RNA synthesis follows the AT/GC rule except that uracil is found in RNA (in other words, transcription follows the AU/GC rule).
- The RNA polymerase core enzyme does not have proofreading activity (no 3' to 5' exonuclease activity). As a result, the mRNA molecule made during transcription sometimes contains mistakes.
- The RNA polymerase core enzyme reforms hydrogen bonds within the two DNA strands after the open complex has passed by. As the RNA polymerase core enzyme rewinds the DNA double helix, the RNA transcript trails behind the core enzyme as a single-stranded RNA molecule.

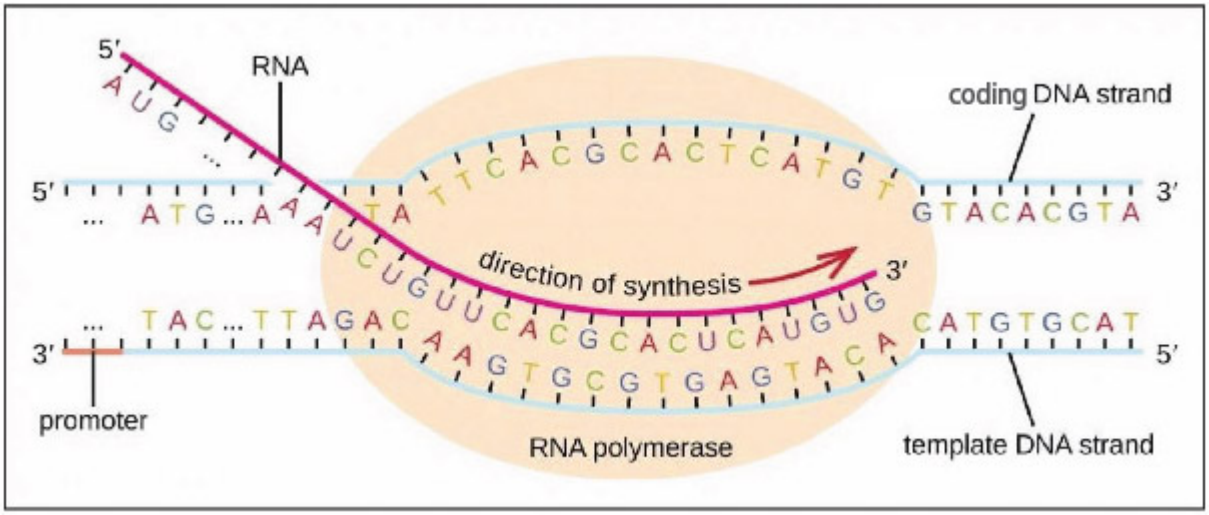


Figure 9.5 ***Transcription Elongation*** *--- Image used from OpenStax (access for free at https://openstax.org/books/biology-2e/pages/1-introduction)*

Key Questions

- What are the similarities and differences between the RNA polymerase core enzyme and the DNA polymerases discussed in Part 6?
- Which protein functions as the DNA helicase for transcription?
- What molecules provide the energy for transcription?

Transcription of Multiple Genes

Not all genes use the same DNA strand as the template strand. In **figure 9.6**, genes A and B use the bottom DNA strand as the template strand for RNA synthesis, because the promoter is located to the left of the gene. Alternatively, gene C

uses the top DNA strand as the template strand, as the promoter is located to the right of the gene. Genes A and B are transcribed left to right, while gene C is transcribed right to left.

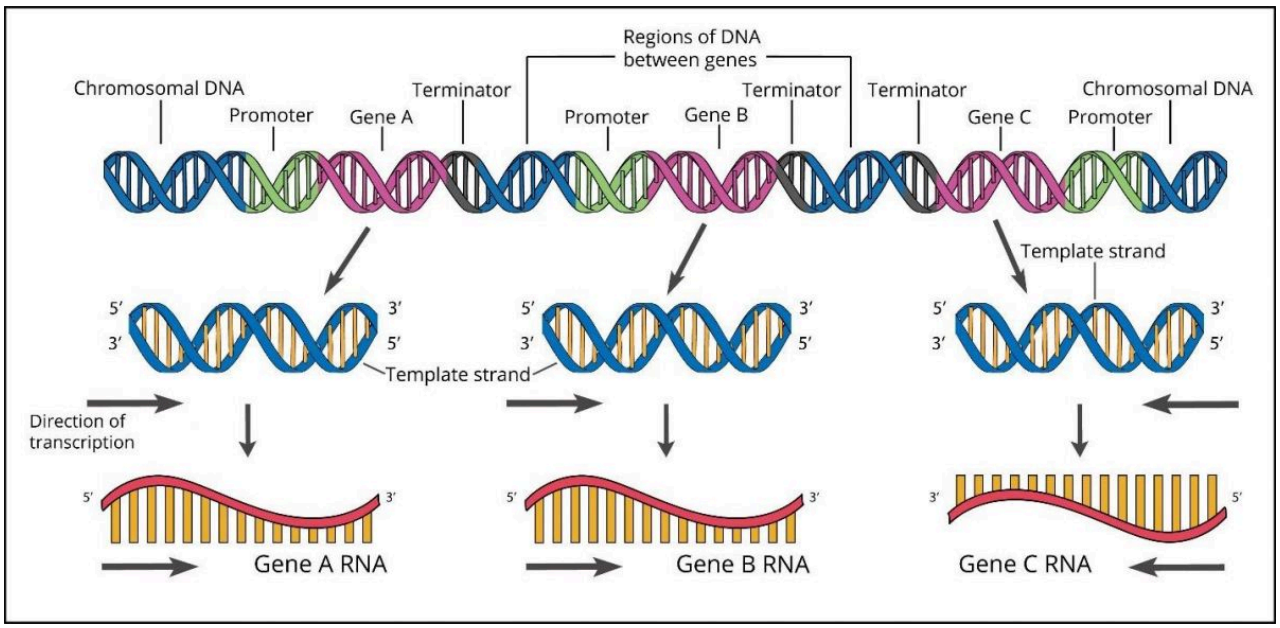


Figure 9.6 ***Transcription of Multiple Genes*** *--- Image created by SL*

Rho (ρ)-Dependent Termination

While the RNA polymerase core enzyme is synthesizing a mRNA molecule, an RNA-DNA double helix molecule is formed within the enzyme. Transcriptional termination involves weakening the hydrogen bonds within this RNA-DNA double helix, resulting in dissociation of the RNA (and the RNA polymerase core enzyme) from the DNA.

Transcriptional termination can occur in two different ways in the bacterium *E. coli*:

- **Rho (ρ)-dependent termination**
- **Rho (ρ)-independent termination**

The rho (ρ)–dependent mechanism of termination requires binding between the **rho (ρ) protein**, a helicase that breaks the hydrogen bonds within an RNA-DNA double helix, and an RNA sequence near the 3’ end of the mRNA transcript called the **rho utilization site (*rut*)** (see **figure 9.7**). The ρ-dependent mechanism of transcription termination also requires the formation of a secondary structure within the RNA transcript called a **stem-loop** or **hairpin loop**. The stem-loop is formed when guanine (G) and cytosine (C) bases are produced in the mRNA as the RNA polymerase core enzyme reads the terminator DNA sequence. The stem-loop, composed of hydrogen bonds between these G and C nucleotides within the same mRNA molecule, slows the RNA polymerase core enzyme during transcription. The rho (ρ) protein then catches up with the RNA polymerase, separates the RNA from the template DNA strand, and releases the RNA transcript and the RNA polymerase core enzyme from the DNA. Transcription is terminated.

Key Questions

- What three components are involved in rho (ρ)-dependent termination?
- What are the functions of each of these components in rho (ρ)-dependent termination?

Rho (ρ)-Independent Termination

The rho (ρ)-independent termination mechanism does not require rho (ρ) protein or the *rut* RNA sequence (see **figure 9.7**). In rho (ρ)-independent termination of transcription, a stem-loop structure is formed in the newly synthesized RNA that slows the RNA polymerase core enzyme. This pausing of the RNA polymerase is aided by the **NusA** protein. While the RNA polymerase slows down, a uracil-rich region is synthesized in the RNA because the RNA polymerase core enzyme is copying an adenine-rich region in the template DNA strand. Recall that each uracil base in the mRNA forms two hydrogen bonds with each adenine base in the template DNA strand. This weak base pairing between U and A bases tends to break spontaneously, releasing the mRNA and RNA polymerase, terminating transcription.

The mechanism that is used for transcription termination depends on the gene. About 50% of *E. coli* genes use the rho (ρ)-dependent mechanism, the other 50% of genes use the rho (ρ)-independent mechanism. An individual gene does not use both termination mechanisms.

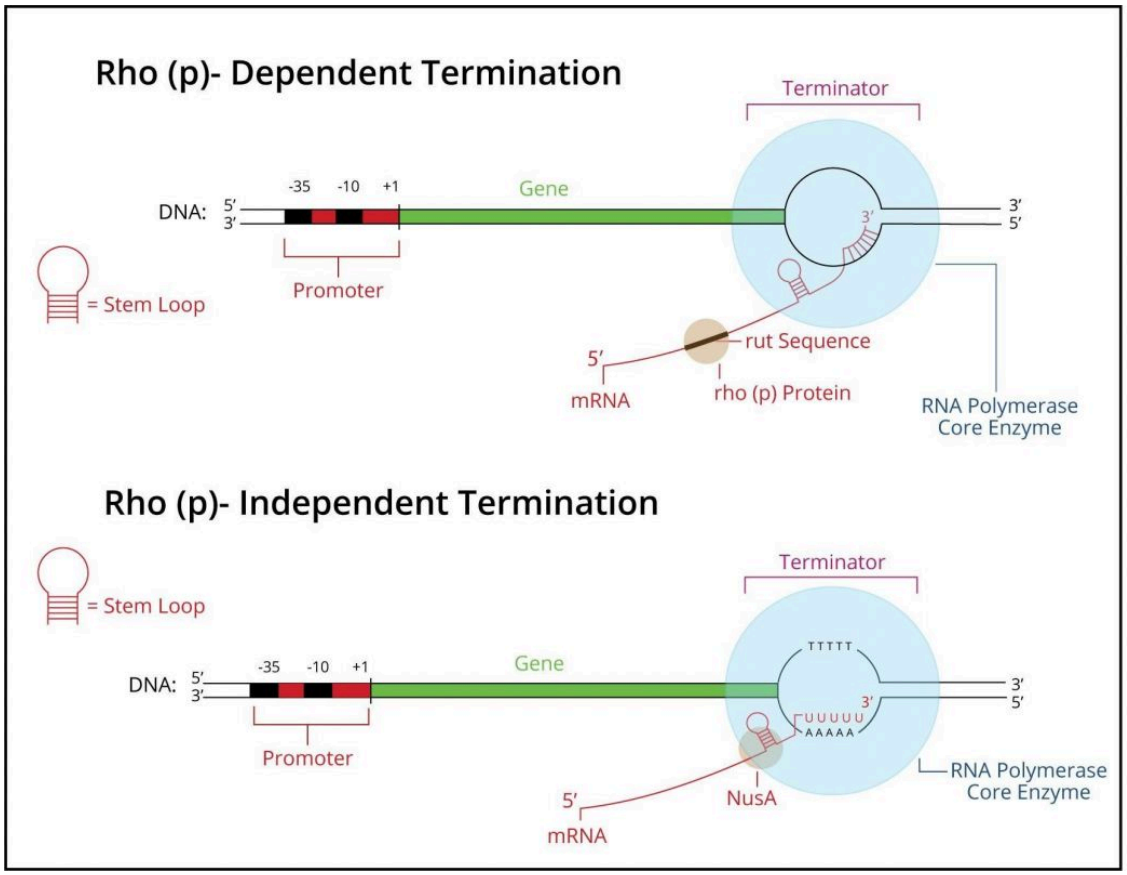


Figure 9.7 ***Transcription Termination in Bacteria*** *--- Image created by SL*

Key Questions

- What three components are involved in rho (ρ)-independent termination?
- What are the functions of each of these components in rho (ρ)-independent termination?

B. Transcription in Eukaryotes

Transcription is important to a eukaryotic cell, as the activation of a structural gene allows eukaryotic cells to adapt to environmental changes (e.g., the presence of a hormone in the blood can activate transcription; see Part 14). Moreover, many eukaryotic organisms are multicellular, so genes need to be transcribed at the right time during development and in the correct cell type. For example, genes involved in building the central nervous system should be transcribed during embryonic development. Genes that encode proteins involved in muscle contraction should be transcribed in muscle cells and not transcribed in other cell types, such as white blood cells. These phenotypic differences are due to transcription, as all cell types (neurons, muscle cells, white blood cells) in the body contain an identical collection of genes.

DNA Sequences Control Eukaryotic Transcription

The transcription of eukaryotic genes is controlled by several types of DNA sequence elements, including the following (see **figure 9.8**):

- **Core promoter.** The core promoter determines where the RNA polymerase will bind to the DNA and begin transcription**.** The core promoter contains two important DNA sequence elements:
  - **TATA box (-25 sequence).** The TATA box (5'-TATAAAA-3' sequence in the coding DNA strand) is located approximately 25 base pairs upstream of the transcriptional start site. The TATA box serves as the binding site for the general transcription factor protein TFIID (see below). The TATA box is also rich in AT base pairs, promoting DNA strand separation.
  - **Transcription start site (+1 site).** The +1 site is the first nitrogenous base in the template DNA strand that is transcribed into an RNA nucleotide.

For a eukaryotic gene to be transcribed, the TATA box and the +1 site must be present. However, if these two sequences are the only DNA sequences present upstream of a gene, the gene is transcribed at a low, yet constant rate, the so-called **basal** level of transcription.

- **Regulatory DNA sequences.** Regulatory DNA sequences function to either transcribe the gene above the basal level or transcribe a gene below the basal level. Regulatory DNA sequences serve as the binding sites for **regulatory transcription factor** proteins that influence the ability of RNA polymerase to recognize the core promoter efficiently. Regulatory DNA sequences include:
  - **Enhancers.** Enhancer DNA sequences stimulate the transcription of the controlled gene above the basal level. Enhancer DNA sequences are the binding sites for **activator** proteins.
  - **Silencers.** Silencer DNA sequences down-regulate transcription of the controlled gene below the basal level. Silencer DNA sequences are the binding sites for **repressor** proteins.

The DNA sequences that influence transcription of an adjacent gene are called ***cis*-acting DNA elements.** *Cis*-acting DNA elements include the core promoter, enhancer, and silencer sequences. The transcription factor proteins that bind to these *cis*-acting DNA elements are called ***trans*-acting factor proteins**. *Trans*-acting factors proteins, also called **transcription factor proteins**, include activator proteins, repressor proteins, and the general transcription factor (GTF) proteins (see below).

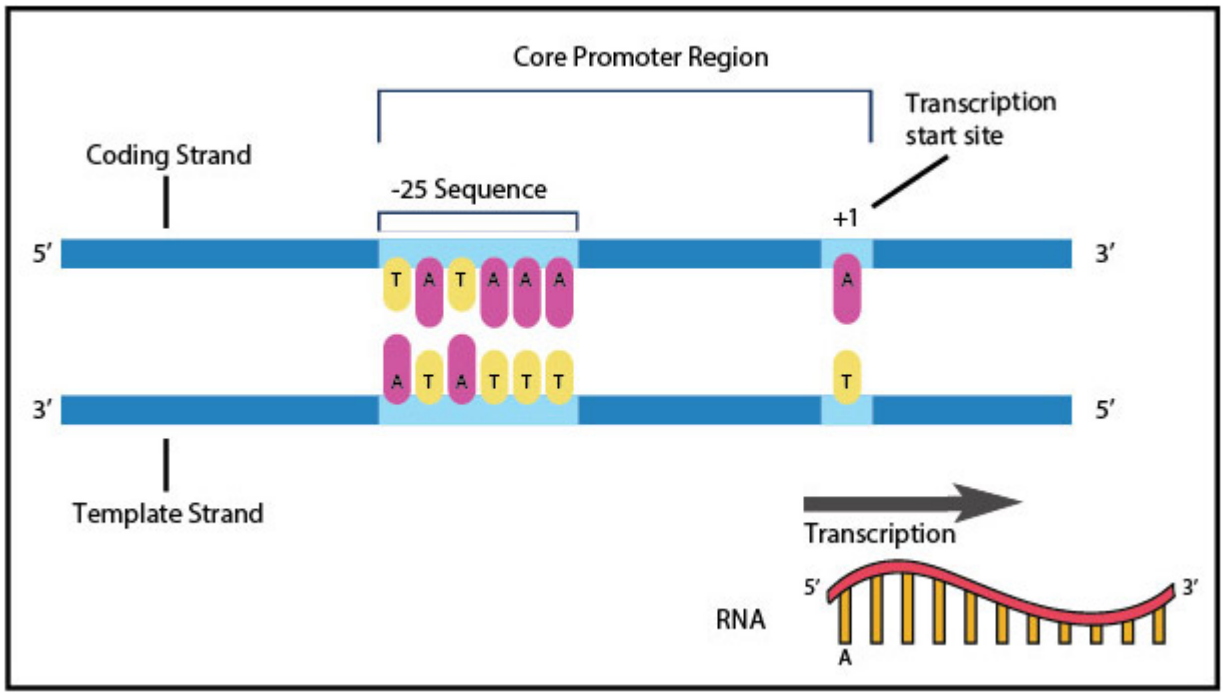


Figure 9.8 ***Eukaryotic Core Promoter*** *--- Image created by SL*

Key Questions

- What are the names of the two sequence features within the core promoter?
- What are the two functions of the TATA box?
- What are names and functions of the two regulatory DNA sequences that influence the transcription of eukaryotic genes?
- What are the names of the proteins that bind to these two regulatory DNA sequences?

RNA Polymerases in Eukaryotes

In eukaryotes, there are three types of RNA polymerases that handle transcription:

- **RNA polymerase I.** RNA polymerase I transcribes most of the eukaryotic ribosomal RNA (rRNA) genes to make rRNA molecules. We will learn in Part 11 that rRNA molecules are noncoding RNA molecules that play a critical role in the translation process.
- **RNA polymerase II.** RNA polymerase II transcribes eukaryotic structural genes. Recall that structural genes produce mRNA molecules upon transcription. In this section, we will focus our attention on RNA polymerase II.
- **RNA polymerase III.** RNA polymerase III transcribes all eukaryotic transfer RNA (tRNA) genes. We will learn in Part 11 that tRNA molecules are noncoding RNA molecules that play a critical role in translation, functioning to deliver amino acids to the ribosome.

Key Questions

- What types of genes do the three eukaryotic RNA polymerases transcribe?

Initiation in Eukaryotes

Both **basal** (constant, low level) transcription and **regulated** (above or below the basal level) transcription of structural genes in eukaryotes require the following proteins (see **figure 9.9**):

- **RNA polymerase II**.
- **General transcription factor (GTF) proteins.** The GTF proteins function like the bacterial sigma (σ) factor protein; the GTFs deliver RNA polymerase II to the core promoter and regulate RNA polymerase II function. There are six major GTF proteins in eukaryotes:
  - **TFIID.** The TFIID protein binds to the core promoter by recognizing the TATA box (-25 sequence). TFIID is actually a multi-subunit protein "machine" composed of multiple protein subunits. One of these protein subunits is the **TATA-binding protein (TBP)** that binds directly to the TATA box (-25 sequence).
  - **TFIIA.** The TFIIA protein helps TFIID bind to the TATA box (-25 DNA sequence).
  - **TFIIB.** The TFIIB protein binds to TFIID and recruits the RNA polymerase II/TFIIF protein complex to the core promoter.
  - **TFIIF.** The TFIIF protein is associated with RNA polymerase II. When the TFIIF protein binds to TFIIB, RNA polymerase II is located at the +1 sequence.
  - **TFIIH.** TFIIH is another multi-subunit protein complex. One protein subunit within the TFIIH complex is a DNA helicase that breaks the hydrogen bonds at the TATA box (-25 sequence). Another protein subunit within the TFIIH complex is a kinase, phosphorylating RNA polymerase II to activate transcription. TFIIH uses the chemical energy within ATP to activate RNA polymerase II.
  - **TFIIE.** TFIIE assists TFIIH to separate the two DNA strands, activating transcription.

The association of RNA polymerase II with the six GTF proteins listed above forms a **preinitiation complex.** The preinitiation complex is also called the **basal transcription apparatus.**

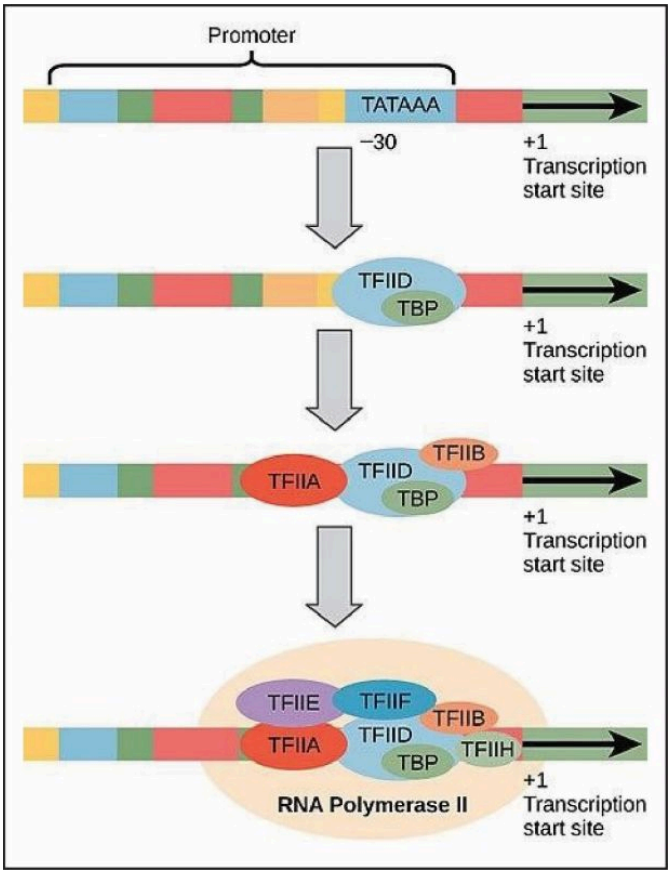


Figure 9.9 ***Transcription Initiation in Eukaryotes*** *--- Image used from OpenStax (access for free at https://openstax.org/books/biology-2e/pages/1-introduction)*

Key Questions

- Which GTF binds to the core promoter?
- Which GTF acts as a bridge to connect the GTF bound to the core promoter to the GTF bound to RNA polymerase II?
- Which GTF is the DNA helicase that separates the two DNA strands?
- Which GTF activates RNA polymerase II?

General and Regulatory Transcription Factors

Transcription factor proteins influence the ability of RNA polymerase II to bind to a eukaryotic core promoter. A huge number of eukaryotic genes encode transcription factor proteins; it is estimated that as many as 1000 human genes encode proteins that regulate transcription! There are two categories of transcription factor proteins:

- **General transcription factor (GTFs) proteins.** The GTFs include the **TFIID, TFIIA, TFIIB, TFIIF, TFIIE**, and **TFIIH** proteins described above. The GTFs function to recruit RNA polymerase II to the core promoter and activate RNA polymerase II to begin transcription. The GTFs are required for all transcription events. If these transcription factors are the only ones involved, the gene is transcribed at a low, yet constant level, the so-called **basal level**. GTFs are also required for transcription rates above and below the basal level.
- **Regulatory transcription factor proteins**. Regulatory transcription factor proteins function to either increase the rate of transcription above the basal level or decrease the rate of transcription below the basal level (see **figure 9.10**). **Activator** proteins are regulatory transcription factor proteins that bind to enhancer DNA sequences and increase the level of transcription above the basal level. Conversely, **repressor** proteins bind to silencer DNA sequences and decrease transcription below the basal level. Many regulatory transcription factors are only expressed in certain cell types or at certain times during embryonic development, thus playing a critical role in cell-specific or time-specific transcription.

The DNA binding sites (core promoter, enhancer, and silencer sequences) for these transcription factor proteins tend to be near the genes they control. As a result, the DNA sequences are called ***cis*-acting DNA elements**. However, these *cis*-acting DNA elements do not need to be immediately adjacent to the core promoter. Some enhancers and silencers can be within the gene they control or can be thousands of base pairs away. The transcription factor proteins (GTFs, activators, and repressors) that bind to the *cis*-acting DNA elements are ***trans*-acting factor proteins**.

Since transcriptional control requires both input from a myriad of DNA sequences and proteins, some component in the cell needs to interpret the various activation and repression signals to provide an overall signal to RNA polymerase II. A large multi-subunit **mediator** protein complex regulates the interaction between RNA polymerase II and the activator and repressor proteins. Mediator thus serves as a link between transcription factors that bind to enhancer and silencer DNA sequences and RNA polymerase II, thereby determining the overall rate of transcription.

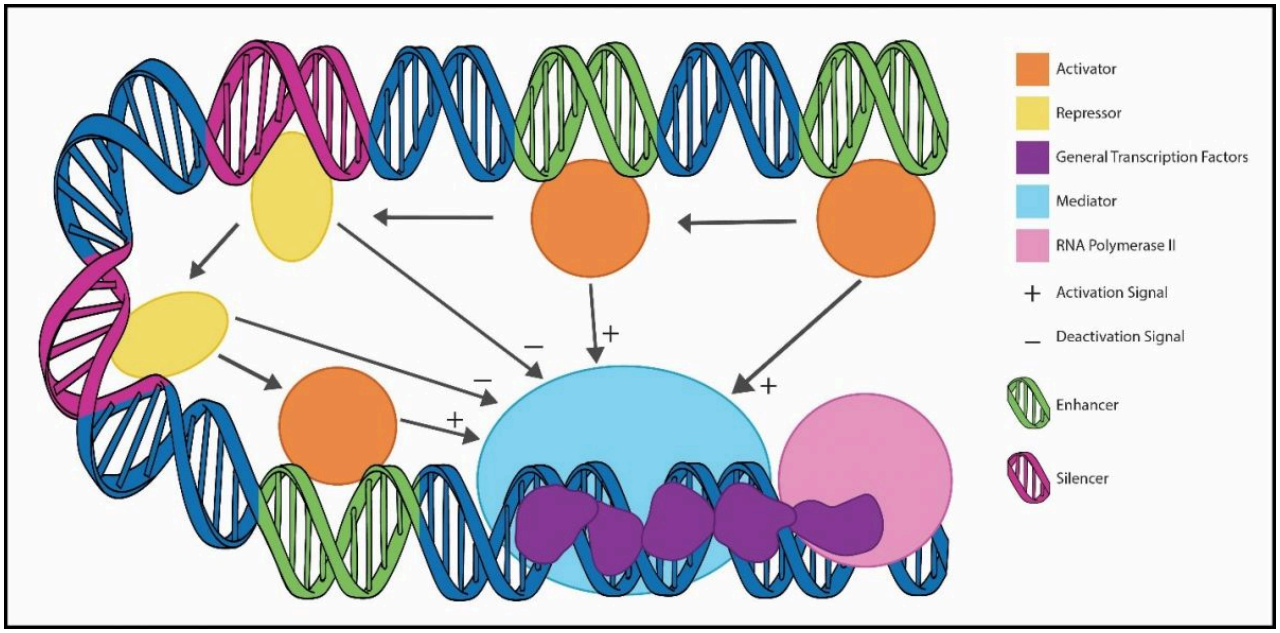


Figure 9.10 ***Regulatory Transcription Factors and Mediator.*** *Mediator (light blue) interprets the activation signals from activator proteins (orange) bound to enhancer DNA sequences (green) and the repression signals from repressor proteins (yellow) bound to silencer DNA sequences (magenta). Mediator then communicates an overall transcription signal (an activation signal in this case) to the general transcription factor proteins (purple) and RNA polymerase II (pink). RNA polymerase II is positioned on the +1 site (not shown) and transcribes the gene towards the right. --- Image created by SL*

Key Questions

- What are three examples of *cis*-acting DNA elements?
- What are three examples of *trans*-acting factor proteins?
- What is the function of the mediator protein complex?

Transcription Elongation in Eukaryotes

The elongation step in eukaryotic transcription is virtually identical to the transcription elongation step in prokaryotes. RNA polymerase II in eukaryotes has the same functional capabilities as the RNA polymerase core enzyme from *E. coli*.

Key Questions

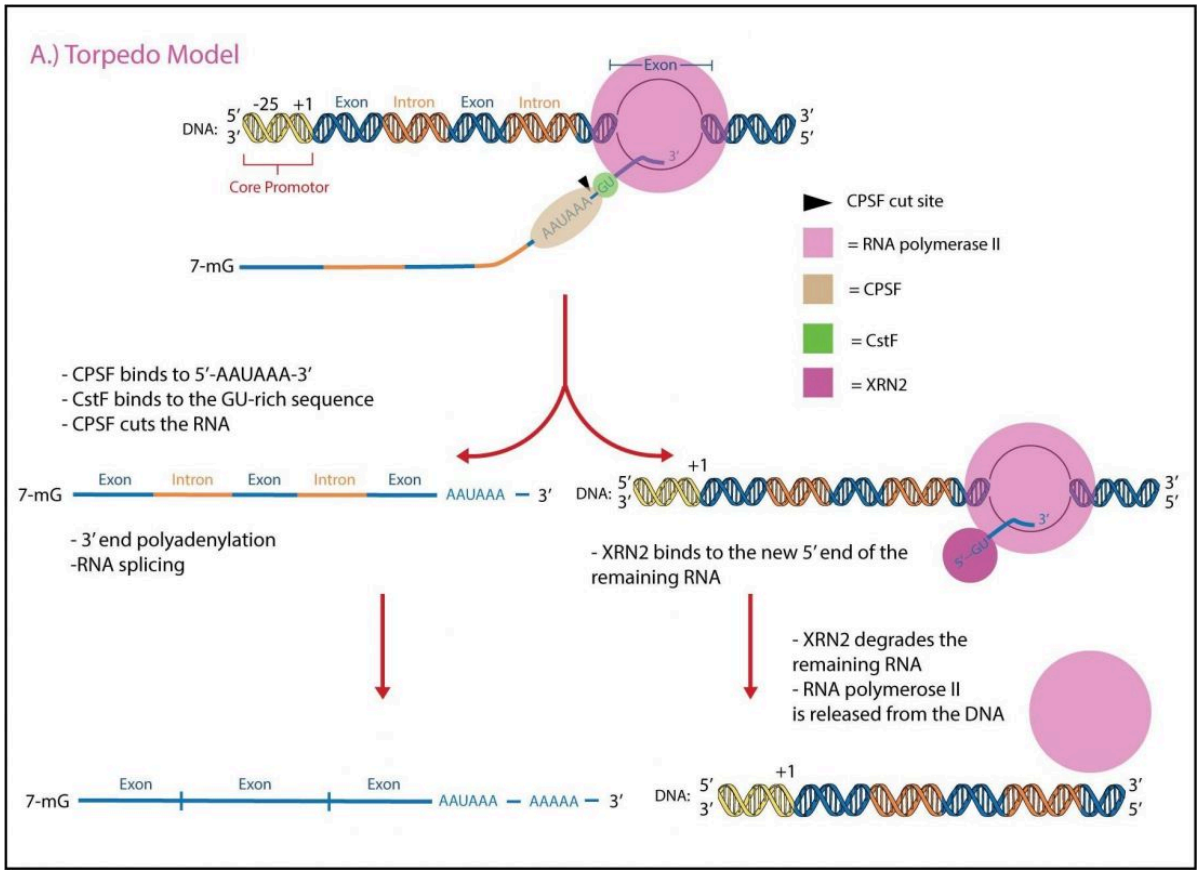
- What are the names of the two proteins that act as DNA helicases in eukaryotic transcription?

Transcription Termination in Eukaryotes

Transcriptional termination in eukaryotes occurs during the process of **3' end polyadenylation**, a modification to the 3' ends of eukaryotic mRNAs. We will cover 3' end polyadenylation in more detail in Part 10. In short, an endonuclease called **cleavage and polyadenylation specificity factor (CPSF)** binds to a **polyadenylation signal sequence** (5'-AAUAAA-3') near the 3' end of the mRNA. CPSF then cuts the mRNA approximately 20 nucleotides downstream (towards the 3' end of the mRNA) from the polyadenylation signal sequence. Cleavage of the mRNA by CPSF releases the mRNA from RNA polymerase II.

After CPSF releases the mRNA from RNA polymerase II, there are two potential ways that RNA polymerase II can be released from the DNA, thereby terminating transcription:

- **Torpedo model**. The torpedo model involves a 5' to 3' exonuclease called **XRN2** degrading the remaining RNA linked to RNA polymerase II and dissociating RNA polymerase II from the DNA (see **figure 9.11a**). Note that the torpedo model shares some similarities to the rho (ρ)-dependent termination mechanism in *E. coli*.
- **Allosteric model**. When RNA polymerase II transcribes the portion of the gene that produces the polyadenylation signal sequence, the RNA polymerase is destabilized and is released from the DNA (see **figure 9.11b**). Note that the allosteric model shares some similarities to the rho (ρ)-independent termination mechanism in *E. coli*.


A.) Torpedo Model
DNA:
-25
+1
Exon
Intron
Exon
Intron
Exon
5′
3′
3′
5′
Core Promotor
AAUAAA
GU
3′
7-mG
CPSF cut site
= RNA polymerase II
= CPSF
= CstF
= XRN2
- CPSF binds to 5′-AAUAAA-3′
- CstF binds to the GU-rich sequence
- CPSF cuts the RNA
7-mG
Exon
Intron
Exon
Intron
Exon
AAUAAA
3′
- 3′ end polyadenylation
-RNA splicing
DNA:
+1
5′
3′
3′
5′
3′
5′-GU
- XRN2 binds to the new 5′ end of the remaining RNA
- XRN2 degrades the remaining RNA
- RNA polymerose II is released from the DNA
7-mG
Exon
Exon
Exon
AAUAAA
AAAAA
3′
DNA:
+1
5′
3′
3′
5′

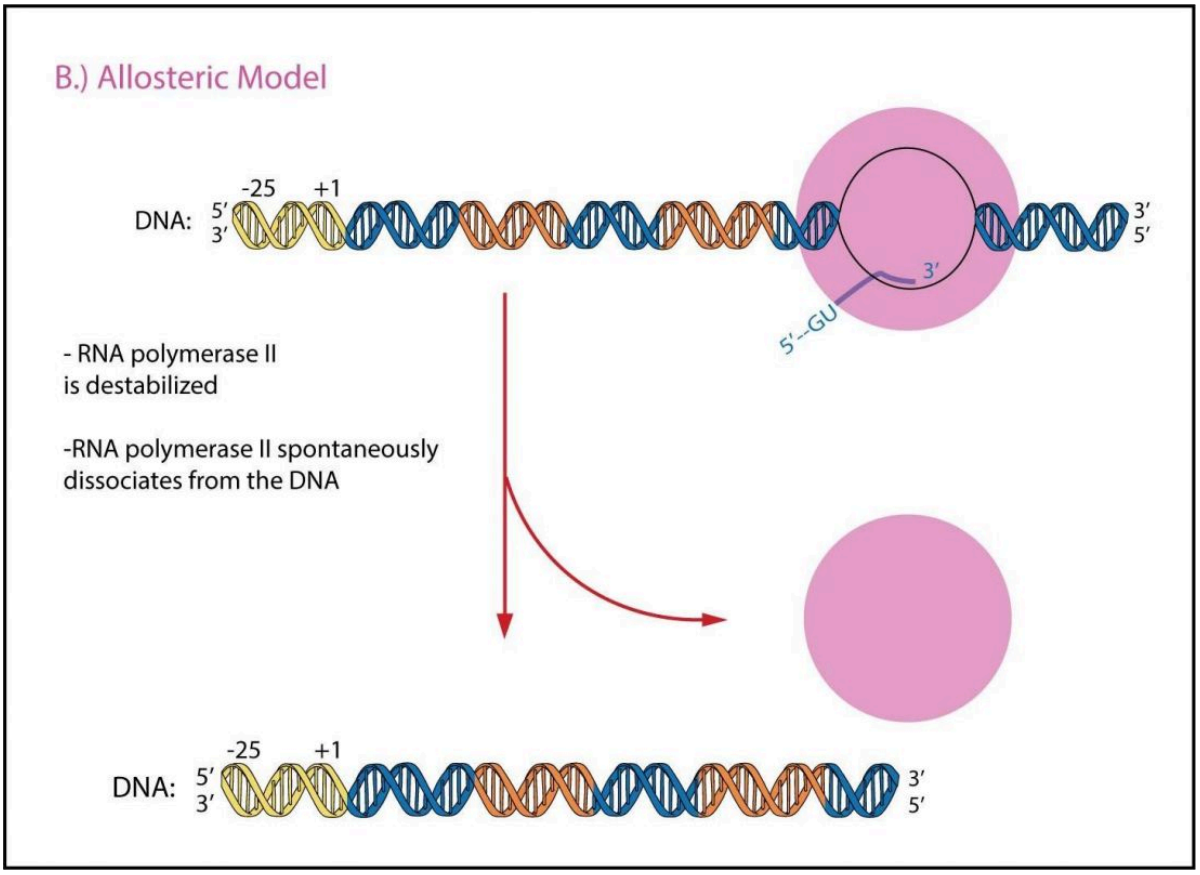


Figure 8.11 ***Transcription Termination in Eukaryotes*** *A) Torpedo Model B) Allosteric Model --- Images created by SL*

Key Questions

- What is the difference between the torpedo and the allosteric models of transcription termination?

Review Questions

Fill in the blank:

1. When structural genes are expressed, they produce _____RNA molecules; when nonstructural genes are expressed, they produce _____RNA molecules.
2. _____ is a GTF protein that has both DNA helicase and kinase activity.
3. The _____ protein binds to the -10 and -35 sequences.
4. The RNA polymerase holoenzyme consists of the _____ protein subunits and the _____ factor protein.
5. The TATA box (-25 sequence) is the binding site for the _____ protein.
6. The _____ protein binds to the *rut* sequence found in 50% of bacterial mRNA molecules.
7. RNA polymerase _____ is responsible for transcribing eukaryotic structural genes.
8. Phosphorylation of _____ helps to activate transcription in eukaryotes.
9. A(n) _____ protein binds to an enhancer sequence in the DNA to activate transcription above the basal level, while a(n) _____ protein binds to a silencer sequence in the DNA to decrease transcription below the basal level.
10. The _____ protein causes the RNA polymerase core enzyme to pause at the stem loop in the rho (ρ)-independent mechanism.
11. DNA replication requires the use of DNA helicase to unwind double-stranded DNA, while transcription in bacteria uses the _____ to unwind double-stranded DNA.