

**Index**

The big picture (HL)

Gene expression and regulation (HL)

Epigenesis (HL)

Effect of the environment on gene expression (HL)

Summary and key terms (HL)

Checklist (HL)

Investigation (HL)

Reflection (HL)

Overview
(/study/app/
422-
cid-
755105/o

Teacher view

Table of
contents

Notebook



Glossary

Reading
assistance

D2. Continuity and change: Cells / D2.2 Gene expression (HL)

The big picture (HL)

Higher level (HL)

? Guiding question(s)

- How is gene expression changed in a cell?
- How can patterns of gene expression be conserved through inheritance?

Keep the guiding questions in mind as you learn the science in this subtopic. You will be ready to answer them at the end of this subtopic. The guiding questions require you to pull together your knowledge and skills from different sections, to see the bigger picture and to build your conceptual understanding.

The Dutch Hunger Winter or *Hongerwinter* was a severe famine that occurred in the Second World War over the winter of 1944–1945 in Nazi-occupied Netherlands (**Figure 1**). The famine was the result of a combination of factors, including strikes and blockades that cut off supplies, and a harsh winter that froze waterways, cutting off boats carrying food and fuel. The Dutch Hunger Winter was responsible for the deaths of tens of thousands of people.



Figure 1. Dutch children eating soup during the famine of 1944–1945.

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(/study/app/bio/sid-422-cid-755105/overview)

This tragic event provided a unique opportunity to study the effects of famine.

One of the biggest findings related to how famine impacted the birth weight and long-term health of the offspring born to women who were pregnant during the famine. Women who experienced famine during their second and third trimesters gave birth to offspring with significantly reduced birth weights, who continued to be small throughout their lives and have lower than expected rates of obesity. Women who experienced famine during their first trimester gave birth to normal weight babies, who experienced significantly higher rates of obesity and cardiovascular diseases in later life [↗](https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2947916/#r3) (<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2947916/#r3>).

What happened to the fetuses affected by this famine to alter their risk of obesity and other conditions?



Theory of Knowledge

The Dutch Hunger Winter offers a rare 'natural experiment' due to its sudden onset and return to normal conditions shortly after the famine ended. The famine impacted the entire population in a relatively small and contained geographic area, which removed confounding factors such as socioeconomic status. Extensive documentation, including detailed ration records, medical records, government reports and personal accounts allowed scientists to conduct long term studies on the impact of famine during pregnancy that would not be ethical to study by other means.



Prior learning

Before you study this subtopic make sure that you understand the following:

- Nucleic acids ([subtopic A1.2](#) [↗](#) (/study/app/bio/sid-422-cid-755105/book/the-big-picture-id-43236/))
- DNA replication ([subtopic D1.1](#) [↗](#) (/study/app/bio/sid-422-cid-755105/book/big-picture-id-43546/))
- Protein synthesis ([subtopic D1.2](#) [↗](#) (/study/app/bio/sid-422-cid-755105/book/big-picture-id-43547/))

D2. Continuity and change: Cells / D2.2 Gene expression (HL)

Gene expression and regulation (HL)

D2.2.1: Gene expression effects on the phenotype (HL) D2.2.2: Regulation of transcription (HL) D2.2.3: Regulation of translation (HL)

Higher level (HL)



Learning outcomes

By the end of this section you should be able to:

- Explain the term gene expression.
- Outline how transcription can be regulated by proteins that bind to DNA.
- Outline how translation can be regulated through the degradation of mRNA.



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(/study/app/
422-
cid-
755105/o

Every somatic (non-sex) cell in your body is genetically identical. But why do different somatic cells have different structures and functions?

Gene expression is the process by which genetic information is used to produce RNA and proteins. Cells produced by fertilisation and during early embryonic development are unspecialised because they express far fewer genes than differentiated cells (see [section B2.3.1–4 \(/study/app/bio/sid-422-cid-755105/book/stem-cells-id-45383/\)](#)). As cells mature and differentiate, variations in the level of expression of different genes between cells enables them to exhibit diverse structures and functions required for their specialised roles (see [section A2.2.12–14 \(/study/app/bio/sid-422-cid-755105/book/endosymbiosis-cell-differentiation-multicellular-organisms-id-44720/\)](#)), allowing phenotypic plasticity ([section D3.2.3–7 \(/study/app/bio/sid-422-cid-755105/book/expression-of-phenotypes-id-46204/\)](#)). Therefore, although the genotype (see [section D3.2.3–7 \(/study/app/bio/sid-422-cid-755105/book/expression-of-phenotypes-id-46204/\)](#)) of a cell does not change, its functions will.

The stages in gene expression are:

- **Transcription:** the DNA sequence of a gene is used as a template to synthesise a complementary RNA molecule called messenger RNA (mRNA) (see [section D1.2.4–6 \(/study/app/bio/sid-422-cid-755105/book/translation-id-46207/\)](#)).
- **Translation:** the mRNA molecule is read by ribosomes to produce a protein product (see [section D1.2.4–6 \(/study/app/bio/sid-422-cid-755105/book/translation-id-46207/\)](#)).
- The protein produced through transcription and translation carries out specific functions either inside or outside of the cell, such as enzymatic activity, signalling and transport.

Promoters, enhancers and transcription factors

For a gene to be transcribed, RNA polymerase must first bind to a section of DNA called the promoter, typically located upstream (located to the 5' end) of a gene (**Figure 1**) ([section D1.2.12–14 \(/study/app/bio/sid-422-cid-755105/book/controlling-transcription-and-translation-hl-id-46505/\)](#)). Promoters are referred to as non-coding regions of DNA because they do not directly encode proteins.

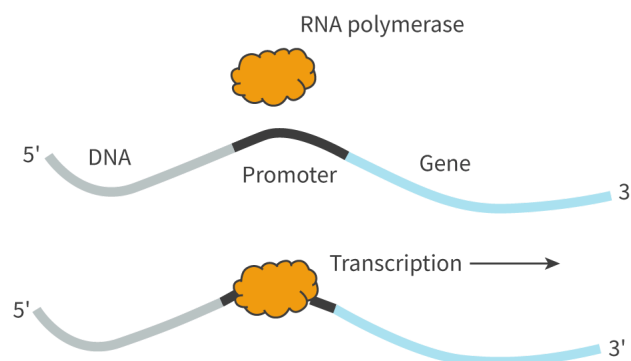


Figure 1. RNA polymerase binds to a promoter to initiate transcription.

More information for figure 1

The diagram illustrates the process of RNA polymerase binding to a segment of DNA to initiate transcription. The image is divided into two parts: the top part shows RNA polymerase not yet attached, with segments labeled 5' (DNA) leading to a promoter and then to a gene segment labeled 3'. The RNA polymerase is depicted as an orange oblong shape above the promoter region. The bottom part shows RNA polymerase bound to the promoter, indicating the start of transcription, with an arrow showing the direction of the process. The segments are again labeled with 5' and 3' to indicate their orientation on the DNA strand. The image conveys the initial step required for gene transcription.

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The interaction of RNA polymerase and a promoter can be influenced by transcription factors, a group of proteins that influence gene expression. Some transcription factors may activate gene expression by encouraging RNA polymerase to bind to the promoter, and some may repress gene expression by blocking RNA polymerase from binding to the promoter. The activity and availability of transcription factors within a cell influence how easily RNA polymerase binds to a promoter and transcribes a gene.

Enhancers are specific regions of DNA that play a role in regulating when and to what extent a gene is expressed, by regulating the transcription of that gene. Like promoters, they are called non-coding DNA. Unlike promoters, which are usually located near the gene they regulate, enhancers can be situated at various distances from a gene, even up to thousands of base pairs away. A group of transcription factors called activator proteins bind to an enhancer, enabling it to form a complex that interacts with the promoter region and aids the binding of RNA polymerase (**Figure 2**).

Section

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Feedback

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Assign

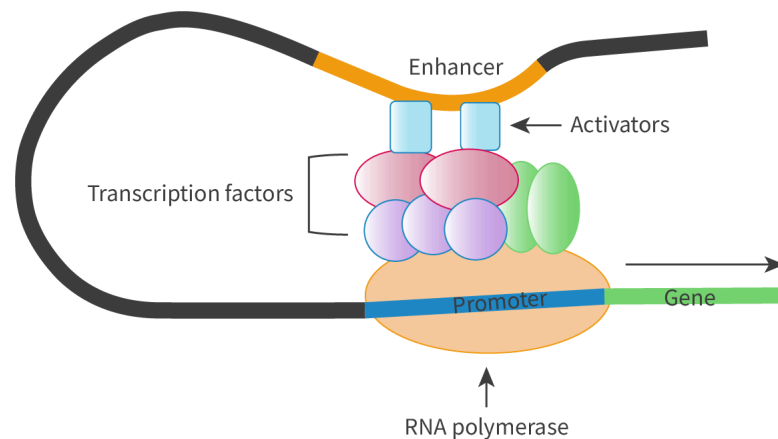


Figure 2. Enhancers are regions of DNA to which activators bind, facilitating the binding of other transcription factors to the promoter to enhance transcription.

More information for figure 2

The diagram illustrates the interaction between various genetic elements involved in transcription regulation. At the top, there is an enhancer region, depicted as a curved line labeled "Enhancer." Below this, activator proteins are shown binding to the enhancer. They are represented as blue rectangles.

Beneath the activators, a group of differently colored oval shapes labeled "Transcription factors" is shown. These transcription factors aid in forming a transcription complex.

Toward the bottom, there is a circular region labeled "Promoter," which serves as the binding site for the transcription complex. An arrow points from the promoter to "RNA polymerase," indicating that the RNA polymerase binds here to begin transcription.

The gene to be transcribed is depicted as a horizontal green line labeled "Gene," with an arrow on the right end, indicating the direction of transcription. The diagram visually explains how enhancers and activators facilitate the recruitment of transcription factors to the promoter region for efficient RNA polymerase binding, enhancing transcription of the target gene.

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A single enhancer can interact with multiple promoters, influencing the transcription of many genes simultaneously. Some genes have multiple promoters, which may be used in different developmental stages, tissue types or environmental conditions. This enables fine tuning of gene expression in different cellular contexts. Additionally, certain genes may share a promoter; a collection of genes with a shared promoter is called an operon. Genes in an operon are usually transcribed together and may have similar or related functions.



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(/study/app/
422-
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755105/o

Repressor proteins are a type of transcription factor that when they bind to specific DNA sequences, prevent the binding of RNA polymerase or other transcription factors, thus inhibiting gene expression. Repressor proteins will be covered in [section D2.2.8–11 \(/study/app/bio/sid-422-cid-755105/book/effect-of-the-environment-on-gene-expression-hl-id-46199/\)](#).

Gene expression is also affected by the presence of **intracellular receptors**, such as steroid hormone receptors. When activated by their specific molecule, the activated receptor undergoes a structural change that enables them to bind to specific DNA sequences to promote transcription of a particular gene (see [section C2.1.10–13 \(/study/app/bio/sid-422-cid-755105/book/mechanism-of-action-of-various-signal-receptors-hl-id-46146/\)](#)).

mRNA persistence

Once an mRNA strand has been synthesised, it can potentially be translated many times. The longer an mRNA strand persists (remains intact and available for translation), the higher the likelihood that it will be translated multiple times, resulting in more of the protein product in the cell.

The synthesized mRNA can persist for varying lengths of time ranging from a few minutes to several days, until it is degraded by **nucleases**, **hydrolytic enzymes** that break down nucleic acids. The lifespan of an mRNA molecule depends on various factors including:

- Chemical modifications to the mRNA, such as the addition of a **guanine cap** at the 5' end of the molecule, and a **poly-A tail** at the 3' end of the molecule (**Figure 3**), which increases the stability of the mRNA (see [section D1.2.15–16 \(/study/app/bio/sid-422-cid-755105/book/modification-and-splicing-hl-id-44257/\)](#)).
- The presence of **stabilising proteins** which can interfere with the activity of nucleases, blocking their active sites and preventing them from binding to and degrading mRNA, extending the lifespan of mRNA. Stabilising proteins can also promote the binding of protective proteins to mRNA. These increase the structural stability of the mRNA molecules, altering the structure of the mRNA and making it less accessible to nucleases.
- The activity and abundance of nucleases in a cell. Cells with higher levels of nuclease activity may experience faster levels of mRNA degradation.
- **Cellular stress**, such as exposure to toxins or heat, which can influence the activity of factors involved in determining the persistence of mRNA.



Figure 3. Guanine caps and poly-A tails increase the stability of mRNA, increasing its persistence.

More information for figure 3

The image is a diagram of mRNA. On the left side, there is a circular shape labeled 'G', representing the 5' cap. A long line stretches from the 5' cap to the right, depicting the mRNA strand. At the end of this line, on the right side, a series of circles labeled 'A', represent the Poly-A tail. The sections are connected in a linear sequence, showing the structure and sections of mRNA with emphasized ends, but without intricate details or text about the phases involved beyond the basic labels.

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Try the activity to help with your understanding of gene expression.



Activity

- **IB learner profile attribute:** Thinker
- **Approaches to learning:** Thinking skills — Combining different ideas in order to create new understandings



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- **Time required to complete activity:** 15 minutes
- **Activity type:** Individual activity

Gel electrophoresis is a technique used to separate DNA or RNA molecules according to their size (see [section D1.1.4—5 \(/study/app/bio/sid-422-cid-755105/book/polymerase-chain-reaction-and-gel-electrophoresis-id-43957/\)\)](#). The DNA or RNA sample is placed in a gel, to which an electric current is applied. The electric current pushes the DNA or RNA molecules through the gel. Smaller molecules move faster through the gel whereas larger molecules move slower. By comparing the position of known DNA or RNA markers to the bands produced by the gel electrophoresis, scientists can deduce which molecules are present in the sample.

Use **Figure 4** to help answer the following questions .

1. The first lane on the left, labelled M, is a DNA ladder. Suggest why this is included.
2. Identify which lane shows the
 - (a) smallest length of DNA
 - (b) largest length of DNA.
3. The band in lane C+35 is 280 base pairs. Estimate the size, in base pairs, of the band in lane C+33.
4. Define the term 'gene expression'.
5. How can the presence of RNA indicate the level of transcription occurring?
6. Compare the expression of the genes in lane C+H with those in lane C+16.

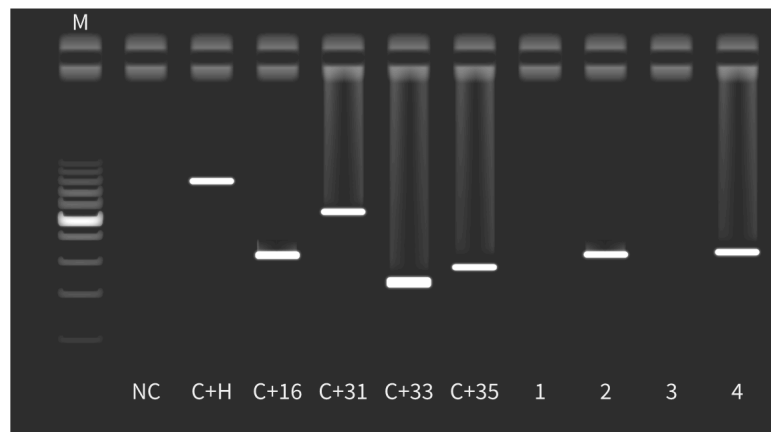


Figure 4. Gel electrophoresis pattern showing the differences between three strains of HPV: 31, 33 and 35. Lanes 1 and 3 are negative samples and are not expected to show any bands. Lanes 2 and 4 are positive samples with a specific marker that is expected to show. M is the DNA marker ladder.

More information for figure 4

The image shows a gel electrophoresis pattern used to differentiate between three strains of HPV: 31, 33, and 35. There are multiple lanes, each labeled with either a letter or a number. From left to right, the lanes are labeled: M (marker), NC, C+H, C+16, C+31, C+33, C+35, 1, 2, 3, and 4. The first lane marked with an 'M' is the marker or DNA ladder, featuring bands at standard intervals. The lanes labeled NC, 1, and 3 are negative controls and do not display any bands. In contrast, lanes labeled C+31, C+33, C+35, and 2 show distinctive bands in the middle of the lane, indicating positive samples. The positions and presence of these DNA bands differentiate the HPV strains present in each sample.

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5 section questions



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D2. Continuity and change: Cells / D2.2 Gene expression (HL)



Epigenesis (HL)

Overview

(/study/app/

422-

cid-

755105/o

D2.2.4: Epigenesis (HL)

D2.2.5: Genome, transcriptome and proteome of individual cells (HL)

D2.2.6: Methylation (HL)

D2.2.7: Epigenetic inheritance (HL)

Higher level (HL)



Learning outcomes

By the end of this section you should be able to:

- Explain the term epigenesis.
- Describe the differences between the genome, transcriptome and proteome of individual cells.
- Outline how methylation can affect gene expression.
- Identify why some epigenetic changes are heritable.

DNA can be modified to result in differences in gene expression between different cells. But how do these modifications occur? And what is their purpose?

A good foundation in DNA replication is required for this section and may be found in [section D2.1.4–6 \(/study/app/bio/sid-422-cid-755105/book/shared-features-of-mitosis-and-meiosis-id-45676/\)](#).

Epigenesis

Epigenesis is the process by which cells and organisms develop from an undifferentiated zygote through the interaction between DNA and environmental factors. More specifically, the presence and level of environmental factors can result in modifications to gene expression patterns, without changes to the DNA sequence (see [section A1.2.5–7 \(/study/app/bio/sid-422-cid-755105/book/rna-and-dna-polymers-id-45990/\)](#)). This means that the phenotype, and not the genotype of an organism is altered (see [section D3.2.3–7 \(/study/app/bio/sid-422-cid-755105/book/expression-of-phenotypes-id-46204/\)](#)).

Epigenetics is the study of how behaviours and the environment can affect gene transcription. During early embryonic development, epigenetic changes play a pivotal role as cells differentiate (see [section A2.2.12–14 \(/study/app/bio/sid-422-cid-755105/book/endosymbiosis-cell-differentiation-multicellular-organisms-id-44720/\)](#)). Gene expression patterns determine cell fate and influence transcription levels and protein synthesis, ultimately driving cellular development and differentiation.

All somatic cells in your body will have the same genome (complete set of DNA, see [section A3.1.8–11 \(/study/app/bio/sid-422-cid-755105/book/comparing-genomes-id-43229/\)](#)). Epigenetic changes, such as DNA methylation and histone modifications, influence gene expression in specific cells or tissues. This results in cells having distinct sets of RNA transcripts (known as transcriptomes) as not all genes are expressed at any given time (see [section D1.2.4–6 \(/study/app/bio/sid-422-cid-755105/book/translation-id-46207/\)](#)). Consequently, differences in transcriptomes lead to different cells having unique proteomes (entire set of proteins), as proteins are synthesised based on the information encoded in RNA transcripts. To maintain a functional proteome, amino acids are continually recycled by proteasomes (see [section D1.2.17–19 \(/study/app/bio/sid-422-cid-755105/book/making%20use%20of%20proteins-hl-id-46212/\)](#)).

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Overview
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DNA methylation

Methylation is the addition of a methyl ($-\text{CH}_3$) group to a molecule. Methylation of cytosine in the DNA of a promoter represses transcription because it prevents transcription factors from binding (**Figure 1**) (see [section D1.2.12–14](#) (/study/app/bio/sid-422-cid-755105/book/controlling-transcription-and-translation-hl-id-46505/)). This results in decreased gene expression or gene silencing.

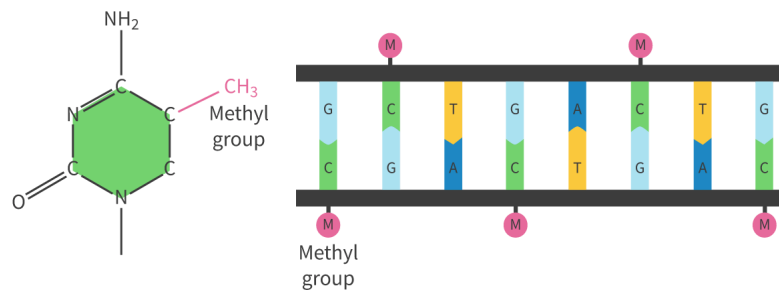


Figure 1. Methylation of cytosine nucleotides in promoter regions makes it harder for RNA polymerase to bind, and therefore downregulates transcription.

More information for figure 1

The image is a diagram that illustrates methylation in DNA. On the left side, it shows the chemical structure of a methylated cytosine. The structure includes a hexagonal ring representing the cytosine base with attached groups such as NH_2 , CH_3 (methyl group), and a carbonyl group ($\text{C}=\text{O}$). The methyl group is highlighted in pink, indicating its addition to the cytosine molecule.

On the right, the diagram depicts a segment of a DNA double helix. The helix features two parallel strands connected by base pairs, which include the nucleotides guanine (G), cytosine (C), adenine (A), and thymine (T). These are color-coded for distinction. Interspersed along the strands are pink circles labeled 'M' to denote methyl groups attached to cytosine bases within the DNA sequence. This indicates regions of promoter methylation, which can inhibit RNA polymerase binding and downregulate gene transcription.

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The level of DNA methylation of a genome or specific gene can be influenced by various factors including age, diet, exposure to infectious agents and environmental conditions during important developmental stages.

Histone acetylation and methylation

Eukaryotic DNA is packaged and organised around histone proteins to form compact structures called nucleosomes (**Figure 2**) (section A1.2.11–13 (/study/app/bio/sid-422-cid-755105/book/dna-base-sequences-hl-id-46211/)). Nucleosomes play a fundamental role in regulating chromatin structure and accessibility to transcriptional machinery.

Histone proteins consist of a core domain and a tail region. The core domain forms the central part of the nucleosome, around which DNA is wrapped, and the tails (N-terminal regions of the proteins) protrude outwards. Histone proteins have a net positive charge, with their tail regions containing a high density of positively charged amino acids. The resulting attraction between the negatively charged DNA and the positively charged histone tails facilitates the formation of nucleosomes and compact chromatin formation.



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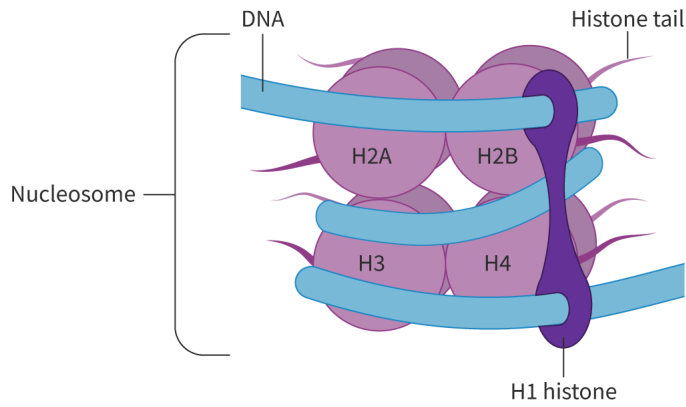


Figure 2. Structure of a nucleosome.

[More information for figure 2](#)

The diagram illustrates the structure of a nucleosome, which consists of a segment of DNA wrapped around histone proteins. The DNA is shown as a blue helical ribbon looping around clusters of pink spheres labeled as histones H2A, H2B, H3, and H4. These histones form the core around which the DNA is wrapped. In addition to the core, the diagram features histone tails protruding from the core and labeled with their respective names. The darker blue chain represents the H1 histone, which binds the DNA strands at the entry and exit points, helping to maintain the compact structure. The diagram provides a visual representation of how DNA is organized in chromatin.

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When DNA is supercoiled (wrapped tightly) around histone proteins, it forms a condensed structure called heterochromatin. In this state, the DNA is less accessible to RNA polymerase and other transcription machinery, resulting in reduced transcription.

When DNA is loosely packed around histone proteins, it is called euchromatin. Euchromatin is more accessible to RNA polymerase and other transcription machinery, resulting in increased transcription and enhanced gene expression (**Figure 3**).

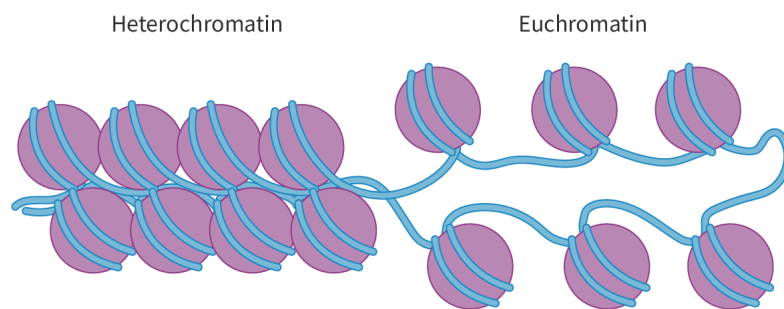


Figure 3. Euchromatin is less condensed, meaning that it is easier for RNA polymerase and other transcriptional machinery to bind to and express the gene. Heterochromatin is highly condensed, and it is therefore harder for RNA polymerase and other transcriptional machinery to bind to and express the gene.

[More information for figure 3](#)

The diagram illustrates the structures of heterochromatin and euchromatin. Heterochromatin is shown on the left, consisting of tightly packed clusters of DNA wrapped around proteins, appearing densely compact. Euchromatin is displayed on the right, with a more loosely packed arrangement, allowing for more space between the clusters. Blue lines represent DNA strands, while purple circles depict nucleosomes. This structural difference demonstrates how euchromatin is more accessible for transcription machinery than heterochromatin.

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Histone tails can be modified by the addition of chemical groups (**Figure 4**). This can alter the nucleosome structure and affect transcription.

Acetylation is the addition of an acetyl, CH_3COO^- group of amino acids in a histone tail. Acetylation decreases the overall charge of the histone protein and reduces the electrostatic attraction between the histone and DNA. As a result, DNA becomes less tightly wrapped around histone proteins. This makes it easier for RNA polymerase and other molecules involved in transcription to access the DNA, usually resulting in increased gene expression. Removal of the acetyl group will reverse this process, resulting in decreased gene expression.

Methylation of amino acids in histones tails can also impact gene expression. Depending on which amino acid is methylated, and the location of the amino acid methylated, and how many methyl groups are added, transcription can be repressed or activated. Methylation and demethylation of histones can recruit various proteins and complexes that can influence the structure of the chromatin and the activity of RNA polymerase and other transcriptional regulators.

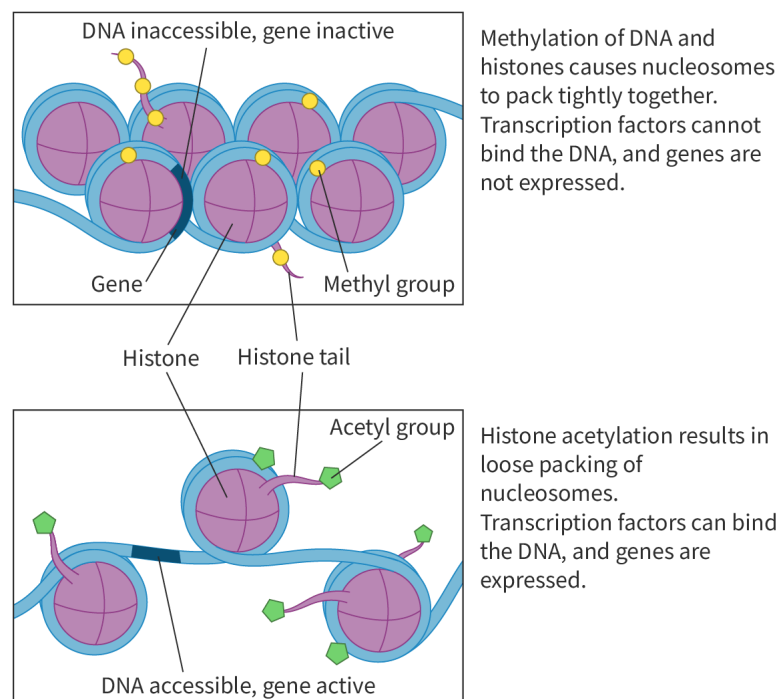


Figure 4. The effect of methylation and acetylation of histone tails on gene expression.

More information for figure 4

The image is divided into two sections, illustrating the effects of methylation and acetylation on histone tails and their impact on gene expression.

Top section: - It shows tightly packed nucleosomes with yellow circles representing methyl groups attached to them. - Labels identify components: Gene, DNA inaccessible, gene inactive, Histone, Histone tail, Methyl group. - A text box explains that methylation of DNA and histones causes nucleosomes to pack tightly, preventing transcription factors from binding to DNA, leading to gene inactivation.

Bottom section: - It shows loosely packed nucleosomes with green polygons symbolizing acetyl groups. - Labels include: Gene, DNA accessible, gene active, Histone tail, Acetyl group. - A text note states that histone acetylation results in loose packing of nucleosomes, allowing transcription factors to bind DNA, leading to gene activation.

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Epigenetic inheritance

Epigenetic inheritance refers to the inheritance of non-genetic information that can influence gene expression and phenotypic traits. For epigenetic inheritance to occur during sexual reproduction, epigenetic changes such as DNA methylation or histone modification must occur in germline cells, and be maintained during meiosis (spermatogenesis and oogenesis) and passed on to the offspring.



Nature of Science

Aspect: Science as a shared endeavour


The term 'epigenetics' was first coined in the mid-20th century, although its modern definition and understanding have changed over time. Currently, epigenetics is a rapidly evolving and dynamic field of scientific research, with ongoing developments, discoveries and interdisciplinary research contributing to our understanding of epigenetic mechanisms and their significance in various biological processes.

Try the activity to help with your understanding of epigenetics.



Activity

- **IB learner profile attribute:**
 - Thinker
 - Inquirer
- **Approaches to learning:** Research skills — Comparing, contrasting and validating information
- **Time required to complete activity:** 20 minutes
- **Activity type:** Individual activity

Lick your rats  (<https://learn.genetics.utah.edu/content/epigenetics/rats/>) is a resource explaining the epigenetic effects of female rats licking their offspring. The original simulation is under development at the time of writing this, but the supporting resource is still available. Study the resource and answer the questions below.

1. Outline the main difference in the phenotypes of the rats who were licked by their mothers as pups, and those who were not.
2. Suggest why each of these phenotypes may be advantageous in different circumstances.
3. High maternal care in rats results in increased expression of the GR gene. Explain the mechanism by which this gene is expressed.
4. Explain why this particular behaviour is classified as epigenetic.

5 section questions ▾

D2. Continuity and change: Cells / D2.2 Gene expression (HL)

Effect of the environment on gene expression (HL)



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Higher level (HL)

Learning outcomes

By the end of this section you should be able to:

- Describe examples of how the environment can affect gene expression.
- Outline consequences of removing epigenetic tags from human gametes.
- Discuss the use of monozygotic twins to study gene expression.
- Describe examples of external factors that can impact gene expression.

Changes in the environment of a cell or organism can impact the expression of genes, resulting in phenotypic plasticity and influencing cellular processes (see [section D3.2.5–7 \(/study/app/bio/sid-422-cid-755105/book/genetics-of-the-y-chromosome-id-46206/\)](#)). What are common examples of environmental changes that can impact gene expression? And how can monozygotic (identical) twins be used to study the effect of the environment on gene expression?

Examples of environmental effects on gene expression in cells and organisms

Exposure to air pollution

Exposure to air pollution, such as nitrous oxides, and particulate matter such as soot has been shown to affect the DNA methylation patterns of genes involved in inflammation, oxidative stress and immune response pathways. This can result in a disruption of normal cellular processes, increased inflammation, increased risk of oxidative damage and a more susceptible immune system.

The precise effects of air pollution on DNA methylation and gene expression can vary depending on individual factors, such as genetic predisposition and general health, and environmental factors such as duration and intensity of the exposure.

Diet

Different foods can affect gene expression. For example, studies in mice have shown that exposure to a high folic acid diet can lead to increased methylation of specific genes related to coat colour, affecting the phenotype of the offspring (**Figure 1**). Mice exposed to a diet high in folic acid during pregnancy were more likely to produce offspring with higher levels of methylation and brown coats. Conversely, the control group, which were given diets containing standard levels of folic acid, exhibited lower levels of methylation and yellow coats.

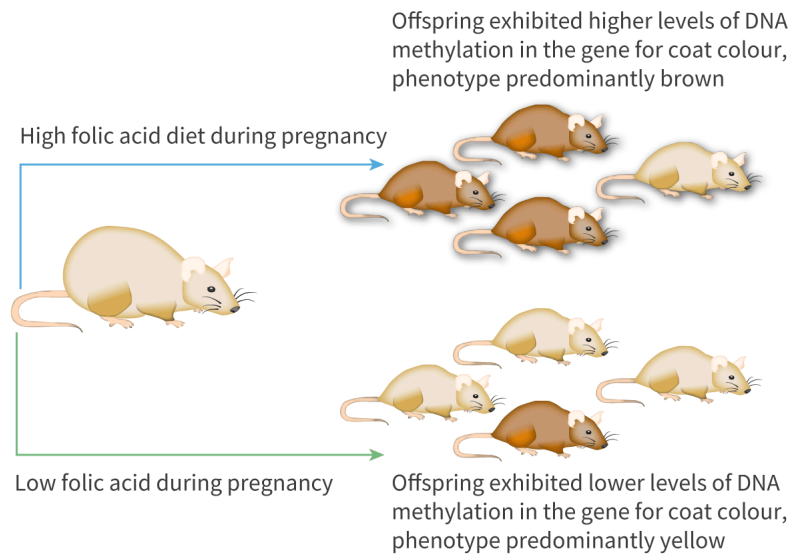


Figure 1. The influence of folic acid on mouse coat colour.

More information for figure 1

The diagram illustrates how the diet during pregnancy affects mice and their offspring's coat color. On the left, there is a large mouse with a caption reading "High folic acid diet during pregnancy" connected by an arrow to a group of several mice. These mice are predominantly brown, indicating higher levels of DNA methylation leading to darker coat colors.

Another arrow from the same large mouse points downwards with the caption "Low folic acid during pregnancy," leading to a group of mostly yellow mice. The caption beside this group states that the offspring exposed to low folic acid exhibited lower levels of DNA methylation, resulting in predominantly yellow coats.

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Omega-3-fatty acids have been shown to influence the expression of genes involved in reducing inflammation, lipid metabolism and cognitive function. Diets high in sugar have been linked to increased inflammation, metabolic dysfunction and insulin resistance.

Temperature

Changes in temperature can impact gene expression. In plants, temperature changes can activate or repress certain genes involved in developmental stages, such as flowering, hibernation or the production of certain pigments.

The sex of many reptiles, including turtles, is determined by the temperature at which their eggs are incubated. Warmer temperatures tend to result in more females, while cooler temperatures lead to the birth of more males. As global temperatures rise due to climate change, this can disrupt the delicate balance, potentially resulting in skewed sex ratios among turtle populations. This imbalance can have profound implications for their reproductive success and long-term survival. Watch **Video 1** for more information.



Overview
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Rising Temperatures Cause Sea Turtles to Turn Female | National Ge...



Video 1. Rising global temperatures can skew the sex-ratio of many reptiles, including turtles.

More information for video 1

The video highlights a critical consequence of climate change: temperature-dependent sex determination (TSD) in sea turtles, particularly green sea turtles at Rine Island, Australia.

In many reptiles, including sea turtles, sex is determined by incubation temperature of eggs in sand nests. Cooler temperatures produce male hatchlings and warmer temperatures produce female hatchlings. Rising global temperatures skew nests toward female-biased populations.

The video begins with a sea turtle swimming in the open sea. The text reads, "WARMING TEMPERATURES OF THE COASTS OF AUSTRALIA MAY BE HAVING A DEVASTATING EFFECT ON GREEN SEA TURTLE POPULATIONS BY TURNING ALMOST ALL THEIR OFFSPRING INTO FEMALES." The footage then shows a baby turtle in a nesting beach. The text reads, "SEX IN SEA TURTLES IS DETERMINED BY THE HEAT OF THE SAND THE EGGS INCUBATE IN."

The scene switches back to the open sea. A man on a boat jumps into the sea to catch a turtle swimming underwater. The text reads, "AS TEMPERATURES RISE DUE TO CLIMATE CHANGE, MORE AND MORE FEMALES ARE BEING BORN." The man catches the turtle and brings him to the surface. The text reads, "ON RAINE ISLANDS, THE PACIFIC OCEAN'S LARGEST AND MOST IMPORTANT GREEN SEA TURTLE ROOKERY, THE SCIENTISTS FOUND THAT FEMALE TURTLES NOW OUTNUMBER MALES 116 TO 1."

The turtle is brought on to the beach and a group of researchers are seen measuring and examining the turtle and then releasing it back into the sea. The text reads "RAINE APPEARS TO HAVE BEEN PRODUCING ALMOST EXCLUSIVELY FEMALES FOR AT LEAST 20 YEARS. IT'S UNCLEAR HOW TURTLES ARE AFFECTED WORLDWIDE, AND OTHER FACTORS LIKE HABITAT CHANGES MAY PLAY A ROLE IN SHIFTING SEX RATIOS."



Creativity, activity, service

Strand: Activity

Learning outcome: Identify own strengths and develop areas for growth

You can positively influence your epigenome by controlling the environment you are in and the activities you partake in. All of the following will have an impact on your epigenome: diet, exercise, stress management, sleep patterns, exposure to toxins, social interactions and overall lifestyle choices.

How can you change your daily schedule to positively affect your epigenome?

Consequences of removal of most but not all epigenetic tags from human ovum and sperm

Epigenetic tags such as methyl groups are molecular markers or modifications that help to regulate gene expression.



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Sperm and ovum are specialised cells that play a crucial role in sexual reproduction (see [sections D3.1.1 \(/study/app/bio/sid-422-cid-755105/book/asexual-and-sexual-reproduction-id-45736/\)](#) and [B2.3.7–10 \(/study/app/bio/sid-422-cid-755105/book/cell-adaptations-hl-id-44445/\)](#)).

Shortly after fertilisation, the majority of epigenetic tags are removed from the parental DNA. This resets the epigenetic environment of the genome by eliminating genetic modifications that have occurred during the lifespan of the parents. It also allows for the development of new epigenetic modifications so that cells can differentiate into various cell types (see [section A2.2.12–14 \(/study/app/bio/sid-422-cid-755105/book/endosymbiosis-cell-differentiation-multicellular-organisms-id-44720/\)](#)).

About 1% of mammalian genes retain their genetic tags and therefore begin the developmental stages with their epigenetic tags already in place. These genes are called imprinted genes. Imprinted genes are inherited from one particular parent.

Female lions tend to mate with many different males and so can give birth to a litter of cubs from many fathers. Large size is imprinted in the male lion, because it is advantageous for his cubs to be as large as possible to compete with their siblings from different fathers. In contrast, it is less advantageous for a female to have large cubs, because increased foetal size may reduce the likelihood of all her cubs [surviving to birth](#) [\[https://onlinelibrary.wiley.com/doi/pdf/10.1002/mrd.22074\]](https://onlinelibrary.wiley.com/doi/pdf/10.1002/mrd.22074). Size is not imprinted in tigers because a litter of tiger cubs comes from a single father.

Tigons and ligers are hybrid animals resulting from the mating of a lion and a tiger. Tigons are the offspring of a male tiger and a female lion (**Figure 2**), whereas ligers are the offspring of a male lion and a female tiger. Tigons and ligers do share some phenotypic similarities with each of their parents, but they also exhibit some distinct phenotypic differences such as variations in size and coat colouration. Many of these differences can be attributed to imprinted genes, which are expressed differently in lions and tigers due to the presence of different epigenetic markers. For example, ligers tend to be larger in size than either tigers or lions, because the gene for size is imprinted and inherited from the male lion. Tigons tend to be the same size or smaller than either tigers or lions because they do not inherit the imprinted gene for large size.



Figure 2. Tigons are the offspring of a male tiger and a female lion.

Credit: HY. JIANG, Getty Images

You can read more about imprinted genes [here](#) [\[https://learn.genetics.utah.edu/content/epigenetics/imprinting\]](https://learn.genetics.utah.edu/content/epigenetics/imprinting).



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Monozygotic twins studies

Monozygotic twins are twins who originate from a single fertilised egg, resulting in genetically identical individuals, making them valuable for studying the effect of the environment on gene expression.

If the twins are brought up together and share the same environment, they will share similar overall patterns of epigenetic tags during this time (epigenome). As the individuals age and their environments differ, differences in their environmental factors, such as exposure to pollution, exercise and diet result in changes in the patterns of epigenetic tags and increasing phenotypic differences.

Click on this link [↗](https://learn.genetics.utah.edu/content/epigenetics/twins) (<https://learn.genetics.utah.edu/content/epigenetics/twins>) and look at the 'Chromosome 3 pairs' image. It shows the similarities in DNA methylation in three-year old monozygotic twins, as shown by the presence of the yellow colour. It also shows the differences in DNA methylation that have accumulated in 50-year-old monozygotic twins, as shown by the presence of the green and red areas.

Where monozygotic twins experience high consistency for certain phenotypic traits, such as genetic diseases, it is indicative of a genetic cause, whereas lower concordance can indicate an environmental and/or epigenetic cause. For example, there is a 45% concordance rate in Alzheimer's rates in male monozygotic twins, meaning that when one twin develops Alzheimer's, there is a 45% chance that the other twin will also develop the condition [↗](#)

(<https://www.sciencedaily.com/releases/2006/02/060206232300.htm#:~:text=Even%20identical%20twins%2C%20whc>) This is in contrast to dizygotic twins.

Theory of Knowledge

The nature/nurture debate revolves around whether certain human behaviours and traits are primarily influenced by genetics (nature) or by environmental factors (nurture).

Improved understanding in the area of epigenetics deepens our understanding of this debate, helping to reveal the complex interplay between environmental factors and their influence on gene expression and phenotypic traits.

Monozygotic twins are particularly useful for epigenetic studies because they have the same genome, with phenotypic changes being attributed to epigenetic differences, such as DNA methylation and histone acetylation. By studying monozygotic twins, scientists can gain insights into the complex relationships between genetics and the environment in shaping individual characteristics.

External factors impacting the pattern of gene expression

The effect of lactose on the expression of the lac operon

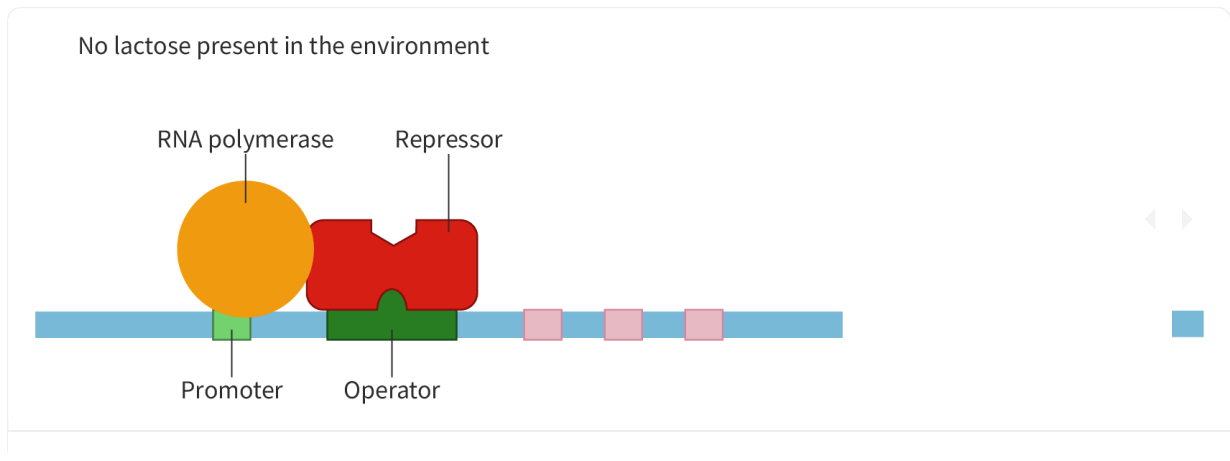
An operon is a cluster of genes that share a promoter, meaning that all of the genes with this single promoter will be transcribed together. The lac operon is a cluster of three genes found in bacterial DNA that code for proteins involved in the digestion of lactose, a disaccharide found in milk. The lac operon includes the gene encoding lactase, the enzyme that hydrolyses lactose, and a lactose membrane transporter.

Bacteria will preferentially use glucose as a food source; however, in the absence of glucose or other more easily digested sugars, bacteria can utilise lactose as an energy source.

When lactose is absent, the lac repressor binds to a region called the operator, preventing the attachment of RNA polymerase to the lac operon promoter and repressing transcription of the gene. When lactose is present, it binds to the repressor, detaching it from the promoter and allowing RNA polymerase to bind and transcribe the lac operon (**Interactive 1**). This means that the genes will only be expressed when lactose is present in the environment.



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Interactive 1. Lactose Expression in Bacteria.

Section

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Feedback



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More information for interactive 1

Assign

The interactive provides a comparison between lactose expression in bacteria with the help of two scenarios, that is, in the presence and absence of lactose. The slider feature on the right side helps toggle between the two scenarios.

Scenario 1

The illustration shows the regulation of the lac operon in bacteria (*E. coli*), in the absence of lactose, demonstrating how gene expression is controlled to conserve cellular energy. The title at the top reads: No lactose present in the environment.

"Promoter" is the binding site for RNA polymerase to initiate transcription of the three genes of the lac operon. The three genes include *lacZ*, *lacY*, and *lacA*. "Operator" is the regulatory sequence where the lac repressor binds. "RNA polymerase" is the enzyme that transcribes the lac operon genes. "Repressor" is the regulatory protein that blocks transcription when lactose is absent.

In the absence of lactose, the repressor binds to the operator, physically obstructing RNA polymerase to bind with the promoter thereby from moving forward. When transcription is blocked, no lac genes are transcribed.

Scenario 2

When the slider is moved from right to left, a new slide with the title: Lactose present, is viewed.

The illustration shows the activation of the lac operon in *E. coli* when lactose is present in the environment. It demonstrates that lactose triggers the expression of genes (*lacZ*, *lacY*, and *lacA*) needed for its metabolism. Lactose binds to the "Repressor", a regulatory protein, and prevents it from binding with the operator. Lactose causes a conformational change in the repressor molecule that inactivates it. The RNA polymerase can now transcribe the genes of the lac operon by binding to the promoter molecule. Finally, the enzymes for lactose digestion are synthesized.

This demonstrates that bacteria efficiently digest lactose only when it is available, conserving energy.

The effect of tryptophan on the expression of the tryptophan operon

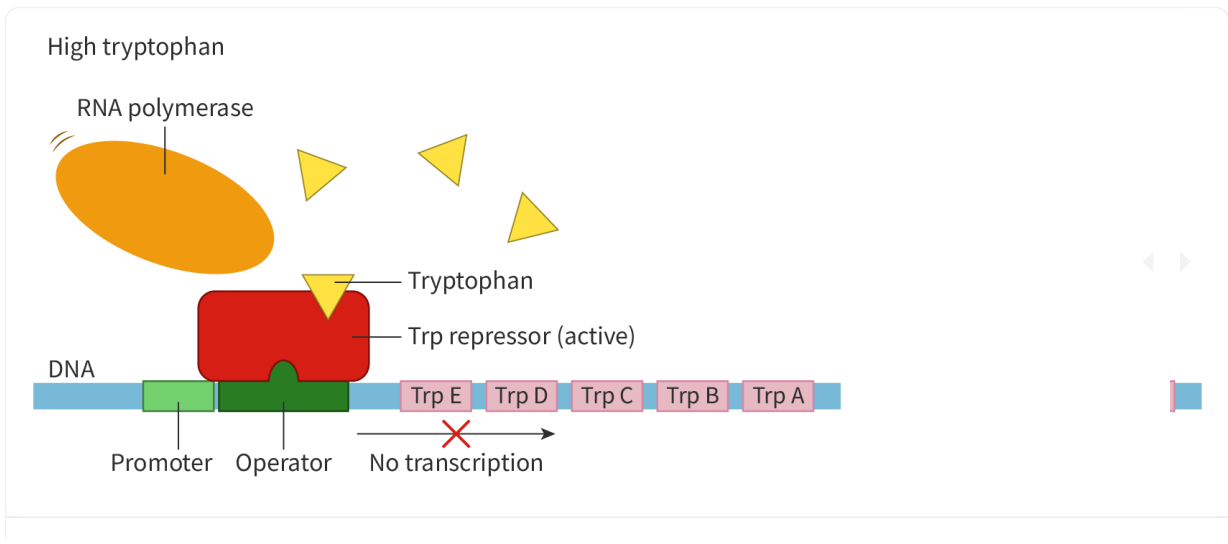
The tryptophan operon is a cluster of five genes found in bacterial DNA that are necessary for the synthesis of the amino acid tryptophan. When tryptophan is absent, RNA polymerase is able to bind to the tryptophan operon and transcribe the genes necessary for the synthesis of tryptophan. This allows bacteria to produce tryptophan when it is not readily available in the environment.

When tryptophan is present, it can bind to a repressor protein, causing the repressor protein to undergo a conformational change, which allows it to bind to the operator region of the tryptophan operon. This inhibits transcription of the tryptophan operon (**Interactive 2**).

This mechanism ensures that the genes necessary to synthesise the amino acid are only transcribed when the amino acid is needed.



Student
view



Interactive 2. Tryptophan Inhibits the Transcription of Genes in the Tryptophan Operon.

More information for interactive 2

The interactive provides a comparison in the regulation of the Tryptophan (*trp*) operon in bacterial DNA when tryptophan amount is high and low. The slider on the right can be moved from right to left to view the two scenarios separately.

Scenario 1

The first illustration, titled, High tryptophan, demonstrates the scenario when tryptophan is abundant in the bacterial cell.

The bacterial DNA has a promoter, operator, and five genes, namely, Trp E, Trp D, Trp C, Trp B, and Trp A. The promoter serves as the binding site for RNA polymerase. The operator is the sequence where the *trp* repressor binds to block transcription. RNA polymerase is the enzyme that transcribes the *trp* operon genes. Trp repressor is normally inactive and requires tryptophan to operate. The tryptophan amino acid is a corepressor that activates the repressor when abundant.

Once the tryptophan binds with the repressor, the repressor becomes active. Once active, it binds to the operator and blocks the RNA polymerase from binding to the promoter thereby halting the transcription. As a result of this, the five genes of tryptophan operon are not transcribed. This prevents unnecessary synthesis of tryptophan when it's already abundant.

Scenario 2

The second illustration, titled, Low tryptophan, demonstrates the scenario when tryptophan is less in the bacterial cell.

As the tryptophan levels are low, the repressor is in its inactive state, and cannot bind to the operator. RNA polymerase now binds to the promoter and transcribes the operon and the five genes for tryptophan production.

The "fullscreen" icon at the top right allows the users to view the illustrations in a zoomed-in version.

Oestradiol

Oestradiol, a steroid hormone, targets cells with oestradiol receptors. These cells are found in many locations within the body and so oestradiol can have diverse and widespread effects on gene expression (**Figure 3**) (see [section C2.1.10–13 \(/study/app/bio/sid-422-cid-755105/book/mechanism-of-action-of-various-signal-receptors-hl-id-46146/\)\)](#)).

As a steroid hormone, oestradiol is able to diffuse freely across cell membranes. Once inside the cell, oestradiol binds to oestradiol receptors, resulting in a conformational change and activation. Once activated, the hormone–receptor complex can move into the nucleus and bind to specific sections of DNA located near target genes (see [section C2.1.10–13 \(/study/app/bio/sid-422-cid-755105/book/mechanism-of-action-of-various-signal-receptors-hl-id-46146/\)\)](#)). Once bound, other proteins such as co-regulatory and co-activator proteins are recruited to the gene, influencing the transcription of the target genes. The specific target genes of oestradiol can vary across different tissues and physiological conditions but include genes related to the development and function of the female reproductive system. For example, the genes for follicle-stimulating hormone and luteinising hormone, genes associated with the development of uterine and breast tissue and genes involved in maintaining bone health.

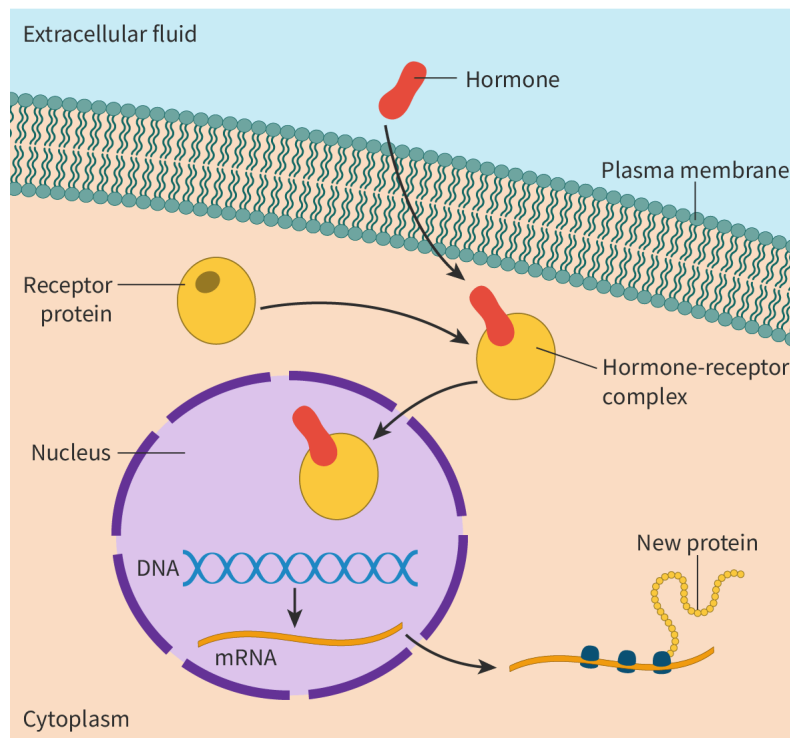


Figure 3. The mechanism of action of a steroid hormone such as oestradiol on gene expression.

[More information for figure 3](#)

This diagram depicts the mechanism of action of a steroid hormone, specifically illustrating the process by which a hormone like oestradiol influences gene expression within a cell. The diagram features several labeled components and arrows demonstrating the sequence and flow of action:

1. **Hormone:** Illustrated as a molecule outside the cell near the extracellular fluid and plasma membrane.
2. **Extracellular Fluid & Plasma Membrane:** The hormone diffuses through the plasma membrane into the cytoplasm.
3. **Receptor Protein:** Once inside, the hormone binds to a receptor protein, causing a conformational change. This forms the hormone-receptor complex.
4. **Hormone-Receptor Complex:** The activated complex translocates to the nucleus.
5. **Nucleus:** Inside the nucleus, the complex interacts with DNA, depicted as a double helix strand.
6. **DNA & mRNA:** The interaction promotes mRNA transcription, shown adjacent to the DNA strand.
7. **New Protein:** The newly transcribed mRNA is translated into a new protein, depicted by ribosome-like structures attaching to the mRNA strand on the cytoplasm side.

This diagram explains how the interaction of hormones and receptors regulates gene expression and protein synthesis within a cell.

[Generated by AI]

🌐 International Mindedness

Most mammals lose the ability to digest lactose, the disaccharide found in milk and other dairy products, after childhood because they stop producing the enzyme lactase, which hydrolyses lactose into glucose and galactose. In the absence of this enzyme, lactose remains in the digestive tract, leading to symptoms such as bloating, gas and diarrhoea. This trait is called lactase non-persistence (often referred to as lactose intolerance) and is exhibited by around 65% of the total global adult population.

Some human populations developed a mutation that allows them to continue producing lactase into adulthood, enabling them to digest lactose and consume dairy products without experiencing digestive issues, a trait known as lactase persistence (**Figure 4**).

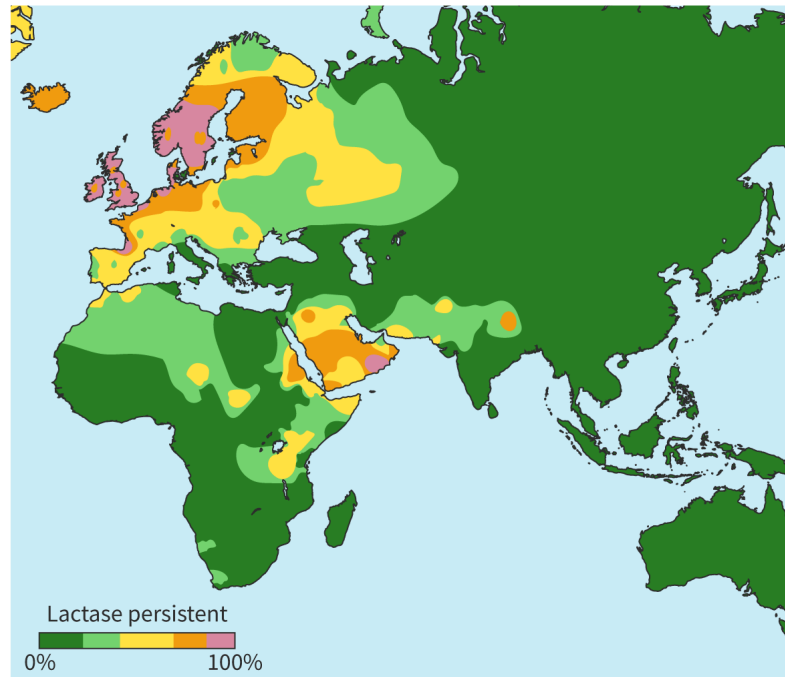



Figure 4. Varying levels of lactase persistence across the world.

 More information for figure 4

The map illustrates the varying levels of lactase persistence across different regions of the world. The color gradient, ranging from red to green, represents the percentage of the population with lactase persistence. Red represents 0% lactase persistence, while green indicates 100%. Northern and western Europe, as well as parts of the Middle East, show higher levels of lactase persistence (yellow to green areas). In contrast, large parts of Africa, Asia, and southern regions exhibit lower levels (orange to red areas), indicating less lactase persistence. This distribution indicates genetic and dietary adaptations across different human populations.

[Generated by AI]

Try the activity to help with your understanding of epigenetic inheritance.

Activity

- **IB learner profile attribute:** Inquirer
- **Approaches to learning:** Research skills — Evaluating information sources for accuracy, bias, credibility and relevance
- **Time required to complete activity:** 15 minutes
- **Activity type:** Individual activity

Watch the video embedded in [this web page](#) 

(<https://learn.genetics.utah.edu/content/epigenetics/twins>) and then research and write a paragraph hypothesising how environmental factors can result in phenotypic differences between identical twins. Consider which environmental factors might have a positive impact on the epigenome, and which might have a negative impact. Discuss your ideas with your classmates.

5 section questions



Overview
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D2. Continuity and change: Cells / D2.2 Gene expression (HL)

Summary and key terms (HL)

Higher level (HL)

- Gene expression is the process by which genetic information is used to produce RNA and proteins. As cells develop and mature from undifferentiated cells, their patterns of gene expression change, where some genes may be turned on or upregulated, and other genes may be turned off or downregulated. The stages in gene expression are transcription, translation and the function of the protein produced.
- Promoters are regions of non-coding DNA to which RNA polymerase binds to initiate transcription. Transcription factors are proteins that can regulate gene expression by altering the ease with which RNA polymerase binds to a promoter. Examples of transcription factors are activator and repressor proteins.
- Once a gene has been transcribed, the mRNA transcript can persist and be translated more than once. The persistence of the mRNA transcript depends on factors such as the presence of endonuclease enzymes and stabilising proteins, chemical modifications to the mRNA and oxidative stress.
- All somatic cells within your body have the same genome, but differences in the environments of the cells lead to differences in gene expression. Examples of epigenetic changes include DNA methylation, and histone acetylation and methylation.
- Some epigenetic changes can be inherited. For this to happen, genetic tags must occur or be maintained in germline cells and passed on to the offspring.
- Environmental factors, such as air pollution, diet and temperature can affect patterns of gene expression. Monozygotic twins are useful for studying the effect of the environment on gene expression as they possess the same genome.
- External factors in the environment of a cell can impact gene expression. Lactose can cause upregulation of the lac operon, a cluster of genes involved in the metabolism of lactose, and tryptophan can cause downregulation of the tryptophan operon, a cluster of genes involved in the production of the amino acid tryptophan. Steroid hormones, such as oestradiol are able to diffuse across cell membranes and bind to specific target receptors within a cell. Once bound, the hormone—receptor complex can bind to specific regions of DNA, recruiting other factors that can cause the up or down regulation of target genes.



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Key terms

Review these key terms. Do you know them all? Fill in as many gaps as you can using the terms in this list.

1. _____ expression is the process by which DNA is used to produce RNA and _____. Although all somatic cells in an individual organism have the same genome, different cells express different genes and this leads to cells having different structures and _____. Some examples are given below.
2. _____ factors are a group of proteins found within a cell that can impact gene expression by altering the ease with which RNA polymerase binds to a _____ region of DNA.
3. _____ of cytosine nucleotides in the promoter region of DNA is an example of a chemical modification. It _____ gene expression.
4. Examples of _____ factors that can impact gene expression include air pollution, diet and temperature.
5. Lactose can cause upregulation of the lac _____ in bacteria, a cluster of genes involved in the digestion of this disaccharide.

proteins promoter Methylation operon decreases functions environmental
Transcription Gene

✓ Check

Interactive 1. Understanding Gene Expression and Regulation Key Terms.

D2. Continuity and change: Cells / D2.2 Gene expression (HL)

Checklist (HL)

Section

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Feedback



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Assign



Higher level (HL)



What you should know

After studying this subtopic you should be able to:

- Explain the term gene expression.
- Outline how transcription can be regulated by proteins that bind to DNA.
- Outline how translation can be regulated through the degradation of mRNA.



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Overview
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- Explain the term epigenesis.
- Describe the differences between the genome, transcriptome and proteome of individual cells.
- Outline how methylation can affect gene expression.
- Identify why some epigenetic changes are heritable.
- Describe examples of how the environment can affect gene expression.
- Outline consequences of removing epigenetic tags from human gametes.
- Discuss the use of monozygotic twins to study gene expression.
- Describe examples of external factors that can impact gene expression.

D2. Continuity and change: Cells / D2.2 Gene expression (HL)

Investigation (HL)

Section

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Assign

Higher level (HL)

- **IB learner profile attribute:** Inquirer
- **Approaches to learning:** Research skills — Evaluating information sources for accuracy, bias, credibility and relevance
- **Time required to complete activity:** 60 minutes
- **Activity type:** Individual and group activity

Your task

In this activity you will have 30 minutes to read and summarise an article related to gene expression. You can search for an article or use one of the suggested articles below.

Once you have done this, present a summary of your findings to a small group of students. While listening to the presentations of your classmates write down at least two questions or comments per presentation. Each presentation should end in a short discussion based on these questions.

- Epigenetics and the Dutch Hunger Winter:
<https://www.naturalhistorymag.com/features/142195/beyond-dna-epigenetics>
(<https://www.naturalhistorymag.com/features/142195/beyond-dna-epigenetics>) (should be accessible to all)
- How our genes respond to our diet:
<https://www.sciencedaily.com/releases/2011/09/110919073845.htm>
(<https://www.sciencedaily.com/releases/2011/09/110919073845.htm>) (should be accessible to all)
- Twins in space:
<https://theconversation.com/twins-in-space-how-space-travel-affects-gene-expression-107936>
(<https://theconversation.com/twins-in-space-how-space-travel-affects-gene-expression-107936>)
- Epigenetics and ageing:
<https://www.science.org/doi/10.1126/sciadv.1600584>
(<https://www.science.org/doi/10.1126/sciadv.1600584>) (advanced reading)
- Queen bees and worker bees:
<https://journals.plos.org/plosbiology/article?id=10.1371/journal.pbio.1000506>
(<https://journals.plos.org/plosbiology/article?id=10.1371/journal.pbio.1000506>) (advanced reading)

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Feedback



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Assign



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Overview
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Study skills

Tips for researching and reading articles:

- Start by searching for articles from valid sources or databases, such as news sites that you know and trust, or well-known databases such as Google Scholar, PubMed or JSTOR. Some articles may require a subscription to read.
- Consider filtering the articles from a search (for example, you might choose to focus on articles published in the last 5 years).
- When deciding whether to read an article, read the abstract to help you determine if the article is relevant to your topic and of interest to you.
- Skim through the article before reading in detail to give you an overview of the main points and help you decide whether to read it in detail.
- When reading in detail, take notes of the main points and any questions or thoughts that you have.
- Check the reference section for additional sources that may be relevant to your research.
- Be critical of the information present, and consider whether it aligns with other reputable sources.

D2. Continuity and change: Cells / D2.2 Gene expression (HL)

Reflection (HL)

Section

Student...

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Feedback



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Assign



Teacher instructions

The goal of this section is to encourage students to reflect on their learning and conceptual understanding of the subject at the end of this subtopic. It asks them to go back to the guiding questions posed at the start of the subtopic and assess how confident they now are in answering them. What have they learned, and what outstanding questions do they have? Are they able to see the bigger picture and the connections between the different topics?

Students can submit their reflections to you by clicking on 'Submit'. You will then see their answers in the 'Insights' part of the Kognity platform.

Higher level (HL)



Reflection

Now that you've completed this subtopic, let's come back to the guiding question introduced in [The big picture \(/study/app/bio/sid-422-cid-755105/book/big-picture-hl-id-43549/\)](/study/app/bio/sid-422-cid-755105/book/big-picture-hl-id-43549/).

- How is gene expression changed in a cell?
- How can patterns of gene expression be conserved through inheritance?

With these questions in mind, take a moment to reflect on your learning so far and type your reflections into the space provided.

You can use the following questions to guide you:

- What main points have you learned from this subtopic?
- Is anything unclear? What questions do you still have?



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- How confident do you feel in answering the guiding questions?
- What connections do you see between this subtopic and other parts of the course?

⚠ Once you submit your response, you won't be able to edit it.

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Submit

Rate subtopic D2.2 Gene expression (HL)

Help us improve the content and user experience.



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