



Photobiology

(Study of the interactions of
light and living organisms)

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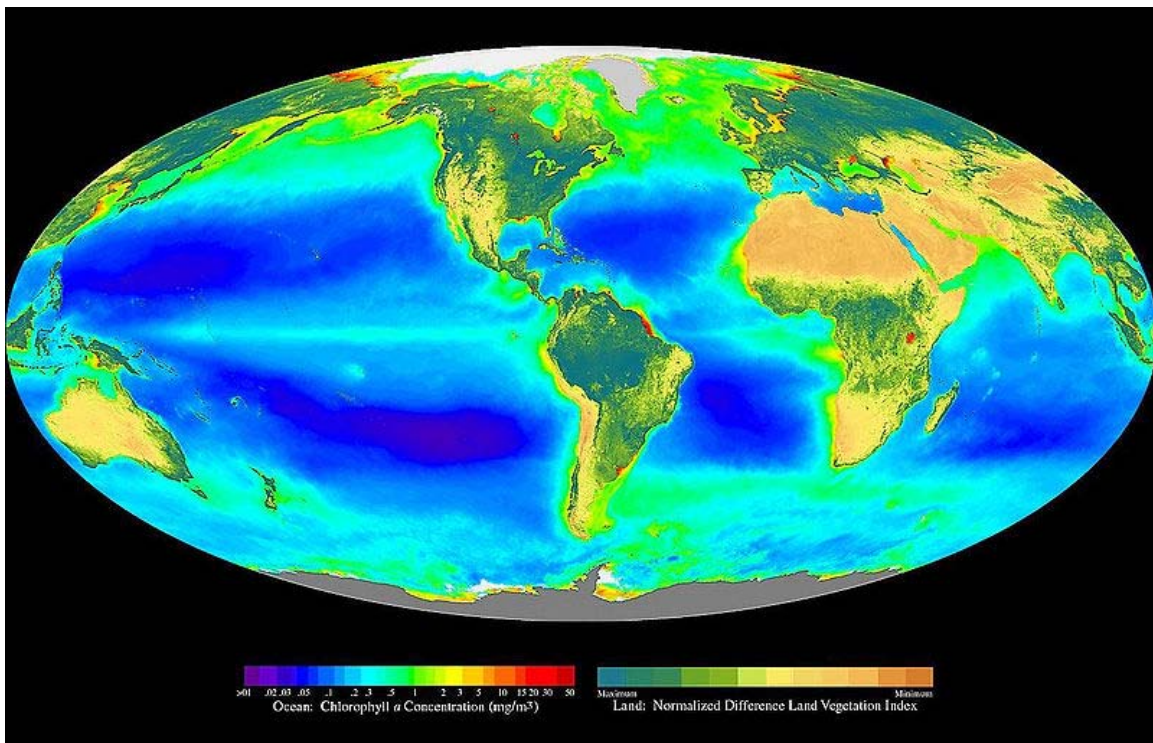
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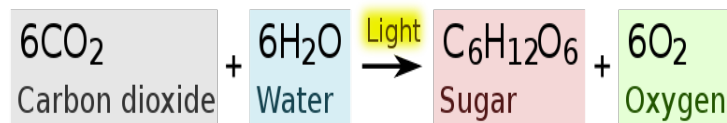
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Chapter 1

Photosynthesis



Composite image showing the global distribution of photosynthesis, including both oceanic phytoplankton and vegetation

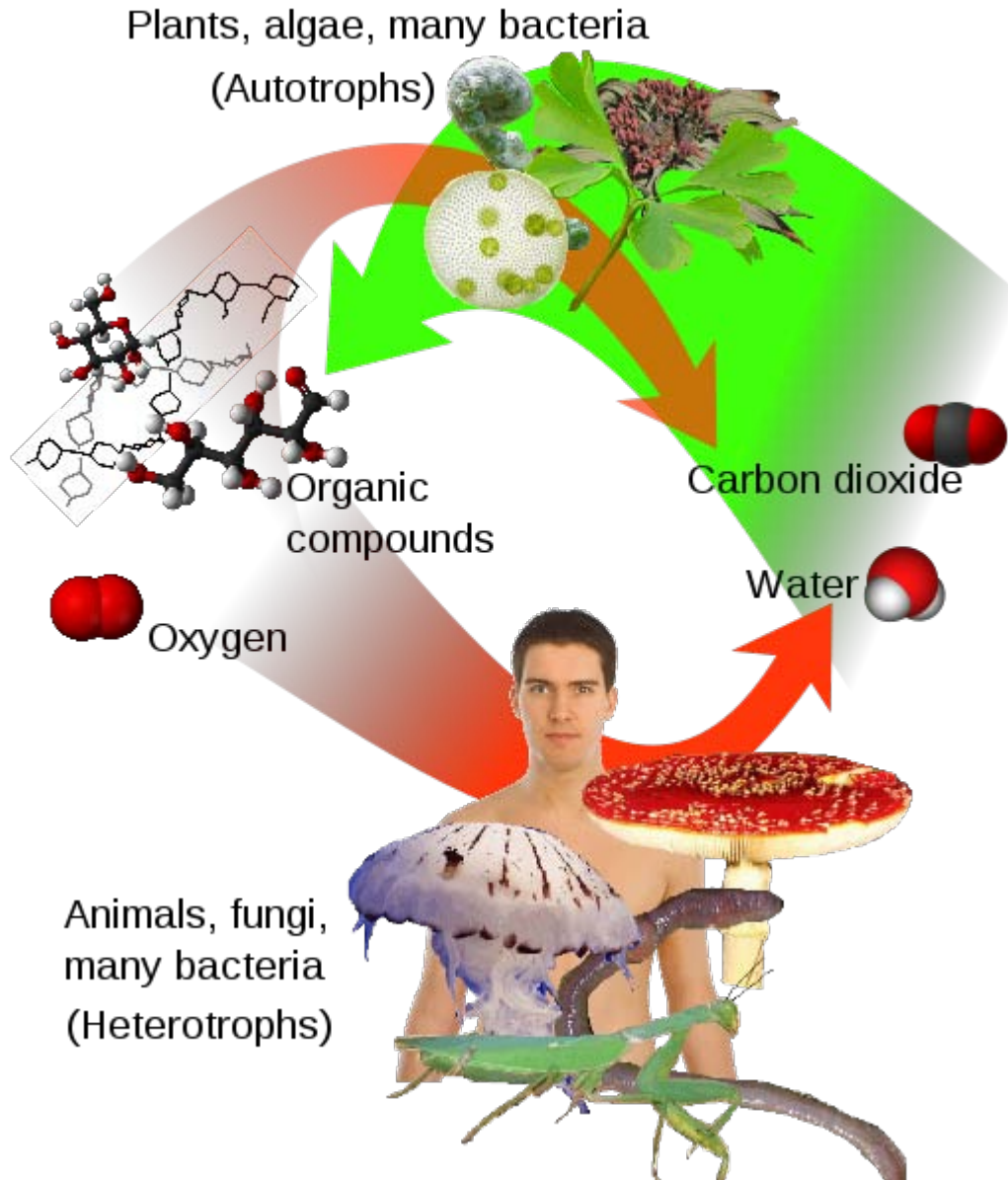


Overall equation for the type of photosynthesis that occurs in plants

Photosynthesis is a process that converts carbon dioxide into organic compounds, especially sugars, using the energy from sunlight. Photosynthesis occurs in plants, algae,

and many species of bacteria, but not in archaea. Photosynthetic organisms are called *photoautotrophs*, since they can create their own food. In plants, algae, and cyanobacteria, photosynthesis uses carbon dioxide and water, releasing oxygen as a waste product. Photosynthesis is vital for all aerobic life on Earth. As well as maintaining the normal level of oxygen in the atmosphere, nearly all life either depends on it directly as a source of energy, or indirectly as the ultimate source of the energy in their food (the exceptions are chemoautotrophs that live in rocks or around deep sea hydrothermal vents). The rate of energy capture by photosynthesis is immense, approximately 100 terawatts, which is about six times larger than the power consumption of human civilization. As well as energy, photosynthesis is also the source of the carbon in all the organic compounds within organisms' bodies. In all, photosynthetic organisms convert around 100–115 teragrams of carbon into biomass per year.

Although photosynthesis can happen in different ways in different species, some features are always the same. For example, the process always begins when energy from light is absorbed by proteins called photosynthetic reaction centers that contain chlorophylls. In plants, these proteins are held inside organelles called chloroplasts, while in bacteria they are embedded in the plasma membrane. Some of the light energy gathered by chlorophylls is stored in the form of adenosine triphosphate (ATP). The rest of the energy is used to remove electrons from a substance such as water. These electrons are then used in the reactions that turn carbon dioxide into organic compounds. In plants, algae and cyanobacteria, this is done by a sequence of reactions called the Calvin cycle, but different sets of reactions are found in some bacteria, such as the reverse Krebs cycle in *Chlorobium*. Many photosynthetic organisms have adaptations that concentrate or store carbon dioxide. This helps reduce a wasteful process called photorespiration that can consume part of the sugar produced during photosynthesis.

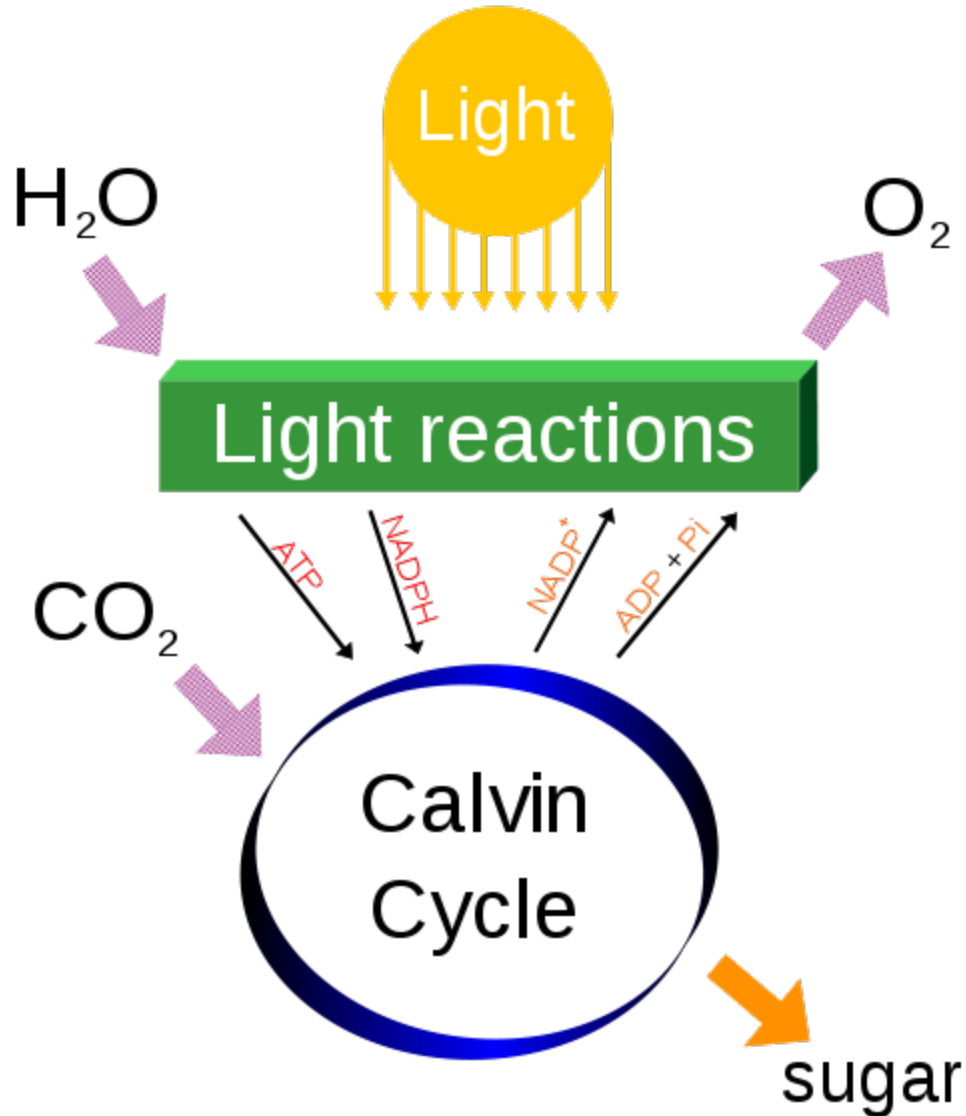


Overview of cycle between autotrophs and heterotrophs. Photosynthesis is the main means by which plants, algae and many bacteria produce organic compounds and oxygen from carbon dioxide and water (green arrow).

The first photosynthetic organisms probably evolved about 3,500 million years ago, early in the evolutionary history of life, when all forms of life on Earth were microorganisms and the atmosphere had much more carbon dioxide. They most likely used hydrogen or hydrogen sulfide as sources of electrons, rather than water. Cyanobacteria appeared later, around 3,000 million years ago, and drastically changed the Earth when they began to oxygenate the atmosphere, beginning about 2,400 million years ago. This new atmosphere allowed the evolution of complex life such as protists. Eventually, no later than a billion years ago, one of these protists formed a symbiotic relationship with a

cyanobacterium, producing the ancestor of many plants and algae. The chloroplasts in modern plants are the descendants of these ancient symbiotic cyanobacteria.

Overview



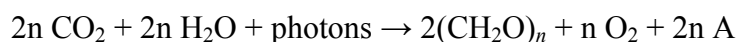
Photosynthesis changes the energy from the sun into chemical energy, splits water to liberate O₂, and fixes CO₂ into sugar.

Photosynthetic organisms are photoautotrophs, which means that they are able to synthesize food directly from carbon dioxide using energy from light. However, not all organisms that use light as a source of energy carry out photosynthesis, since *photoheterotrophs* use organic compounds, rather than carbon dioxide, as a source of carbon. In plants, algae and cyanobacteria, photosynthesis releases oxygen. This is called *oxygenic photosynthesis*. Although there are some differences between oxygenic

photosynthesis in plants, algae and cyanobacteria, the overall process is quite similar in these organisms. However, there are some types of bacteria that carry out anoxygenic photosynthesis, which consumes carbon dioxide but does not release oxygen.

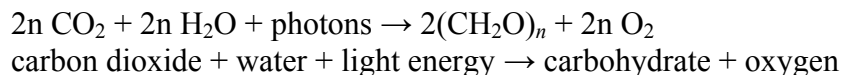
Carbon dioxide is converted into sugars in a process called carbon fixation. Carbon fixation is a redox reaction, so photosynthesis needs to supply both a source of energy to drive this process, and the electrons needed to convert carbon dioxide into carbohydrate, which is a reduction reaction. In general outline, photosynthesis is the opposite of cellular respiration, where glucose and other compounds are oxidized to produce carbon dioxide, water, and release chemical energy. However, the two processes take place through a different sequence of chemical reactions and in different cellular compartments.

The general equation for photosynthesis is therefore:

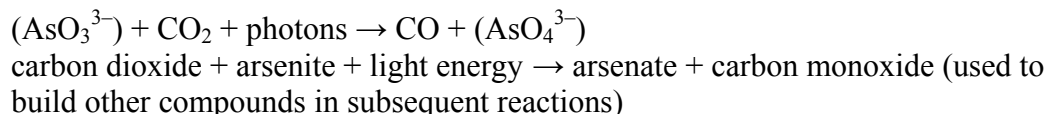


Carbon dioxide + electron donor + light energy → carbohydrate + oxygen + oxidized electron donor

Since water is used as the electron donor in oxygenic photosynthesis, the equation for this process is:



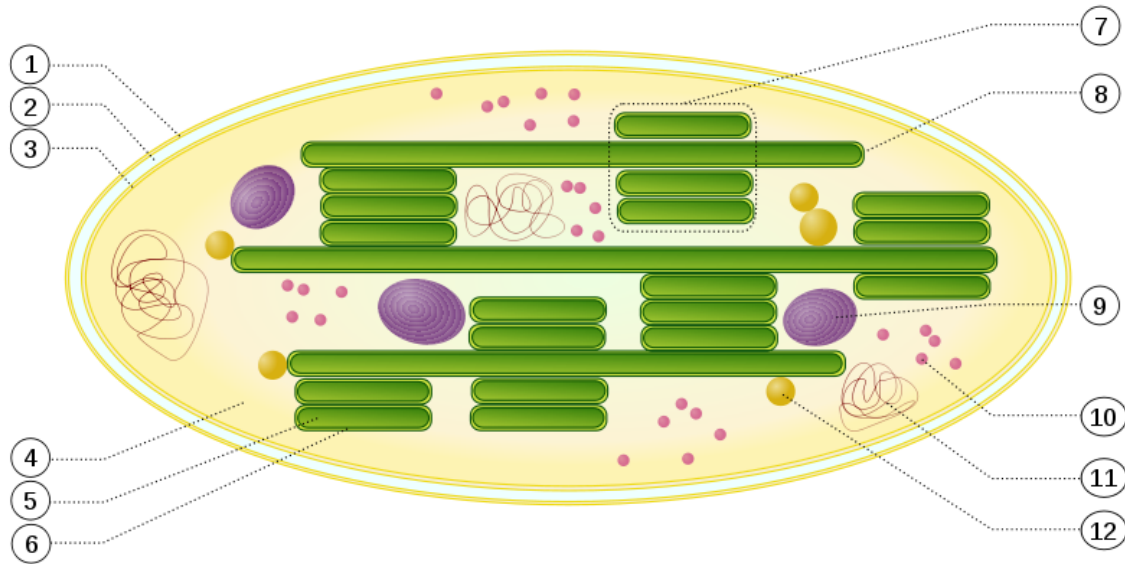
Other processes substitute other compounds (such as arsenite) for water in the electron-supply role; the microbes use sunlight to oxidize arsenite to arsenate: The equation for this reaction is:



Photosynthesis occurs in two stages. In the first stage, *light-dependent reactions* or *light reactions* capture the energy of light and use it to make the energy-storage molecules ATP and NADPH. During the second stage, the *light-independent reactions* use these products to capture and reduce carbon dioxide.

Most organisms that utilize photosynthesis to produce oxygen use visible light to do so, although at least three use infrared radiation.

Photosynthetic membranes and organelles



Chloroplast ultrastructure:

1. outer membrane
2. intermembrane space
3. inner membrane (1+2+3: envelope)
4. stroma (aqueous fluid)
5. thylakoid lumen (inside of thylakoid)
6. thylakoid membrane
7. granum (stack of thylakoids)
8. thylakoid (lamella)
9. starch
10. ribosome
11. plastidial DNA
12. plastoglobule (drop of lipids)

The proteins that gather light for photosynthesis are embedded within cell membranes. The simplest way these are arranged is in photosynthetic bacteria, where these proteins are held within the plasma membrane. However, this membrane may be tightly folded into cylindrical sheets called thylakoids, or bunched up into round vesicles called *intracytoplasmic membranes*. These structures can fill most of the interior of a cell, giving the membrane a very large surface area and therefore increasing the amount of light that the bacteria can absorb.

In plants and algae, photosynthesis takes place in organelles called chloroplasts. A typical plant cell contains about 10 to 100 chloroplasts. The chloroplast is enclosed by a membrane. This membrane is composed of a phospholipid inner membrane, a phospholipid outer membrane, and an intermembrane space between them. Within the membrane is an aqueous fluid called the stroma. The stroma contains stacks (grana) of thylakoids, which are the site of photosynthesis. The thylakoids are flattened disks,

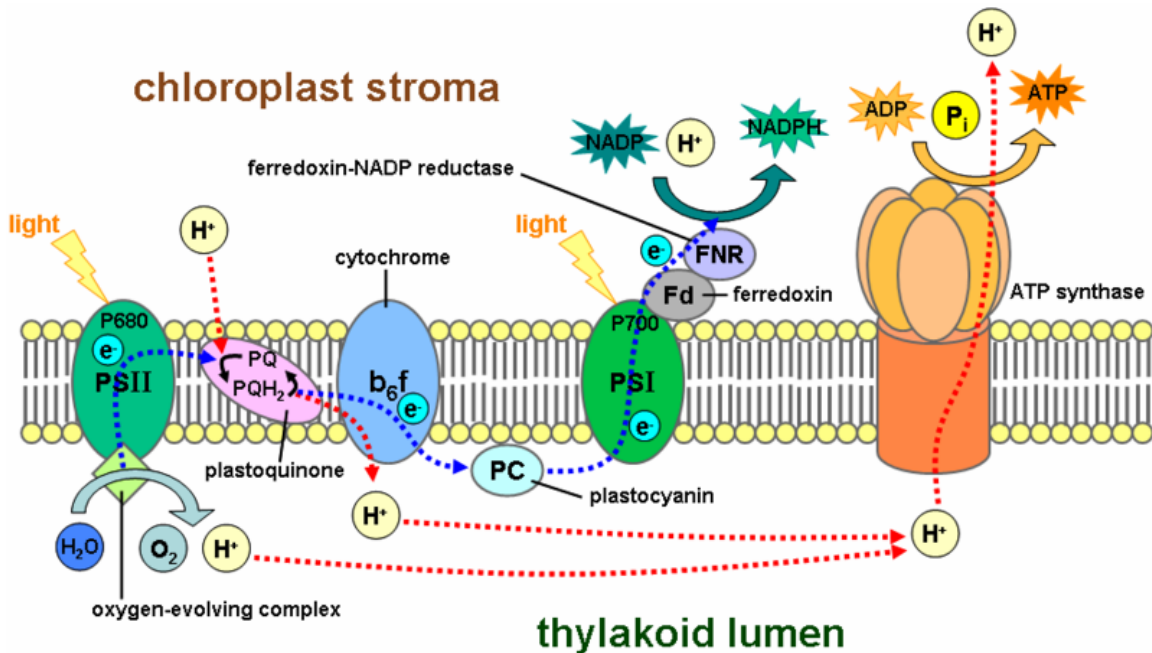
bounded by a membrane with a lumen or thylakoid space within it. The site of photosynthesis is the thylakoid membrane, which contains integral and peripheral membrane protein complexes, including the pigments that absorb light energy, which form the photosystems.

Plants absorb light primarily using the pigment chlorophyll, which is the reason that most plants have a green color. Besides chlorophyll, plants also use pigments such as carotenes and xanthophylls. Algae also use chlorophyll, but various other pigments are present as phycocyanin, carotenes, and xanthophylls in green algae, phycoerythrin in red algae (rhodophytes) and fucoxanthin in brown algae and diatoms resulting in a wide variety of colors.

These pigments are embedded in plants and algae in special antenna-proteins. In such proteins all the pigments are ordered to work well together. Such a protein is also called a light-harvesting complex.

Although all cells in the green parts of a plant have chloroplasts, most of the energy is captured in the leaves. The cells in the interior tissues of a leaf, called the mesophyll, can contain between 450,000 and 800,000 chloroplasts for every square millimeter of leaf. The surface of the leaf is uniformly coated with a water-resistant waxy cuticle that protects the leaf from excessive evaporation of water and decreases the absorption of ultraviolet or blue light to reduce heating. The transparent epidermis layer allows light to pass through to the palisade mesophyll cells where most of the photosynthesis takes place.

Light reactions



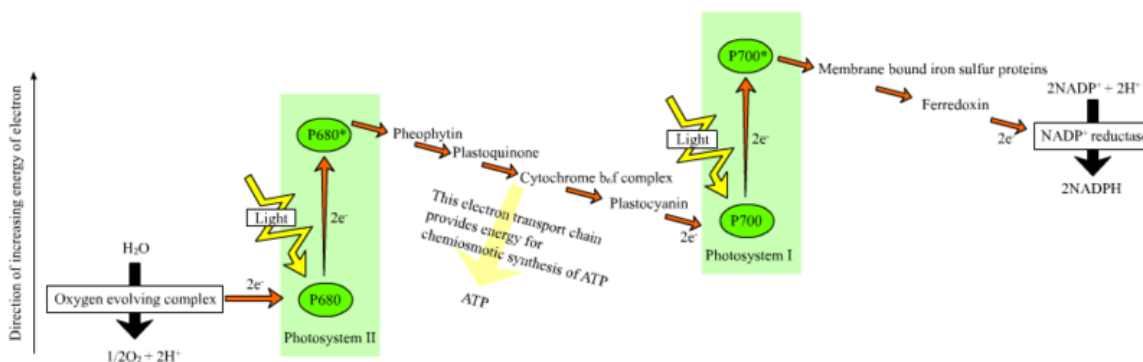
Light-dependent reactions of photosynthesis at the thylakoid membrane

In the light reactions, one molecule of the pigment chlorophyll absorbs one photon and loses one electron. This electron is passed to a modified form of chlorophyll called pheophytin, which passes the electron to a quinone molecule, allowing the start of a flow of electrons down an electron transport chain that leads to the ultimate reduction of NADP to NADPH. In addition, this creates a proton gradient across the chloroplast membrane; its dissipation is used by ATP synthase for the concomitant synthesis of ATP. The chlorophyll molecule regains the lost electron from a water molecule through a process called photolysis, which releases a dioxygen (O₂) molecule. The overall equation for the light-dependent reactions under the conditions of non-cyclic electron flow in green plants is:



Not all wavelengths of light can support photosynthesis. The photosynthetic action spectrum depends on the type of accessory pigments present. For example, in green plants, the action spectrum resembles the absorption spectrum for chlorophylls and carotenoids with peaks for violet-blue and red light. In red algae, the action spectrum overlaps with the absorption spectrum of phycobilins for blue-green light, which allows these algae to grow in deeper waters that filter out the longer wavelengths used by green plants. The non-absorbed part of the light spectrum is what gives photosynthetic organisms their color (e.g., green plants, red algae, purple bacteria) and is the least effective for photosynthesis in the respective organisms.

Z scheme



The "Z scheme"

In plants, light-dependent reactions occur in the thylakoid membranes of the chloroplasts and use light energy to synthesize ATP and NADPH. The light-dependent reaction has two forms: cyclic and non-cyclic. In the non-cyclic reaction, the photons are captured in the light-harvesting antenna complexes of photosystem II by chlorophyll and other accessory pigments. When a chlorophyll molecule at the core of the photosystem II reaction center obtains sufficient excitation energy from the adjacent antenna pigments, an electron is transferred to the primary electron-acceptor molecule, pheophytin, through a process called photoinduced charge separation. These electrons are shuttled through an electron transport chain, the so called **Z-scheme** shown in the diagram, that initially

functions to generate a chemiosmotic potential across the membrane. An ATP synthase enzyme uses the chemiosmotic potential to make ATP during photophosphorylation, whereas NADPH is a product of the terminal redox reaction in the *Z-scheme*. The electron enters a chlorophyll molecule in Photosystem I. The electron is excited due to the light absorbed by the photosystem. A second electron carrier accepts the electron, which again is passed down lowering energies of electron acceptors. The energy created by the electron acceptors is used to move hydrogen ions across the thylakoid membrane into the lumen. The electron is used to reduce the co-enzyme NADP, which has functions in the light-independent reaction. The cyclic reaction is similar to that of the non-cyclic, but differs in the form that it generates only ATP, and no reduced NADP (NADPH) is created. The cyclic reaction takes place only at photosystem I. Once the electron is displaced from the photosystem, the electron is passed down the electron acceptor molecules and returns back to photosystem I, from where it was emitted, hence the name *cyclic reaction*.

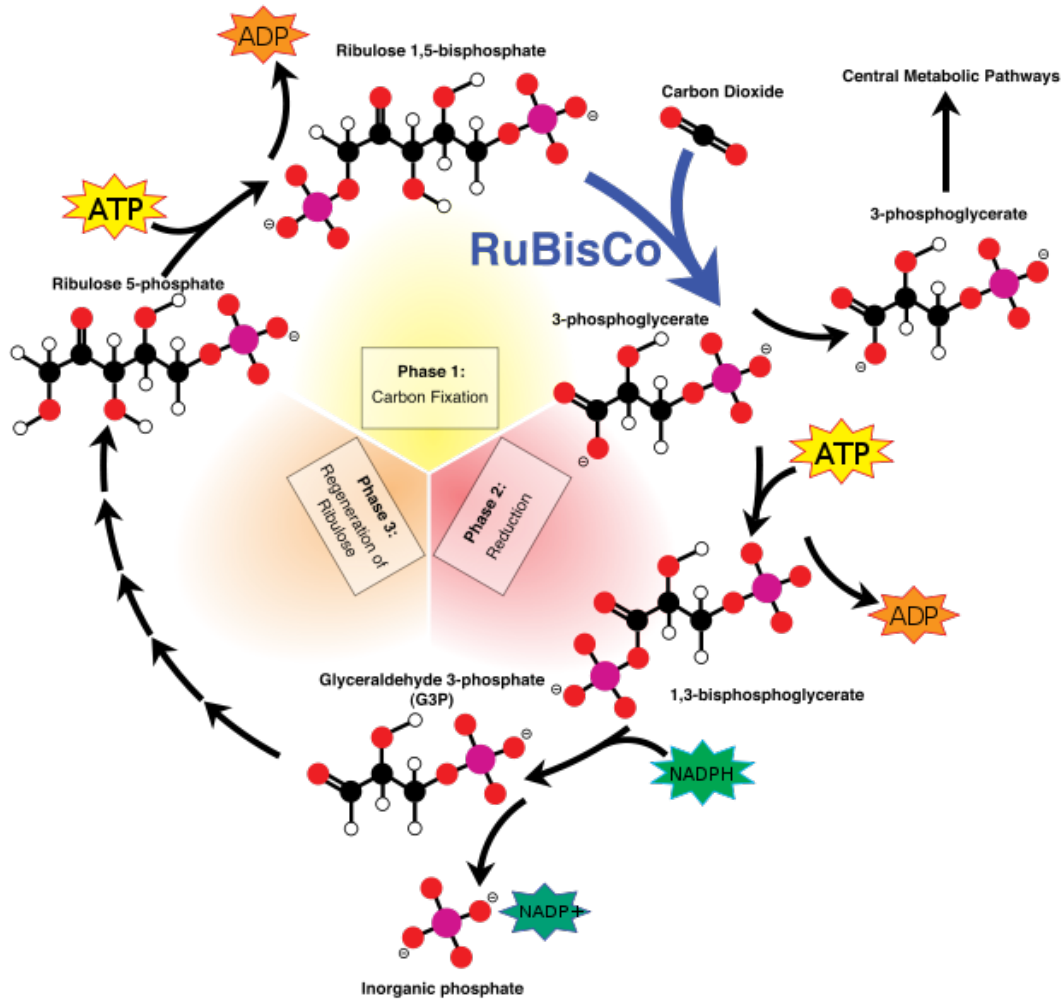
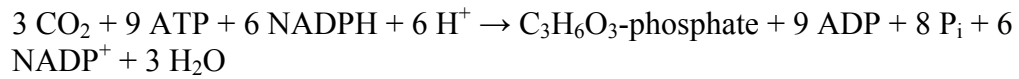
Water photolysis

The NADPH is the main reducing agent in chloroplasts, providing a source of energetic electrons to other reactions. Its production leaves chlorophyll with a deficit of electrons (oxidized), which must be obtained from some other reducing agent. The excited electrons lost from chlorophyll in photosystem I are replaced from the electron transport chain by plastocyanin. However, since photosystem II includes the first steps of the *Z-scheme*, an external source of electrons is required to reduce its oxidized **chlorophyll *a*** molecules. The source of electrons in green-plant and cyanobacterial photosynthesis is water. Two water molecules are oxidized by four successive charge-separation reactions by photosystem II to yield a molecule of diatomic oxygen and four hydrogen ions; the electron yielded in each step is transferred to a redox-active tyrosine residue that then reduces the photooxidized paired-chlorophyll *a* species called P680 that serves as the primary (light-driven) electron donor in the photosystem II reaction center. The oxidation of water is catalyzed in photosystem II by a redox-active structure that contains four manganese ions and a calcium ion; this oxygen-evolving complex binds two water molecules and stores the four oxidizing equivalents that are required to drive the water-oxidizing reaction. Photosystem II is the only known biological enzyme that carries out this oxidation of water. The hydrogen ions contribute to the transmembrane chemiosmotic potential that leads to ATP synthesis. Oxygen is a waste product of light-dependent reactions, but the majority of organisms on Earth use oxygen for cellular respiration, including photosynthetic organisms.

Light-independent reactions

The Calvin Cycle

In the Light-independent or dark reactions the enzyme RuBisCO captures CO₂ from the atmosphere and in a process that requires the newly formed NADPH, called the Calvin-Benson Cycle, releases three-carbon sugars, which are later combined to form sucrose and starch. The overall equation for the light-independent reactions in green plants is:



Overview of the Calvin cycle and carbon fixation

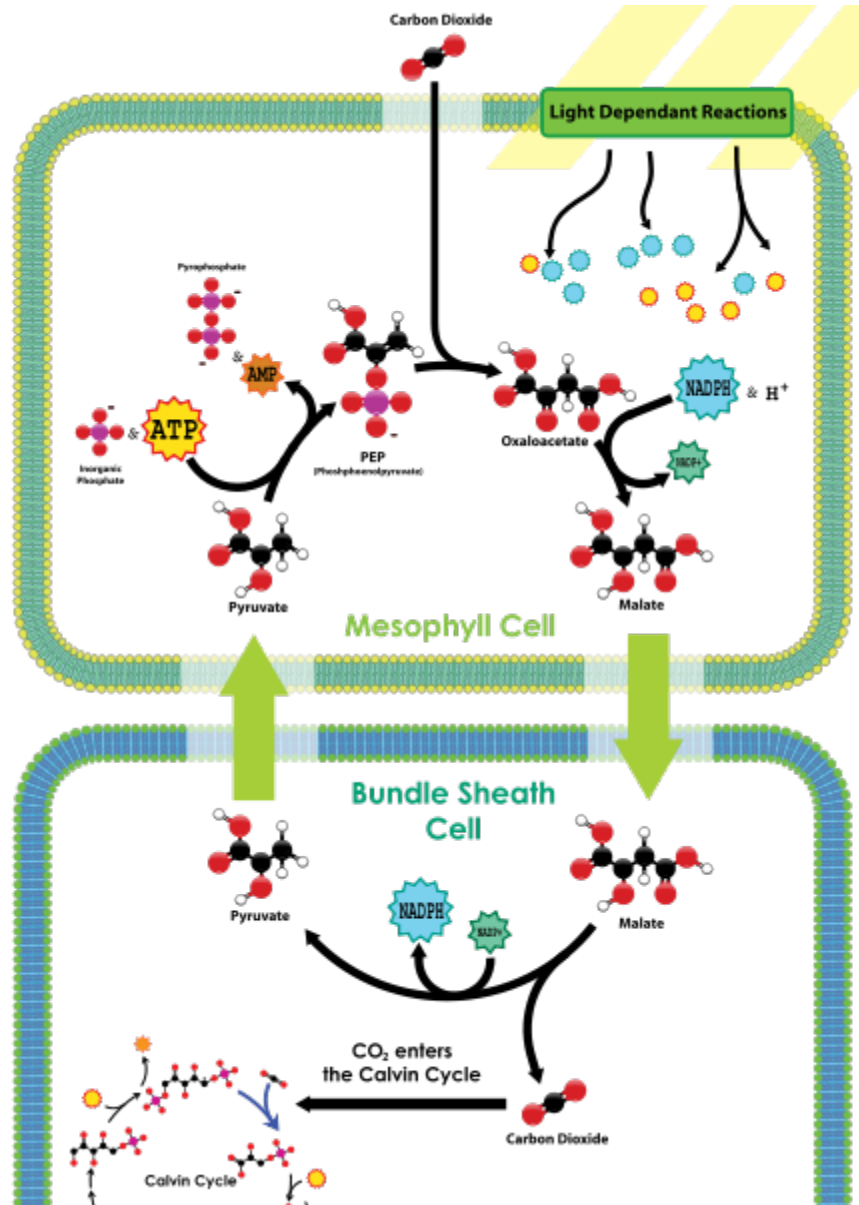
To be more specific, carbon fixation produces an intermediate product, which is then converted to the final carbohydrate products. The carbon skeletons produced by photosynthesis are then variously used to form other organic compounds, such as the building material cellulose, as precursors for lipid and amino acid biosynthesis, or as a fuel in cellular respiration. The latter occurs not only in plants but also in animals when the energy from plants gets passed through a food chain.

The fixation or reduction of carbon dioxide is a process in which carbon dioxide combines with a five-carbon sugar, ribulose 1,5-bisphosphate (RuBP), to yield two molecules of a three-carbon compound, glycerate 3-phosphate (GP), also known as 3-phosphoglycerate (PGA). GP, in the presence of ATP and NADPH from the light-dependent stages, is reduced to glyceraldehyde 3-phosphate (G3P). This product is also referred to as 3-phosphoglyceraldehyde (PGAL) or even as triose phosphate. Triose is a 3-carbon sugar. Most (5 out of 6 molecules) of the G3P produced is used to regenerate

RuBP so the process can continue. The 1 out of 6 molecules of the triose phosphates not "recycled" often condense to form hexose phosphates, which ultimately yield sucrose, starch and cellulose. The sugars produced during carbon metabolism yield carbon skeletons that can be used for other metabolic reactions like the production of amino acids and lipids.

Carbon concentrating mechanisms

On land



Overview of C4 carbon fixation

In hot and dry conditions, plants close their stomata to prevent the loss of water. Under these conditions, CO₂ will decrease, and oxygen gas, produced by the light reactions of photosynthesis, will decrease in the stem, not leaves, causing an increase of photorespiration by the oxygenase activity of ribulose-1,5-bisphosphate carboxylase/oxygenase and decrease in carbon fixation. Some plants have evolved mechanisms to increase the CO₂ concentration in the leaves under these conditions.

C₄ plants chemically fix carbon dioxide in the cells of the mesophyll by adding it to the three-carbon molecule phosphoenolpyruvate (PEP), a reaction catalyzed by an enzyme called PEP carboxylase and which creates the four-carbon organic acid, oxaloacetic acid. Oxaloacetic acid or malate synthesized by this process is then translocated to specialized bundle sheath cells where the enzyme, rubisco, and other Calvin cycle enzymes are located, and where CO₂ released by decarboxylation of the four-carbon acids is then fixed by rubisco activity to the three-carbon sugar 3-phosphoglyceric acids. The physical separation of rubisco from the oxygen-generating light reactions reduces photorespiration and increases CO₂ fixation and thus photosynthetic capacity of the leaf. C₄ plants can produce more sugar than C₃ plants in conditions of high light and temperature. Many important crop plants are C₄ plants, including maize, sorghum, sugarcane, and millet. Plants that do not use PEP-carboxylase in carbon fixation are called C₃ plants because the primary carboxylation reaction, catalyzed by rubisco, produces the three-carbon sugar 3-phosphoglyceric acids directly in the Calvin-Benson cycle. Over 90% of plants use C₃ carbon fixation, compared to 3% that use C₄ carbon fixation.

Xerophytes, such as cacti and most succulents, also use PEP carboxylase to capture carbon dioxide in a process called Crassulacean acid metabolism (CAM). In contrast to C₄ metabolism, which *physically* separates the CO₂ fixation to PEP from the Calvin cycle, CAM *temporally* separates these two processes. CAM plants have a different leaf anatomy from C₃ plants, and fix the CO₂ at night, when their stomata are open. CAM plants store the CO₂ mostly in the form of malic acid via carboxylation of phosphoenolpyruvate to oxaloacetate, which is then reduced to malate. Decarboxylation of malate during the day releases CO₂ inside the leaves, thus allowing carbon fixation to 3-phosphoglycerate by rubisco. 16,000 species of plants use CAM.

In water

Cyanobacteria possess carboxysomes which increase the concentration of CO₂ around rubisco to increase the rate of photosynthesis. This operates by carbonic anhydrase producing hydrocarbonate ions (HCO₃⁻) which are then pumped into the carboxysome, before being processed by a different carbonic anhydrase to produce CO₂. Pyrenoids in algae and hornworts also act to concentrate CO₂ around rubisco.

Order and kinetics

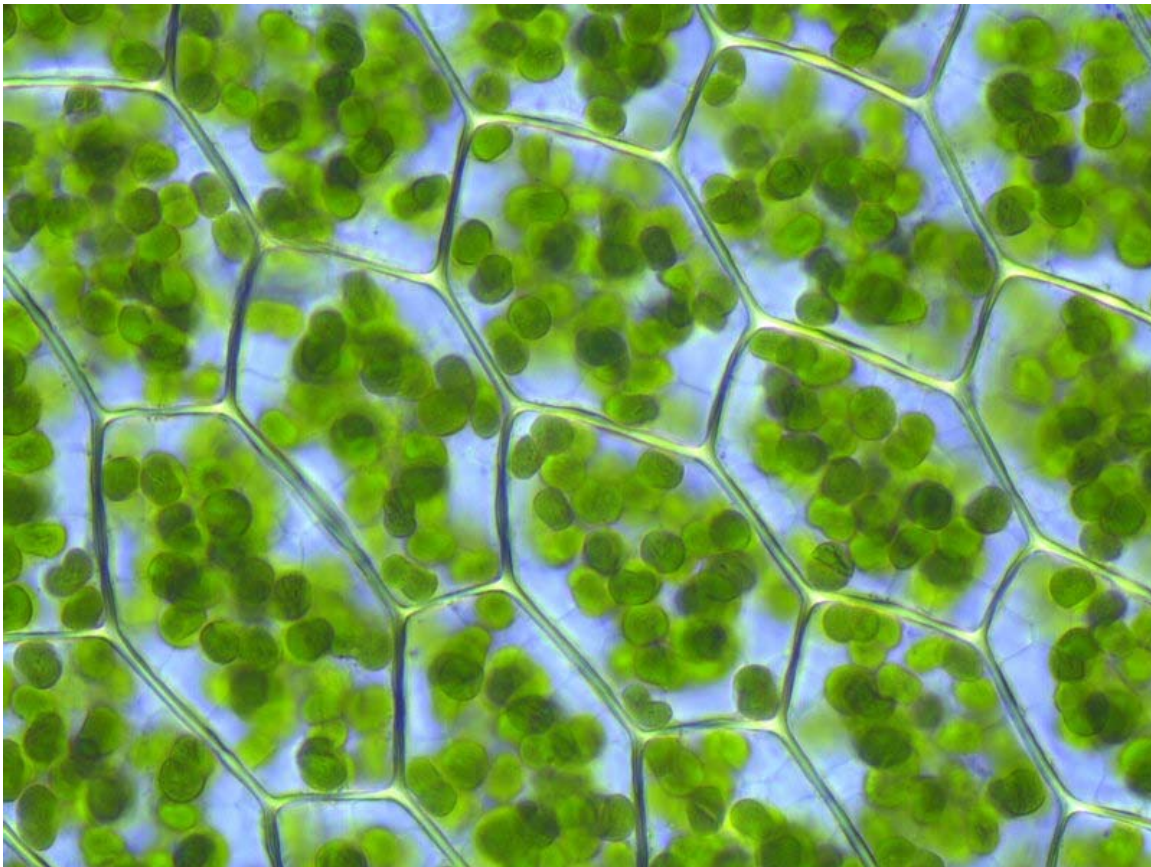
The overall process of photosynthesis takes place in four stages. The first, energy transfer in antenna chlorophyll takes place in the femtosecond (1 femtosecond (fs) = 10⁻¹⁵ s) to picosecond (1 picosecond (ps) = 10⁻¹² s) time scale. The next phase, the transfer of

electrons in photochemical reactions, takes place in the picosecond to nanosecond time scale (1 nanosecond (ns) = 10^{-9} s). The third phase, the electron transport chain and ATP synthesis, takes place on the microsecond (1 microsecond (μ s) = 10^{-6} s) to millisecond (1 millisecond (ms) = 10^{-3} s) time scale. The final phase is carbon fixation and export of stable products and takes place in the millisecond to second time scale. The first three stages occur in the thylakoid membranes.

Efficiency

Plants usually convert light into chemical energy with a photosynthetic efficiency of 3–6%. Actual plants' photosynthetic efficiency varies with the frequency of the light being converted, light intensity, temperature and proportion of carbon dioxide in the atmosphere, and can vary from 0.1% to 8%. By comparison, solar panels convert light into electric energy at an efficiency of approximately 6–20% for mass-produced panels, and up to 41% in a research laboratory.

Evolution



Plant cells with visible chloroplasts (from a moss, *Plagiomnium affine*)

Early photosynthetic systems, such as those from green and purple sulfur and green and purple nonsulfur bacteria, are thought to have been anoxygenic, using various molecules

as electron donors. Green and purple sulfur bacteria are thought to have used hydrogen and sulfur as an electron donor. Green nonsulfur bacteria used various amino and other organic acids. Purple nonsulfur bacteria used a variety of nonspecific organic molecules. The use of these molecules is consistent with the geological evidence that the atmosphere was highly reduced at that time.

Fossils of what are thought to be filamentous photosynthetic organisms have been dated at 3.4 billion years old.

The main source of oxygen in the atmosphere is oxygenic photosynthesis, and its first appearance is sometimes referred to as the oxygen catastrophe. Geological evidence suggests that oxygenic photosynthesis, such as that in cyanobacteria, became important during the Paleoproterozoic era around 2 billion years ago. Modern photosynthesis in plants and most photosynthetic prokaryotes is oxygenic. Oxygenic photosynthesis uses water as an electron donor, which is oxidized to molecular oxygen (O_2) in the photosynthetic reaction center.

Symbiosis and the origin of chloroplasts

Several groups of animals have formed symbiotic relationships with photosynthetic algae. These are most common in corals, sponges and sea anemones, possibly due to these animals having particularly simple body plans and large surface areas compared to their volumes. In addition, a few marine mollusks *Elysia viridis* and *Elysia chlorotica* also maintain a symbiotic relationship with chloroplasts they capture from the algae in their diet and then store in their bodies. This allows the molluscs to survive solely by photosynthesis for several months at a time. Some of the genes from the plant cell nucleus have even been transferred to the slugs, so that the chloroplasts can be supplied with proteins that they need to survive.

An even closer form of symbiosis may explain the origin of chloroplasts. Chloroplasts have many similarities with photosynthetic bacteria, including a circular chromosome, prokaryotic-type ribosomes, and similar proteins in the photosynthetic reaction center. The endosymbiotic theory suggests that photosynthetic bacteria were acquired (by endocytosis) by early eukaryotic cells to form the first plant cells. Therefore, chloroplasts may be photosynthetic bacteria that adapted to life inside plant cells. Like mitochondria, chloroplasts still possess their own DNA, separate from the nuclear DNA of their plant host cells and the genes in this chloroplast DNA resemble those in cyanobacteria. DNA in chloroplasts codes for redox proteins such as photosynthetic reaction centers. The CoRR Hypothesis proposes that this **Co**-location is required for **Redox Regulation**.

Cyanobacteria and the evolution of photosynthesis

The biochemical capacity to use water as the source for electrons in photosynthesis evolved once, in a common ancestor of extant cyanobacteria. The geological record indicates that this transforming event took place early in Earth's history, at least 2450–2320 million years ago (Ma), and possibly much earlier. Available evidence from

geobiological studies of Archean (>2500 Ma) sedimentary rocks indicates that life existed 3500 Ma, but the question of when oxygenic photosynthesis evolved is still unanswered. A clear paleontological window on cyanobacterial evolution opened about 2000 Ma, revealing an already-diverse biota of blue-greens. Cyanobacteria remained principal primary producers throughout the Proterozoic Eon (2500–543 Ma), in part because the redox structure of the oceans favored photoautotrophs capable of nitrogen fixation. Green algae joined blue-greens as major primary producers on continental shelves near the end of the Proterozoic, but only with the Mesozoic (251–65 Ma) radiations of dinoflagellates, coccolithophorids, and diatoms did primary production in marine shelf waters take modern form. Cyanobacteria remain critical to marine ecosystems as primary producers in oceanic gyres, as agents of biological nitrogen fixation, and, in modified form, as the plastids of marine algae.

A 2010 study by researchers at Tel Aviv University discovered that the Oriental hornet (*Vespa orientalis*) converts sunlight into electric power using a pigment called xanthopterin. This is the first scientific evidence of a member of the animal kingdom engaging in photosynthesis.

Discovery

Although some of the steps in photosynthesis are still not completely understood, the overall photosynthetic equation has been known since the 19th century.

Jan van Helmont began the research of the process in the mid-17th century when he carefully measured the mass of the soil used by a plant and the mass of the plant as it grew. After noticing that the soil mass changed very little, he hypothesized that the mass of the growing plant must come from the water, the only substance he added to the potted plant. His hypothesis was partially accurate—much of the gained mass also comes from carbon dioxide as well as water. However, this was a signaling point to the idea that the bulk of a plant's biomass comes from the inputs of photosynthesis, not the soil itself.

Joseph Priestley, a chemist and minister, discovered that when he isolated a volume of air under an inverted jar, and burned a candle in it, the candle would burn out very quickly, much before it ran out of wax. He further discovered that a mouse could similarly "injure" air. He then showed that the air that had been "injured" by the candle and the mouse could be restored by a plant.

In 1778, Jan Ingenhousz, court physician to the Austrian Empress, repeated Priestley's experiments. He discovered that it was the influence of sunlight on the plant that could cause it to revive a mouse in a matter of hours.

In 1796, Jean Senebier, a Swiss pastor, botanist, and naturalist, demonstrated that green plants consume carbon dioxide and release oxygen under the influence of light. Soon afterwards, Nicolas-Théodore de Saussure showed that the increase in mass of the plant as it grows could not be due only to uptake of CO₂, but also to the incorporation of water.

Thus the basic reaction by which photosynthesis is used to produce food (such as glucose) was outlined.

Cornelis Van Niel made key discoveries explaining the chemistry of photosynthesis. By studying purple sulfur bacteria and green bacteria he was the first scientist to demonstrate that photosynthesis is a light-dependent redox reaction, in which hydrogen reduces carbon dioxide.

Robert Emerson discovered two light reactions by testing plant productivity using different wavelengths of light. With the red alone, the light reactions were suppressed. When blue and red were combined, the output was much more substantial. Thus, there were two photosystems, one absorbing up to 600 nm wavelengths, the other up to 700. The former is known as PSII, the latter is PSI. PSI contains only chlorophyll a, PSII contains primarily chlorophyll a with most of the available chlorophyll b, among other pigments.

Further experiments to prove that the oxygen developed during the photosynthesis of green plants came from water, were performed by Robert Hill in 1937 and 1939. He showed that isolated chloroplasts give off oxygen in the presence of unnatural reducing agents like iron oxalate, ferricyanide or benzoquinone after exposure to light. The Hill reaction is as follows:



where A is the electron acceptor. Therefore, in light the electron acceptor is reduced and oxygen is evolved. Cyt b_6 , now known as a plastoquinone, is one electron acceptor.

Samuel Ruben and Martin Kamen used radioactive isotopes to determine that the oxygen liberated in photosynthesis came from the water.

Melvin Calvin and Andrew Benson, along with James Bassham, elucidated the path of carbon assimilation (the photosynthetic carbon reduction cycle) in plants. The carbon reduction cycle is known as the Calvin cycle, which inappropriately ignores the contribution of Bassham and Benson. Many scientists refer to the cycle as the Calvin-Benson Cycle, Benson-Calvin, and some even call it the Calvin-Benson-Bassham (or CBB) Cycle.

A Nobel Prize winning scientist, Rudolph A. Marcus, was able to discover the function and significance of the electron transport chain.

Otto Heinrich Warburg and Dean Burk discovered the I-quantum photosynthesis reaction that splits the CO₂, activated by the respiration.

Factors



The leaf is the primary site of photosynthesis in plants.

There are three main factors affecting photosynthesis and several corollary factors. The three main are:

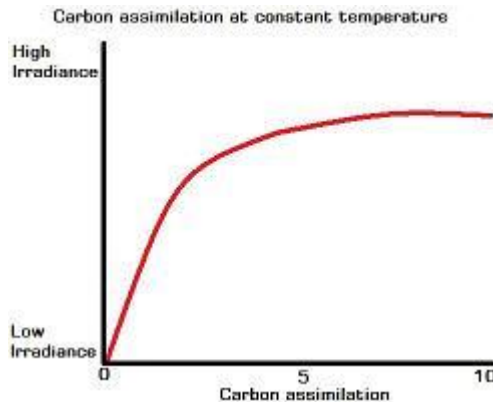
- Light irradiance and wavelength
- Carbon dioxide concentration
- Temperature.

Light intensity (irradiance), wavelength and temperature

In the early 20th century Frederick Frost Blackman along with Albert Einstein investigated the effects of light intensity (irradiance) and temperature on the rate of carbon assimilation.

- At constant temperature, the rate of carbon assimilation varies with irradiance, initially increasing as the irradiance increases. However at higher irradiance this relationship no longer holds and the rate of carbon assimilation reaches a plateau.
- At constant irradiance, the rate of carbon assimilation increases as the temperature is increased over a limited range. This effect is only seen at high irradiance levels.

At low irradiance, increasing the temperature has little influence on the rate of carbon assimilation.



Carbon assimilation at a constant temperature.

These two experiments illustrate vital points: firstly, from research it is known that photochemical reactions are not generally affected by temperature. However, these experiments clearly show that temperature affects the rate of carbon assimilation, so there must be two sets of reactions in the full process of carbon assimilation. These are of course the light-dependent 'photochemical' stage and the light-independent, temperature-dependent stage. Second, Blackman's experiments illustrate the concept of limiting factors. Another limiting factor is the wavelength of light. Cyanobacteria, which reside several meters underwater, cannot receive the correct wavelengths required to cause photoinduced charge separation in conventional photosynthetic pigments. To combat this problem, a series of proteins with different pigments surround the reaction center. This unit is called a phycobilisome.

Carbon dioxide levels and photorespiration

As carbon dioxide concentrations rise, the rate at which sugars are made by the light-independent reactions increases until limited by other factors. RuBisCO, the enzyme that captures carbon dioxide in the light-independent reactions, has a binding affinity for both carbon dioxide and oxygen. When the concentration of carbon dioxide is high, RuBisCO will fix carbon dioxide. However, if the carbon dioxide concentration is low, RuBisCO will bind oxygen instead of carbon dioxide. This process, called photorespiration, uses energy, but does not produce sugars.

RuBisCO oxygenase activity is disadvantageous to plants for several reasons:

1. One product of oxygenase activity is phosphoglycolate (2 carbon) instead of 3-phosphoglycerate (3 carbon). Phosphoglycolate cannot be metabolized by the Calvin-Benson cycle and represents carbon lost from the cycle. A high oxygenase activity, therefore, drains the sugars that are required to recycle ribulose 5-bisphosphate and for the continuation of the Calvin-Benson cycle.

2. Phosphoglycolate is quickly metabolized to glycolate that is toxic to a plant at a high concentration; it inhibits photosynthesis.
3. Salvaging glycolate is an energetically expensive process that uses the glycolate pathway and only 75% of the carbon is returned to the Calvin-Benson cycle as 3-phosphoglycerate. The reactions also produce ammonia (NH₃) which is able to diffuse out of the plant leading to a loss of nitrogen.

A highly simplified summary is:



The salvaging pathway for the products of RuBisCO oxygenase activity is more commonly known as photorespiration, since it is characterized by light-dependent oxygen consumption and the release of carbon dioxide.

Chapter 2

Photomorphogenesis

In developmental biology, **photomorphogenesis** is light-mediated development. The photomorphogenesis of plants is often studied by using tightly-frequency-controlled light sources to grow the plants.

Germination

Light has profound effects on the development of plants. The light-mediated changes in plant growth and development are called photomorphogenesis. The most striking effects of light are observed when a germinating seedling emerges from the soil and is exposed to light for the first time.

Normally the seedling radicle (root) emerges first from the seed, and the shoot appears as the root becomes established. Later, with growth of the shoot (particularly when it emerges into the light) there is increased secondary root formation and branching. This coordinated progression of developmental responses are early manifestations of correlative growth phenomena where the root affects the growth of the shoot and vice versa. To a large degree, these coordinated differential growth responses are hormone mediated.

In the absence of light, plants develop an etiolated growth pattern. Etiolation of the seedling adapts it to emerging from the soil.

Comparison of dark-grown (etiolated) and light-grown (de-etiolated) seedlings

Etiolated characteristics:

- Distinct "apical hook" (dicot) or coleoptile (monocot)
- No leaf growth

- No chlorophyll
- Rapid stem elongation
- Limited radial expansion of stem
- Limited root elongation
- Limited production of lateral roots

De-etiolated characteristics:

- Apical hook opens or coleoptile splits open
- Leaf growth promoted
- Chlorophyll produced
- Stem elongation suppressed
- Radial expansion of stem
- Root elongation promoted
- Lateral root development accelerated

The developmental changes characteristic of photomorphogenesis shown by de-etiolated seedlings, are induced by light. Typically, plants are responsive to wavelengths of light in the blue, red and far-red regions of the spectrum through the action of several different photosensory systems. The photoreceptors for red and far-red wavelengths are known as phytochromes. There are at least 5 members of the phytochrome family of photoreceptors. There are several blue light photoreceptors.

Photoreceptor systems in plants

Plants use phytochrome to detect and respond to red and far-red wavelengths.

Phytochromes are proteins with a light absorbing pigment attached (chromophore).

The chromophore is a linear tetrapyrrole called phytochromobilin.

The phytochrome apoprotein is synthesized in the Pr form. Upon binding the chromophore, the holoprotein becomes sensitive to light. If it absorbs red light it will change conformation to the biologically active Pfr form. The Pfr form can absorb red light and switch back to the Pr form.

Most plants have multiple phytochromes encoded by different genes. The different forms of phytochrome control different responses but there is also a lot of redundancy so that in the absence of one phytochrome, another may take on the missing functions.

Arabidopsis has 5 phytochromes - PHYA, PHYB, PHYC, PHYD, PHYE

Molecular analyses of phytochrome and phytochrome-like genes in higher plants (ferns, mosses, algae) and photosynthetic bacteria have shown that phytochromes evolved from prokaryotic photoreceptors that predated the origin of plants.

Blue light systems

As for the red/far-red system, plants contain multiple blue light photoreceptors which have different functions.

Based on studies with action spectra, mutants and molecular analyses, it has been determined that higher plants contain at least 4, and probably 5, different blue light photoreceptors.

Cryptochromes were the first blue light receptors to be isolated and characterized from any organism. The proteins use a flavin as a chromophore. The cryptochromes have evolved from microbial DNA-photolyase, an enzyme that carries out light-dependent repair of UV damaged DNA.

Two cryptochromes have been identified in plants.

Cryptochromes control stem elongation, leaf expansion, circadian rhythms and flowering time.

In addition to blue light, cryptochromes also perceive long wavelength UV irradiation (UV-A).

Phototropin is the blue light photoreceptor that controls phototropism. It also uses flavin as chromophore. Only one phototropin has been identified so far (NPH1). Phototropin also perceives long wavelength UV irradiation (UV-A) in addition to blue light.

Recent experiments indicate that a 4th blue light receptor exists that uses a carotenoid as a chromophore. This new photoreceptor controls blue light induction of stomatal opening. However, the gene and protein have not yet been found.

Other blue light responses exist that seem to function in plants that are missing the cryptochrome, phototropin and carotenoid photoreceptors suggesting that at least one more will be found.

Since the cryptochromes were discovered in plants, several labs have identified homologous genes and photoreceptors in a number of other organisms, including

humans, mice and flies. It appears that in mammals and flies, the cryptochromes function in entrainment of the biological clock. Indeed, in flies, a cryptochrome may be a functional part of the clock mechanism.

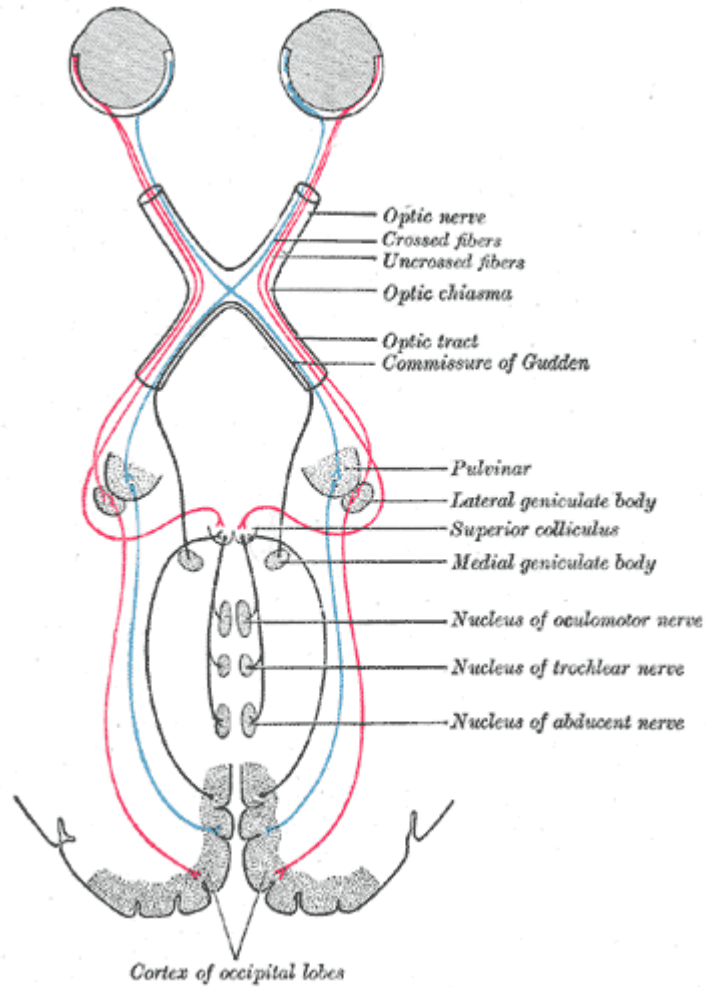
UV systems

Based on various responses to UV light, it is assumed that there are UV-specific photoreceptors....

Chapter 3

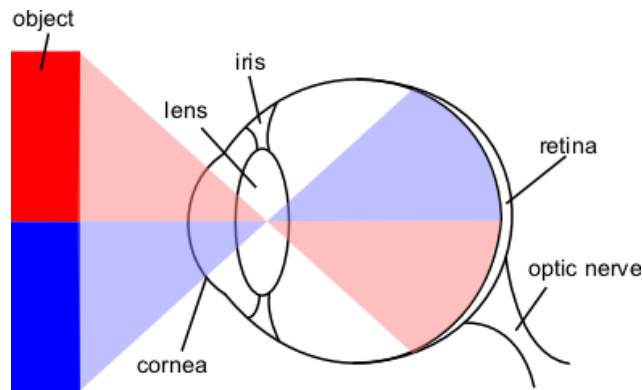
Visual System

The **visual system** is the part of the central nervous system which enables organisms to process visual detail, as well as enabling several non-image forming photoresponse functions. It interprets information from visible light to build a representation of the surrounding world. The visual system accomplishes a number of complex tasks, including the reception of light and the formation of monocular representations; the construction of a binocular perception from a pair of two dimensional projections; the identification and categorization of visual objects; assessing distances to and between objects; and guiding body movements in relation to visual objects. The psychological manifestation of visual information is known as visual perception, a lack of which is called blindness. Non-image forming visual functions, independent of visual perception, include the pupillary light reflex (PLR) and circadian photoentrainment.



The visual system includes the eyes, the connecting pathways through to the visual cortex and other parts of the brain. The illustration shows the mammalian system.

Introduction



Optical layout of the eye

The image projected onto the retina is inverted due to the optics of the eye.

Here we mostly describes the visual system of mammals, although other "higher" animals have similar visual systems. In this case, the visual system consists of:

- The eye, especially the retina
- The optic nerve
- The optic chiasma
- The optic tract
- The lateral geniculate body
- The optic radiation
- The visual cortex
- The visual association cortex.

Different species are able to see different parts of the light spectrum; for example, bees can see into the ultraviolet, while pit vipers can accurately target prey with their pit organs, which are sensitive to infrared radiation.

History

In the second half of the 19th century, many motifs of the nervous system were identified such as the neuron doctrine and brain localisation, which related to the neuron being the basic unit of the nervous system and functional localisation in the brain, respectively. These would become tenets of the fledgling neuroscience and would support further understanding of the visual system.

The notion that the cerebral cortex is divided into functionally distinct cortices now known to be responsible for capacities such as touch (somatosensory cortex), movement (motor cortex), and vision (visual cortex), was first proposed by Franz Joseph Gall in 1810. Evidence for functionally distinct areas of the brain (and, specifically, of the cerebral cortex) mounted throughout the 19th century with discoveries by Paul Broca of the language center (1861), and Gustav Fritsch and Edouard Hitzig of the motor cortex (1871). Based on selective damage to parts of the brain and the functional effects this would produce (lesion studies), David Ferrier proposed that visual function was localised to the parietal lobe of the brain in 1876. In 1881, Hermann Munk more accurately located vision in the occipital lobe, where the primary visual cortex is now known to be.

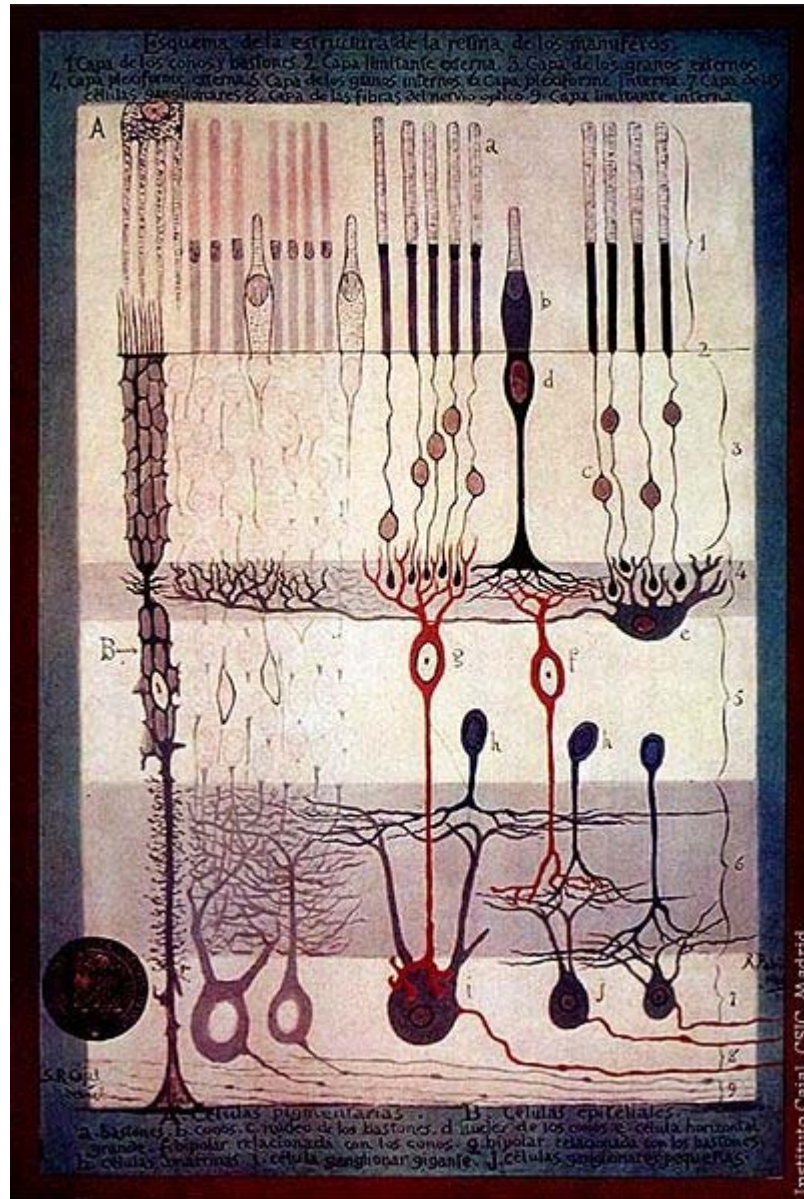
Biology of the visual system

Eye

The eye is a complex biological device. The functioning of a camera is often compared with the workings of the eye, mostly since both focus light from external objects in the field of view onto a light-sensitive medium. In the case of the camera, this medium is film or an electronic sensor; in the case of the eye, it is an array of visual receptors. With this simple geometrical similarity, based on the laws of optics, the eye functions as a transducer, as does a CCD camera.

Light entering the eye is refracted as it passes through the cornea. It then passes through the pupil (controlled by the iris) and is further refracted by the lens. The cornea and lens act together as a compound lens to project an inverted image onto the retina.

Retina



S. Ramón y Cajal, *Structure of the Mammalian Retina*, 1900

The retina consists of a large number of photoreceptor cells which contain particular protein molecules called opsins. In humans, two types of opsins are involved in conscious vision: rod opsins and cone opsins. (A third type, melanopsin in some of the retinal ganglion cells (RGC), part of the body clock mechanism, is probably not involved in conscious vision, as these RGC do not project to the lateral geniculate nucleus (LGN) but

to the pretectal olivary nucleus (PON).) An opsin absorbs a photon (a particle of light) and transmits a signal to the cell through a signal transduction pathway, resulting in hyperpolarization of the photoreceptor.

Rods and cones differ in function. Rods are found primarily in the periphery of the retina and are used to see at low levels of light. Cones are found primarily in the center (or fovea) of the retina. There are three types of cones that differ in the wavelengths of light they absorb; they are usually called short or blue, middle or green, and long or red. Cones are used primarily to distinguish color and other features of the visual world at normal levels of light.

In the retina, the photoreceptors synapse directly onto bipolar cells, which in turn synapse onto ganglion cells of the outermost layer, which will then conduct action potentials to the brain. A significant amount of visual processing arises from the patterns of communication between neurons in the retina. About 130 million photoreceptors absorb light, yet roughly 1.2 million axons of ganglion cells transmit information from the retina to the brain. The processing in the retina includes the formation of center-surround receptive fields of bipolar and ganglion cells in the retina, as well as convergence and divergence from photoreceptor to bipolar cell. In addition, other neurons in the retina, particularly horizontal and amacrine cells, transmit information laterally (from a neuron in one layer to an adjacent neuron in the same layer), resulting in more complex receptive fields that can be either indifferent to color and sensitive to motion or sensitive to color and indifferent to motion. **Mechanism of generating visual signals:** The retina adapts to its change in light through the use of the rods. In the dark, the retinal has a bent shape called cis-retinal. When light is present, the retinal changes to a straight form called trans-retinal and breaks away from the opsin. This is called bleaching because the purified rhodopsin changes from violet to colorless in the light. In the dark, the rhodopsin absorbs no light therefore releasing glutamate cells which inhibit the bipolar cell. This inhibits the release of neurotransmitters to the ganglion cell. In the light, glutamate secretion ceases which no longer inhibits the bipolar cell from releasing neurotransmitters to the ganglion cell and therefore an image can be detected.

The final result of all this processing is five different populations of ganglion cells that send visual (image-forming and non-image-forming) information to the brain:

1. M cells, with large center-surround receptive fields that are sensitive to depth, indifferent to color, and rapidly adapt to a stimulus;
2. P cells, with smaller center-surround receptive fields that are sensitive to color and shape;
3. K cells, with very large center-only receptive fields that are sensitive to color and indifferent to shape or depth;
4. another population that is intrinsically photosensitive; and
5. a final population that is used for eye movements.

A 2006 University of Pennsylvania study calculated the approximate bandwidth of human retinas to be about 8960 kilobits per second, whereas guinea pig retinas transfer at about 875 kilobits.

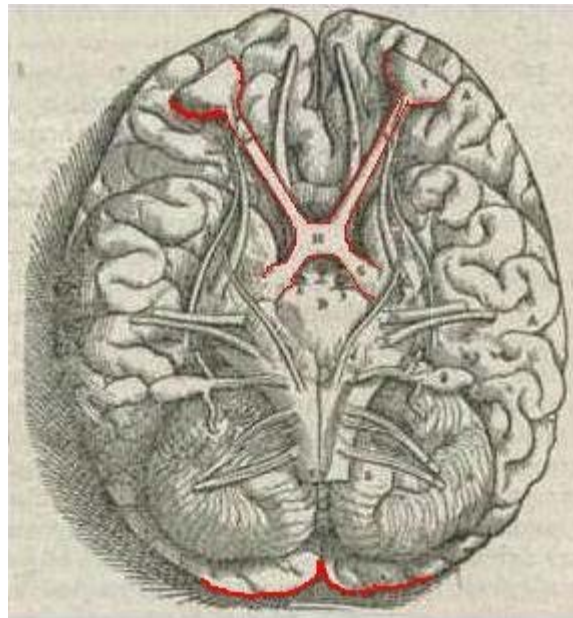
In 2007 Zaidi and co-researchers on both sides of the Atlantic studying patients without rods and cones, discovered that the novel photoreceptive ganglion cell in humans also has a role in conscious and unconscious visual perception. The peak spectral sensitivity was 481 nm. This shows that there are two pathways for sight in the retina – one based on classic photoreceptors (rods and cones) and the other, newly discovered, based on photoreceptive ganglion cells which act as rudimentary visual brightness detectors.

Photochemistry

In the visual system, **retinal**, technically called *retinene₁* or "retinaldehyde", is a light-sensitive retinene molecule found in the rods and cones of the retina. Retinal is the fundamental structure involved in the transduction of light into visual signals, i.e. nerve impulses in the ocular system of the central nervous system. In the presence of light, the retinal molecule changes configuration and as a result a nerve impulse is generated.

Fibers to thalamus

Optic nerve



Information flow from the eyes (top), crossing at the optic chiasma, joining left and right eye information in the optic tract, and layering left and right visual stimuli in the lateral geniculate nucleus. V1 in red at bottom of image. (1543 image from Andreas Vesalius' *Fabrica*)

The information about the image via the eye is transmitted to the brain along the optic nerve. Different populations of ganglion cells in the retina send information to the brain through the optic nerve. About 90% of the axons in the optic nerve go to the lateral geniculate nucleus in the thalamus. These axons originate from the M, P, and K ganglion cells in the retina, see above. This parallel processing is important for reconstructing the visual world; each type of information will go through a different route to perception. Another population sends information to the superior colliculus in the midbrain, which assists in controlling eye movements (saccades) as well as other motor responses.

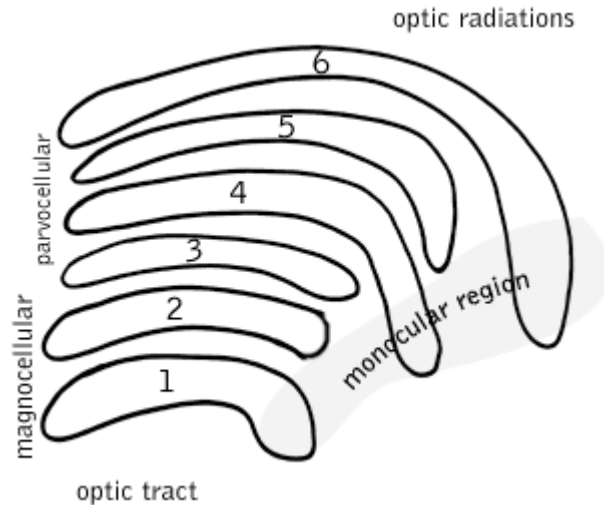
A final population of photosensitive ganglion cells, containing melanopsin, sends information via the retinohypothalamic tract (RHT) to the pretectum (pupillary reflex), to several structures involved in the control of circadian rhythms and sleep such as the suprachiasmatic nucleus (SCN, the biological clock), and to the ventrolateral preoptic nucleus (VLPO, a region involved in sleep regulation). A recently discovered role for photoreceptive ganglion cells is that they mediate conscious and unconscious vision – acting as rudimentary visual brightness detectors as shown in rodless coneless eyes.

Optic chiasm

The optic nerves from both eyes meet and cross at the optic chiasm, at the base of the hypothalamus of the brain. At this point the information coming from both eyes is combined and then splits according to the visual field. The corresponding halves of the field of view (right and left) are sent to the left and right halves of the brain, respectively, to be processed. That is, the right side of primary visual cortex deals with the left half of the *field of view* from both eyes, and similarly for the left brain. A small region in the center of the field of view is processed redundantly by both halves of the brain.

Optic tract

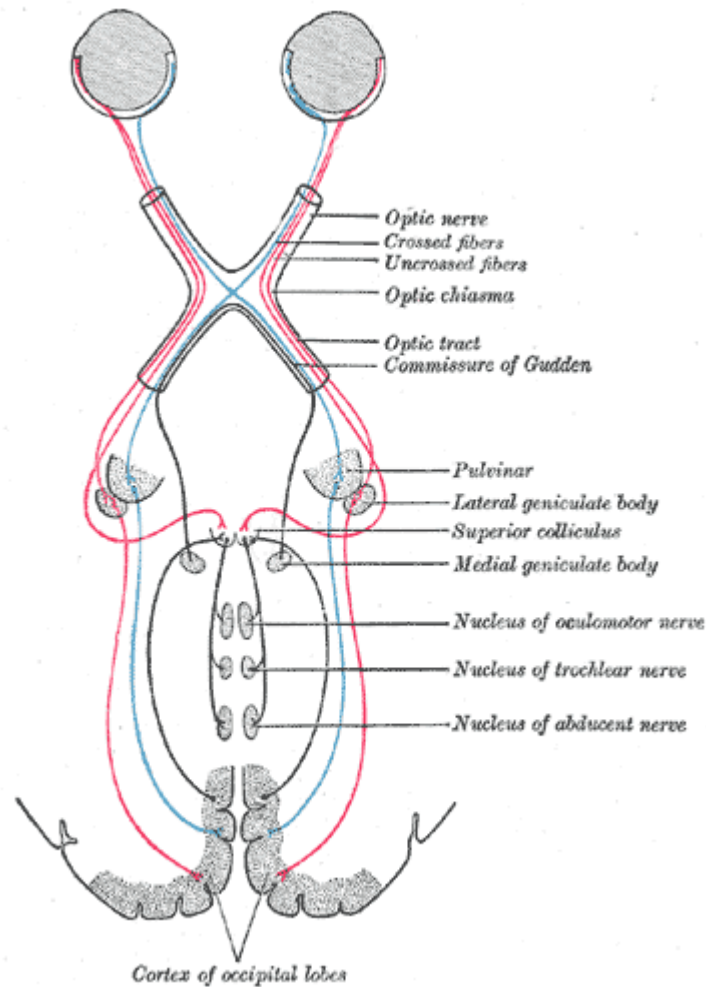
Information from the right *visual field* (now on the left side of the brain) travels in the left optic tract. Information from the left *visual field* travels in the right optic tract. Each optic tract terminates in the lateral geniculate nucleus (LGN) in the thalamus.



Six layers in the LGN

Lateral geniculate nucleus

The **lateral geniculate nucleus** (LGN) is a sensory relay nucleus in the thalamus of the brain. The LGN consists of six layers in humans and other primates starting from catarhinians, including cercopithecidae and apes. Layers 1, 4, and 6 correspond to information from the contralateral (crossed) fibers of the nasal visual field; layers 2, 3, and 5 correspond to information from the ipsilateral (uncrossed) fibers of the temporal visual field. Layer one (1) contains M cells which correspond to the M (magnocellular) cells of the optic nerve of the opposite eye and are concerned with depth or motion. Layers four and six (4 & 6) of the LGN also connect to the opposite eye, but to the P cells (color and edges) of the optic nerve. By contrast, layers two, three and five (2, 3, & 5) of the LGN connect to the M cells and P (parvocellular) cells of the optic nerve for the same side of the brain as its respective LGN. Spread out, the six layers of the LGN are the area of a credit card and about three times its thickness. The LGN is rolled up into two ellipsoids about the size and shape of two small birds' eggs. In between the six layers are smaller cells that receive information from the K cells (color) in the retina. The neurons of the LGN then relay the visual image to the primary visual cortex (V1) which is located at the back of the brain (caudal end) in the occipital lobe in and close to the calcarine sulcus. The LGN is not just a simple relay station but it's also a center for processing; it receives reciprocal input from the cortical and subcortical and reciprocal innervation from the visual cortex.



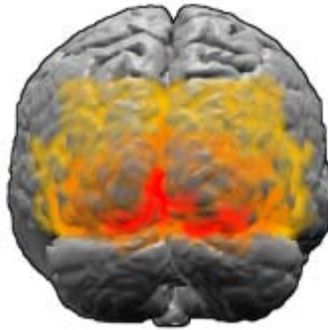
Scheme showing central connections of the optic nerves and optic tracts.

Optic radiation

The **optic radiations**, one on each side of the brain, carry information from the thalamic lateral geniculate nucleus to layer 4 of the visual cortex. The P layer neurons of the LGN relay to V1 layer 4C β . The M layer neurons relay to V1 layer 4C α . The K layer neurons in the LGN relay to large neurons called blobs in layers 2 and 3 of V1.

There is a direct correspondence from an angular position in the field of view of the eye, all the way through the optic tract to a nerve position in V1. At this juncture in V1, the image path ceases to be straightforward; there is more cross-connection within the visual cortex.

Visual cortex



Visual cortex: V1, V2, V3, V4, V5 (also called MT)

The visual cortex is the largest system in the human brain and is responsible for processing the visual image. It lies at the rear of the brain (highlighted in the image), above the cerebellum. The region that receives information directly from the LGN is called the primary visual cortex, (also called V1 and striate cortex). Visual information then flows through a cortical hierarchy. These areas include V2, V3, V4 and area V5/MT (the exact connectivity depends on the species of the animal). These secondary visual areas (collectively termed the extrastriate visual cortex) process a wide variety of visual primitives. Neurons in V1 and V2 respond selectively to bars of specific orientations, or combinations of bars. These are believed to support edge and corner detection. Similarly, basic information about color and motion is processed here.

Visual association cortex

As visual information passes forward through the visual hierarchy, the complexity of the neural representations increase. Whereas a V1 neuron may respond selectively to a line segment of a particular orientation in a particular retinotopic location, neurons in the lateral occipital complex respond selectively to complete object (e.g., a figure drawing), and neurons in visual association cortex may respond selectively to human faces, or to a particular object.

Along with this increasing complexity of neural representation may come a level of specialization of processing into two distinct pathways: the dorsal stream and the ventral stream (the Two Streams hypothesis, first proposed by Ungerleider and Mishkin in 1982). The dorsal stream, commonly referred to as the "where" stream, is involved in spatial attention (covert and overt), and communicates with regions that control eye movements and hand movements. More recently, this area has been called the "how" stream to emphasize its role in guiding behaviors to spatial locations. The ventral stream, commonly referred as the "what" stream, is involved in the recognition, identification and categorization of visual stimuli.

However, there is still much debate about the degree of specialization within these two pathways, since they are in fact heavily interconnected.

Chapter 4

Circadian Rhythm

A **circadian rhythm** is an endogenously driven roughly 24-hour cycle in biochemical, physiological, or behavioural processes. Circadian rhythms have been widely observed, in plants, animals, fungi and cyanobacteria. The term "circadian" comes from the Latin *circa*, meaning "around", and *diem* or *dies*, meaning "day". The formal study of biological temporal rhythms such as daily, tidal, weekly, seasonal, and annual rhythms is called chronobiology. Although circadian rhythms are endogenous ("built-in", self-sustained), they are adjusted (entrained) to the environment by external cues called zeitgebers, the primary one of which is daylight.

History

The earliest known account of a circadian process dates from the 4th century BC, when Androsthenes, a ship captain serving under Alexander the Great, described diurnal leaf movements of the tamarind tree. The first modern observation of endogenous circadian oscillation was by the French scientist Jean-Jacques d'Ortous de Mairan in the 18th century; he noted that 24-hour patterns in the movement of the leaves of the plant *Mimosa pudica* continued even when the plants were kept in constant darkness.

In 1896, Patrick and Gilbert observed that during a prolonged period of sleep deprivation, sleepiness increases and decreases with a period of approximately 24 hours. In 1918, J.S. Szymanski showed that animals are capable of maintaining 24-hour activity patterns in the absence of external cues such as light and changes in temperature. Joseph Takahashi discovered the first mammalian 'clock gene' in 1994.

The term "circadian" was coined by Franz Halberg in the late 1950s.

Criteria

To be called circadian, a biological rhythm must meet these four general criteria:

1. **The rhythms repeat once a day (they have a 24-hour period).** In order to keep track of the time of day, a clock must be at the same point at the same time each day, i.e. repeat every 24 hours.
2. **The rhythms persist in the absence of external cues (endogenous).** The rhythm persists in constant conditions with a period of about 24 hours. The rationale for this criterion is to distinguish circadian rhythms from simple responses to daily external cues. A rhythm cannot be said to be endogenous unless it has been tested in conditions without external periodic input.
3. **The rhythms can be adjusted to match the local time (entrainable).** The rhythm can be reset by exposure to external stimuli (such as light and heat), a process called entrainment. The rationale for this criterion is to distinguish circadian rhythms from other imaginable endogenous 24-hour rhythms that are immune to resetting by external cues and, hence, do not serve the purpose of estimating the local time. Travel across time zones illustrates the necessity of the ability to adjust the biological clock so that it can reflect the local time and anticipate what will happen next. As their circadian clock is resetting, people will usually experience jet lag.
4. **The rhythms maintain circadian periodicity over a range of physiological temperatures (exhibit temperature compensation).** Some organisms live at a broad range of temperatures, and the thermal energy will affect the kinetics of all molecular processes in their cell(s). In order to keep track of time, the organism's circadian clock must maintain a roughly 24-hour periodicity despite the changing kinetics, a property known as temperature compensation.

Origin

Photosensitive proteins and circadian rhythms are believed to have originated in the earliest cells, with the purpose of protecting the replicating of DNA from high ultraviolet radiation during the daytime. As a result, replication was relegated to the dark. The fungus *Neurospora*, which exists today, retains this clock-regulated mechanism.

Circadian rhythms allow organisms to anticipate and prepare for precise and regular environmental changes; they have great value in relation to the outside world. The rhythmicity appears to be as important in regulating and coordinating internal metabolic processes, as in coordinating with the environment. This is suggested by the maintenance (heritability) of circadian rhythms in fruit flies after several hundred generations in constant laboratory conditions, as well as in creatures in constant darkness in the wild, and by the experimental elimination of behavioural but not physiological circadian rhythms in quail.

The simplest known circadian clock is that of the prokaryotic cyanobacteria. Recent research has demonstrated that the circadian clock of *Synechococcus elongatus* can be reconstituted *in vitro* with just the three proteins of their central oscillator. This clock has been shown to sustain a 22-hour rhythm over several days upon the addition of ATP. Previous explanations of the prokaryotic circadian timekeeper were dependent upon a DNA transcription/translation feedback mechanism.

In 1971, Ronald J. Konopka and Seymour Benzer first identified a genetic component of the biological clock using the fruit fly as a model system. Three mutant lines of flies displayed aberrant behaviour: one had a shorter period, another had a longer one, and the third had none. All three mutations mapped to the same gene, which was named "period". The same gene was identified to be defective in the sleep disorder FASPS (Familial advanced sleep phase syndrome) in human beings thirty years later, underscoring the conserved nature of the molecular circadian clock through evolution. Many more genetic components of the biological clock are now known. Their interactions result in an interlocked feedback loop of gene products resulting in periodic fluctuations that the cells of the body interpret as a specific time of the day.

A great deal of research on biological clocks was done in the latter half of the 20th century. It is now known that the molecular circadian clock can function within a single cell; i.e., it is cell-autonomous. At the same time, different cells may communicate with each other resulting in a synchronised output of electrical signaling. These may interface with endocrine glands of the brain to result in periodic release of hormones. The receptors for these hormones may be located far across the body and synchronise the peripheral clocks of various organs. Thus, the information of the time of the day as relayed by the eyes travels to the clock in the brain, and, through that, clocks in the rest of the body may be synchronised. This is how the timing of, for example, sleep/wake, body temperature, thirst, and appetite are coordinately controlled by the biological clock.

Importance in animals

Circadian rhythmicity is present in the sleeping and feeding patterns of animals, including human beings. There are also clear patterns of core body temperature, brain wave activity, hormone production, cell regeneration and other biological activities. In addition, photoperiodism, the physiological reaction of organisms to the length of day or night, is vital to both plants and animals, and the circadian system plays a role in the measurement and interpretation of day length.

“ Timely prediction of seasonal periods of weather conditions, food availability or predator activity is crucial for survival of many species. Although not the only parameter, the changing length of the photoperiod ('daylength') is the most predictive environmental cue for the seasonal timing of physiology and behavior, most notably for timing of migration, hibernation and reproduction. ”

Impact of light–dark cycle

The rhythm is linked to the light–dark cycle. Animals, including humans, kept in total darkness for extended periods eventually function with a freerunning rhythm. Each "day", their sleep cycle is pushed back or forward, depending on whether their endogenous period is shorter or longer than 24 hours. The environmental cues that reset the rhythms each day are called *zeitgebers* (from the German, "time-givers"). It is interesting to note

that totally-blind subterranean mammals (e.g., blind mole rat *Spalax* sp.) are able to maintain their endogenous clocks in the apparent absence of external stimuli. Although they lack image-forming eyes, their photoreceptors (detect light) are still functional; as well, they do surface periodically.

Freerunning organisms that normally have one or two consolidated sleep episodes will still have them when in an environment shielded from external cues, but the rhythm is, of course, not entrained to the 24-hour light–dark cycle in nature. The sleep–wake rhythm may, in these circumstances, become out of phase with other circadian or ultradian rhythms such as metabolic, hormonal, CNS electrical, or neurotransmitter rhythms.

Recent research has influenced the design of spacecraft environments, as systems that mimic the light–dark cycle have been found to be highly beneficial to astronauts.

Arctic animals

Norwegian researchers at the University of Tromsø have shown that some Arctic animals (ptarmigan, reindeer) show circadian rhythms only in the parts of the year that have daily sunrises and sunsets. In one study of reindeer, animals at 70 degrees North showed circadian rhythms in the autumn, winter, and spring, but not in the summer. Reindeer at 78 degrees North showed such rhythms only autumn and spring. The researchers suspect that other Arctic animals as well may not show circadian rhythms in the constant light of summer and the constant dark of winter.

However, another study in northern Alaska found that ground squirrels and porcupines strictly maintained their circadian rhythms through 82 days and nights of sunshine. The researchers speculate that these two small mammals see that the apparent distance between the sun and the horizon is shortest once a day, and, thus, a sufficient signal to adjust by.

Butterfly migration

The navigation of the fall migration of the Eastern North American monarch butterfly (*Danaus plexippus*) to their overwintering grounds in central Mexico uses a time-compensated sun compass that depends upon a circadian clock in their antennae.

In plants

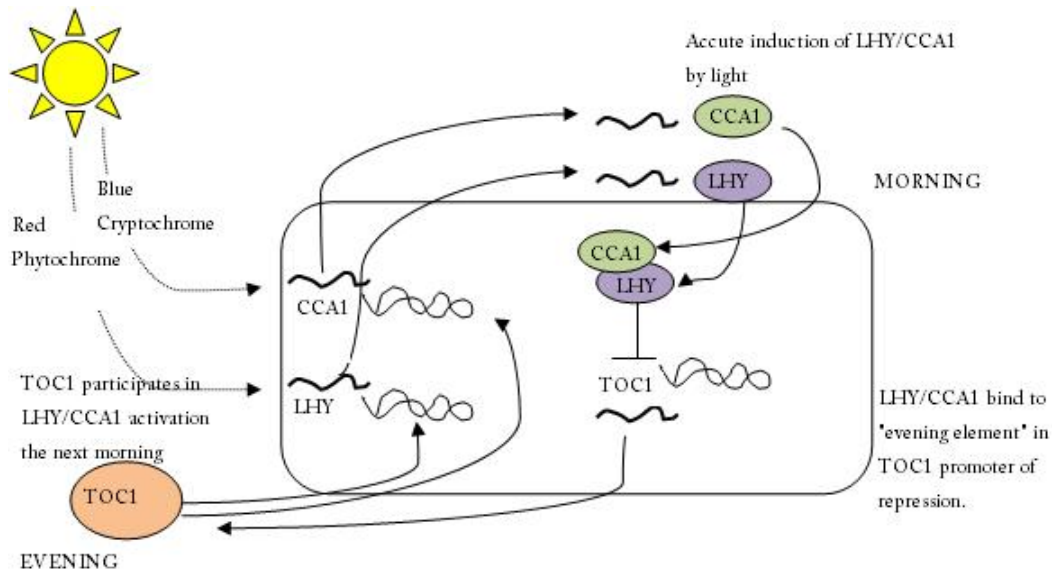


Diagram showing a small portion of the transcriptional feedback loop in *Arabidopsis*. LHY and CCA1 are considered negative elements due to its repression against TOC1 in the morning while TOC1 is considered a positive element because it results in increased transcription of LHY and CCA1 during the evening because of its accumulation.

Plant circadian rhythms tell the plant what season it is in and when to flower for the best chance of attracting insects to pollinate them and can include leaf movement, growth, germination, stomatal/gas exchange, enzyme activity, photosynthetic activity, and fragrance emission. Circadian rhythms occur as a biological rhythm with light, are endogenously generated and self sustaining, and are relatively constant over a range of ambient temperatures. Circadian rhythms feature a transcriptional feedback loop, a presence of PAS proteins, and several photoreceptors that fine-tune the clock to different light conditions. Anticipation of changes in the environment changes the physiological state that provides plants with an adaptive advantage. A better understanding of plant circadian rhythms has applications in agriculture such as helping farmers stagger crop harvests thus extending crop availability, and to secure against massive losses due to weather.

Clocks are set through signals such as light, temperature, and nutrient availability, so that the internal time matches the local time. Light is the signal and is sensed by a wide variety of photoreceptors. Red and blue light are absorbed through several phytochromes and cryptochromes. One phytochrome, phyA, is the main phytochrome in dark-grown seedlings, but rapidly degrades in light to produce Cry1. Phytochromes B–E are more stable with phyB the main phytochrome in light-grown seedlings. The cryptochrome (cry) gene is also a light-sensitive component of the circadian clock. Cryptochromes 1–2 (involved in blue–UVA) help to maintain the period length in the clock through a whole range of light conditions.

The central oscillator generates a self-sustaining rhythm and is made of two genes: CCA1 (Circadian and Clock Associated 1) and LHY (Late Elongated Hypocotyl) that encode closely related MYB transcription factors that regulate circadian rhythms in *Arabidopsis*. When CCA1 and LHY are overexpressed (under constant light or dark conditions) plants become arrhythmic and mRNA signals reduce contributing to a negative feedback loop. CCA1 and LHY expression oscillates and peaks in early morning while TOC1 oscillates and peaks in early evening. From past observations and studies, it is hypothesised that these three components model a negative feedback loop in which over-expressed CCA1 and LHY repress TOC1 and over-expressed TOC1 is a positive regulator CCA1 and LHY.

Biological clock in mammals

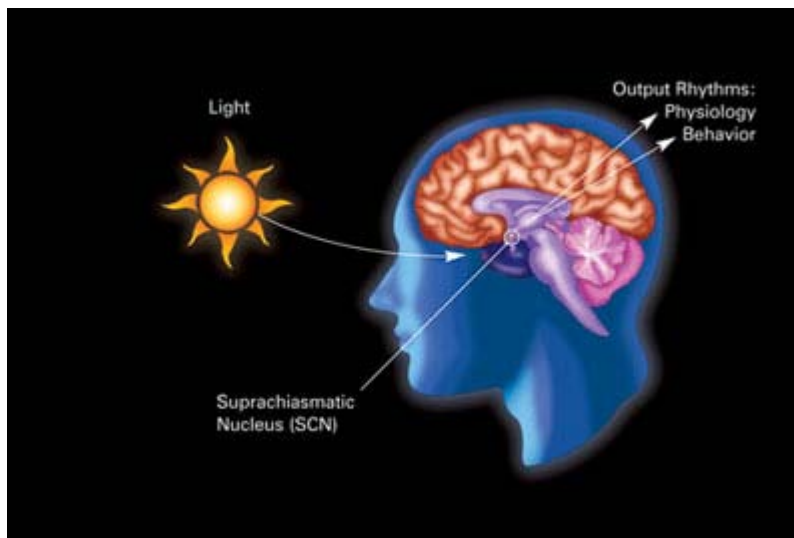


Diagram illustrating the influence of light and darkness on circadian rhythms and related physiology and behaviour through the suprachiasmatic nucleus in humans.

The primary circadian "clock" in mammals is located in the suprachiasmatic nucleus (or nuclei) (SCN), a pair of distinct groups of cells located in the hypothalamus. Destruction of the SCN results in the complete absence of a regular sleep–wake rhythm. The SCN receives information about illumination through the eyes. The retina of the eye contains "classical" photoreceptors ("rods" and "cones"), which are used for conventional vision. But the retina also contains specialized ganglion cells which are directly photosensitive,

and project directly to the SCN where they help in the entrainment of this master circadian clock.

These cells contain the photopigment melanopsin and their signals follow a pathway called the retinohypothalamic tract, leading to the SCN. If cells from the SCN are removed and cultured, they maintain their own rhythm in the absence of external cues.

The SCN takes the information on the lengths of the day and night from the retina, interprets it, and passes it on to the pineal gland, a tiny structure shaped like a pine cone and located on the epithalamus. In response, the pineal secretes the hormone melatonin. Secretion of melatonin peaks at night and ebbs during the day and its presence provides information about night-length.

Several studies have indicated that pineal melatonin feeds back on SCN rhythmicity to modulate circadian patterns of activity and other processes. However, the nature and system-level significance of this feedback are unknown.

The circadian rhythms of humans can be entrained to slightly shorter and longer periods than the Earth's 24 hours. Researchers at Harvard have recently shown that human subjects can at least be entrained to a 23.5-hour cycle and a 24.65-hour cycle (the latter being the natural solar day-night cycle on the planet Mars).

Determining the human circadian rhythm

The classic phase markers for measuring the timing of a mammal's circadian rhythm are:

- melatonin secretion by the pineal gland
- core body temperature
- plasma level of cortisol.

For temperature studies, subjects must remain awake but calm and semi-reclined in near darkness while their rectal temperatures are taken continuously. The average human adult's temperature reaches its minimum at about 05:00 (5 a.m.), about two hours before habitual wake time, though variation is great among normal chronotypes.

Melatonin is absent from the system or undetectably low during daytime. Its onset in dim light, *dim-light melatonin onset* (DLMO), at about 21:00 (9 p.m.) can be measured in the blood or the saliva. Its major metabolite can also be measured in morning urine. Both DLMO and the midpoint (in time) of the presence of the hormone in the blood or saliva have been used as circadian markers. However, newer research indicates that the melatonin *offset* may be the more reliable marker. Benloucif et al. in Chicago in 2005 found that melatonin phase markers were more stable and more highly correlated with the timing of sleep than the core temperature minimum. They found that both sleep offset and melatonin offset were more strongly correlated with the various phase markers than sleep onset. In addition, the declining phase of the melatonin levels was more reliable and stable than the termination of melatonin synthesis.

One method used for measuring melatonin offset is to analyse a sequence of urine samples throughout the morning for the presence of the melatonin metabolite 6-sulphatoxymelatonin (aMT6s). Laberge et al. in Quebec in 1997 used this method in a study that confirmed the frequently found delayed circadian phase in healthy adolescents.

A third marker of the human pacemaker is the timing of the maximum plasma cortisol level. Klerman *et al.* in 2002 compared cortisol and temperature data to eight different analysis methods of plasma melatonin data, and found that "methods using plasma melatonin data may be considered more reliable than methods using CBT or cortisol data as an indicator of circadian phase in humans."

Outside the "master clock"

More-or-less independent circadian rhythms are found in many organs and cells in the body outside the suprachiasmatic nuclei (SCN), the "master clock". These clocks, called peripheral oscillators, are found in the oesophagus, lungs, liver, pancreas, spleen, thymus, and the skin. Though oscillators in the skin respond to light, a systemic influence has not been proven so far. There is also some evidence that the olfactory bulb and prostate may experience oscillations when cultured, suggesting that these structures may also be weak oscillators.

Furthermore, liver cells, for example, appear to respond to feeding rather than to light. Cells from many parts of the body appear to have freerunning rhythms.

Light and the biological clock

Light resets the biological clock in accordance with the phase response curve (PRC). Depending on the timing, light can advance or delay the circadian rhythm. Both the PRC and the required illuminance vary from species to species and lower light levels are required to reset the clocks in nocturnal rodents than in humans.

Lighting levels that affect the circadian rhythm in humans are higher than the levels usually used in artificial lighting in homes. According to some researchers the illumination intensity that excites the circadian system has to reach up to 1000 lux striking the retina.

In addition to light intensity, wavelength (or colour) of light is a factor in the entrainment of the body clock. Melanopsin is most efficiently excited by light from the blue part of the spectrum (420–440 nm according to some researchers while others have reported 470–485 nm). These blue wavelengths are present in virtually all light sources, therefore their elimination requires special lights or filters which appear amber.

It is thought that the direction of the light may have an effect on entraining the circadian rhythm; light coming from above, resembling an image of a bright sky, has greater effect than light entering our eyes from below.

According to a 2010 study completed by the Lighting Research Center, daylight has a direct effect on circadian rhythms and, consequently, on performance and well-being. The research showed that students who experience disruption in lighting schemes in the morning consequently experience disruption in sleeping patterns. The change in sleeping patterns may lead to negatively impacted student performance and alertness. Removing circadian light in the morning delays the dim light melatonin onset by 6 minutes a day, for a total of 30 minutes for five days.

Enforced longer cycles

Modern research under very controlled conditions has shown the human period for adults to be just slightly longer than 24 hours on average. Czeisler et al. at Harvard found the range for normal, healthy adults of all ages to be quite narrow: 24 hours and 11 minutes \pm 16 minutes. The "clock" resets itself daily to the 24-hour cycle of the Earth's rotation.

The *28-hour day* is presented as a concept of time management. It builds on the fact that the week of seven days at 24 hours and a "week" of six days at 28 hours both equal a week of 168 hours. To live on the 28-hour day and six-day week would require staying awake for 19 to 20 hours and sleeping for eight to nine hours. Each "day" on this system has a unique light/dark pattern.

Studies by Nathaniel Kleitman in 1938 and by Derk-Jan Dijk and Charles Czeisler in 1994/5 have put human subjects on enforced 28-hour sleep-wake cycles, in constant dim light and with other time cues suppressed, for over a month. Because normal people cannot entrain to a 28-hour day in dim light if at all, this is referred to as a forced desynchrony protocol. Sleep and wake episodes are uncoupled from the endogenous circadian period of about 24.18 hours and researchers are allowed to assess the effects of circadian phase on aspects of sleep and wakefulness including sleep latency and other functions.

Early research into circadian rhythms suggested that most people preferred a day closer to 25 hours when isolated from external stimuli like daylight and timekeeping. Early investigators determined the human circadian period to be 25 hours or more. They went to great lengths to shield subjects from time cues and daylight, but they were not aware of the effects of indoor electric lights. The subjects were allowed to turn on light when they were awake and to turn it off when they wanted to sleep. Electric light in the evening delayed their circadian phase. These results became well-known. Researchers allowed subjects to keep electric lighting on in the evening, as it was thought at that time that a couple of 60W bulbs would not have a resetting effect on the circadian rhythms of humans. More recent research has shown that adults have a built-in day, which averages just over 24 hours, that indoor lighting does affect circadian rhythms and that most people attain their best-quality sleep during their chronotype-determined sleep periods.

Human health

Timing of medical treatment in coordination with the body clock may significantly increase efficacy and reduce drug toxicity or adverse reactions. For example, appropriately timed treatment with angiotensin converting enzyme inhibitors (ACEi) may reduce nocturnal blood pressure and also benefit left ventricular (reverse) remodelling.



A short nap during the day does not affect circadian rhythms.

A number of studies have concluded that a short period of sleep during the day, a power-nap, does not have any measurable effect on normal circadian rhythms, but can decrease stress and improve productivity.

There are many health problems associated with disturbances of the human circadian rhythm, such as seasonal affective disorder (SAD), delayed sleep phase syndrome (DSPS) and other circadian rhythm disorders. Circadian rhythms also play a part in the reticular activating system, which is crucial for maintaining a state of consciousness. In addition, a reversal in the sleep-wake cycle may be a sign or complication of uremia, azotemia or acute renal failure.

Studies have also shown that light has a direct effect on human health because of the way it influences the circadian rhythms.

Circadian rhythm and airline pilots

Due to the work nature of airline pilots, who often traverse multiple timezones and regions of sunlight and darkness in one day, and spend many hours awake both day and

night, they are often unable to maintain sleep patterns that correspond to the natural human circadian rhythm; this situation can easily lead to fatigue. The NTSB cites this situation as a contributing factor to many accidents and has conducted multiple research studies in order to find methods of combating fatigue in pilots.

Disruption

Disruption to rhythms usually has a negative effect. Many travellers have experienced the condition known as jet lag, with its associated symptoms of fatigue, disorientation and insomnia.

A number of other disorders, for example bipolar disorder and some sleep disorders, are associated with irregular or pathological functioning of circadian rhythms. Recent research suggests that circadian rhythm disturbances found in bipolar disorder are positively influenced by lithium's effect on clock genes.

Disruption to rhythms in the longer term is believed to have significant adverse health consequences on peripheral organs outside the brain, particularly in the development or exacerbation of cardiovascular disease. The suppression of melatonin production associated with the disruption of the circadian rhythm may increase the risk of developing cancer.

Effect of drugs

Circadian rhythms and clock genes expressed in brain regions outside the SCN may significantly influence the effects produced by drugs such as cocaine. Moreover, genetic manipulations of clock genes profoundly affect cocaine's actions.

Chapter 5

Bioluminescence



Flying and glowing firefly, a.k.a. *Photinus pyralis*,



Female of *Lampyris noctiluca*, the Common Glowworm.

Bioluminescence is the production and emission of light by a living organism. Its name is a hybrid word, originating from the Greek *bios* for "living" and the Latin *lumen* "light". Bioluminescence is a naturally occurring form of chemiluminescence where energy is released by a chemical reaction in the form of light emission. Fireflies, anglerfish, and other creatures produce the chemicals luciferin (a pigment) and luciferase (an enzyme). The luciferin reacts with oxygen to create light. The luciferase acts as a catalyst to speed up the reaction, which is sometimes mediated by cofactors such as calcium ions or ATP. The chemical reaction can occur either inside or outside the cell. In bacteria, the expression of genes related to bioluminescence is controlled by an operon called the Lux operon.

Bioluminescence occurs in marine vertebrates and invertebrates, as well as microorganisms and terrestrial animals. Symbiotic organisms carried within larger organisms are also known to bioluminesce.

Characteristics

Bioluminescence is a form of luminescence, or "cold light" emission; less than 20% of the light generates thermal radiation. It should not be confused with fluorescence, phosphorescence or refraction of light.

Ninety percent of deep-sea marine life are estimated to produce bioluminescence in one form or another. Most marine light-emission belongs in the blue and green light spectrum, the wavelengths that can transmit through the seawater most easily. However, certain loose-jawed fishes emit red and infrared light and the genus *Tomopteris* emits yellow bioluminescence.

Non-marine bioluminescence is less widely distributed, but a larger variety in colours is seen. The two best-known forms of land bioluminescence are fireflies and glow worms. Other insects, insect larvae, annelids, arachnids and even species of fungi have been noted to possess bioluminescent abilities.

Some forms of bioluminescence are brighter (or only exist) at night, following a circadian rhythm.

Adaptations for bioluminescence

There are five main theories for bioluminescent traits:

Counterillumination camouflage

In some squid species bacterial bioluminescence is used for counterillumination so the animal matches the overhead environmental light seen from below. In these animals, photoreceptive vesicles have been found that control the contrast of this illumination to create optimal matching. Usually these light organs are separate from the tissue containing the bioluminescent bacteria. However, in one species *Euprymna scolopes* these bacteria make up an integral component of the animal's light organ. Fireflies use their light mainly for attracting the opposite sex for mating.

Attraction



Firefly larva

Bioluminescence is used as a lure to attract prey by several deep sea fish such as the anglerfish. A dangling appendage that extends from the head of the fish attracts small animals to within striking distance of the fish. Some fish, however, use a non-bioluminescent lure.

The cookiecutter shark uses bioluminescence for camouflage, but a small patch on its underbelly remains dark and appears as a small fish to large predatory fish like tuna and mackerel swimming beneath it. When these fish try to consume the "small fish", they are bitten by the shark, which gouges out small circular "cookie cutter" shaped chunks of flesh from its hosts.

Dinoflagellates have an interesting twist on this mechanism. When a predator of plankton is sensed through motion in the water, the dinoflagellate luminesces. This in turn attracts even larger predators which will consume the would-be predator of the dinoflagellate.

The attraction of mates is another proposed mechanism of bioluminescent action. This is seen actively in fireflies, which use periodic flashing in their abdomens to attract mates in the mating season. In the marine environment this has only been well-documented in

certain small crustaceans called ostracod. It has been suggested that pheromones may be used for long-distance communication, and bioluminescence used at close range to "home in" on the target.

Repulsion

Certain squid and small crustaceans use bioluminescent chemical mixtures or bioluminescent bacterial slurries in the same way as many squid use ink. A cloud of luminescence is expelled, confusing or repelling a potential predator while the squid or crustacean escapes to safety. Every species of firefly has larvae that glow to repel predators.

Communication

Communication between bacteria (quorum sensing) plays a role in the regulation of luminescence in many bacterial species. Using small extracellularly secreted molecules, they are able to adapt their behavior to only turn on genes for light production when they are at high cell densities.

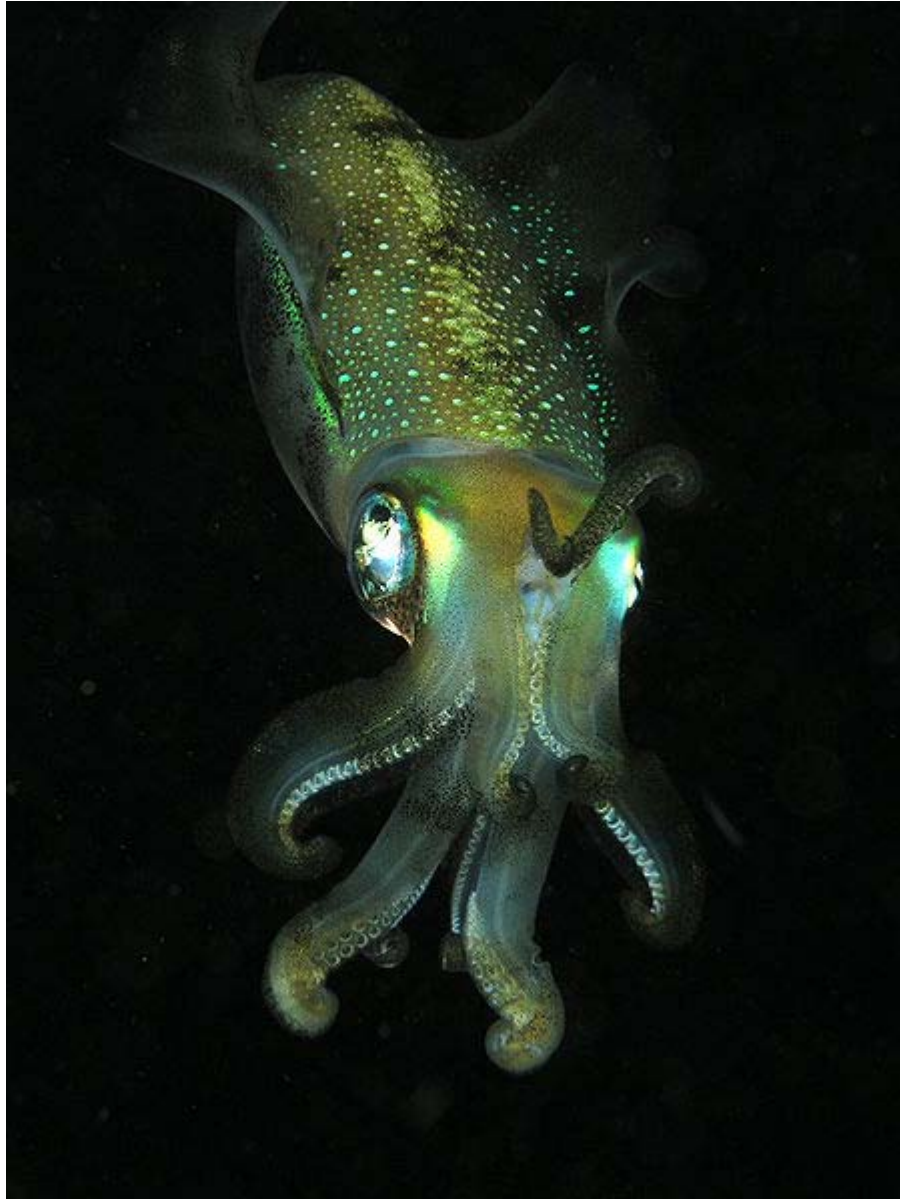
Illumination

While most marine bioluminescence is green to blue, the Black Dragonfish produces a red glow. This adaptation allows the fish to see red-pigmented prey, which are normally invisible in the deep ocean environment where red light has been filtered out by the water column.

Biotechnology



Artistic rendering of bioluminescent Antarctic krill



Sepioteuthis lessoniana, one of many bioluminescent squid - 63 out of 100 genera of cuttlefish and squid contain species with the ability.

Bioluminescent organisms are a target for many areas of research. Luciferase systems are widely used in the field of genetic engineering as reporter genes. Luciferase systems have also been harnessed for biomedical research using bioluminescence imaging.

Vibrio symbiosis with numerous marine invertebrates and fish, namely the Hawaiian Bobtail Squid (*Euprymna scolopes*), are key experimental models for symbiosis, quorum sensing, and bioluminescence.

The structures of photophores, the light producing organs in bioluminescent organisms, are being investigated by industrial designers.

Proposed applications of engineered bioluminescence

Some proposed applications of engineered bioluminescence include:

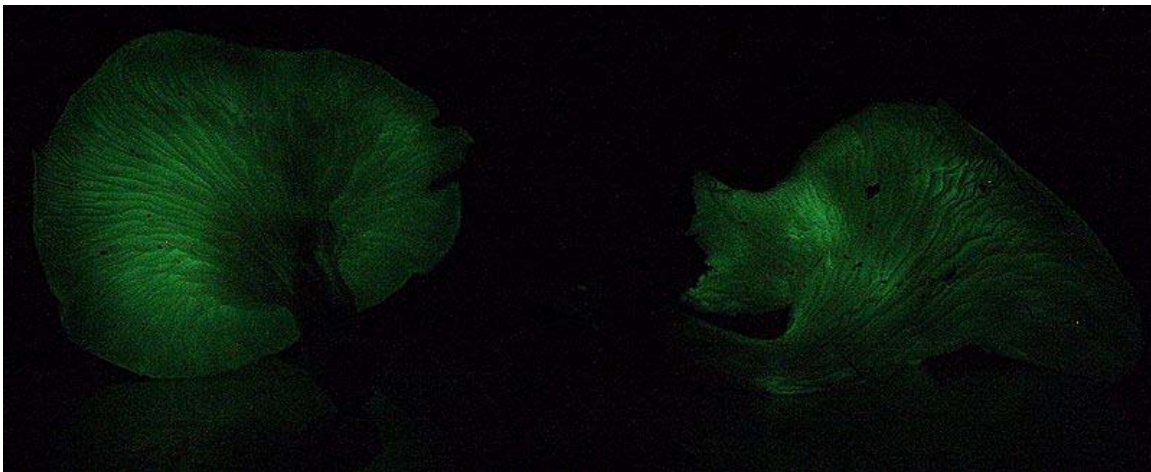
- Glowing trees to line highways to save government electricity bills
- Christmas trees that do not need lights, reducing danger from electrical fires
- Agricultural crops and domestic plants that luminesce when they need watering
- New methods for detecting bacterial contamination of meats and other foods
- Bio-identifiers for escaped convicts and mental patients
- Detecting bacterial species in suspicious corpses
- Novelty pets that bioluminesce (rabbits, mice, fish etc.)

Bioluminescent organisms

Omphalotus nidiformis



Example of a bioluminescent species of mushroom...



...glowing with the lights off.



Firefly (species unknown) with and without flash.



The fungus *Panellus stipticus* displaying bioluminescence.

All cells produce some form of bioluminescence within the electromagnetic spectrum, but most are neither visible nor noticeable to the naked eye. Every organism's bioluminescence is unique in wavelength, duration, timing and regularity of flashes. Below follows a list of organisms which have been observed to have visible bioluminescence.

Terrestrial organisms

Animals:

- certain arthropods
 - fireflies
 - click beetles
 - glow worms
 - railroad worms
 - certain mycetophilid flies
 - certain centipedes
 - certain millipedes
- a terrestrial mollusc (a tropical land snail)
 - *Quantula striata*
- annelids

Fungi:

- Mushrooms
 - Jack O'Lantern mushroom (*Omphalotus olearius*)
 - ghost fungus (*Omphalotus nidiformis*)
 - Honey mushroom
 - *Panellus stipticus*
 - several species of *Mycena*

Fish

- Anglerfish
- Cookie-cutter shark
- Flashlight fish
- Gulper eel
- Lanternfish
- Marine hatchetfish
- Midshipman fish
- Pineconefish
- Viperfish

Marine invertebrates

- many cnidarians
 - Sea pens
 - coral
 - *Aequorea victoria*, a jellyfish
- certain Ctenophores or "comb jellies"
- certain echinoderms (e.g. Ophiurida)
- certain crustaceans
 - ostracods
 - copepods
 - krill
- certain chaetognaths
- certain molluscs
 - certain clams, bivalves
 - certain nudibranchs, sea slugs
 - Octopus
 - Bolitaenidae
 - the order Teuthida
 - Colossal Squid
 - Mastigoteuthidae
 - Sepiolidae
 - Sparkling Enope Squid
 - Vampire squid



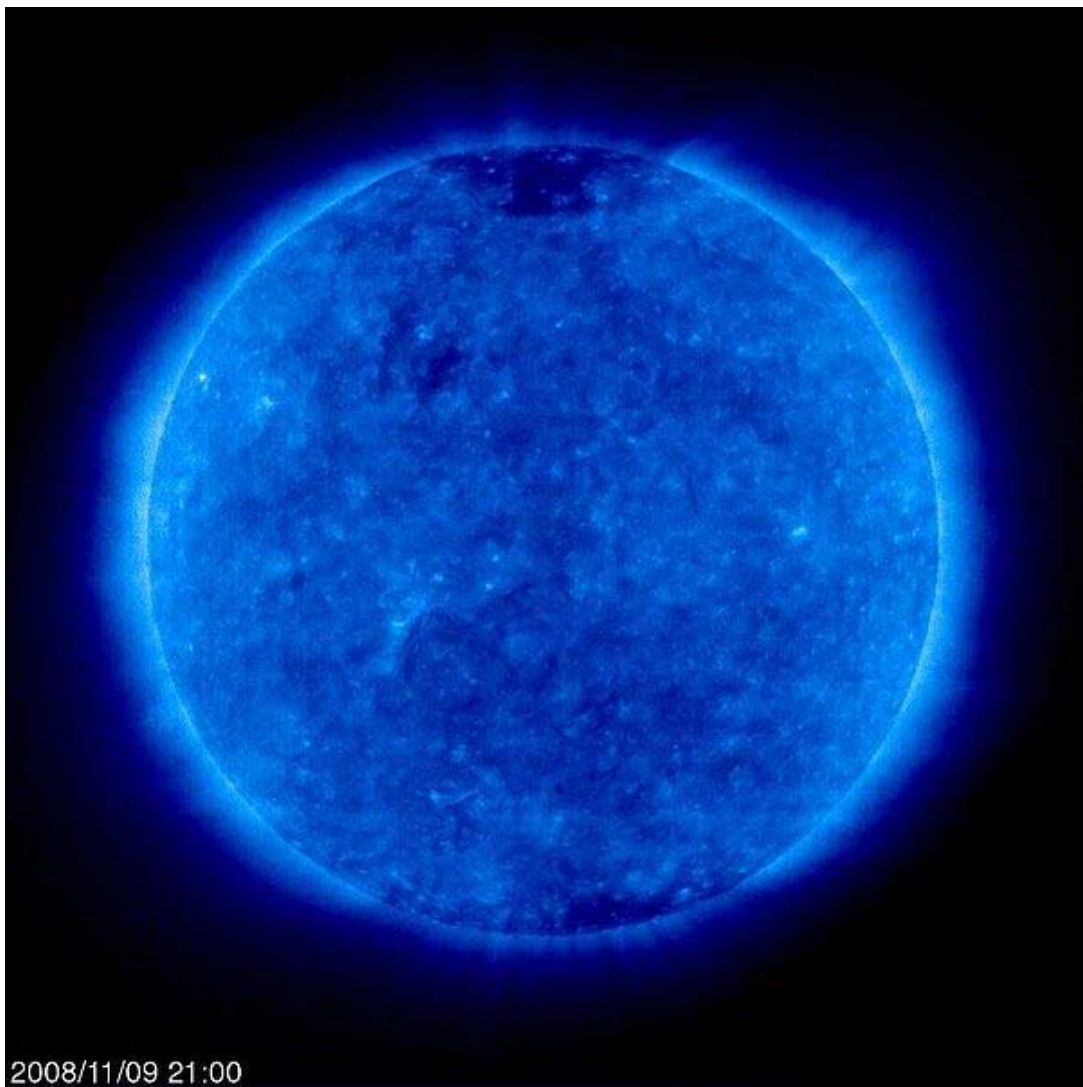
Blue ocean glow caused by myriad tiny organisms, such as Noctiluca.

Microorganisms

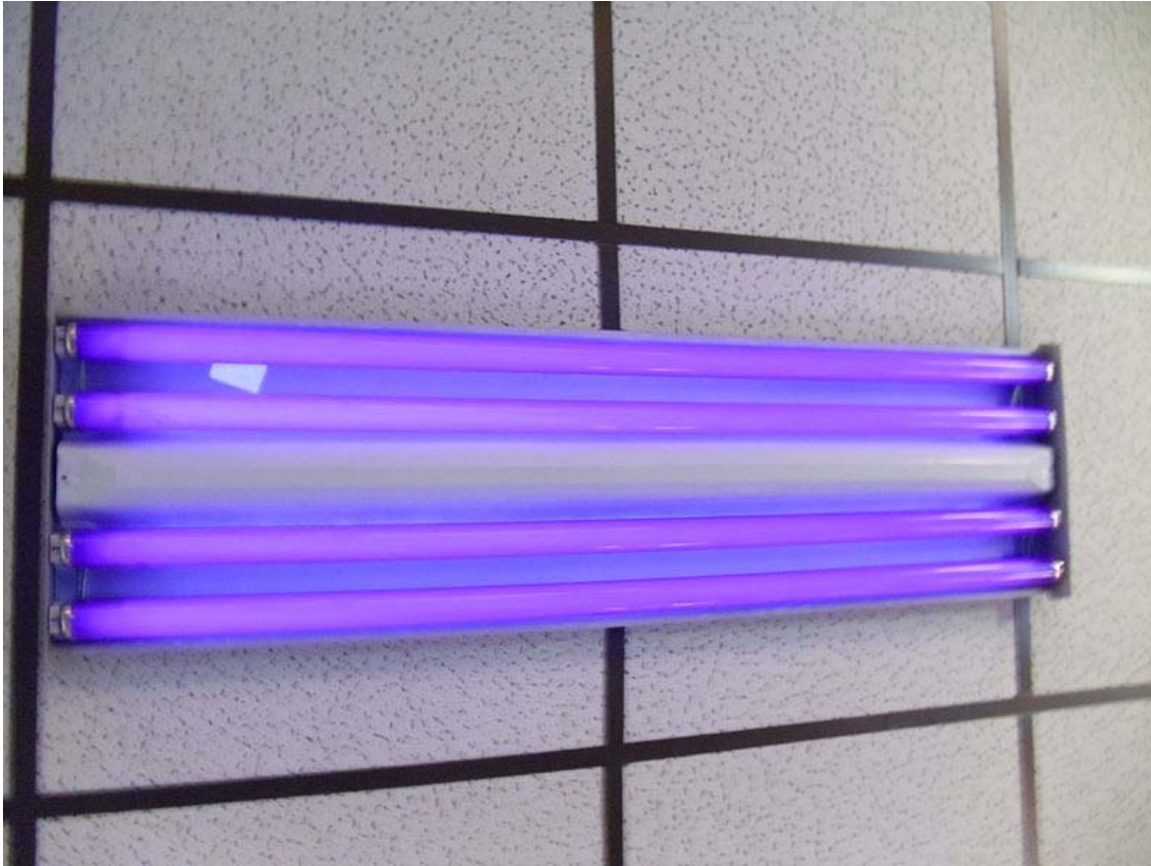
- Dinoflagellates
- Vibrionaceae (e.g. *Vibrio fischeri*, *Vibrio harveyi*, *Vibrio phosphoreum*)
- Members of the marine bacterial family Shewanellaceae, *Shewanella hanedai* and *Shewanella woodyi* have also been shown to be bioluminescent
- Fungi - A total of 71 species are bioluminescent including species of *Armillaria*, *Omphalotus*, *Mycena*, *Gerronema*, *Pleurotus*.

Chapter 6

Ultraviolet



False-color image of the Sun's corona as seen in deep ultraviolet by the Extreme ultraviolet Imaging Telescope



Black light fluorescent tubes, a common source of long wave (UVA) ultraviolet.

Ultraviolet (UV) light is electromagnetic radiation with a wavelength shorter than that of visible light, but longer than X-rays, in the range 10 nm to 400 nm, and energies from 3eV to 124 eV. It is so named because the spectrum consists of electromagnetic waves with frequencies higher than those that humans identify as the color violet.

Although ultraviolet is invisible to the human eye, most people are aware of the effects of UV through the painful condition of sunburn, but the UV spectrum has many other effects, both beneficial and damaging, to human health.

UV light is found in sunlight and is emitted by electric arcs and specialized lights such as black lights. It can cause chemical reactions, and causes many substances to glow or fluoresce. Most ultraviolet is classified as non-ionizing radiation. The higher energies of the ultraviolet spectrum from about 150 nm ('vacuum' ultraviolet) are ionizing, but this type of ultraviolet is not very penetrating and is blocked by air.

Discovery

The discovery of UV radiation was intimately associated with the observation that silver salts darken when exposed to sunlight. In 1801, the German physicist Johann Wilhelm Ritter made the hallmark observation that invisible rays just beyond the violet end of the

visible spectrum were especially effective at lightening silver chloride-soaked paper. He called them "oxidizing rays" to emphasize chemical reactivity and to distinguish them from "heat rays" at the other end of the invisible spectrum. The simpler term "chemical rays" was adopted shortly thereafter, and it remained popular throughout the 19th century. The terms chemical and heat rays were eventually dropped in favour of ultraviolet and infrared radiation, respectively.

The discovery of the ultraviolet radiation below 200 nm, named vacuum ultraviolet because it is strongly absorbed by air, was made in 1893 by the German physicist Victor Schumann.

Origin of the term

The name means "beyond violet" (from Latin *ultra*, "beyond"), violet being the color of the shortest wavelengths of visible light. UV light has a shorter wavelength than violet light.

Subtypes

The electromagnetic spectrum of ultraviolet light can be subdivided in a number of ways. The draft ISO standard on determining solar irradiances (ISO-DIS-21348) describes the following ranges:

Name	Abbreviation	Wavelength range in nanometers	Energy per photon
Ultraviolet A, long wave, or black light	UVA	400 nm–315 nm	3.10–3.94 eV
Near	NUV	400 nm–300 nm	3.10–4.13 eV
Ultraviolet B or medium wave	UVB	315 nm–280 nm	3.94–4.43 eV
Middle	MUV	300 nm–200 nm	4.13–6.20 eV
Ultraviolet C, short wave, or germicidal	UVC	280 nm–100 nm	4.43–12.4 eV
Far	FUV	200 nm–122 nm	6.20–10.2 eV
Vacuum	VUV	200 nm–100 nm	6.20–12.4 eV
Low	LUV	100 nm–88 nm	12.4–14.1 eV
Super	SUV	150 nm–10 nm	8.28–124 eV
Extreme	EUV	121 nm–10 nm	10.2–124 eV

In photolithography and laser technology, the term *deep ultraviolet* or *DUV* refers to wavelengths below 300 nm. Extreme Ultraviolet stands here for discrete spectral ranges of around 13.5 nm (in future planned also 6.x nm) of about 2 % bandwidth. In fields like

analytics and life sciences, the acronym "XUV" is used for Extreme Ultraviolet for characterizing the broader spectral range, such as to distinguish from EUV. XUV is separated from x-rays and VUV, by the fact that the photoelectron ionization of innershell electrons is the - by orders of magnitudes - dominating photon-matter interaction effect. This is in contrast to x-rays, where scatter is relevant and VUV where the interaction is mainly with outer ("chemical active") electrons of the atoms and molecules.

"Vacuum UV" is so named because it is absorbed strongly by air and is, therefore, used in a vacuum. In the long-wave limit of this region, roughly 150–200 nm, the principal absorber is the oxygen in air. Work in this region can be performed in an oxygen-free atmosphere, pure nitrogen being commonly used, which avoids the need for a vacuum chamber.

Sources of UV

Natural sources of UV

The sun emits ultraviolet radiation in the UVA, UVB, and UVC bands. The Earth's ozone layer blocks 97-99% of this UV radiation from penetrating through the atmosphere. Of the ultraviolet radiation that reaches the Earth's surface, 98.7% is UVA. (UVC and more energetic radiation is responsible for the generation of the ozone layer, and formation of the ozone there). Extremely hot stars emit proportionally more UV radiation than the sun; the star R136a1 has a thermal energy of 4.57 eV, which falls in the near-UV range.

Ordinary glass is partially transparent to UVA but is opaque to shorter wavelengths, whereas Silica or quartz glass, depending on quality, can be transparent even to vacuum UV wavelengths. Ordinary window glass passes about 90% of the light above 350 nm, but blocks over 90% of the light below 300 nm.

The onset of vacuum UV, 200 nm, is defined by the fact that ordinary air is opaque at shorter wavelengths. This opacity is due to the strong absorption of light of these wavelengths by oxygen in the air. Pure nitrogen (less than about 10 ppm oxygen) is transparent to wavelengths in the range of about 150–200 nm. This has wide practical significance now that semiconductor manufacturing processes are using wavelengths shorter than 200 nm. By working in oxygen-free gas, the equipment does not have to be built to withstand the pressure differences required to work in a vacuum. Some other scientific instruments, such as circular dichroism spectrometers, are also commonly nitrogen-purged and operate in this spectral region.

Extreme UV is characterized by a transition in the physics of interaction with matter: Wavelengths longer than about 30 nm interact mainly with the chemical valence electrons of matter, whereas wavelengths shorter than that interact mainly with inner shell electrons and nuclei. The long end of the EUV/XUV spectrum is set by a prominent He⁺ spectral line at 30.4 nm. XUV is strongly absorbed by most known materials, but it is possible to synthesize multilayer optics that reflect up to about 50% of XUV radiation at

normal incidence. This technology has been used to make telescopes for solar imaging; it was pioneered by the NIXT and MSSTA sounding rockets in the 1990s; (current examples are SOHO/EIT and TRACE) and for nanolithography (printing of traces and devices on microchips).

"Black light"

A black light, or Wood's light, is a lamp that emits long wave UV radiation and very little visible light. They are sometimes referred to as a "UV light". Fluorescent black lights are typically made in the same fashion as normal fluorescent lights except that only one phosphor is used, and the clear glass envelope of the bulb may be replaced by a deep-bluish-purple glass called Wood's glass, a nickel-oxide-doped glass, which blocks almost all visible light above 400 nanometres. The color of such lamps is often referred to in the trade as "blacklight blue" or "BLB." This is to distinguish these lamps from "bug zapper" blacklight ("BL") lamps that do not have the blue Wood's glass. The phosphor typically used for a near 368 to 371 nanometre emission peak is either europium-doped strontium fluoroborate ($\text{SrB}_4\text{O}_7\text{F}:\text{Eu}^{2+}$) or europium-doped strontium borate ($\text{SrB}_4\text{O}_7:\text{Eu}^{2+}$) while the phosphor used to produce a peak around 350 to 353 nanometres is lead-doped barium silicate ($\text{BaSi}_2\text{O}_5:\text{Pb}^+$). "Blacklight Blue" lamps peak at 365 nm.

While "black lights" do produce light in the UV range, their spectrum is confined to the longwave UVA region. Unlike UVB and UVC, which are responsible for the direct DNA damage that leads to skin cancer, black light is limited to lower-energy, longer waves and does not cause sunburn. However, UVA is capable of causing damage to collagen fibers and destroying vitamins A and D in skin.

A black light may also be formed by simply using Wood's glass instead of clear glass as the envelope for a common incandescent bulb. This was the method used to create the very first black light sources. Though it remains a cheaper alternative to the fluorescent method, it is exceptionally inefficient at producing UV light (less than 0.1% of the input power), owing to the black body nature of the incandescent light source. Incandescent UV bulbs, due to their inefficiency, may also become dangerously hot during use. More rarely still, high-power (hundreds of watts) mercury-vapor black lights that use a UV-emitting phosphor and an envelope of Wood's glass can be found. These lamps are used mainly for theatrical and concert displays, and also become very hot during normal use.

Some UV fluorescent bulbs specifically designed to attract insects use the same near-UV emitting phosphor as normal blacklights, but use plain glass instead of the more expensive Wood's glass. Plain glass blocks less of the visible mercury emission spectrum, making them appear light-blue to the naked eye. These lamps are referred to as "blacklight" or "BL" in most lighting catalogs.

Ultraviolet light can also be generated by some light-emitting diodes.

Ultraviolet fluorescent lamps

Fluorescent lamps without a phosphorescent coating to convert UV to visible light, emit ultraviolet light with two peaks at 253.7 nm and 185 nm due to the peak emission of the mercury within the bulb. Eighty-five to ninety percent of the UV produced by these lamps is at 253.7 nm, while only five to ten percent is at 185 nm. Germicidal lamps use quartz (glass) doped with an additive to block the 185 nm wavelength. With the addition of a suitable phosphorescent coating, they can be modified to produce a UVA, UVB, or visible light spectrum (all fluorescent tubes used for domestic and commercial lighting are mercury (Hg) UV emission bulbs at heart).

Such low-pressure mercury lamps are used extensively for disinfection, and in standard form have an optimum operating temperature of about 30 degrees Celsius. Use of a mercury amalgam allows operating temperature to rise to 100 degrees Celsius, and UVC emission to about double or triple per unit of light-arc length. These low-pressure lamps have a typical efficiency of approximately thirty to thirty-five percent, meaning that for every 100 watts of electricity consumed by the lamp, it will produce approximately 30-35 watts of total UV output.

Ultraviolet LEDs

Light-emitting diodes (LEDs) can be manufactured to emit light in the ultraviolet range, although practical LED arrays are very limited below 365 nm. LED efficiency at 365 nm is about 5-8%, whereas efficiency at 395 nm is closer to 20%, and power outputs at these longer UV wavelengths are also better. Such LED arrays are beginning to be used for UV curing applications, and are already successful in digital print applications and inert UV curing environments. Power densities approaching 3,000 mW/cm² (30 kW/m²) are now possible, and this, coupled with recent developments by photoinitiator and resin formulators, makes the expansion of LED-cured UV materials likely.

Ultraviolet lasers

UV laser diodes and UV solid-state lasers can be manufactured to emit light in the ultraviolet range. Wavelengths available include 262, 266, 349, 351, 355, and 375 nm. Ultraviolet lasers have applications in industry (laser engraving), medicine (dermatology and keratectomy), secure communications, and computing (optical storage). They can be made by applying frequency conversion to lower-frequency lasers, or from Ce:LiSAF crystals (cerium doped with lithium strontium aluminum fluoride), a process developed in the 1990s at Lawrence Livermore National Laboratory.

Gas-discharge lamps

Argon and deuterium lamps are often used as stable sources, either windowless or with various windows such as magnesium fluoride.

Detecting and measuring UV radiation

Ultraviolet detection and measurement technology can vary with the part of the spectrum under consideration. While some silicon detectors are used across the spectrum, and in fact the US NIST has characterized simple silicon diodes that work with visible light too, many specializations are possible for different applications. Many approaches seek to adapt visible light-sensing technologies, but these can suffer from unwanted response to visible light and various instabilities. A variety of solid-state and vacuum devices have been explored for use in different parts of the UV spectrum. Ultraviolet light can be detected by suitable photodiodes and photocathodes, which can be tailored to be sensitive to different parts of the UV spectrum. Sensitive ultraviolet photomultipliers are available.

Near UV

Between 200-400 nm, a variety of detector options exist.

Vacuum UV

Technology for VUV instrumentation has been largely driven by solar physics for many decades and more recently some photolithography applications for semiconductors. While optics can be used to remove unwanted visible light that contaminates the VUV, in general, detectors can be limited by their response to non-VUV radiation, and the development of "solar-blind" devices has been an important area of research. Wide-gap solid-state devices or vacuum devices with high-cutoff photocathodes can be attractive compared to silicon diodes. Recently, a diamond-based device flew on the LYRA

Human health-related effects of UV radiation

Beneficial effects

Vitamin D

UVB exposure induces the production of vitamin D in the skin at a rate of up to 1,000 IUs per minute. The majority of positive health effects are related to this vitamin. It has regulatory roles in calcium metabolism (which is vital for normal functioning of the nervous system, as well as for bone growth and maintenance of bone density), immunity, cell proliferation, insulin secretion, and blood pressure.

Aesthetics

Too little UVB radiation may lead to a lack of vitamin D. Too much UVB radiation may lead to direct DNA damage, sunburn, and skin cancer. An appropriate amount of UVB (which varies according to skin color) leads to a limited amount of direct DNA damage. This is recognized and repaired by the body, then melanin production is increased, which leads to a long-lasting tan. This tan occurs with a 2-day lag phase after irradiation, but it is much less harmful and is longer-lasting than the one obtained from UVA.

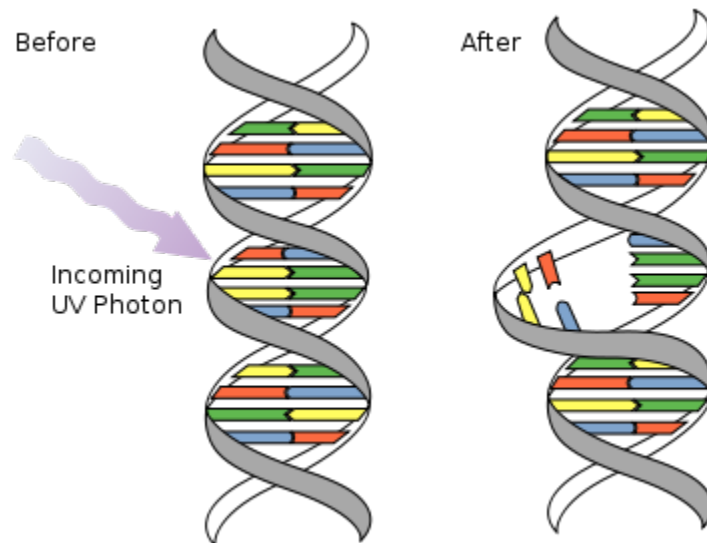
Medical applications

Ultraviolet radiation has other medical applications, in the treatment of skin conditions such as psoriasis and vitiligo. UVA radiation has been much used in conjunction with psoralens (PUVA treatment) for psoriasis, although this treatment is less used now because the combination produces dramatic increases in skin cancer, and because treatment with UVB radiation by itself is more effective. In cases of psoriasis and vitiligo, UV light with wavelength of 311 nm is most effective.

Harmful effects

An overexposure to UVB radiation can cause sunburn and some forms of skin cancer. However the most deadly form - malignant melanoma - is mostly caused by the indirect DNA damage (free radicals and oxidative stress). In humans, prolonged exposure to solar UV radiation may result in acute and chronic health effects on the skin, eye, and immune system. This can be seen from the absence of a UV-signature mutation in 92% of all melanoma.

UVC rays are the highest energy, most dangerous type of ultraviolet light. Little attention has been given to UVC rays in the past since they are filtered out by the atmosphere. However, their use in equipment such as pond sterilization units may pose an exposure risk, if the lamp is switched on outside of its enclosed pond sterilization unit.



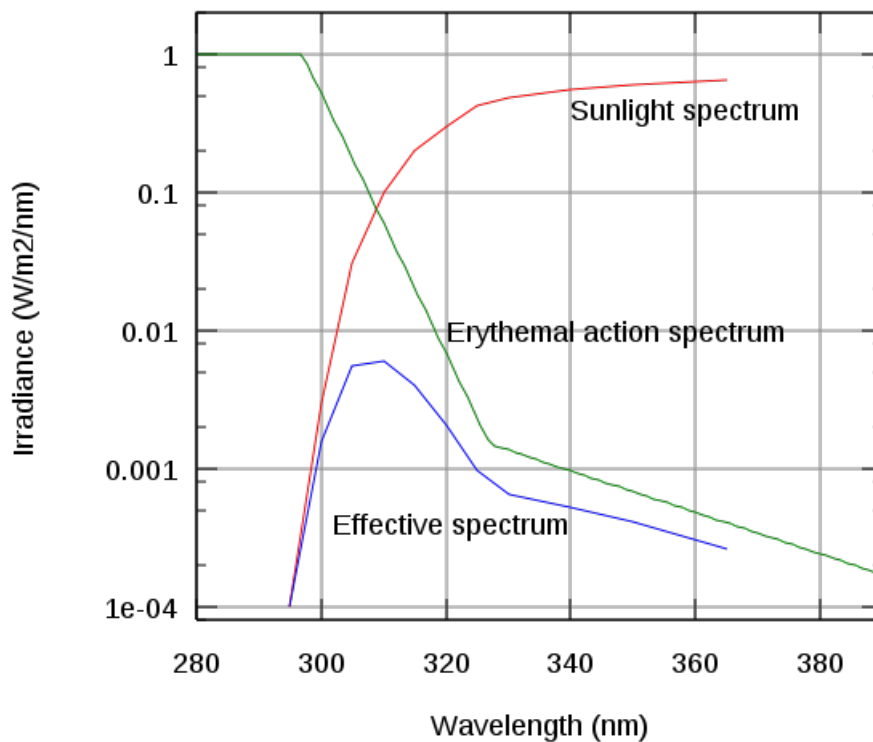
Ultraviolet photons harm the DNA molecules of living organisms in different ways. In one common damage event, adjacent thymine bases bond with each other, instead of across the "ladder". This "thymine dimer" makes a bulge, and the distorted DNA molecule does not function properly.

Skin

“ Ultraviolet (UV) irradiation present in sunlight is an environmental human carcinogen. The toxic effects of UV from natural sunlight and therapeutic artificial lamps are a major concern for human health. The major acute effects of UV irradiation on normal human skin comprise sunburn inflammation erythema, tanning, and local or systemic immunosuppression. ”

— Matsumura and Ananthaswamy , (2004)

UVA, UVB, and UVC can all damage collagen fibers and, therefore, accelerate aging of the skin. Both UVA and UVB destroy vitamin A in skin, which may cause further damage. In the past, UVA was considered less harmful, but today it is known it can contribute to skin cancer via indirect DNA damage (free radicals and reactive oxygen species). It penetrates deeply, but it does not cause sunburn. UVA does not damage DNA directly like UVB and UVC, but it can generate highly reactive chemical intermediates, such as hydroxyl and oxygen radicals, which in turn can damage DNA. Because it does not cause reddening of the skin (erythema), it cannot be measured in SPF testing. There is no good clinical measurement for blockage of UVA radiation, but it is important for sunscreen to block both UVA and UVB. Some scientists blame the absence of UVA filters in sunscreens for the higher melanoma risk found for sunscreen users.



The reddening of the skin due to the action of sunlight depends both on the amount of sunlight and on the sensitivity of the skin ("erythmal action spectrum") over the UV spectrum.

UVB light can cause direct DNA damage. The radiation excites DNA molecules in skin cells, causing aberrant covalent bonds to form between adjacent cytosine bases, producing a dimer. When DNA polymerase comes along to replicate this strand of DNA, it reads the dimer as "AA" and not the original "CC". This causes the DNA replication mechanism to add a "TT" on the growing strand. This mutation can result in cancerous growths, and is known as a "classical C-T mutation". The mutations caused by the direct DNA damage carry a UV signature mutation that is commonly seen in skin cancers. The mutagenicity of UV radiation can be easily observed in bacterial cultures. This cancer connection is one reason for concern about ozone depletion and the ozone hole. UVB causes some damage to collagen, but at a very much slower rate than UVA.

As a defense against UV radiation, the amount of the brown pigment melanin in the skin increases when exposed to moderate (depending on skin type) levels of radiation; this is commonly known as a sun tan. The purpose of melanin is to absorb UV radiation and dissipate the energy as harmless heat, blocking the UV from damaging skin tissue. UVA gives a quick tan that lasts for days by oxidizing melanin that was already present, and triggers the release of the melanin from melanocytes. UVB yields a tan that takes roughly 2 days to develop because it stimulates the body to produce more melanin. The photochemical properties of melanin make it an excellent photoprotectant. Older and more widespread sunscreen chemicals cannot dissipate the energy of the excited state as efficiently as melanin, and, therefore, the penetration of these sunscreen ingredients into the lower layers of the skin may increase the amount of free radicals and reactive oxygen species (ROS). In recent years, improved filtering substances have come into use in commercial sunscreen lotions that do not significantly degrade or lose their capacity to protect the skin as the exposure time increases (*photostable* substances).

Sunscreen prevents the direct DNA damage that causes sunburn. Most of these products contain an SPF rating to show how well they block UVB rays. The SPF rating, however, offers no data about UVA protection. In the US, the Food and Drug Administration is considering adding a star rating system to show UVA protection. A similar system is already used in some European countries. Some sunscreen lotions now include compounds such as titanium dioxide, which helps protect against UVA rays. Other UVA blocking compounds found in sunscreen include zinc oxide and avobenzone.

Sunscreen safety debate

Medical organizations recommend patients protect themselves from UV radiation by using sunscreen. Five sunscreen ingredients have been shown to protect mice against skin tumors.

However, some sunscreen chemicals produce potentially harmful substances if they are illuminated while in contact with living cells. The amount of sunscreen that penetrates

through the stratum corneum may or may not be large enough to cause damage. In one study of sunscreens, the authors write:

The question whether UV filters acts on or in the skin has so far not been fully answered. Despite the fact that an answer would be a key to improve formulations of sun protection products, many publications carefully avoid addressing this question.

In an experiment by Hanson et al. published in 2006, the amount of harmful reactive oxygen species (ROS) was measured in untreated and in sunscreen treated skin. In the first 20 minutes, the film of sunscreen had a protective effect and the amount of ROS was smaller. After 60 minutes, however, the amount of absorbed sunscreen was so high, the amount of ROS was higher in the sunscreen treated skin than in the untreated skin.

Such effects can be avoided by using newer generations of filter substances or combinations that maintain their UV protective properties even after several hours of solar exposure. Sunscreen products containing photostable filters like drometrizole trisiloxane, bisoctrizole, or bemotrizinol have been available for many years throughout the world, but are not yet available in the U.S., whereas another high-quality filter, ecamsule, has also been available in the U.S. since 2006.

Eye

High intensities of UVB light are hazardous to the eyes, and exposure can cause *welder's flash* (photokeratitis or arc eye) and may lead to cataracts, pterygium, and pinguecula formation.

UV light is absorbed by molecules known as chromophores, which are present in the eye cells and tissues. Chromophores absorb light energy from the various wavelengths at different rates - a pattern known as absorption spectrum. If too much UV light is absorbed, eye structures such as the cornea, the lens and the retina can be damaged.

Protective eyewear is beneficial to those who are working with or those who might be exposed to ultraviolet radiation, particularly short wave UV. Given that light may reach the eye from the sides, full coverage eye protection is usually warranted if there is an increased risk of exposure, as in high altitude mountaineering. Mountaineers are exposed to higher than ordinary levels of UV radiation, both because there is less atmospheric filtering and because of reflection from snow and ice.

Ordinary, untreated eyeglasses give some protection. Most plastic lenses give more protection than glass lenses, because, as noted above, glass is transparent to UVA and the common acrylic plastic used for lenses is less so. Some plastic lens materials, such as polycarbonate, inherently block most UV. There are protective treatments available for eyeglass lenses that need it, which will give better protection. But even a treatment that *completely* blocks UV will not protect the eye from light that arrives around the lens.

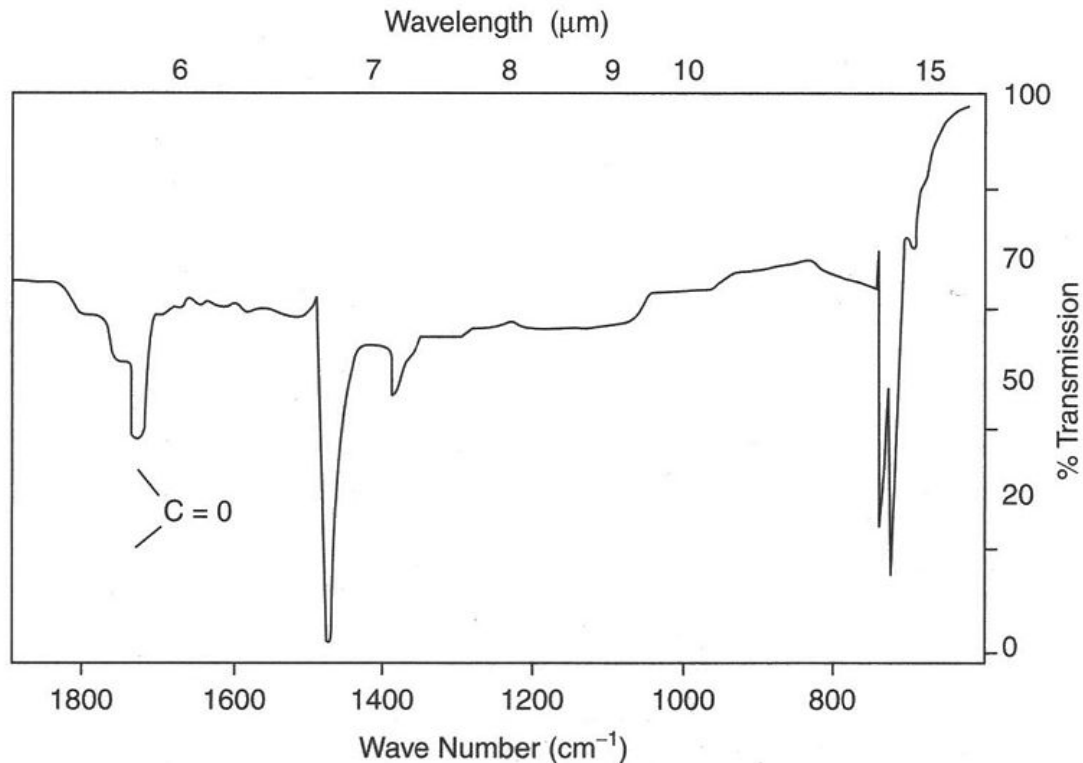
Degradation of polymers, pigments and dyes



UV damaged polypropylene rope (left) and new rope (right)

Many polymers used in consumer products are degraded by UV light, and need addition of UV absorbers to inhibit attack, especially if the products are exposed to sunlight. The problem appears as discoloration or fading, cracking, and, sometimes, total product disintegration if cracking has proceeded sufficiently. The rate of attack increases with exposure time and sunlight intensity.

It is known as UV degradation, and is one form of polymer degradation. Sensitive polymers include thermoplastics, such as polypropylene, polyethylene, and poly(methyl methacrylate) as well as speciality fibers like aramids. UV absorption leads to chain degradation and loss of strength at sensitive points in the chain structure. They include tertiary carbon atoms, which in polypropylene occur in every repeat unit. Aramid rope must be shielded with a sheath of thermoplastic if it is to retain its strength. The impact of UV on polymers is used in nanotechnology, transplantology, X-ray lithography and others fields for modification of properties (roughness, hydrophobicity) of polymer surface. For example, it is known about smoothing effect of vacuum ultraviolet (VUV) on a poly(methyl methacrylate) surface.



IR spectrum showing carbonyl absorption due to UV degradation of polyethylene

In addition, many pigments and dyes absorb UV and change colour, so paintings and textiles may need extra protection both from sunlight and fluorescent bulbs, two common sources of UV radiation. Old and antique paintings such as watercolour paintings, for example, usually must be placed away from direct sunlight. Common window glass provides some protection by absorbing some of the harmful UV, but valuable artifacts need extra shielding. Many museums place black curtains over watercolour paintings and ancient textiles, for example. Since watercolours can have very low pigment levels, they need extra protection from UV light.

Blockers and absorbers

Ultraviolet Light Absorbers (UVAs) are molecules used in organic materials (polymers, paints, etc.) to absorb UV light to reduce the UV degradation (photo-oxidation) of a material. A number of different UVAs with different absorption properties exist. UVAs can disappear over time, so monitoring of UVA levels in weathered materials is necessary.

In sunscreen, ingredients that absorb UVA/UVB rays, such as avobenzone and octyl methoxycinnamate, are known as absorbers. They are contrasted with physical "blockers" of UV radiation such as titanium dioxide and zinc oxide.

Applications of UV

By wavelength:

- **13.5 nm:** Extreme Ultraviolet Lithography
- **230-400 nm:** Optical sensors, various instrumentation
- **230-365 nm:** UV-ID, label tracking, barcodes
- **240-280 nm:** Disinfection, decontamination of surfaces and water (DNA absorption has a peak at 260 nm)
- **250-300 nm:** Forensic analysis, drug detection
- **270-300 nm:** Protein analysis, DNA sequencing, drug discovery
- **280-400 nm:** Medical imaging of cells
- **300-400 nm:** Solid-state lighting
- **300-365 nm:** Curing of polymers and printer inks
- **300-320 nm:** Light therapy in medicine
- **350-370 nm:** Bug zappers (flies are most attracted to light at 365 nm)

Security



A bird appears on many Visa credit cards when held under a UV light source

To help prevent counterfeiters, sensitive documents (e.g., credit cards, driver's licenses, passports) may also include a UV watermark that is visible only under a UV-emitting light. Passports issued by most countries usually contain UV sensitive inks and security threads. Visa stamps and stickers on passports of visitors contain large detailed seals

invisible under normal light, but strongly visible under UV illumination. Passports issued by many nations have UV sensitive watermarks on all pages. Currencies of various countries' banknotes have an image, as well as many multicolored fibers, that are visible only under ultraviolet light.

Some brands of pepper spray will leave an invisible chemical (UV dye) that is not easily washed off on a pepper sprayed attacker, which would help police identify them later.

Forensics

UV is an investigative tool at the crime scene helpful in locating and identifying bodily fluids (semen, blood, bile etc.). E.g., ejaculated fluids or saliva are detected by high-power UV, irrespective of the structure or colour of the surface the fluid is deposited upon.

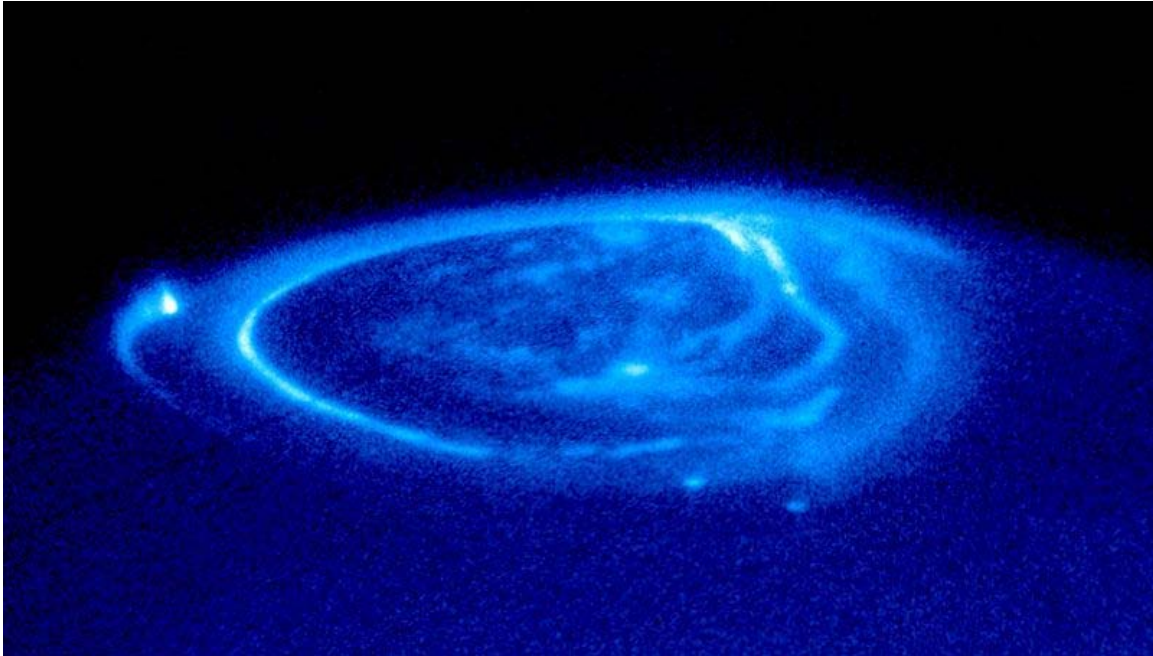
Fluorescent lamps

Fluorescent lamps produce UV radiation by ionising low-pressure mercury vapour. A phosphorescent coating on the inside of the tubes absorbs the UV and converts it to visible light.

The main mercury emission wavelength is in the UVC range. Unshielded exposure of the skin or eyes to mercury arc lamps that do not have a conversion phosphor is quite dangerous.

The light from a mercury lamp is predominantly at discrete wavelengths. Other practical UV sources with more continuous emission spectra include xenon arc lamps (commonly used as sunlight simulators), deuterium arc lamps, mercury-xenon arc lamps, metal-halide arc lamps, and tungsten-halogen incandescent lamps.

Astronomy



Aurora at Jupiter's north pole as seen in ultraviolet light by the Hubble Space Telescope.

In astronomy, very hot objects preferentially emit UV radiation. Because the ozone layer blocks many UV frequencies from reaching telescopes on the surface of the Earth, most UV observations are made from space.

Biological surveys and pest control

Some animals, including birds, reptiles, and insects such as bees, can see near-ultraviolet light. Many fruits, flowers, and seeds stand out more strongly from the background in ultraviolet wavelengths as compared to human color vision. Scorpions glow or take on a yellow to green color under UV illumination, thus assisting in the control of these arachnids. Many birds have patterns in their plumage that are invisible at usual wavelengths but observable in ultraviolet, and the urine and other secretions of some animals, including dogs, cats, and human beings, is much easier to spot with ultraviolet. Urine trails of rodents can be detected by pest control technicians for proper treatment of infested dwellings.

Butterflies use ultraviolet as a communication system for sex recognition and mating behavior.

Many insects use the ultraviolet wavelength emissions from celestial objects as references for flight navigation. A local ultraviolet emitter will normally disrupt the navigation process and will eventually attract the flying insect.



Entomologist using a UV light for collecting beetles in the Paraguayan Chaco.

Ultraviolet traps called bug zappers are used to eliminate various small flying insects. They are attracted to the UV light, and are killed using an electric shock, or trapped once they come into contact with the device. Different designs of ultraviolet light traps are also used by entomologists for collecting nocturnal insects during faunistic survey studies.

Spectrophotometry

UV/VIS spectroscopy is widely used as a technique in chemistry, to analyze chemical structure, the most notable one being conjugated systems. UV radiation is often used in visible spectrophotometry to determine the fluorescence of a given sample. In biological research, UV light is used for quantification of nucleic acids.

Sanitary compliance

UV lamps including newer LEDs (light-emitting diode) aid in the detection of organic mineral deposits that remain on surfaces where periodic cleaning and sanitizing may not be properly accomplished. Both urine and phosphate soaps are easily detected using UV inspection. Pet urine deposits in carpeting or other hard surfaces can be detected for accurate treatment and removal of mineral tracers and the odor-causing bacteria that feed on proteins within. Many hospitality industries use UV lamps to inspect for unsanitary

bedding to determine lifecycle for mattress restoration as well as general performance of the cleaning staff. A perennial news feature for many television news organizations involves an investigative reporter's using a similar device to reveal unsanitary conditions in hotels, public toilets, hand rails, and such.

Air purification

Using a catalytic reaction from titanium dioxide and UV light exposure, a strong oxidative effect occurs on any organic objects that pass through the media, converting otherwise irritating pathogens, pollens, and mold spores into harmless inert byproducts. The cleansing mechanism of UV is a photochemical process. The contaminants that pollute the indoor environment are almost entirely based upon organic or carbon-based compounds. These compounds break down when exposed to high-intensity UV at 240 to 280 nm. Short-wave ultraviolet light can destroy DNA in living microorganisms and break down organic material found in indoor air. UVC's effectiveness is directly related to intensity and exposure time.

UV light has also been shown (by KJ Scott *et al*) as effective in reducing gaseous contaminants such as carbon monoxide and VOCs. Scott and his colleagues demonstrated that the correct mixture of UV lamps radiating at 184 and 254 nm can remove LOW concentrations hydrocarbons and carbon monoxide, if the lamps are held in a radiation chamber (a box or drum) and the air is recycled between the room and the reaction chamber. This arrangement prevents the introduction of ozone into the treated air. Alternatively, air may be treated by passing by a single UV source operating at 184 nm and subsequent catalysis with iron oxide. The iron oxides remove the ozone produced by the UV lamp.

Analyzing minerals



A collection of mineral samples brilliantly fluorescing at various wavelengths as seen while being irradiated by UV light.

Ultraviolet lamps are also used in analyzing minerals and gems, and in other detective work including authentication of various collectibles. Materials may look the same under visible light, but fluoresce to different degrees under ultraviolet light, or may fluoresce differently under short wave ultraviolet versus long wave ultraviolet.

Authentication

In other detective work including authentication of various collectibles and art, and detecting counterfeit currency absent of marker dyes. Materials may look the same under visible light, but fluoresce to different degrees under ultraviolet light, or may fluoresce differently under short-wave ultraviolet versus long-wave ultraviolet.

Chemical markers

UV fluorescent dyes are used in many applications (for example, biochemistry and forensics). The Green Fluorescent Protein (GFP) is often used in genetics as a marker. Many substances, such as proteins, have significant light absorption bands in the ultraviolet that are of use and interest in biochemistry and related fields. UV-capable spectrophotometers are common in such laboratories.

Photochemotherapy

Exposure to UVA light while the skin is hyper-photosensitive by taking psoralens is an effective treatment for psoriasis called PUVA. Due to the potential of psoralens to cause damage to the liver, PUVA may be used only a limited number of times over a patient's lifetime.

Phototherapy

Exposure to UVB light, in particular, the 310 nm narrowband UVB range, is an effective long-term treatment for many skin conditions like psoriasis, vitiligo, eczema, and others. UVB phototherapy does not require additional medications or topical preparations for the therapeutic benefit; only the light exposure is needed. However, phototherapy can be effective when used in conjunction with certain topical treatments such as anthralin, coal tar, and Vitamin A and D derivatives, or systemic treatments such as methotrexate and soriatane.

Typical treatment regimes involve short exposure to UVB rays 3 to 5 times a week at a hospital or clinic, and up to 30 or more sessions may be required before results are noticeable. Almost all of the conditions that respond to UVB light are chronic problems, so continuous treatment is required to keep those problems in check. Home UVB systems are common solutions for those whose conditions respond to treatment. Home systems permit patients to treat themselves every other day (the ideal treatment regimen for most) without the frequent, costly trips to the office/clinic and back.

Side-effects may include itching and redness of the skin due to UVB exposure, and possibly sunburn, if patients do not minimize exposure to natural UV rays during treatment days. Cataracts can frequently develop if the eyes are not protected from UVB light exposure. There is no link between an increase in the patient's risk for skin cancer and the proper use of UVB phototherapy]]. "Proper use" is generally defined as reaching the "Sub-Erythemic Dose" (S.E.D.), the maximum amount of UVB your skin can receive *without* burning.

Certain fungal growths under the toenail can be treated using a specific wavelength of UV delivered from a high-power LED (light-emitting diode) and can be safer than traditional systemic drugs.

Photolithography

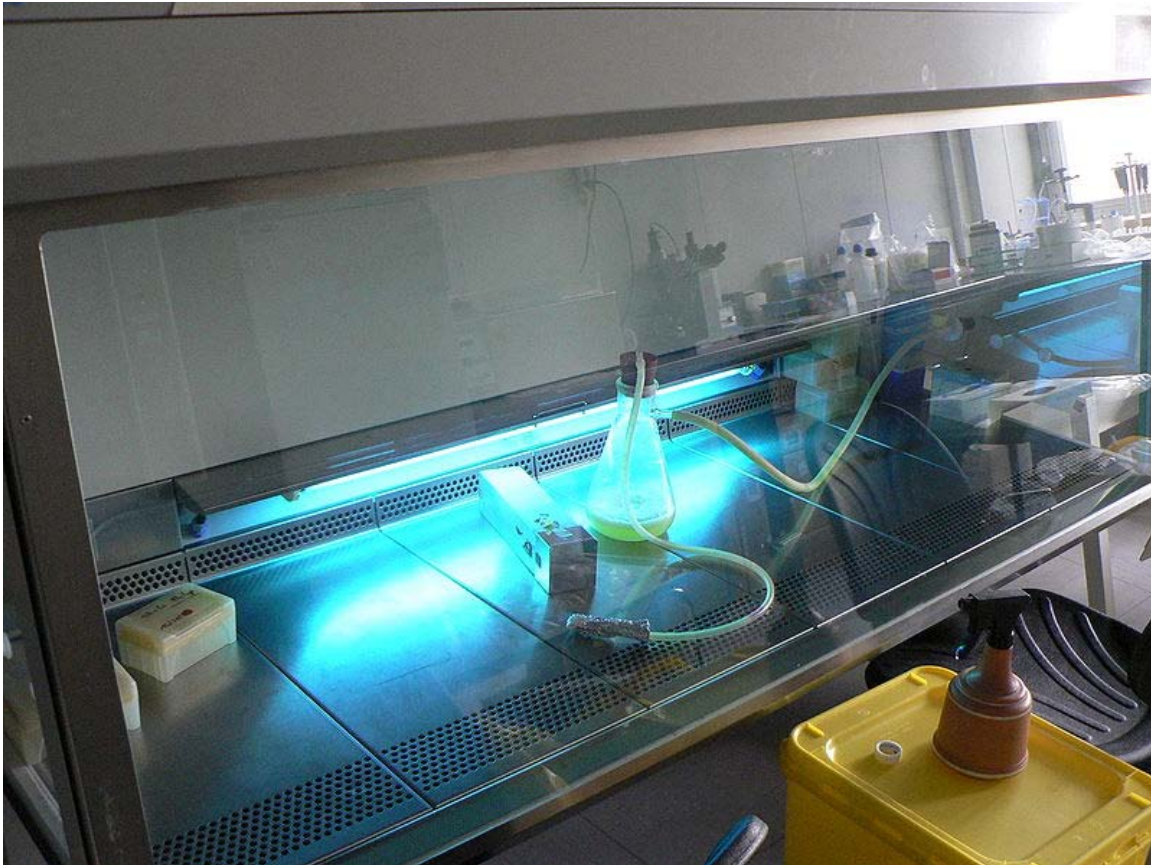
Ultraviolet radiation is used for very fine resolution photolithography, a procedure wherein a chemical called a photoresist is exposed to UV radiation that has passed through a mask. The light causes chemical reactions to occur in the photoresist, and, after development (a step that removes either the exposed or the unexposed photoresist), a pattern determined by the mask remains on the sample. Steps may then be taken to "etch" away areas of the sample where no photoresist remains.

UV radiation is used extensively in the electronics industry because photolithography is used in the manufacture of semiconductors, integrated circuit components, and printed circuit boards.

Checking electrical insulation

An application of UV is to detect corona discharge (often called "corona") on electrical apparatus. Degradation of insulation in electrical apparatus or pollution causes corona, wherein a strong electric field ionizes the air and excites nitrogen molecules, causing the emission of ultraviolet radiation. The corona degrades the insulation level of the apparatus. Corona produces ozone and to a lesser extent nitrogen oxide, which may subsequently react with water in the air to form nitrous acid and nitric acid vapour in the surrounding air.

Sterilization



A low pressure mercury vapor discharge tube floods the inside of a hood with shortwave UV light when not in use, sterilizing microbiological contaminants from irradiated surfaces.

Ultraviolet lamps are used to sterilize workspaces and tools used in biology laboratories and medical facilities. Commercially available low-pressure mercury-vapor lamps emit

about 86% of their light at 254 nanometers (nm), which coincides very well with one of the two peaks of the germicidal effectiveness curve (i.e., effectiveness for UV absorption by DNA). One of these peaks is at about 265 nm and the other is at about 185 nm. Although 185 nm is better absorbed by DNA, the quartz glass used in commercially available lamps, as well as environmental media such as water, are more opaque to 185 nm than 254 nm (C. von Sonntag et al., 1992). UV light at these germicidal wavelengths causes adjacent thymine molecules on DNA to dimerize; if enough of these defects accumulate on a microorganism's DNA, its replication is inhibited, thereby rendering it harmless (even though the organism may not be killed outright). However, since microorganisms can be shielded from ultraviolet light in small cracks and other shaded areas, these lamps are used only as a supplement to other sterilization techniques.

Disinfecting drinking water

UV radiation can be an effective viricide and bactericide. Disinfection using UV radiation is commonly used in wastewater treatment applications and is finding an increased usage in drinking water treatment. Many bottlers of spring water use UV disinfection equipment to sterilize their water. Solar water disinfection is the process of using PET bottles and sunlight to disinfect water.

New York City has approved the construction of a 2-billion-US-gallon-per-day (7,600,000 m³/d) ultraviolet drinking water disinfection facility. There are also several facilities under construction and several in operation that treat waste water with several stages of filters, hydrogen peroxide, and UV light to bring the water up to drinking standards. One such facility exists in Orange County, California. NASA has examined the use of this technology, using titanium dioxide as catalyst, for breaking down harmful products in spacecraft waste water.

It used to be thought that UV disinfection was more effective for bacteria and viruses, which have more exposed genetic material, than for larger pathogens that have outer coatings or that form cyst states (e.g., Giardia) that shield their DNA from the UV light. However, it was recently discovered that ultraviolet radiation can be somewhat effective for treating the microorganism Cryptosporidium. The findings resulted in the use of UV radiation as a viable method to treat drinking water. Giardia in turn has been shown to be very susceptible to UV-C when the tests were based on infectivity rather than excystation. It has been found that protists are able to survive high UV-C doses but are sterilized at low doses.

Solar water disinfection (SODIS) has been extensively researched in Switzerland and has proven ideal to treat small quantities of water cheaply using natural sunlight. Contaminated water is poured into transparent plastic bottles and exposed to full sunlight for six hours. The sunlight treats the contaminated water through two synergetic mechanisms: UV-A irradiation and increased water temperature. If the water temperatures rises above 50 °C (120 °F), the disinfection process is three times faster.

Food processing

As consumer demand for fresh and "fresh-like" food products increases, the demand for nonthermal methods of food processing is likewise on the rise. In addition, public awareness regarding the dangers of food poisoning is also raising demand for improved food processing methods. Ultraviolet radiation is used in several food processes to kill unwanted microorganisms. UV light can be used to pasteurize fruit juices by flowing the juice over a high-intensity ultraviolet light source. The effectiveness of such a process depends on the UV absorbance of the juice.

Fire detection

Ultraviolet detectors generally use either a solid-state device, such as one based on silicon carbide or aluminium nitride, or a gas-filled tube as the sensing element. UV detectors that are sensitive to UV light in any part of the spectrum respond to irradiation by sunlight and artificial light. A burning hydrogen flame, for instance, radiates strongly in the 185- to 260-nanometer range and only very weakly in the IR region, whereas a coal fire emits very weakly in the UV band yet very strongly at IR wavelengths; thus, a fire detector that operates using both UV and IR detectors is more reliable than one with a UV detector alone. Virtually all fires emit some radiation in the UVC band, whereas the Sun's radiation at this band is absorbed by the Earth's atmosphere. The result is that the UV detector is "solar blind", meaning it will not cause an alarm in response to radiation from the Sun, so it can easily be used both indoors and outdoors.

UV detectors are sensitive to most fires, including hydrocarbons, metals, sulfur, hydrogen, hydrazine, and ammonia. Arc welding, electrical arcs, lightning, X-rays used in nondestructive metal testing equipment (though this is highly unlikely), and radioactive materials can produce levels that will activate a UV detection system. The presence of UV-absorbing gases and vapors will attenuate the UV radiation from a fire, adversely affecting the ability of the detector to detect flames. Likewise, the presence of an oil mist in the air or an oil film on the detector window will have the same effect.

Herpetology

Reptiles need long wave UV light for de novo synthesis of vitamin D. Vitamin D is needed to metabolize calcium for bone and egg production. Thus, in a typical reptile enclosure, a fluorescent UV lamp should be available for vitamin D synthesis. This should be combined with the provision of heat for basking, either in the same or by another lamp.

Curing of electronic potting resins

Electronic components that require clear transparency for light to exit or enter (photo voltaic panels and sensors) can be potted using acrylic resins that are cured using UV light energy. The advantages are low VOC emissions and rapid curing.

Curing of inks, adhesives, varnishes and coatings

Certain inks, coatings, and adhesives are formulated with photoinitiators and resins. When exposed to the correct energy and irradiance in the required band of UV light, polymerization occurs, and so the adhesives harden or cure. Usually, this reaction is very quick, a matter of a few seconds. Applications include glass and plastic bonding, optical fiber coatings, the coating of flooring, UV Coating and paper finishes in offset printing, and dental fillings. Curing of decorative finger nail "gels".

An industry has developed around the manufacture of UV sources for UV curing applications. This includes UV lamps, UV LEDs, and Excimer Flash lamps. Fast processes such as flexo or offset printing require high-intensity light focused via reflectors onto a moving substrate and medium; and high-pressure Hg (mercury) or Fe (iron, doped)-based bulbs are used, which can be energized with electric arc or microwaves. Lower-power sources (fluorescent lamps, LED) can be used for static applications, and, in some cases, small high-pressure lamps can have light focused and transmitted to the work area via liquid-filled or fiber-optic light guides.

Sun tanning

Sun tanning describes a darkening of the skin in a natural physiological response stimulated by exposure to ultraviolet radiation from sunshine (or a sunbed). With excess exposure to the sun, a suntanned area can also develop sunburn. The increased production of melanin is triggered by the direct DNA damage. This kind of damage is recognized by the body and as a defense against UV radiation the skin produces more melanin. Melanin dissipates the UV energy as harmless heat, and therefore it is an excellent photoprotectant. Melanin protects against the direct DNA damage and against the indirect DNA damage. Sunscreen protects only against the direct DNA damage, but increases the indirect DNA damage. Some studies suggest that this may be the cause of the higher incidence of melanoma found in sunscreen users compared to non-users.

Erasing EPROM modules

Some EPROM (erasable programmable read-only memory) modules are erased by exposure to UV radiation. These modules often have a transparent glass (quartz) window on the top of the chip that allows the UV radiation in. These have been largely superseded by EEPROM and flash memory chips in most devices.

Preparing low surface energy polymers

UV radiation is useful in preparing low surface energy polymers for adhesives. Polymers exposed to UV light will oxidize, thus raising the surface energy of the polymer. Once the surface energy of the polymer has been raised, the bond between the adhesive and the polymer is stronger.

Reading otherwise illegible papyruses

Using multi-spectral imaging it is possible to read illegible papyruses, such as the burned papyruses of the Villa of the Papyri or of Oxyrhynchus, or the Archimedes palimpsest. The technique involves taking pictures of the illegible papyruses using different filters in the infrared or ultraviolet range, finely tuned to capture certain wavelengths of light. Thus, the optimum spectral portion can be found for distinguishing ink from paper on the papyrus surface.

Lasers

Ultraviolet lasers have applications in industry (laser engraving), medicine (dermatology and keratectomy), free air secure communications and computing (optical storage). They can be made by applying frequency conversion to lower-frequency lasers, or from Ce:LiSAF crystals (cerium doped with lithium strontium aluminum fluoride), a process developed in the 1990s at Lawrence Livermore National Laboratory.

UV solar cells and UV degradation of solar cells

Japan's National Institute of Advanced Industrial Science and Technology (AIST) has succeeded in developing a transparent solar cell that uses ultraviolet light to generate electricity but allows visible light to pass through it. Most conventional solar cells use visible and infrared light to generate electricity. In contrast, the innovative new solar cell uses ultraviolet radiation. Used to replace conventional window glass, the installation surface area could be large, leading to potential uses that take advantage of the combined functions of power generation, lighting and temperature control.

Also PEDOT-PSS solar cells is an ultraviolet (UV) light-selective and -sensitive photovoltaic cell easily fabricated.

On the other hand, a nanocrystalline layer of Cu_2O in the construction of photovoltaic cells increases their ability to utilize UV radiations for photocurrent generation.

Nondestructive testing

UV light of a specified spectrum and intensity is used to stimulate fluorescent dyes so as to highlight defects in a broad range of materials. These dyes may be carried into surface-breaking defects by capillary action (liquid penetrant inspection) or they may be bound to ferrite particles caught in magnetic leakage fields in ferrous materials (magnetic particle inspection).

Evolutionary significance

Evolution of early reproductive proteins and enzymes is attributed in modern models of evolutionary theory to ultraviolet light. UVB light causes thymine base pairs next to each other in genetic sequences to bond together into thymine dimers, a disruption in the

strand that reproductive enzymes cannot copy. This leads to frameshifting during genetic replication and protein synthesis, usually killing the organism. As early prokaryotes began to approach the surface of the ancient oceans, before the protective ozone layer had formed, blocking out most wavelengths of UV light, they almost invariably died out. The few that survived had developed enzymes that verified the genetic material and broke up thymine dimer bonds, known as base excision repair enzymes. Many enzymes and proteins involved in modern mitosis and meiosis are similar to excision repair enzymes, and are believed to be evolved modifications of the enzymes originally used to overcome UV light.

Chapter 7

Light Therapy



Bright light therapy is a common treatment for seasonal affective disorder and for circadian rhythm disorders.

Light therapy or **phototherapy** (classically referred to as **heliotherapy**) consists of exposure to daylight or to specific wavelengths of light using lasers, light-emitting diodes, fluorescent lamps, dichroic lamps or very bright, full-spectrum light, usually controlled with various devices. The light is administered for a prescribed amount of time and, in some cases, at a specific time of day.

Commercially, the common use of the term is associated with the treatment of skin, sleep disorder and some psychiatric disorders. Light therapy directed at the skin is used to treat acne vulgaris and neonatal jaundice. Light therapy which strikes the retina of the eyes is used to treat circadian rhythm disorders such as delayed sleep phase syndrome and can also be used to treat seasonal affective disorder, with some support for its use also with non-seasonal psychiatric disorders.

The medical (mainstream and complementary and alternative medicine) applications of light therapy also include pain management, accelerated wound healing, hair growth, acupuncture, improvement in blood properties and blood circulation, and sinus-related diseases and disorders. Many of these use low level laser therapy and red light therapy in the 620–660 nm range.

The National Center for Complementary and Alternative Medicine has listed "Light Therapy" as a practice that involves "veritable forms of energy that include those involving electromagnetic fields".

History

Indian medical literature dating to 1500 BC describes a treatment combining herbs with natural sunlight to treat non-pigmented skin areas. Buddhist literature from about 200 AD and 10th-century Chinese documents made similar references.

Danish physician Nils Finsen is believed to be the father of modern phototherapy. He developed the first artificial light source for this purpose, and used his invention to treat lupus vulgaris. He received the Nobel Prize in Physiology or Medicine in 1903.

Since then a large array of treatments have been developed from the use of controlled light. Though the popular consumer understanding of "light therapy" is associated with treating seasonal affective disorder, other applications, growing in recognition include the application of low level laser, red light, near-infrared and ultraviolet lights for pain management, hair growth, skin treatments, accelerated wound healing. The modalities include light-based acupuncture, directing light on painful areas, blood irradiation therapy and photodynamic therapy.

Skin related

Acne vulgaris

Sunlight was long known to improve acne, and this was thought to be due to antibacterial and other effects of the ultraviolet spectrum which cannot be used as a long-term treatment due to the likelihood of skin damage.

It was found that some of the visible violet light present in sunlight (in the range 415–430 nm) activates a porphyrin (Coproporphyrin III) in *Propionibacterium acnes* which

damages and ultimately kills the bacteria by releasing singlet oxygen. A total of 320 J/cm² of light within this range renders the bacteria non-viable.

The use of light therapy for three consecutive days has been shown to reduce the bacteria in the pores by 99.9%. Since there are few porphyrins naturally found in the skin, the treatment is believed safe except in patients with porphyria; although eye protection is used due to light-sensitive chemicals in the retina. The light is usually created by superluminous LEDs. This form of treatment has been approved by the FDA for some lightwave systems . Overall improvements of on average 76% for 80% of patients occurs over three months; most studies show that it performs better than benzoyl peroxide and the treatment is far better tolerated. However, approximately 10% of users see no improvement.

Psoriasis and eczema

A feature of psoriasis is localized inflammation mediated by the immune system. UV radiation is known to suppress the immune system and reduce inflammatory responses. Light therapy for skin conditions like psoriasis or eczema use UV-A (315–400 nm wavelength) or UV-B (280–315 nm wavelength) light waves. UV-A, combined with a drug taken orally, is known as PUVA treatment. Narrow band UV-B is the 310 nm wavelength and is given as a light therapy treatment rather than full spectrum UV-B.

Tanning

Tanning is caused by the effects of two different spectrums of ultraviolet radiation: UV-A and UV-B.

Wound healing

Lightwave therapy has been suggested for use in healing of wounds. Some say that low-level laser therapy does not appear to be effective, while others find that it can be effective. Lightwave therapy is used clinically in many areas outside the United States including Canada, Europe and Asia.

Photodynamic therapy

Visible blue light is used with aminolevulinic acid for the treatment of actinic keratosis. This is not a U.S. FDA-approved treatment for acne vulgaris.

Mood and sleep related

Light boxes

The production of the hormone melatonin, a sleep regulator, is inhibited by light and permitted by darkness as registered by photosensitive ganglion cells in the retina. To

some degree, the reverse is true for serotonin, which has been linked to mood disorders. Hence, for the purpose of manipulating melatonin levels or timing, light boxes providing very specific types of artificial illumination to the retina of the eye are effective.

Light therapy either uses a lightbox which emits up to 10,000 lux of light, much brighter than a customary incandescent lamp, or a lower intensity of specific wavelengths of light from the blue (470 nm) to the green (525 nm) areas of the visible spectrum. Newer light therapy devices use LED technology, making them much smaller and more convenient for users. A 1995 study showed that green light therapy at doses of 350 lux produces melatonin suppression and phase shifts equivalent to 10,000 lux bright light therapy and another study published in May 2010 suggests that the blue light often used for SAD treatment should perhaps be replaced by green or white illumination.

In treatment, the patient's eyes are to be at a prescribed distance from the light source with the light striking the retina. This does not require looking directly into the light.

Seasonal affective disorder

While full sunlight is preferred for seasonal affective disorder (SAD), light boxes may be effective for the treatment of the condition. Light boxes for seasonal affective disorder are designed to filter out most UV light, which can cause eye and skin damage. The U.S. Food and Drug Administration has not approved the use of light boxes to treat SAD due to unclear results in clinical trials, but light therapy is still seen as the main form of treatment for SAD. Direct sunlight, reflected into the windows of a home or office by a computer-controlled mirror device called a heliostat, has also been used as a type of light therapy for the treatment of SAD.

It is possible that response to light therapy for SAD could be season dependent.

Non-seasonal depression

Light therapy has also been suggested in the treatment of non-seasonal depression and other psychiatric disturbances, including major depressive disorder, bipolar disorder and postpartum depression. A meta-analysis by the Cochrane Collaboration concluded that "For patients suffering from non-seasonal depression, light therapy offers modest though promising antidepressive efficacy."

Circadian rhythm sleep disorders

Chronic CRSD

In the management of circadian rhythm disorders such as delayed sleep phase syndrome (DSPS), the timing of light exposure is critical. For DSPS, the light must be provided to the retina as soon after spontaneous awakening as possible to achieve the desired effect, as shown by the phase response curve for light in humans. Some users have reported success with lights that turn on shortly *before* awakening (dawn simulation). Morning use

may also be effective for non-24-hour sleep-wake syndrome, while evening use is recommended for advanced sleep phase syndrome.

Situational CRSD

Light therapy has been tested for individuals on shift work, and for jet lag.

Neonatal jaundice



A newborn infant undergoing white-light phototherapy to treat neonatal jaundice.

Light therapy is used to treat cases of neonatal jaundice through the isomerization of the bilirubin and consequently transformation into compounds that the newborn can excrete via urine and stools. A common treatment of neonatal jaundice is the Bili light.

Parkinson's disease

Bright light therapy may ease Parkinson's disease by reducing patients' tremors.

Safety

Ultraviolet light causes progressive damage to human skin. This is mediated by genetic damage, collagen damage, as well as destruction of vitamin A and vitamin C in the skin and free radical generation. Ultraviolet light is also known to be a factor in formation of

cataracts. Researchers have questioned whether limiting blue light exposure could reduce the risk of age-related macular degeneration.

Modern phototherapy lamps used in the treatment of seasonal affective disorder and sleep disorders either filter out or do not emit ultraviolet light and are considered safe and effective for the intended purpose, as long as photosensitizing drugs are not being taken at the same time and in the absence of any existing eye conditions. Light therapy is a mood altering treatment, and just as with drug treatments, there is a possibility of triggering a manic state from a depressive state, causing anxiety and other side effects. While these side effects are usually controllable, it is recommended that patients undertake light therapy under the supervision of an experienced clinician, rather than attempting to self-medicate.

It is reported that bright light therapy may activate the production of reproductive hormones, such as testosterone, luteinizing hormone, follicle-stimulating hormone, and estradiol.

There are few absolute contraindications to light therapy, although there are some circumstances in which caution is required. These include when a patient has a condition that might render his or her eyes more vulnerable to phototoxicity, has a tendency toward mania, has a photosensitive skin condition, or is taking a photosensitizing herb (such as St. John's wort) or medication. Patients with porphyria should avoid most forms of light therapy. Patients on certain drugs like methotrexate or chloroquine should use caution with light therapy as there is a chance that these drugs could cause porphyria.

Side effects

Side effects of light therapy for sleep phase disorders include jumpiness or jitteriness, headache, and nausea. Some nondepressive physical complaints (such as poor vision and skin rash or irritation) may improve with light therapy.

Chapter 8

Light Effects on Circadian Rhythm and Scotobiology

Light effects on circadian rhythm

Numerous organisms maintain inherent individual daily rhythms to biological processes, known as **circadian rhythms**, that assist the organism in maintaining functional periodicity relative to the 24-hour day/night cycle of the earth. These rhythms are maintained by the individual organisms, but due to variable individuality and environmental pressures, must continually or repeatedly be reset to synch with the natural environmental cycle. In order for this to be accomplished, external factors must play some role in the synchronization, or entrainment, of the internal circadian rhythm with the external environment. Of the various factors that influence this entrainment, light exposure to the eyes is the strongest effector.

Demonstrated effects

All of the mechanisms of light-effected entrainment are not yet fully known, however numerous studies have demonstrated the effectiveness of light entrainment to the day/night cycle. Studies have shown that:

- The timing of exposure to light influences entrainment; as seen on the phase response curve for light for a given species.
 - In diurnal species, exposure to bright light after waking advances the circadian rhythm, whereas exposure before sleeping delays the rhythm.
- The length of exposure influences entrainment.
 - Longer exposures have a greater effect than shorter exposures.
 - Consistent exposure has a greater effect than intermittent exposure.
 - In rats, constant exposure eventually disrupts the cycle to the point that functions like memory and stress coping may be impaired.
- Intensity and wavelength of light influence entrainment.
 - Brighter light is more effective than dim light.

- Dim light can effect entrainment relative to darkness.
- In humans, low intensity short wavelength (blue/violet) light may be equally effective as high intensity white light.

Internal regulators

Light's effect on the circadian rhythms of all or most animals has been well-documented. However, since circadian rhythms are internal functions, the influence of external factors like light and an individual's sensitivity to them can to some degree be regulated by internal mechanisms.

- In zebrafish, evidence of a negative regulation of light-dependent gene transcription has been found. In one study, overabundance of the enzyme catalase reduced the transcription of genes that were dependent on light, whereas inhibition of the enzyme resulted in increased transcription.
- Another study found that a deficit of the oligopeptide angiotensin in the brain of laboratory rats resulted in delayed adjustment to changes in the day/night pattern.
- Similarly, deficits of TrkB tyrosine kinase in mice, a receptor for brain-derived neurotrophic factor (BDNF), result in a decrease of the ability to entrain to shifts in the day–night cycle.

Internal conditions may thus sway the effectiveness of entrainment to light. All mechanisms behind the process are not yet fully understood.

Other factors

Although many researchers consider light to be the strongest cue for entrainment, it is by no means the only factor acting on circadian rhythms. Other factors may enhance or decrease the effectiveness of entrainment. For instance, physical activity like exercise when coupled with light exposure results in a somewhat stronger entrainment response. Other factors such as music and administration of the neurohormone melatonin have shown similar effects. Numerous other factors affect entrainment as well. These include feeding schedules, temperature, pharmacology, locomotor stimuli, social interaction, sexual stimuli and stress.

Scotobiology

The term *scotobiology* describes the study of biology as directly and specifically affected by darkness, as opposed to photobiology, which describes the biological effects of light.

Overview

The science of scotobiology gathers together under a single descriptive heading a wide range of approaches to the study of the biology of darkness. This includes work on the effects of darkness on the behavior and metabolism of animals, plants, and microbes.

Some of this work has been going on for over a century, and lays the foundation for understanding the importance of dark night skies, not only for humans but for all biological species.

The great majority of biological systems have evolved in a world of alternating day and night and have become irrevocably adapted to and dependent on the seasonally changing patterns of light and darkness. Light is essential for many biological activities such as sight and photosynthesis. These are the focus of the science of photobiology. But the presence of uninterrupted periods of darkness, as well as their alternation with light, is just as important to biological behaviour. Scotobiology studies the positive responses of biological systems to the presence of darkness, and not merely the negative effects caused by the absence of light.

Effects of darkness

Many of the biological and behavioural activities of plants, animals (including birds and amphibians), insects, and microorganisms are either adversely affected by light pollution at night or can only function effectively either during or as the consequence of nightly darkness. Such activities include foraging, breeding and social behavior in higher animals, amphibians, and insects, which are all affected in various ways if light pollution occurs in their environment. These are not merely photobiological phenomena; light pollution acts by interrupting critical dark-requiring processes.

But perhaps the most important scotobiological phenomena relate to the regular periodic alternation of light and darkness. These include breeding behavior in a range of animals, the control of flowering and the induction of winter dormancy in many plants, and the operational control of the human immune system. In many of these biological processes the critical point is the length of the dark period rather than that of the light. For example, "short-day" and "long-day" plants are, in fact, "long-night" and "short-night" respectively. That is to say, plants do not measure the length of the light period, but of the dark period. One consequence of light pollution is that even brief periods of relatively bright light during the night may prevent plants or animals (including humans) from measuring the length of the dark period, and therefore from behaving in a normal or required manner. This is a critical aspect of scotobiology, and one of the major areas in the study of the responses of biological systems to darkness.

In discussing scotobiology, it is important to remember that darkness (the absence of light) is seldom absolute. An important aspect of any scotobiological phenomenon is the level and quality (wavelength) of light that is below the threshold of detection for that phenomenon and in any specific organism. This important variable in scotobiological studies is not always properly noted or examined. There are substantial levels of natural light pollution at night, of which moonlight is usually the strongest. For example, plants that rely on night length to program their behaviour have the capacity to ignore full moonlight during an otherwise dark night. If this ability had not evolved, plants would not be able to respond to changing night-length for such behavioural programs as the initiation of flowering and the onset of dormancy. On the other hand, some animal

behavioural patterns are strongly responsive to moonlight. It is thus most important in any scotobiological study to determine the threshold level of light that may be required to interfere with or negate the normal pattern of dark-night activity.

Etymology

In 2003, at a symposium on the Ecology of the Night held in Muskoka, Ontario, Canada, discussion centered around the many effects of night-time light pollution on the biology of a wide range of organisms, but it went far beyond this in describing darkness as a biological imperative for the functioning of biological systems. Presentations focused on the absolute requirement of darkness for many aspects of normal behaviour and metabolism of many organisms and for the normal progression of their life cycles. Because there was no suitable term to describe the Symposium's main focus, the term *scotobiology* was introduced. The word is derived from the Greek *scotos* (dark), and relates to *photobiology*, which describes the biological effects of light (*photos*). This term appears not to have been used previously, although related terms such as *skototropism* and *scotophyle* have appeared in the literature.