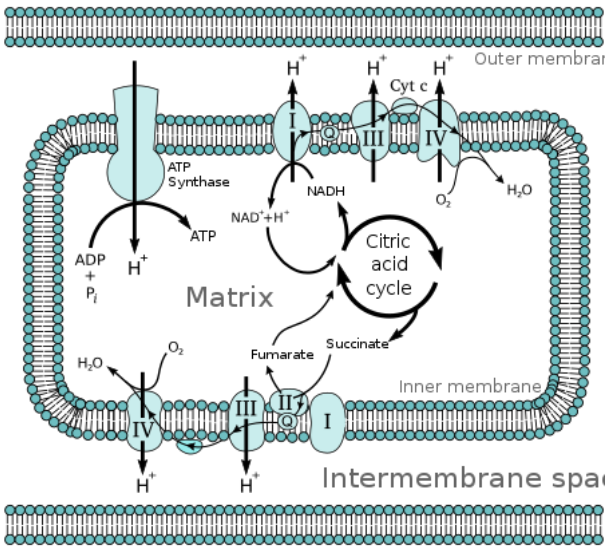
Electron transport chain

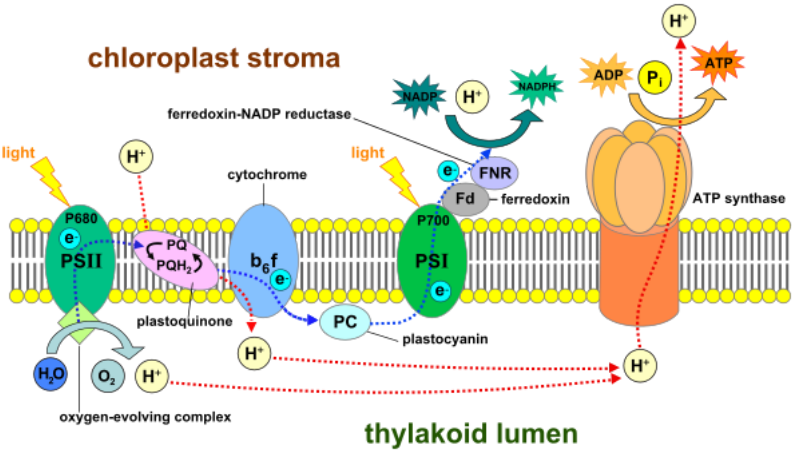
The **electron transport chain** (**ETC; respiratory chain**[1]) is a series of protein complexes that transfer electrons from electron donors to electron acceptors via redox reactions (both reduction and oxidation occurring simultaneously) and couples this electron transfer with the transfer of protons (H^+ ions) across a membrane. The electron transport chain is built up of peptides, enzymes, and other molecules.



The electron transport chain in the mitochondrion is the site of oxidative phosphorylation in eukaryotes. The NADH and succinate generated in the citric acid cycle are oxidized, providing energy to power ATP synthase.

The flow of electrons through the electron transport chain is an exergonic process. The energy from the redox reactions create an electrochemical proton gradient that drives the synthesis of adenosine triphosphate (ATP). In aerobic respiration, the flow of electrons terminates with molecular oxygen being the final electron acceptor. In anaerobic respiration, other electron acceptors are used, such as sulfate.

In the electron transport chain, the redox reactions are driven by the Gibbs free energy state of the components. Gibbs free energy is related to a quantity called the redox potential. The complexes in the electron transport chain harvest the energy of the redox reactions that occur when transferring electrons from a low redox potential to a higher redox potential, creating an electrochemical gradient. It is the electrochemical gradient created that drives the synthesis of ATP via coupling with oxidative phosphorylation with ATP synthase.[2]



Photosynthetic electron transport chain of the thylakoid membrane.

In eukaryotic organisms the electron transport chain, and site of oxidative phosphorylation, is found on the inner mitochondrial membrane. The energy stored from the process of respiration in reduced compounds (such as NADH and FADH) is used by the electron transport chain to pump protons into the intermembrane space, generating the electrochemical gradient over the inner mitochondrial membrane. In photosynthetic eukaryotes, the electron transport chain is found on the thylakoid membrane. Here, light energy drives the reduction of components of the electron transport chain and therefore causes subsequent synthesis of ATP. In bacteria, the electron transport chain can vary over species but it always constitutes a set of redox reactions that are coupled to the synthesis of ATP, through the generation of an electrochemical gradient, and oxidative phosphorylation through ATP synthase.[3]

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Mitochondrial electron transport chains

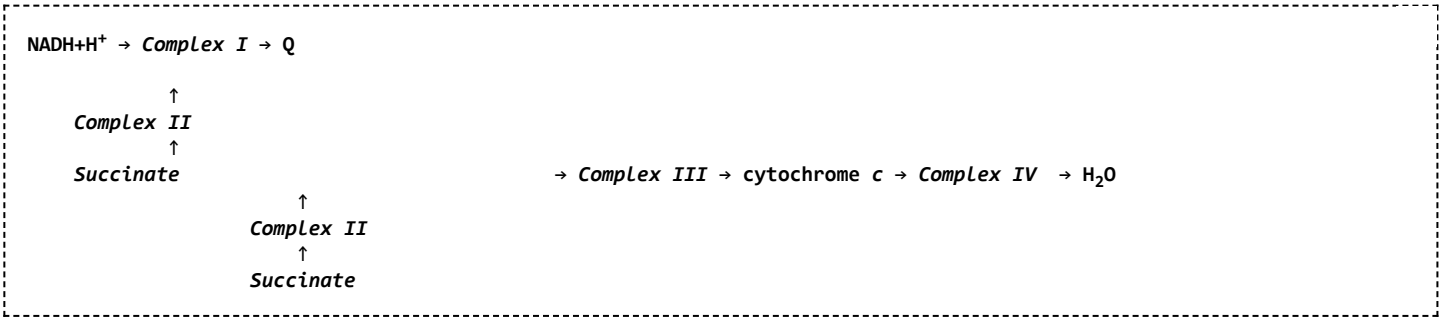
Most eukaryotic cells have mitochondria, which produce ATP from products of the citric acid cycle, fatty acid oxidation, and amino acid oxidation. At the inner mitochondrial membrane, electrons from NADH and $FADH_2$ pass through the electron transport chain to oxygen, which is reduced to water.[4] The electron transport chain comprises an enzymatic series of electron donors and acceptors. Each electron donor will pass electrons to a more electronegative acceptor, which in turn donates these electrons to another acceptor, a process that continues down the series until electrons are passed to oxygen, the most electronegative and terminal electron acceptor in the chain. Passage of electrons between donor and acceptor releases energy, which is used to generate a proton gradient across the mitochondrial membrane by "pumping" protons into the intermembrane space, producing a thermodynamic state that has the potential to do work. This entire process is called oxidative phosphorylation since ADP is phosphorylated to ATP by using the electrochemical gradient established by the redox reactions of the electron transport chain.

Mitochondrial redox carriers

Energy obtained through the transfer of electrons down the electron transport chain is used to pump protons from the mitochondrial matrix into the intermembrane space, creating an electrochemical proton gradient (ΔpH) across the inner mitochondrial membrane. This proton gradient is largely but not exclusively responsible for the mitochondrial membrane potential ($\Delta\Psi_M$).[5] It allows ATP synthase to use the flow of H^+ through the enzyme back into the matrix to generate ATP from adenosine diphosphate (ADP) and inorganic phosphate. Complex I (NADH coenzyme Q reductase; labeled I) accepts electrons from the Krebs cycle electron carrier nicotinamide adenine dinucleotide (NADH), and passes them to coenzyme Q (ubiquinone; labeled Q), which also receives electrons from complex II (succinate dehydrogenase; labeled II). Q passes electrons to complex III (cytochrome bc_1

complex; labeled III), which passes them to cytochrome *c* (cyt *c*). Cyt *c* passes electrons to complex IV (cytochrome *c* oxidase; labeled IV), which uses the electrons and hydrogen ions to reduce molecular oxygen to water.

Four membrane-bound complexes have been identified in mitochondria. Each is an extremely complex transmembrane structure that is embedded in the inner membrane. Three of them are proton pumps. The structures are electrically connected by lipid-soluble electron carriers and water-soluble electron carriers. The overall electron transport chain:



Complex I

In complex I (NADH ubiquinone oxireductase, Type I NADH dehydrogenase, or mitochondrial complex I; EC 1.6.5.3 (https://enzyme.expasy.org/EC/1.6.5.3)), two electrons are removed from NADH and transferred to a lipid-soluble carrier, ubiquinone (Q). The reduced product, ubiquinol (QH_2), freely diffuses within the membrane, and Complex I translocates four protons (H^+) across the membrane, thus producing a proton gradient. Complex I is one of the main sites at which premature electron leakage to oxygen occurs, thus being one of the main sites of production of superoxide.[6]

The pathway of electrons is as follows:

NADH is oxidized to NAD^+, by reducing Flavin mononucleotide to $FMNH_2$ in one two-electron step. $FMNH_2$ is then oxidized in two one-electron steps, through a semiquinone intermediate. Each electron thus transfers from the $FMNH_2$ to an Fe-S cluster, from the Fe-S cluster to ubiquinone (Q). Transfer of the first electron results in the free-radical (semiquinone) form of Q, and transfer of the second electron reduces the semiquinone form to the ubiquinol form, QH_2. During this process, four protons are translocated from the mitochondrial matrix to the intermembrane space. [7] As the electrons become continuously oxidized and reduced throughout the complex an electron current is produced along the 180 Angstrom width of the complex within the membrane. This current powers the active transport of four protons to the intermembrane space per two electrons from NADH.[8]

Complex II

In complex II (succinate dehydrogenase or succinate-CoQ reductase; EC 1.3.5.1 (https://enzyme.expasy.org/EC/1.3.5.1)) additional electrons are delivered into the quinone pool (Q) originating from succinate and transferred (via flavin adenine dinucleotide (FAD)) to Q. Complex II consists of four protein subunits: succinate dehydrogenase, (SDHA); succinate dehydrogenase [ubiquinone] iron-sulfur subunit, mitochondrial, (SDHB); succinate dehydrogenase complex subunit C, (SDHC) and succinate dehydrogenase complex, subunit D, (SDHD). Other electron donors (e.g., fatty acids and glycerol 3-phosphate) also direct electrons into Q (via FAD). Complex II is a parallel electron transport pathway to complex 1, but unlike complex 1, no protons are transported to the intermembrane space in this pathway. Therefore, the pathway through complex II contributes less energy to the overall electron transport chain process.

Complex III

In complex III (cytochrome bc_1 complex or $CoQH_2$-cytochrome *c* reductase; EC 1.10.2.2 (https://enzyme.expasy.org/EC/1.10.2.2)), the Q-cycle contributes to the proton gradient by an asymmetric absorption/release of protons. Two electrons are removed from QH_2 at the Q_O site and sequentially transferred to two molecules of cytochrome *c*, a water-soluble electron carrier located within the intermembrane space. The two other electrons sequentially pass across the protein to the Q_i site where the quinone part of ubiquinone is reduced to quinol. A proton gradient is formed by one quinol ($2\,H_2^+\,e^-$) oxidations at the Q_o site to form one quinone ($2\,H_2^+\,e^-$) at the Q_i site. (In total, four protons are translocated: two protons reduce quinone to quinol and two protons are released from two ubiquinol molecules.)

$$QH_2 + 2\ \text{cytochrome}\ c(Fe^{III}) + 2\,H^+_{in} \longrightarrow Q + 2\ \text{cytochrome}\ c(Fe^{II}) + 4\,H^+_{out}$$

When electron transfer is reduced (by a high membrane potential or respiratory inhibitors such as antimycin A), Complex III may leak electrons to molecular oxygen, resulting in superoxide formation.

This complex is inhibited by dimercaprol (British Antilewisite, BAL), Napthoquinone and Antimycin.

Complex IV

In complex IV (cytochrome *c* oxidase; EC 1.9.3.1 (https://enzyme.expasy.org/EC/1.9.3.1)), sometimes called cytochrome AA3, four electrons are removed from four molecules of cytochrome *c* and transferred to molecular oxygen (O_2), producing two molecules of water. The complex contains coordinated copper ions and several heme groups. At the same time, eight protons are removed from the mitochondrial matrix (although only four are translocated across the membrane), contributing to the proton gradient. The exact details of proton pumping in complex IV are still under study.[9] Cyanide is an inhibitor of complex 4.

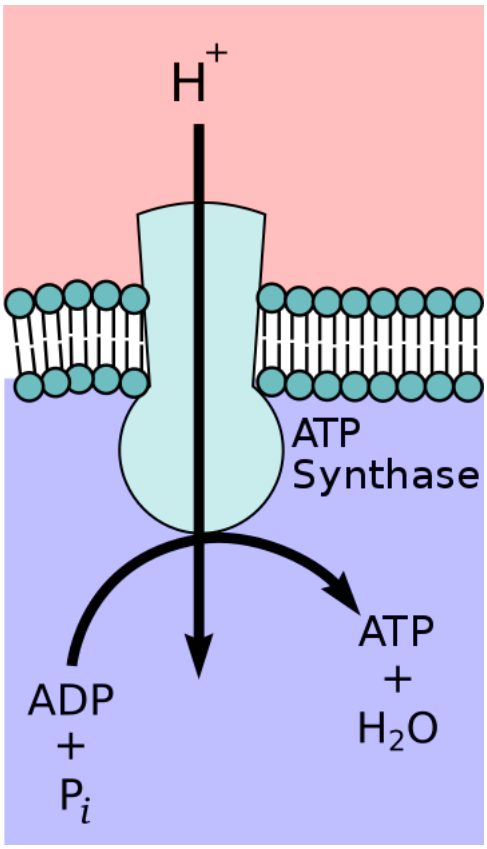
Coupling with oxidative phosphorylation

The chemiosmotic coupling hypothesis, proposed by Nobel Prize in Chemistry winner Peter D. Mitchell, the electron transport chain and oxidative phosphorylation are coupled by a proton gradient across the inner mitochondrial membrane. The efflux of protons from the mitochondrial matrix creates an electrochemical gradient (proton gradient). This gradient is used by the F_OF_1 ATP synthase complex to make ATP via oxidative phosphorylation. ATP synthase is sometimes described as *Complex V* of the electron transport chain.[10] The F_O component of ATP synthase acts as an ion channel that provides for a proton flux back into the mitochondrial matrix. It is composed of a, b and c subunits. Protons in the inter-membranous space of mitochondria first enters the ATP synthase complex through *a* subunit channel. Then protons move to the c subunits.[11] The number of c subunits it has determines how many protons it will require to make the F_O turn one full revolution. For example, in humans, there are 8 c subunits, thus 8 protons are required.[12] After *c* subunits, protons finally enters matrix using *a* subunit channel that opens into the mitochondrial matrix.[11] This reflux releases free energy produced during the generation of the oxidized forms of the electron carriers (NAD^+ and Q). The free energy is used to drive ATP synthesis, catalyzed by the F_1 component of the complex.[13]

Coupling with oxidative phosphorylation is a key step for ATP production. However, in specific cases, uncoupling the two processes may be biologically useful. The uncoupling protein, thermogenin—present in the inner mitochondrial membrane of brown adipose tissue—provides for an alternative flow of protons back to the inner mitochondrial matrix. Thyroxine is also a natural uncoupler. This alternative flow results in thermogenesis rather than ATP production.[14]

Reverse electron flow

Reverse electron flow, is the transfer of electrons through the electron transport chain through the reverse redox reactions. Usually requiring a significant amount of energy to be used, this can result in reducing the oxidised form of electron donors. For example, NAD+ can be reduced to NADH by complex I.[15] There are several factors that have been shown to induce reverse electron flow. However, more work needs to be done to confirm this. One such example is blockage of ATP production by ATP synthase, resulting in a build-up of protons and therefore a higher proton-motive force, inducing reverse electron flow.[16]



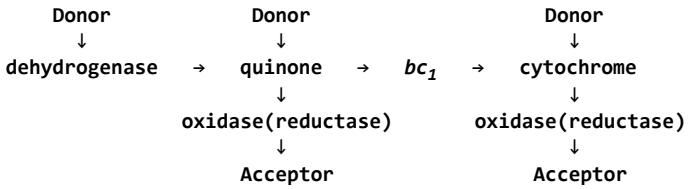
Depiction of ATP synthase, the site of oxidative phosphorylation to generate ATP.

Bacterial electron transport chains

In eukaryotes, NADH is the most important electron donor. The associated electron transport chain is

NADH → *Complex I* → Q → *Complex III* → cytochrome *c* → *Complex IV* → O_2 where *Complexes I, III* and *IV* are proton pumps, while Q and cytochrome *c* are mobile electron carriers. The electron acceptor is molecular oxygen.

In prokaryotes (bacteria and archaea) the situation is more complicated, because there are several different electron donors and several different electron acceptors. The generalized electron transport chain in bacteria is:



Electrons can enter the chain at three levels: at the level of a dehydrogenase, at the level of the quinone pool, or at the level of a mobile cytochrome electron carrier. These levels correspond to successively more positive redox potentials, or to successively decreased potential differences relative to the terminal electron acceptor. In other words, they correspond to successively smaller Gibbs free energy changes for the overall redox reaction *Donor* → *Acceptor*.

Individual bacteria use multiple electron transport chains, often simultaneously. Bacteria can use a number of different electron donors, a number of different dehydrogenases, a number of different oxidases and reductases, and a number of different electron acceptors. For example, *E. coli* (when growing aerobically using glucose as an energy source) uses two different NADH dehydrogenases and two different quinol oxidases, for a total of four different electron transport chains operating simultaneously.

A common feature of all electron transport chains is the presence of a proton pump to create an electrochemical gradient over a membrane. Bacterial electron transport chains may contain as many as three proton pumps, like mitochondria, or they may contain only one or two. They always contain at least one proton pump.

Electron donors

In the present day biosphere, the most common electron donors are organic molecules. Organisms that use organic molecules as an electron source are called *organotrophs*. Organotrophs (animals, fungi, protists) and *phototrophs* (plants and algae) constitute the vast majority of all familiar life forms.

Some prokaryotes can use inorganic matter as an energy source. Such an organism is called a *lithotroph* ("rock-eater"). Inorganic electron donors include hydrogen, carbon monoxide, ammonia, nitrite, sulfur, sulfide, manganese oxide, and ferrous iron. Lithotrophs have been found growing in rock formations thousands of meters below the surface of Earth. Because of their volume of distribution, lithotrophs may actually outnumber organotrophs and phototrophs in our biosphere.

The use of inorganic electron donors as an energy source is of particular interest in the study of evolution. This type of metabolism must logically have preceded the use of organic molecules as an energy source.

Complex I and II

Bacteria can use a number of different electron donors. When organic matter is the energy source, the donor may be NADH or succinate, in which case electrons enter the electron transport chain via NADH dehydrogenase (similar to *Complex I* in mitochondria) or succinate dehydrogenase (similar to *Complex II*). Other dehydrogenases may be used to process different energy sources: formate dehydrogenase, lactate dehydrogenase, glyceraldehyde-3-phosphate dehydrogenase, H_2 dehydrogenase (hydrogenase), electron transport chain. Some dehydrogenases are also proton pumps; others funnel electrons into the quinone pool. Most dehydrogenases show induced expression in the bacterial cell in response to metabolic needs triggered by the environment in which the cells grow. In the case of lactate dehydrogenase in E.coli, the enzyme is used aerobically and in combination with other dehydrogenases. It is inducible and is expressed when there is high concentration of DL- lactate present in the cell.

Quinone carriers

Quinones are mobile, lipid-soluble carriers that shuttle electrons (and protons) between large, relatively immobile macromolecular complexes embedded in the membrane. Bacteria use ubiquinone (Coenzyme Q, the same quinone that mitochondria use) and related quinones such as menaquinone (Vitamin K_2). Archaea in the genus *Sulfolobus* use caldariellaquinone.[17] The use of different quinones is due to slightly altered redox potentials. These changes in redox potential are caused by changes in structure of quinone. The Change in redox potentials of these quinones may be suited to changes in the electron acceptors or variations of redox potentials in bacterial complexes.[18]

Proton pumps

A *proton pump* is any process that creates a proton gradient across a membrane. Protons can be physically moved across a membrane; this is seen in mitochondrial *Complexes I* and *IV*. The same effect can be produced by moving electrons in the opposite direction. The result is the disappearance of a proton from the cytoplasm and the appearance of a proton in the periplasm. Mitochondrial *Complex III* uses this second type of proton pump, which is mediated by a quinone (the Q cycle).

Some dehydrogenases are proton pumps; others are not. Most oxidases and reductases are proton pumps, but some are not. Cytochrome bc_1 is a proton pump found in many, but not all, bacteria (it is not found in *E. coli*). As the name implies, bacterial bc_1 is similar to mitochondrial bc_1 (*Complex III*).

Cytochrome electron carriers

Cytochromes are pigments that contain iron. They are found in two very different environments.

Some cytochromes are water-soluble carriers that shuttle electrons to and from large, immobile macromolecular structures imbedded in the membrane. The mobile cytochrome electron carrier in mitochondria is cytochrome *c*. Bacteria use a number of different mobile cytochrome electron carriers.

Other cytochromes are found within macromolecules such as *Complex III* and *Complex IV*. They also function as electron carriers, but in a very different, intramolecular, solid-state environment.

Electrons may enter an electron transport chain at the level of a mobile cytochrome or quinone carrier. For example, electrons from inorganic electron donors (nitrite, ferrous iron, electron transport chain.) enter the electron transport chain at the cytochrome level. When electrons enter at a redox level greater than NADH, the electron transport chain must operate in reverse to produce this necessary, higher-energy molecule.

Terminal oxidases and reductases

When bacteria grow in aerobic environments, the terminal electron acceptor (O_2) is reduced to water by an enzyme called an *oxidase*. When bacteria grow in anaerobic environments, the terminal electron acceptor is reduced by an enzyme called a reductase. In mitochondria the terminal membrane complex (*Complex IV*) is cytochrome oxidase. Aerobic bacteria use a number of different terminal oxidases. For example, *E. coli* (a facultative anaerobe) does not have a cytochrome oxidase or a bc_1 complex. Under aerobic conditions, it uses two different terminal quinol oxidases (both proton pumps) to reduce oxygen to water.

Bacterial Complex IV can be split into classes according to the molecules act as terminal electron acceptors. Class I oxidases are cytochrome oxidases and use oxygen as the terminal electron acceptor. Class II oxidases are Quinol oxidases and can use a variety of terminal electron acceptors. Both of these classes can be subdivided into categories based on what redox active components they contain. E.g. Heme aa3 Class 1 terminal oxidases are much more efficient than Class 2 terminal oxidases[2]

Anaerobic bacteria, which do not use oxygen as a terminal electron acceptor, have terminal reductases individualized to their terminal acceptor. For example, *E. coli* can use fumarate reductase, nitrate reductase, nitrite reductase, DMSO reductase, or trimethylamine-N-oxide reductase, depending on the availability of these acceptors in the environment.

Most terminal oxidases and reductases are *inducible*. They are synthesized by the organism as needed, in response to specific environmental conditions.

Electron acceptors

Just as there are a number of different electron donors (organic matter in organotrophs, inorganic matter in lithotrophs), there are a number of different electron acceptors, both organic and inorganic. In aerobic bacteria and facultative anaerobes if oxygen is available, it is invariably used as the terminal electron acceptor, because it generates the greatest Gibbs free energy change and produces the most energy.[19]

In anaerobic environments, different electron acceptors are used, including nitrate, nitrite, ferric iron, sulfate, carbon dioxide, and small organic molecules such as fumarate.

Photosynthetic

In oxidative phosphorylation, electrons are transferred from a low-energy electron donor such as NADH to an acceptor such as O_2) through an electron transport chain. In photophosphorylation, the energy of sunlight is used to *create* a high-energy electron donor which can subsequently reduce redox active components. These components are then coupled to ATP synthesis via proton translocation by the electron transport chain.[9]

Photosynthetic electron transport chains, like the mitochondrial chain, can be considered as a special case of the bacterial systems. They use mobile, lipid-soluble quinone carriers (phylloquinone and plastoquinone) and mobile, water-soluble carriers (cytochromes, electron transport chain.). They also contain a proton pump. The proton pump in *all* photosynthetic chains resembles mitochondrial *Complex III*. The commonly-held theory of symbiogenesis believes that both organelles descended from bacteria.

See also

- Charge-transfer complex
- CoRR hypothesis
- Electron equivalent
- Hydrogen hypothesis
- Respirasome

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External links

- Electron+Transport+Chain+Complex+Proteins (https://meshb.nlm.nih.gov/record/ui?name=Electron%20Transport%20Chain%20Complex%20Proteins) at the US National Library of Medicine Medical Subject Headings (MeSH)
- Khan Academy, video lecture (https://www.khanacademy.org/video/electron-transport-chain?playlist=Biology)