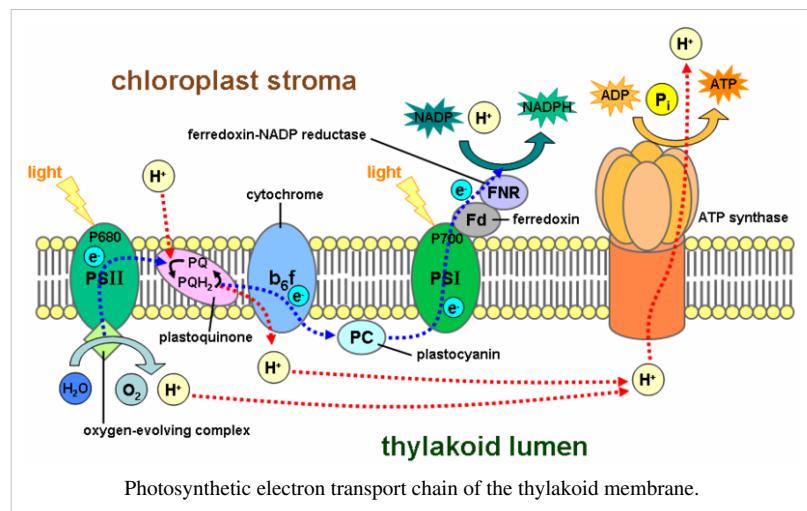
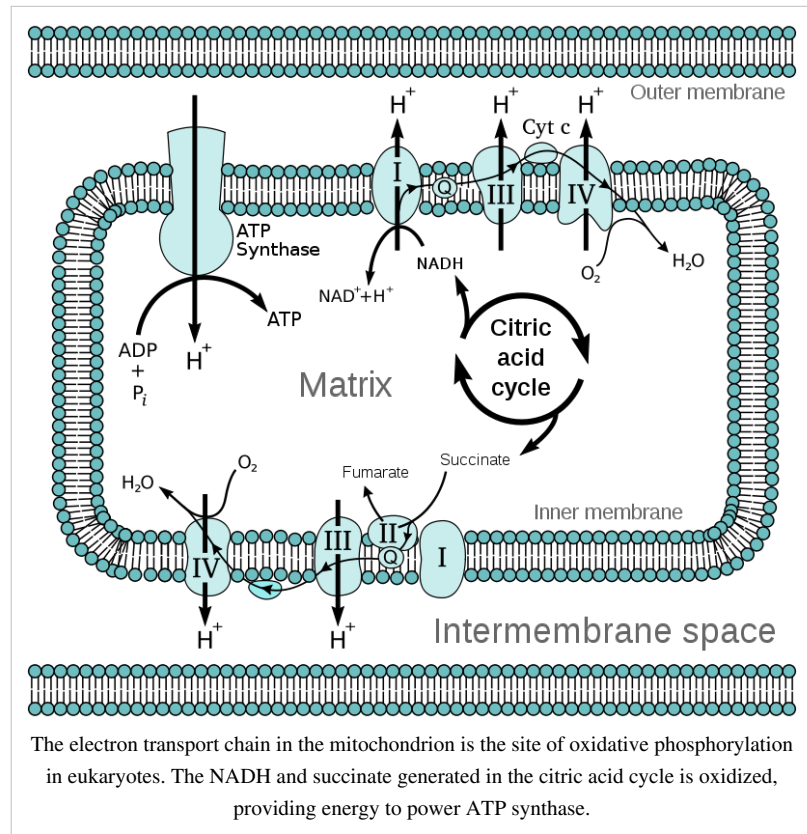


Electron transport chain

An **electron transport chain (ETC)** couples a chemical reaction between an electron donor (such as NADH) and an electron acceptor (such as O_2) to the transfer of H^+ ions across a membrane, through a set of mediating biochemical reactions. These H^+ ions are used to produce adenosine triphosphate (ATP), the main energy intermediate in living organisms, as they move back across the membrane. Electron transport chains are used for extracting energy from sunlight (photosynthesis) and from redox reactions such as the oxidation of sugars (respiration).

In chloroplasts, light drives the conversion of water to oxygen and $NADP^+$ to NADPH and a transfer of H^+ ions. NADPH is used as an electron donor for carbon fixation. In mitochondria, it is the conversion of oxygen to water, NADH to NAD^+ and succinate to fumarate that drives the transfer of H^+ ions. While some bacteria have electron transport chains similar to those in chloroplasts or mitochondria, other bacteria use different electron donors and acceptors. Both the respiratory and photosynthetic electron transport chains are major sites of premature electron leakage to oxygen, thus being major sites of superoxide production and drivers of oxidative stress.



Background

The electron transport chain is also called the **ETC**. An enzyme called ATP synthase catalyzes a reaction to generate ATP. The structure of this enzyme and its underlying genetic code is remarkably conserved in all known forms of life.

ATP synthase is powered by a transmembrane electrochemical gradient in the form of a proton gradient^{[1] [2]}. The function of the electron transport chain is to produce this gradient^{[3] [4]}. In all living organisms, a series of redox reactions is used to produce a transmembrane electrochemical potential gradient.

Redox reactions are chemical reactions in which electrons are transferred from a donor molecule to an acceptor molecule. The underlying force driving these reactions is the Gibbs free energy of the reactants and products. The Gibbs free energy is the energy available ("free") to do work. Any reaction that decreases the overall Gibbs free energy of a system will proceed spontaneously.

The transfer of electrons from a high-energy molecule (the donor) to a lower-energy molecule (the acceptor) can be *spatially* separated into a series of intermediate redox reactions. This is an electron transport chain.

The fact that a reaction is thermodynamically possible does not mean that it will actually occur; for example, a mixture of hydrogen gas and oxygen gas does not spontaneously ignite. It is necessary either to supply an activation energy or to lower the intrinsic activation energy of the system, in order to make most biochemical reactions proceed at a useful rate. Living systems use complex macromolecular structures (enzymes) to lower the activation energies of biochemical reactions.

It is possible to couple a thermodynamically favorable reaction (a transition from a high-energy state to a lower-energy state) to a thermodynamically unfavorable reaction (such as a separation of charges, or the creation of an osmotic gradient), in such a way that the overall free energy of the system decreases (making it thermodynamically possible), while useful work is done at the same time. Biological macromolecules that catalyze a thermodynamically unfavorable reaction *if and only if a thermodynamically favorable reaction occurs simultaneously* underlie all known forms of life.

Electron transport chains capture energy in the form of a transmembrane electrochemical potential gradient. This energy can then be harnessed to do useful work. The gradient can be used to transport molecules across membranes. It can be used to do mechanical work, such as rotating bacterial flagella, and also to produce ATP, a high-energy molecule which can go on to power other cellular reactions.

A small amount of ATP is available from substrate-level phosphorylation (for example, in glycolysis). Some organisms can obtain ATP exclusively by fermentation. In most organisms, however, the majority of ATP is generated by electron transport chains.

Electron transport chains in mitochondria

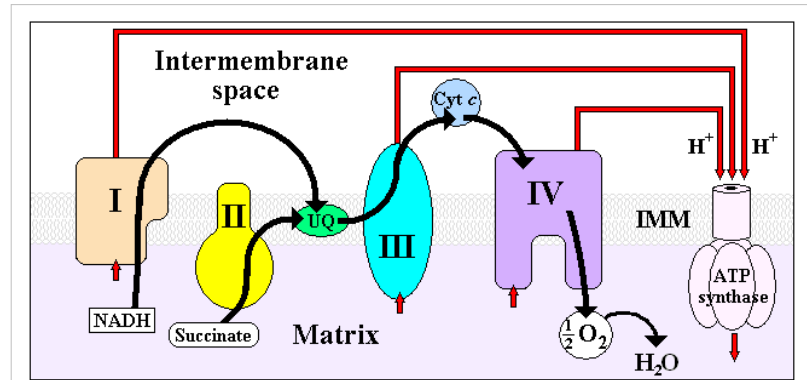
The cells of almost all eukaryotes contain intracellular organelles called mitochondria, which produce ATP. Energy sources such as glucose are initially metabolized in the cytoplasm. The products are imported into mitochondria. Mitochondria continue the process of catabolism using metabolic pathways including the Krebs cycle, fatty acid oxidation, and amino acid oxidation.

The end result of these pathways is the production of two kinds of energy-rich electron donors, NADH and succinate. Electrons from these donors are passed through an electron transport chain to oxygen, which is reduced to water. This is a multi-step redox process that occurs on the mitochondrial inner membrane. The enzymes that catalyze these reactions have the ability to simultaneously create a proton gradient across the membrane, producing a thermodynamically unlikely high-energy state with the potential to do work. Although electron transport occurs with great efficiency, a small percentage of electrons are prematurely leaked to oxygen, resulting in the formation of the toxic free-radical superoxide.

The similarity between intracellular mitochondria and free-living bacteria is striking. The known structural, functional, and DNA similarities between mitochondria and bacteria provide strong evidence that mitochondria evolved from intracellular bacterial symbionts (*see Endosymbiotic theory*).

Mitochondrial redox carriers

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



Stylized representation of the ETC. Energy obtained through the transfer of electrons

$\text{NADH} \rightarrow \text{Complex I} \rightarrow \text{Q} \rightarrow \text{Complex III} \rightarrow \text{cytochrome } c \rightarrow \text{Complex IV} \rightarrow \text{O}_2$
 ↑
 Complex II

Complex I

Complex I (NADH dehydrogenase, also called NADH:ubiquinone oxidoreductase; EC 1.6.5.3 [5]) removes two electrons from NADH

and transfers them to a lipid-soluble carrier, *ubiquinone* (Q). The reduced product, *ubiquinol* (QH₂) is free to diffuse within the membrane. At the same time, *Complex I* moves four protons (H⁺) across the membrane, producing a proton gradient. Complex I is one of the main sites at which premature electron leakage to oxygen occurs, thus being one of main sites of production of a harmful free radical called superoxide.

The pathway of electrons occurs as follows:

NADH is oxidized to NAD⁺, reducing Flavin mononucleotide to FMNH₂ in one two-electron step. The next electron carrier is a Fe-S cluster, which can only accept one electron at a time to reduce the ferric ion into a ferrous ion. In a convenient manner, FMNH₂ can be oxidized in only two one-electron steps, through a semiquinone intermediate. The electron thus travels from the FMNH₂ to the Fe-S cluster, then from the Fe-S cluster to the oxidized Q to give the free-radical (semiquinone) form of Q. This happens again to reduce the semiquinone form to the ubiquinol form, QH₂. During this process, four protons are translocated across the inner mitochondrial membrane, from the matrix to the intermembrane space. This creates a proton gradient that will be later used to generate ATP through oxidative phosphorylation.

Complex II

Complex II (succinate dehydrogenase; EC 1.3.5.1 ^[6]) is not a proton pump. It serves to funnel additional electrons into the quinone pool (Q) by removing electrons from succinate and transferring them (via FAD) to Q. Complex II consists of four protein subunits: SDHA, SDHB, SDHC, and SDHD. Other electron donors (e.g., fatty acids and glycerol 3-phosphate) also funnel electrons into Q (via FAD), again without producing a proton gradient.

Complex III

Complex III (cytochrome *bc_L* complex; EC 1.10.2.2 ^[7]) removes in a stepwise fashion two electrons from QH₂ at the Q_O site and sequentially transfers them to two molecules of cytochrome *c*, a water-soluble electron carrier located within the intermembrane space. The two other electrons are sequentially passed across the protein to the Q_I site where quinone part of ubiquinone is reduced to quinol. A proton gradient is formed because it takes 2 quinol (4H+4e-) oxidations at the Q_O site to form one quinol (2H+2e-) at the Q_I site. (in total 6 protons: 2 protons reduce quinone to quinol and 4 protons are released from 2 ubiquinol). The bc_L complex does NOT 'pump' protons, it helps build the proton gradient by an asymmetric absorption/release of protons.

When electron transfer is reduced (by a high membrane potential, point mutations or respiratory inhibitors such as antimycin A), Complex III may leak electrons to molecular oxygen, resulting in the formation of superoxide, a highly-toxic reactive oxygen species, which is thought to contribute to the pathology of a number of diseases and to processes involved in aging.

Complex IV

Complex IV (cytochrome *c* oxidase; EC 1.9.3.1 ^[8]) removes four electrons from four molecules of cytochrome *c* and transfers them to molecular oxygen (O₂), producing two molecules of water (H₂O). At the same time, it moves four protons across the membrane, producing a proton gradient. In cyanide poisoning, this enzyme is inhibited.

Coupling with oxidative phosphorylation

The chemiosmotic coupling hypothesis, as proposed by Nobel Prize in Chemistry winner Peter D. Mitchell, explains that the electron transport chain and oxidative phosphorylation are coupled by a proton gradient across the inner mitochondrial membrane. The efflux of protons creates both a pH gradient and an electrochemical gradient. This proton gradient is used by the F_OF₁ ATP synthase complex to make ATP via oxidative phosphorylation. ATP synthase is sometimes regarded as *complex V* of the electron transport chain. The F_O component of ATP synthase acts as an ion channel for return of protons back to mitochondrial matrix. During their return, the free energy produced during the generation of the oxidized forms of the electron carriers (NAD⁺ and Q) is released. This energy is used to drive ATP synthesis, catalyzed by the F₁ component of the complex.

Coupling with oxidative phosphorylation is a key step for ATP production. However, in certain cases, uncoupling may be biologically useful. The inner mitochondrial membrane of brown adipose tissue contains a large amount of thermogenin (an uncoupling protein), which acts as uncoupler by forming an alternative pathway for the flow of protons back to matrix. This results in consumption of energy in thermogenesis rather than ATP production. This may be useful in cases when heat production is required, for example in colds or during arise of hibernating animals. Synthetic uncouplers (e.g., 2,4-dinitrophenol) also exist, and, at high doses, are lethal.

Summary

The mitochondrial electron transport chain removes electrons from an electron donor (NADH or QH_2) and passes them to a terminal electron acceptor (O_2) via a series of redox reactions. These reactions are coupled to the creation of a proton gradient across the mitochondrial inner membrane. There are three proton pumps: *I*, *III*, and *IV*. The resulting transmembrane proton gradient is used to make ATP via ATP synthase.

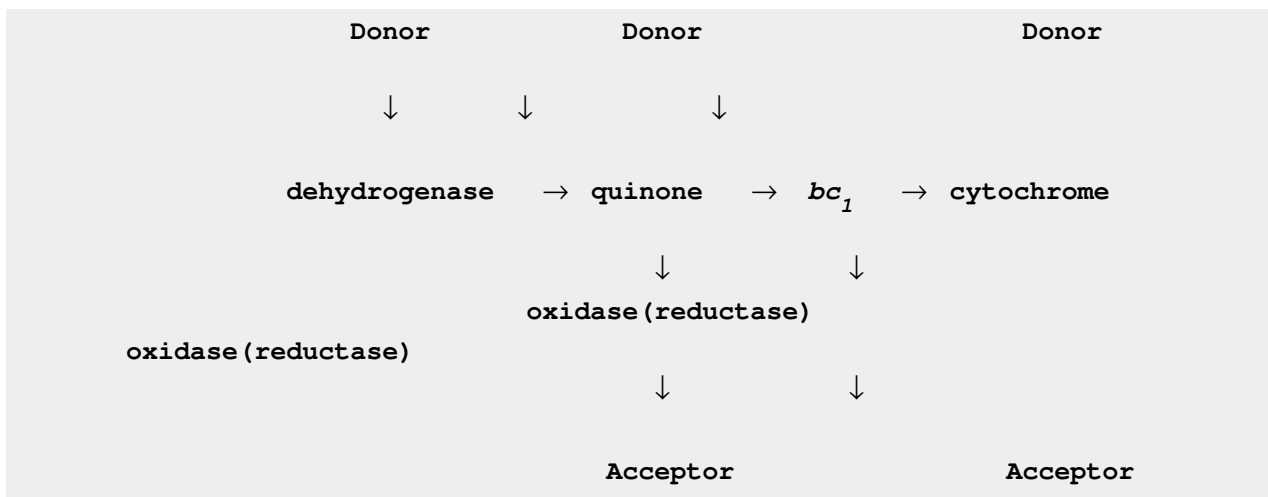
The reactions catalyzed by *Complex I* and *Complex III* exist roughly at equilibrium. This means that these reactions are readily reversible, simply by increasing the concentration of the products relative to the concentration of the reactants (for example, by increasing the proton gradient). ATP synthase is also readily reversible. Thus ATP can be used to make a proton gradient, which in turn can be used to make NADH. This process of **reverse electron transport** is important in many prokaryotic electron transport chains.

Electron transport chains in bacteria

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

$\text{NADH} \rightarrow \text{Complex I} \rightarrow \text{Q} \rightarrow \text{Complex III} \rightarrow \text{cytochrome } c \rightarrow \text{Complex IV} \rightarrow \text{O}_2$ 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 is a number of different electron donors and a number of different electron acceptors. The generalized electron transport chain in bacteria is:



Note that 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 a transmembrane proton gradient. 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 energy 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 organisms are called *lithotrophs* ("rock-eaters"). Inorganic electron donors include hydrogen, carbon monoxide, ammonia, nitrite, sulfur, sulfide, 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.

Dehydrogenases

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, H₂ dehydrogenase (hydrogenase), etc. Some dehydrogenases are also proton pumps; others simply funnel electrons into the quinone pool.

Most of dehydrogenases are synthesized only when needed. Depending on the environment in which they find themselves, bacteria select different enzymes from their DNA library and synthesize only those that are needed for growth. Enzymes that are synthesized only when needed are said to be 'inducible'.

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* (the same quinone that mitochondria use) and related quinones such as *menaquinone*.

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_L* is a proton pump found in many, but not all, bacteria (it is not found in *E. coli*). As the name implies, bacterial *bc_L* is similar to mitochondrial *bc_L* (*Complex III*).

Proton pumps are the heart of the electron transport process. They produce the transmembrane electrochemical gradient that supplies energy to the cell.

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, etc.) 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* does not have a cytochrome oxidase or a *bc₁* complex. Under aerobic conditions, it uses two different terminal quinol oxidases (both proton pumps) to reduce oxygen to water.

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. 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.

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

Since electron transport chains are redox processes, they can be described as the sum of two redox pairs. For example, the mitochondrial electron transport chain can be described as the sum of the $NAD^+/NADH$ redox pair and the O_2/H_2O redox pair. NADH is the electron donor and O_2 is the electron acceptor.

Not every donor-acceptor combination is thermodynamically possible. The redox potential of the acceptor must be more positive than the redox potential of the donor. Furthermore, actual environmental conditions may be far different from *standard* conditions (1 molar concentrations, 1 atm partial pressures, pH = 7), which apply to *standard* redox potentials. For example, hydrogen-evolving bacteria grow at an ambient partial pressure of hydrogen gas of 10^{-4} atm. The associated redox reaction, which is thermodynamically favorable in nature, is thermodynamically impossible under “standard” conditions.

Summary

Bacterial electron transport pathways are, in general, inducible. Depending on their environment, bacteria can synthesize different transmembrane complexes and produce different electron transport chains in their cell membranes. Bacteria select their electron transport chains from a DNA library containing multiple possible dehydrogenases, terminal oxidases and terminal reductases. The situation is often summarized by saying that electron transport chains in bacteria are *branched*, *modular*, and *inducible*.

Photosynthetic electron transport chains

In **oxidative phosphorylation**, electrons are transferred from a high-energy electron donor (e.g., NADH) to an electron acceptor (e.g., O₂) through an electron transport chain. In **photophosphorylation**, the energy of sunlight is used to *create* a high-energy electron donor and an electron acceptor. Electrons are then transferred from the donor to the acceptor through another electron transport chain.

Photosynthetic electron transport chains have many similarities to the oxidative chains discussed above. They use mobile, lipid-soluble carriers (quinones) and mobile, water-soluble carriers (cytochromes, etc.). They also contain a proton pump. It is remarkable that the proton pump in *all* photosynthetic chains resembles mitochondrial *Complex III*.

Photosynthetic electron transport chains are discussed in greater detail in the articles Photophosphorylation, Photosynthesis, Photosynthetic reaction center and Light-dependent reaction.

Summary

Electron transport chains are redox reactions that transfer electrons from an electron donor to an electron acceptor. The transfer of electrons is coupled to the translocation of protons across a membrane, producing a proton gradient. The proton gradient is used to produce useful work.

The coupling of thermodynamically favorable to thermodynamically unfavorable biochemical reactions by biological macromolecules is an example of an **emergent property** – a property that could not have been predicted, even given full knowledge of the primitive geochemical systems from which these macromolecules evolved. It is an open question whether such emergent properties evolve only by chance, or whether they *necessarily* evolve in any large biogeochemical system, given the underlying laws of physics.

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See also

- CoRR Hypothesis
- Hydrogen hypothesis

External links

- MeSH *Electron+Transport+Chain+Complex+Proteins* (http://www.nlm.nih.gov/cgi/mesh/2009/MB_cgi?mode=&term=Electron+Transport+Chain+Complex+Proteins)
 - UMich Orientation of Proteins in Membranes *families/superfamily-3* (<http://opm.phar.umich.edu/families.php?superfamily=3>) - Complexes with cytochrome b-like domains
 - UMich Orientation of Proteins in Membranes *families/superfamily-4* (<http://opm.phar.umich.edu/families.php?superfamily=4>) - Bacterial and mitochondrial cytochrome c oxidases
 - UMich Orientation of Proteins in Membranes *families/superfamily-2* (<http://opm.phar.umich.edu/families.php?superfamily=2>) - Photosynthetic reaction centers and photosystems
 - UMich Orientation of Proteins in Membranes *families/superfamily-78* (<http://opm.phar.umich.edu/families.php?superfamily=78>) - Cytochrome c family
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