ALQUSOUR ACADEMY

أكاديمية القصور

BIOCHEMISTRY

Subject: Final Exam - Chapter Twenty

للاستفسار والتسجيل

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Electron Transport & Oxidative Phosphorylation

☒ Introduction:

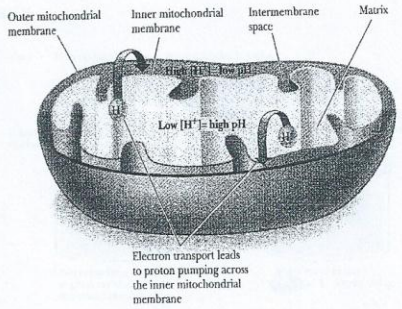
- We said in the previous chapter that citric acid cycle produce only one direct molecule of ATP, when one acetyl CoA enters the cycle.
- In order to complete oxidation of glucose to H_2O and CO_2, glucose needs to pass through **3 pathways**:
  1) Glycolysis (an **anaerobic** process that occurs in the **cytosol**).
  2) Citric acid cycle (**aerobic** process that occurs in **mitochondria**)
  3) Oxidative phosphorylation and ETC (**aerobic** process that occurs in mitochondria).
- In the last pathway, ATP will be generated under the power of electrons transport from one complex to another, until the electrons reach their final destination O_2 (then reduced to H_2O).
- O_2 is the main oxidizing agent in the cell, and in this chapter we will discuss the role of **oxygen** in metabolisms as a **final acceptor of electrons**.

☒ What role does electron transport play in metabolism?

As a summary to what will happen in this pathway

1) The NADH and $FADH_2$ generated from the Krebs cycle and glycolysis will transfer their electrons to the oxygen, this happen in a series of reaction called **electrons transport chain (ETC).** Where, all the reactions of ETC take place on the inner metochondrial membrane.

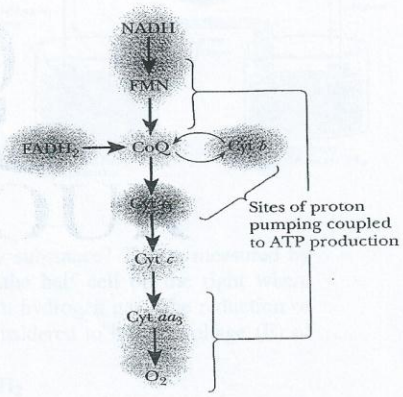
   And this transport catalyzed by **4 types of enzyme complexes** embedded in the innermitochondrial membrane, so a series of **oxidation reduction reactions** occur in these complexes ended in transfer of electrons to the oxygen.



2) As general outline, NADH (or FADH2) passes electrons to co-enzyme Q (an electron carrier). Electrons are then passed from Co-enzyme Q to a series of proteins called cytochromes and, eventually, to **oxygen**.

3) The energy of the electrons transport can be used (**by only three of the four complexes**) to pump the protons across the inner membrane out in the intermediate space, creating a **pH gradient** (**proton gradient**).

4) The reverse flow of protons through the membrane back into inner matrix will drive the production of ATP, by **oxidative Phosphorylation.**



NOTE: Each NADH will give 2.5 ATP, and each $FADH_2$ will give 1.5 ATP.

- We have 2 separate reactions but tightly coupled to each other:
  1) **Electron transport to oxygen**. It is an exergonic process, its ΔG is negative.
  2) **Oxidative Phosphorylation:** in which ADP is phosphorylated to produce ATP. It is an endergonic reaction where $\Delta G = 30.5$ KJ/mole.

☒ What are the reduction potentials for the electron transport chain?

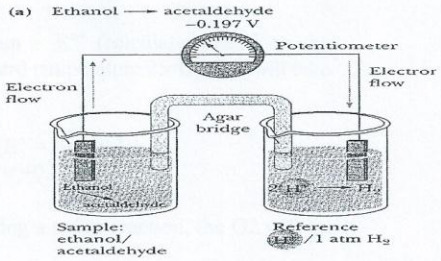
- We said that hydrolysis of ATP into ADP and Pi is an **exergonic reaction**, and the energy released can be used to drive a reaction that needs energy.

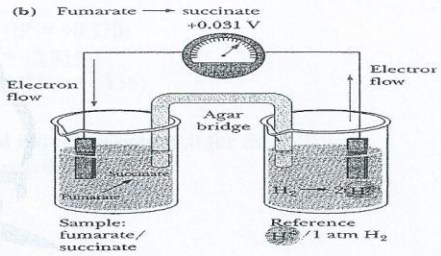
- Also we said that the reverse reaction in which ADP with Pi to give ATP is an **endergonic reaction** can be derived by a high exergonic reaction.

- Each reduction reaction should be accompanied by an oxidation reaction. **How would we know which one of them will be reduced (gain the electrons)?**

- The answer will be according to the **reduction potential** for every substance, which indicates the tendency of a substance to gain the electron (to be reduced).

- A molecule with **high reduction potential** will tend to be reduced if it is paired with a molecule with a **lower reduction potential**. In other words, if we put 2 molecules with different reduction potential, the one with high reduction potential will be reduced, and the other will be oxidized.





- **But** how we measure the reduction potential for every substance? This is measured by making a simple battery cell; the reference point is the half cell on the right where hydrogen ion is in aqueous solution in equilibrium with hydrogen gas. The reduction of hydrogen ion to hydrogen gas is the control and is considered to have a voltage (E) of zero.

$$2H^+ + 2e^- \rightarrow H_2$$

- The sample to be test is in the other half cell. The electric circuit is completed by bridge with a salt-containing agar gel.

❖ If we put ethanol and acetaldehyde in the sample half cell, the electrons will flow from the sample cell to the reference cell, this means the ethanol will be oxidized (lose the electrons) to acetaldehyde, and the hydrogen ions will be reduced (gain the electrons) to hydrogen gas, This means that hydrogen/H^+ pair has a higher reduction potential than ethanol/ acetaldehyde pair.

❖ If we put fumarate and succinate in the sample cell, the electrons will flow from the reference cell to the sample cell, meaning that the hydrogen gas will be oxidized (lose the electrons) to hydrogen ions, and the fumarate will be reduced (gain the electrons) to succinate, so the succinate/fumarate pair has a higher reduction potential than hydrogen/H^+ pair.

- The standard biological voltage of each half reaction = $E^{\circ\prime}$ (calculated based on the compounds in the cell being at 1M, pH being 7, standard temperature 25°C). We will take an example to confirm the idea of reduction potential:

$$NAD^+ + 2H^+ + 2e^- \rightarrow NADH + H^+ \ (E^{\circ\prime} = -0.320\ V)$$
$$1/2O_2 + 2H^+ + 2e^- \rightarrow H2O \ (E^{\circ\prime} = +0.816\ V)$$

- This means that, if the two half reaction are paired during a redox reaction, the O2 will be reduced to water, and the NADH will be oxidized.

$$NADH + H^+ \rightarrow NAD^+ + 2H^+ + 2e^- \ (E^{\circ\prime} = +0.320)$$
$$\underline{1/2O_2 + 2H^+ + 2e^- \rightarrow H_2O \ (E^{\circ\prime} = +0.816)}$$
$$NADH + 1/2O_2 + H^+ \rightarrow NAD^+ + H_2O \ (E^{\circ\prime} = +1.136)$$

- **Note that we had to change the sign on the standard reduction potential for the NADH because we had to reverse the direction of the reaction.**

- The $\Delta G^\circ$of a redox reaction is calculated using

$$\Delta G^\circ = -nF\,\Delta E^{\circ\prime}$$

n (the number of the moles of electrons transferred).
F (is Faraday`s constant = 96.485 KJ V^{-1} $mole^{-1}$).
$\Delta E^{\circ\prime}$ is the total voltage for the two half reactions.

- Notice that the ΔG° is negative when the $\Delta E^{\circ\prime}$ is positive.

- The differences between ΔG, ΔG°, and $\Delta G^{\circ\prime}$ are similar to differences between ΔE, ΔE°, and $\Delta E^{\circ\prime}$.

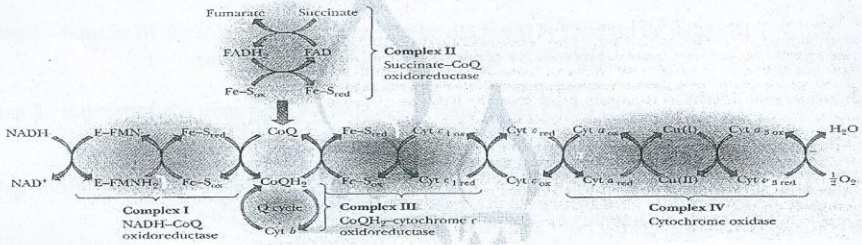
- ΔG, ΔE ➔ Free energy change, and reduction potential under any condition.
- ΔG°, ΔE°➔ free energy change, and reduction potential under standard state.
- $\Delta G^{\circ\prime}$, $\Delta E^{\circ\prime}$➔ free energy change and reduction potential under standard condition expect that PH=7 here; because it is impossible to have[H+]=1M, where the PH=0

☒ How the electrons transport complexes are organized?

- The electron transport apparatus found in the inner mitochondrial membrane consists of 4 complexes (**respiratory complex**); the apparatus can be resolved into its component parts by a process called **fractionation.**

- In addition to the respiratory complexes, two electron carriers, coenzyme Q and cytochrome *c,* are not bound to the complexes but are free to move within and along the membrane, respectively

- Each complex is a multienzymes system, like pyruvate dehydrogenase complex and α-ketoglutarate dehydrogenase complex. We will talk about each complex separately.



Complex I: Also called ***NADH-CoQ oxidoreductase,*** it catalyzes the transport of electrons from **NADH** to coenzyme Q (**CoQ** or also called **ubiquinone).**

- This complex contains many subunit of **(iron-sulfur cluster, flavoprotein)** the total number of subunits is more than **20.** The flavoprotein has a flavin coenzyme, called flavin mononucleotide or FMN, which differs from FAD in not having an adenine nucleotide..

- The transfer of electrons occurs in multi-steps, started with **NADH** and ended with $\mathbf{CoQH_2}$.

Step 1:-transfer of electrons from **NADH** to the **flavin** portion of the flavoprotein.

$$\mathbf{NADH + H^+ + E\text{-}FMN \rightarrow NAD^+ + E\text{-}FMNH_2}$$

Step 2:- transfer of electrons from **FMNH2 (**to be oxidized) to the **iron-sulfer cluster** (to be reduced) $\mathbf{E\text{-}FMNH_2 + 2Fe\text{-}S_{oxidized} \rightarrow E\text{-}FMN + 2Fe\text{-}S_{reduced} + 2H^+}$

Step 3:- transfer of electrons from **Fe-S cluster** to the **coenzyme Q** (ubiquonone).

$$\mathbf{2Fe\text{-}S_{reduced} + CoQ + 2H^+ \rightarrow 2Fe\text{-}S_{oxidized} + CoQH_2}$$

Some important notes about this complex:-

- The net reaction of this complex is one of the three **responsible for the proton pumping** that create the pH gradient, the $\Delta G^{\circ\prime}$ for this reaction is **-81** KJ/mole, indicates that it release enough energy to drive the phospholylation of ADP to ATP.
- Although all electron carriers can be present in an oxidized or reduced form, but there is an order to which ones will tend to reduce the others.
- Some electrons carrier carry the electrons and hydrogens in their reduced form (like NADH), while other *carry only the electrons (Fe-S cluster); this is the basis of proton pumping.*
- The final electron receptor is CoQ, is mobile, free to move in the membrane and to pass electron to the third complex for further transport to oxygen.

Complex II: - also called ***succinate-CoQ oxidoreductase,*** it catalyzes the transfer of electrons from the **succinate** to the **CoQ**, Also in multi-steps.

Step 1:- transfer of electrons from succinate (to be oxidized) to FAD (to be reduced)

$$\textbf{succinate} + \textbf{E-FAD} \rightarrow \textbf{fumarate} + \textbf{E-FADH}_2$$

Step 2:- transfer of electrons from $\mathbf{FADH_2}$ to the **iron-sulfer** group

$$\textbf{E-FADH}_2 + \textbf{Fe-S}_{\textbf{oxidized}} \rightarrow \textbf{E-FAD} + \textbf{Fe-S}_{\textbf{reduced}}$$

Step 3:- transfer of electrons from Fe-S to the CoQ

$$\textbf{Fe-S}_{\textbf{reduced}} + \textbf{CoQ} + 2\textbf{H}^+ \rightarrow \textbf{Fe-S}_{\textbf{oxidized}} + \textbf{CoQH}_2$$

Some important notes about this complex:-

- The first step in this reaction is catalyzed by ***succinate dehydrogenase***, although we saw it in the citric acid cycle but it has been shown to be a part of complex II.
- The other components of complex II are a ***b*-type cytochrome** and two **iron-sulfer proteins**.
- Through this complex there is **no pumping of hydrogen ions or ATP** production because the energy released is not enough.

Complex III: - also called ***$CoQH_2$-cytochrome c oxidoreductase or cytochrome reductase,*** it catalyzes the transport of electrons from $\mathbf{CoQH_2}$ to the **cytochrome** ***c***, also in multi-steps.

But let us talk about the **cytochroms** first:

- These are proteins contain a heme group, and in each heme group the iron is reduced to Fe(II) and oxidized to Fe(III), and this is differ from the heme in the hemoglobin, which remain in the reduced form.

$$\text{Fe (III)} + \text{e-} \rightarrow \text{Fe (II)} \text{ (reduction)}$$
$$\text{Fe (II)} \rightarrow \text{Fe (III)} + \text{e-} \text{ (oxidation)}$$

- There are many different types of cytochroms that differ in their structure and in their tendency to participate in redox reaction, like cytochromes(*a, b, c*) also there is c_1 …
- The components of this complex include cytochrome *b* (two types; b_H, b_L), cytochrome c_1, and several iron-sulfer cluster.
- Back to complex III; the flow of electrons from the reduced coenzyme Q ($CoQH_2$) to the other components of the complex does not make a simple direct path. It is known that there is a cyclic flow of electrons involves coenzyme Q twice in what is called **Q cycle**.

☒ **In Q cycle:**

➢ One electron passed from the reduced form of CoQ ($CoQH_2$ = upiquinol) to Fe-S then to the cytochrome c_1 leaving CoQ in the semiquinone form (CoQ^-).

NOTE: the semiquinone is an intermediate between the oxidized (CoQ) and the reduced forms of coenzyme Q ($CoQH_2$).

➢ The semiquinone, along with the oxidized and reduced forms of CoQ participates in a cyclic process in which the two *b* cytochromes are reduced and oxidized in turn.

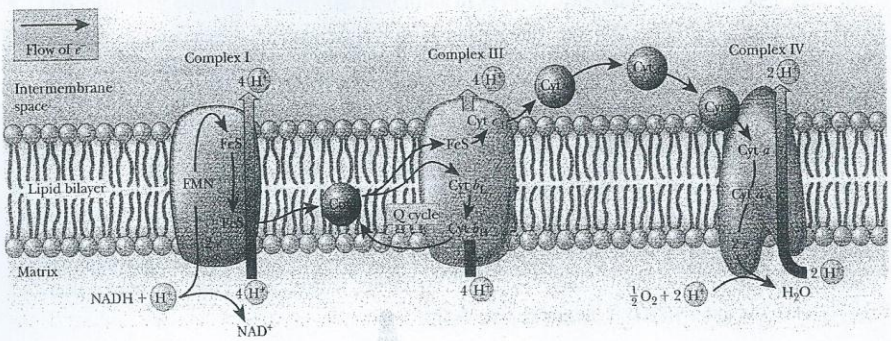
➢ Then a second molecules of $CoQH_2$ transfer a second electron to cytochrome c_1, and then to the mobile cytochrome *c* leaving another semiquinone.

➢ The net result is the same as one molecule of $CoQH_2$ had lost two electrons.

➢ One of the two molecules of $CoQH_2$ involved in the Q cycle is regenerated and the other oxidized to CoQ.

➢ So, two molecules of cytochrome *c* are required for every molecule of coenzyme Q.
The overall reaction is:

$$\mathbf{CoQH_2 + 2\ Cyt\ c[Fe\ (III)] \rightarrow CoQ + 2\ Cyt\ c[Fe\ (II)] + 2H^+}$$



Important Notes:

- Cytochrome *c* behaves like CoQ in which it is also mobile through the membrane for easy transfer of electron from one complex to another.
- Cytochrome *c* itself is not part of the complex but is loosely bound to the outer surface of the inner mitochondrial membrane, facing the intermembrane space and can move freely in the membrane, just like CoQ.
- Cytochromes can carry electrons but not hydrogen. So, the net reaction of this complex is also one of the three **responsible for the proton pumping** that create the pH gradient. The $\Delta G^{\circ\prime}$ for this reaction is **-34.2** KJ/mole, indicates that it release enough energy to drive the phospholylation of ADP to ATP.

Complex IV: - also called ***cytochrome c oxidase***, it catalyzes the final step of electron transport from the cytochrome *c* to the oxygen.

- This complex contains cytochrome *a*, a_3, and 2 Cu^{+2} ions. Also **proton pumping** and ATP formation take place in this complex.
- The transfer of electron occurs in multi-steps:

Transfer of electron from cytochrome *c* to the cytochrome *a*, then to Cu^{+2}, then to the cytochrome a_3, and finally to O_2.

$$\textbf{Cyt c} \rightarrow \textbf{Cyt a} \rightarrow \textbf{Cu}^{+2} \rightarrow \textbf{Cyt a}_3 \rightarrow \textbf{O}_2$$

- **The following equation shows the reactions of cytochromes more exciplicitly:**

Cyt *c* [reduced, Fe (II)] + Cyt aa_3 [oxidized, Fe (III)] →
Cyt aa_3 [reduced, Fe (II)] + Cyt *c* [oxidized, Fe (III)]

Cytochromes *a* and a_3 taken together from the complex known as cytochrome oxidase.

- **When the oxygen gains the electrons it will be reduced to H_2O, we have finally seen the link to molecular oxygen in aerobic metabolism.**

The overall reaction is:
2 Cyt aa_3 [reduced, Fe (II)] + $1/2O_2$ + $2H^+$ →
2 Cyt aa_3 [oxidized, Fe (III)] + H_2O

Cytochromes and other iron containing protein of electron transport:

- We see that cytochromes located in the mitochondria, but they can also occur in the endoplasmic reticulum.
- All cytochromes contain a heme group that participate in the oxidation-reduction reaction, not like the heme present in hemoglobin or myoglobin which link to oxygen.
- The differences between cytochromes lie in their structure, they differ in the polypeptide chain and in the way the polypeptide attached to the heme group.
- **Nonheme iron proteins** don't contain a heme group, but may contain sulfer, like iron-sulfer protein. (Here the iron bound to cysteine or S^{-2}).

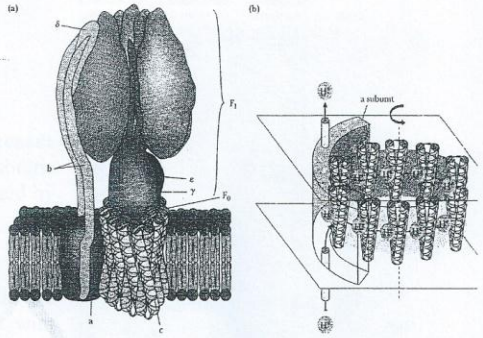
What is the connection between electron transport and phosphorylation?

- We said that the energy released from the oxidation reaction is used to drive the phosphorylation of ADP to ATP.
- We mentioned that three of the four respiratory complex release energy used to pump the proton across the inner membrane to generate a pH gradient across the membrane.
- In addition to this pH gradient there is also a voltage difference across the membrane (due to different concentration of ions between in and out), and this electrochemical potential (voltage drop) across the membrane is converted to a chemical energy of ATP by the coupling process.

- A coupling factor is needed to link oxidation and phosphorylation. ***ATP synthase*** is the protein that serves this function and catalyzes the synthesis of ATP.

☒ **ATP synthase:**

- It is an oligomer separate from the electron transport complexes.
- It spans the inner mitochondrial membrane and projects into the matrix as well.
- F0 (the portion that spans the membrane) consists of 3 different polypeptide (a, b, c).
- F1 (the portion that project to the matrix) consists of 5 different polypeptide in the ratio of $\alpha 3\beta 3\gamma\delta\varepsilon$.
- F0 is the channel for protons.
- F1 sphere is the site of ATP synthesis.



- From the figure; a, b, α, β, and δ subunits constitute the stator of the ATP synthase, and c, γ, and ε subunits form the rotor. Flow of protons through the structure turns the rotor and drives the cycle of conformational changes in α and β that synthesize ATP.
- ATP synthase is also called **mitochondrial ATPase** because the hydrolysis and the synthesis of ATP can be catalyzed by the same enzyme (ATP synthase).
- The **discoverers** of ATP synthase are P. Boyer, John Walker and Jens Skon.

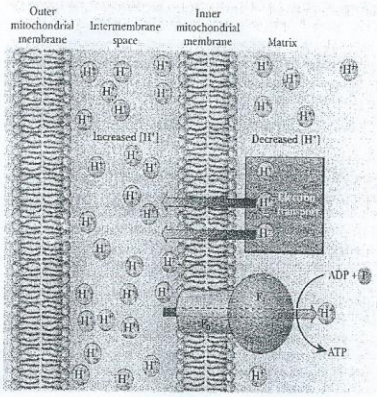
- **Uncoupler**:- these are compounds that inhibits the phosphorylation of ADP without affecting the electron transport, like:
  - ***2,4-dinitrophenol***.
  - Some antibiotics (***valinomycine, gramicidineA)***
- When an uncoupler is present the O2 in the mitochondria will be reduced to H2O, but there will be no production of ATP. But once they are removed, ATP synthesis resumes.
- **P/O ratio:** is used to indicate the coupling of ATP production to electron transport.
- This ratio gives the number of moles of Pi consumed in the phosphorylation of ADP for each mole of oxygen atoms consumed in the reduction of it to H2O.

- The P/O ratio of 1 mole of NADH is 2.5, while 1 mole of FADH2 is 1.5.

☒ **What is the mechanism of coupling in oxidative phosphorylation?**

There are many mechanisms have been proposed for coupling between the electron transport and ATP production, we will talk about two:

- Chemiosmotic coupling.
- Conformational coupling.



Chemiosmotic coupling:

- This mechanism was based entirely on the differences in proton concentration between the intermembrane space and the matrix, this proton gradient established by 3 of the 4 respiratory complexes.

- The proton gradient exists because the various proteins that serve as electron carries in the respiratory chain are not symmetrically oriented with respect to the 2 sides of the inner metochondarial membrane, nor they react in the same way with respect to the matrix and intermembrane space.

- When the electrons transported by a complex, it take up the protons from the matrix and transport them to the intermemebrane space.

  Complex I or III → transfer $4H^+$
  Complex IV → transfer $2H^+$

- The **intermembrane space** has **a higher** concentration of proton and **lower pH** than the **matrix.**

- ATP production will take place when the hydrogen ions flow back to the matrix through the ion channels of the ATP synthase. (As we said the ATP production occur at F1 unit which projects in the matrix).

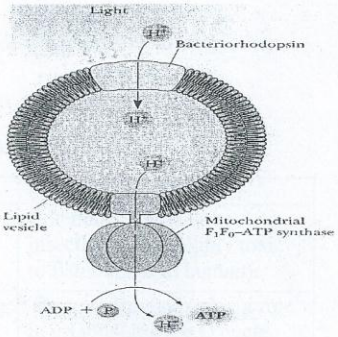
The evidences that support this mechanism (suggested by Peter Mitchell):

1) A system with definite inside and outside compartments (closed vesicles) is essential for oxidative phosphorylation, the process does not occur in soluble preparations or in membrane fragment without compartmentalization.

2) Sub mitochondrial preparations that contain closed vesicles can be prepared, such vesicles can carry out oxidative phosphorylation, and the asymmetrical orientation of the respiratory complex with respect to the membrane can be demonstrated.

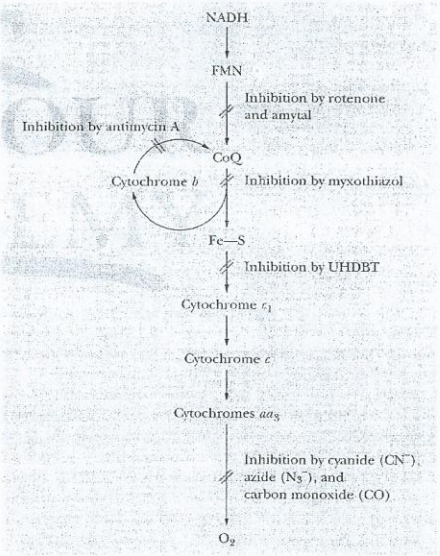
3) A model system for oxidative phosphorylation can be constructed with proton pumping in the absence of electron transport, the model system consist of reconstituted membrane vesicles, mitochondrial ATP synthase, and a proton pump. The pump is bacteriorhodopsin, a protein found in the membrane of halobacteria, the proton pumping takes place when the protein is illuminated.

4) The existence of the pH gradient has been demonstrated and confirmed experimentally.



How the uncouplers work based on this mechanism?

- **Dinitrophenol** is an acid, and the actual uncoupler is its conjugate base dinitrophenolate anion, which can react with the protons in the intermembrane space reducing the pH gradient.
- **Valinomycine** (a cyclic trimer of 4 repeating units) and **GramicidineA** are ionophores creating a channel through which ions such as H^+, K^+, Na^+ can pass through the membrane, so reducing the pH gradient.



How are respiratory inhibitors used to study electron transport?

- What will happen if the flow of electrons through the **ETC** is blocked?
  - Reduced compounds will accumulate before the blocking point in the pathway.
  - Compounds come after the blocking point will be lacking electron and tend to be found in the oxidized form.

So, by using the respiratory inhibitor we can determine:

- ✓ The order of the electron transport chain, depending on the relative amount of oxidized and reduced form of electron carriers.
- ✓ The oxidized and reduce forms of cytochromes.

Note: the oxidized and reduced forms of cytochrome can be distinguished from each other by spectroscopic techniques (wavelengths).

There are three sites in the ETC at which inhibitors have an effect:-

Inhibitor site	Examples	Comments
1) block the transfer of electrons from the flavoprotein NADH reductase to coenzyme Q	Barbiturates (ex; amytal), Rotenone	Rotenone is used as insecticide, it is highly toxic to fish but not to human).
2) Block electrons transfer involving the b cytochromes, coenzyme Q, cytochromes c1.	antimycin A, myxothiazol, 5-n-undecyl-6-hydroxy-4,7-dioxobenzothiazol (UHDBT)	These compounds play a role in establishing the Q cycle.
3) block the transfer of electrons frome the cytochrom aa3 complex to oxygen	Cyanide(CN^-), azide(N_3^-), carbon monoxide(CO)	

Note: Notice that each of the 3 sites of action of respiratory inhibitors corresponds to one of the respiratory complexes.

☒ What is the ATP yield from complete oxidation of glucose?

Look to the table 20.3 and notice:

- ➢ A complete oxidation of glucose will give **30 ATP** molecules if we use **glycerol-phosphate shuttle.** It is observed in mammalian muscle and brain.
- ➢ A complete oxidation of glucose will give **32 ATP** molecules if we use **malate-aspartate shuttle.** It is found in mammalian kidney, liver and heart.

Table 20.3
Yield of ATP from Glucose Oxidation

Pathway	ATP Yield per Glucose: Glycerol–Phosphate Shuttle	Malate–Aspartate Shuttle	NADH	$FADH_2$
Glycolysis: glucose to pyruvate (cytosol)				
Phosphorylation of glucose	−1	−1		
Phosphorylation of fructose-6-phosphate	−1	−1		
Dephosphorylation of 2 molecules of 1,3-BPG	+2	+2		
Dephosphorylation of 2 molecules of PEP	+2	+2		
Oxidation of 2 molecules of glyceraldehyde-3-phosphate yields 2 NADH			+2	
Pyruvate conversion to acetyl-CoA (mitochondria)				
2 NADH produced			+2	
Citric acid cycle (mitochondria)				
2 molecules of GTP from 2 molecules of succinyl-CoA	+2	+2		
Oxidation of 2 molecules each of isocitrate, α-ketoglutarate, and malate yields 6 NADH			+6	
Oxidation of 2 molecules of succinate yields 2 $FADH_2$				+2
Oxidative phosphorylation (mitochondria)				
2 NADH from glycolysis yield 1.5 ATP each if NADH is oxidized by glycerol–phosphate shuttle; 2.5 ATP by malate–aspartate shuttle	+3	+5	−2	
Oxidative decarboxylation of 2 pyruvate to 2 acetyl-CoA: 2 NADH produce 2.5 ATP each	+5	+5	−2	
2 $FADH_2$ from each citric acid cycle produce 1.5 ATP each	+3	+3		−2
6 NADH from citric acid cycle produce 2.5 ATP each	+15	+15	−6	
Net Yield	+30	+32	0	0

Questions:

1-Oxidative phosphorylation and ETC occur in:
a- mitochondria b- ER
c- cytosol d- a+b

2-The final electron accepter in ETC:
a- O2 b- CO2
c- H2O d- FADH

3-In ETC NADH can drive the production of:
a- 1.5 ATP b- 2.5 ATP
c- 3ATP d- 4ATP

4-Which of the following compound is\are uncoupler:
a- 2,4dinitrophenol b- valinomycin
c- tetracyclin d- a+b

5- How many ATP produced if we use glycerol phosphate shuttle:
a- 32 ATP b- 30ATP
c- 10 ATP d- 15ATP

6-In which of the following complex, there is no production of ATP
a- complex 1 b- complex 2
c- complex 3 d- complex 4

7-The enzyme complex of ETC embedded in:
a- inner mitochondrial membrane b- outer mitochondrial membrane
c- plasma membrane d- all of the above

8-Which of the following complex called cytochrome c oxidase:
a- complex 1 b- complex 2
c- complex 3 d- complex 4

9-Which of the following complex transfer $2H^+$:
a- complex 1 b- complex 2
c- complex 3 d- complex 4

Answer sheet

Question#	Answer
1	a- mitochondria
2	a- O2
3	b- 2.5 ATP
4	d- a+b
5	b- 30ATP
6	b- complex 2
7	a- inner mitochondrial membrane
8	d- complex 4
9	d- complex 4