

AN INTRODUCTION TO METABOLISM

Part 2: Aerobic Metabolism and the RQ Concept*

Summary: This is a generalized overview of aerobic metabolic pathways. After the overview, we will introduce the concept of respiratory quotient (RQ) and its usefulness in metabolic studies. **The material that does not matter so much to us, interesting as it is, is in blue.**

I. Introduction

A. In most animals, most of the **supply reactions responsible for the generation of ~P** occur in the mitochondria (e.g., Krebs cycle, oxidative phosphorylation, β -oxidation of fatty acids). They are closely related to other reactions that occur in the cytosol (glycolysis and some types of protein and lipid metabolism).

1. **In aerobic organisms most ~P comes from the mitochondria.** For our purposes we will treat the mitochondria as **BLACK BOXES containing two reaction systems** that we need to be concerned with

(a) **KREBS CYCLE (TCA):** degrades 2C (acetyl) compounds (or sometimes other things that feed into the various steps of the cycle) into lots of high-energy electrons and some ~P.

(i) Nearly all of the energy is removed from the fuel molecules in the form of high-energy electrons. The carriers that actually move the electrons are the coenzymes **NAD⁺ or NAD_{oxidized}** and **FAD**. When these are reduced by the addition of electrons, they become **NADH (NAD_{reduced})** and **FADH₂** respectively. We will see below that the energy in these electrons is ultimately extracted by the electron transport system (ETS) and is used to produce ~P by a process we will term **oxidative phosphorylation** (or **ox-phos** for short).

(ii) Some ~P is also produced by a process called **substrate-level phosphorylation**. Substrate-level phosphorylation can be defined as the process where a ~P is created on a substrate molecule and is then transferred to some other molecule -- for instance ADP or GDP to make ATP or GDP. In the case of the Krebs cycle, the substrate-level phosphorylation involves the production of GTP. However, in terms of energy content, GTP carries same amount of energy as ATP in the same manner. In fact, the ~P on GTP is generally quickly transferred to ADP to make ATP. Thus, we often simply count it as an ATP. A single ~P is produced by substrate level phosphorylation per 2C that enters the Krebs Cycle.

(iii) The **rate of the Krebs Cycle** is controlled by:

1. availability of appropriate 2C compounds
2. availability of **electron acceptors (NAD⁺ and**

FAD).

3. the concentrations of certain enzyme

modulators such as ADP and ATP.

(iv) the **Krebs cycle gets its fuels from one of three**

sources:

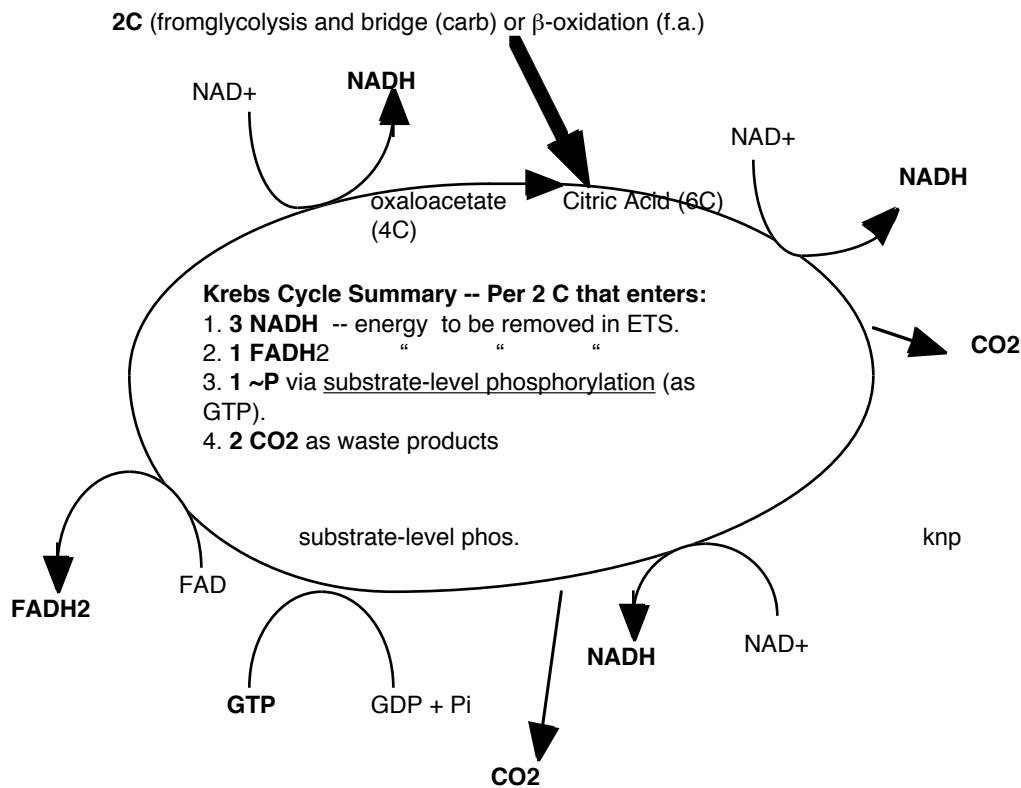
1. **carbohydrate**, 2C fragments after processing in glycolysis (cytosol) and the mitochondrial "bridge reaction (PDH complex rx)".

2. **fatty acids via β -oxidation** in the mitochondria -- this feeds 2 C fragments in to the cycle at the same place as carbs enter.

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3. Sometimes (rarely in humans) by oxidation of the skeletons of amino acids -- these are basically what are left of an amino acid after it has been deaminated (after the -NH_2 is removed). Strictly speaking, the remains of deamination of amino acids come in all sizes and shapes and not simply as 2 C fragments (nearly all are not 2 C).
 (v) **CO_2 is the Krebs cycle waste product.**

Here is an overview of a single turn of the Krebs Cycle:



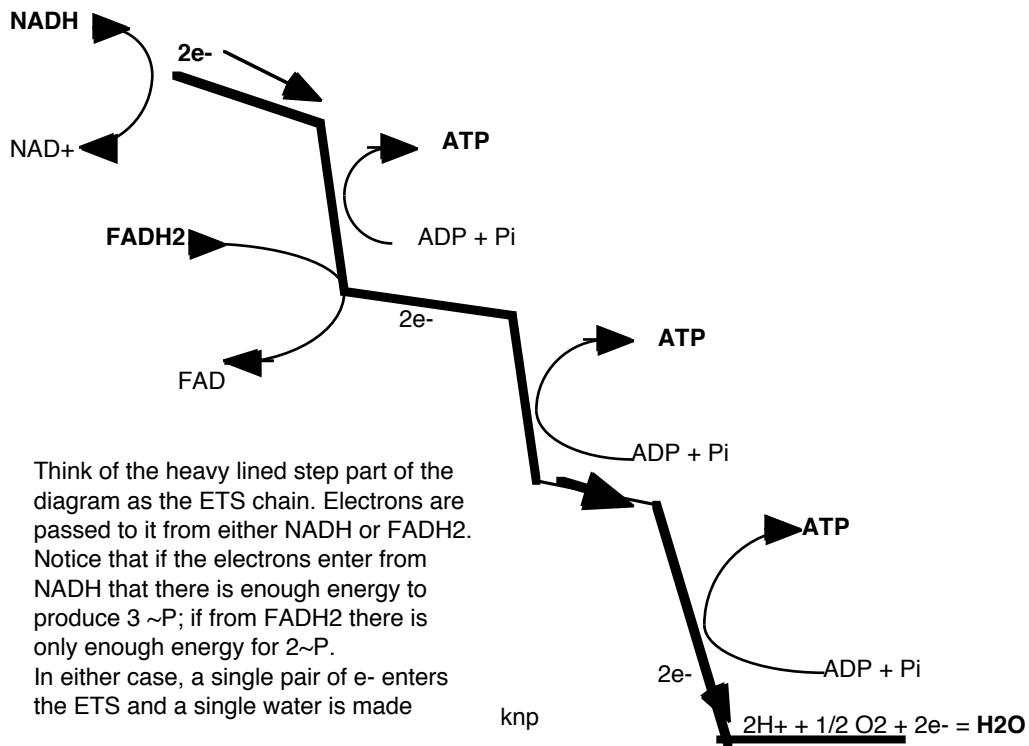
(b) **The CYTOCHROME ELECTRON TRANSPORT SYSTEM (ETS):** (This is a look into a black box that we will not make much of – I would love to, but it is more for a biochemistry course).

(i) The ETS accepts high-energy electrons produced by the Krebs cycle and by other mitochondrial and cytosol reactions such as glycolysis and β -oxidation.

(ii) These electrons are eventually transferred in an orderly manner from one carrier to the next until they eventually combine with oxygen and form water.

(iii) In the process, energy from the electrons is used to form ATP from ADP and Pi by a process involving pumping and re-entry of H^+ (Mitchell's chemiosmotic model). The details of this process need not concern us although they are fascinating and at the center of cellular energetics.

(iv) The amount of energy that can be conserved in ~P depends on the source of the electrons. Electrons from NADH are more energetic than those from FADH₂. The ETS is able to conserve 3 ~P per electron pair from NADH (one pair NADH) and 2 ~P per FADH₂ (one pair of electrons per FADH₂). Here is a potential energy "step" model of the ETS:



(v). The ETS is controlled by:

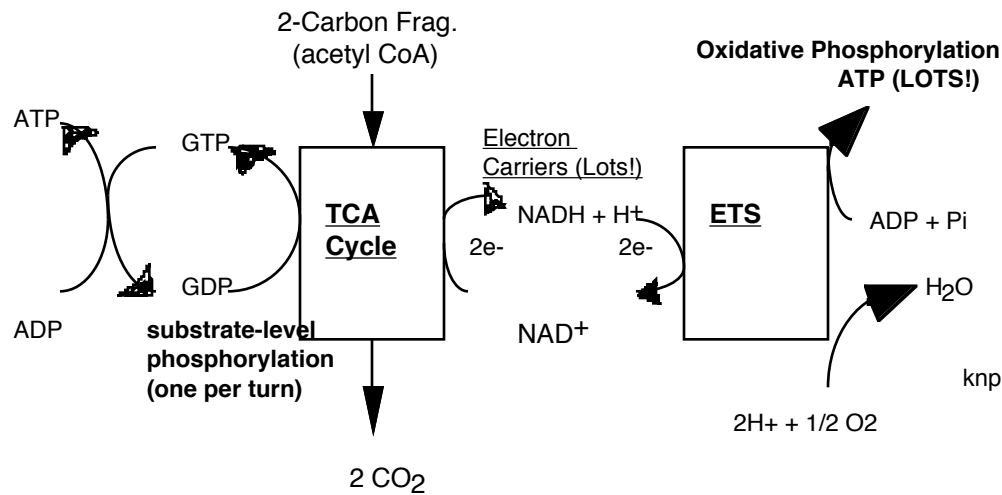
1. Foremost -- the **availability of O₂**.
2. Availability of **NADH or FADH₂**.
3. Ratio of ATP to ADP --ADP must be

present to allow the system to work (except in an exotic process called "uncoupled phosphorylation" which we will consider later).

(c) **Putting together the Krebs Cycle and the ETS.**

1. At this point, if not before, you should realize that most of the ~P in the body will be made by the ETS. We can go so far as to view the Krebs cycle as simply a means to supply high-energy electrons to the ETS. They are, after all, the most numerous products of the ETS. The diagram below emphasizes the sources of ~P from the mitochondria but it does not show them in their correct amounts. We'll do that shortly:

The Krebs Cycle and ETS



? In the diagram above, which form of NAD is reduced? Oxidized? Which form contains more potential energy? Why?

2. **Keeping track of conserved energy:** Per 2C that entered the Krebs cycle, we got:
- (a) 1 ~P directly by substrate level phosphorylation
 - (b) 3 NADH, each of which will give up their electrons to the ETS and produce 3 ~P -- so the total amount of ~P made from the NADH yielded in one turn of the Krebs cycle is 3* 3 = 9.
 - (c) there was 1 FADH₂ which will give a pair of electrons to the ETS and yield 2 ~P.
 - (d) So the **total is 12 ~P.**

We have just considered two important mitochondrial systems for conserving energy in ~P. In addition, β -oxidation of fatty acids also occurs there but we will not consider it. This leaves a very important cytoplasmic process, glycolysis

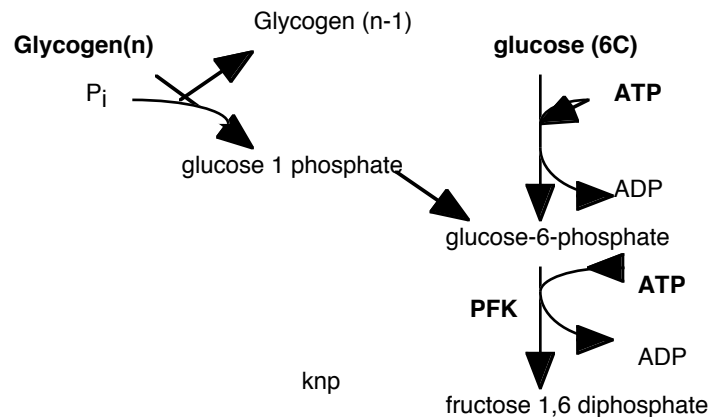
b. **GLYCOLYSIS:** a system that is resident in the cytosol. It takes glucose (and other substances) and converts to them into 3C fragments. Energy-wise, ATP is generated from ADP and Pi via substrate-level phosphorylations and high-energy electrons are produced and captured by NAD⁺. However, these can only be used to synthesize ~P under aerobic conditions. The concentrations of ATP, AMP (derived from ADP) and certain other substances are very important in the regulation of glycolysis. Here is a more detailed (but still very simple) overview of the process:

- (i) fuel sources and preparation: The input is always a hexose sugar or hexose derivative. It can either be **glucose** (or a number of other hexoses) or **glycogen**. If we start from glucose, two ~P are expended in preparing the molecule for the

degradative parts of glycolysis. If we start from glycogen, only one is needed because a hexose is cleaved from glycogen using a P_i .

It is very important to realize that you are not really getting something for nothing by starting from glycogen. Recall from the previous set of notes (QT2 p.7) that the addition of one glucose residue to glycogen requires 2 $\sim P$ bonds. Only one is "gotten back" when glycogen is cleaved for fuel. As always, there is a cost involved in anabolism. On the other hand, during the exercise, there is certainly an advantage to the extra $\sim P$ when using glycogen as a fuel -- but this advantage was gained by "banking" the $\sim P$ in glycogen along with paying a 1 $\sim P$ "deposit fee".

Here is a quick overview:



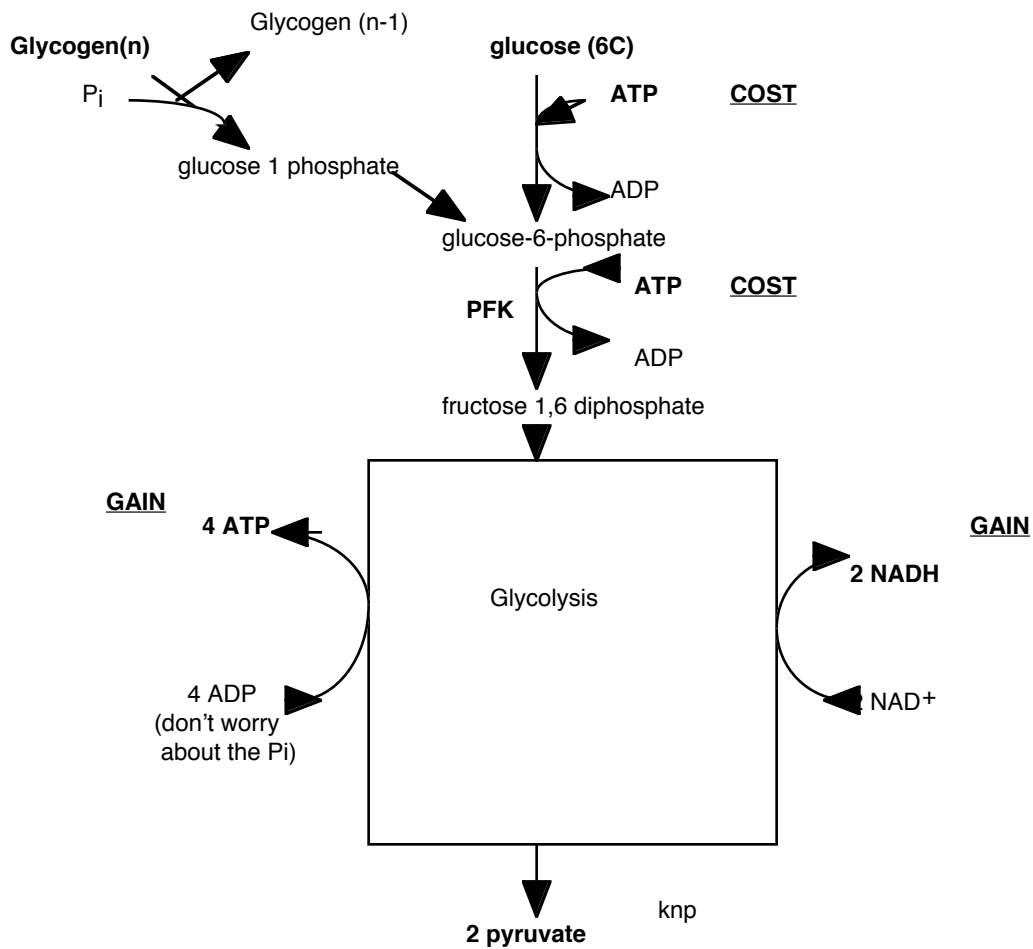
(note: the only important thing for you to remember is that the hexose sources are either glucose in which case 2 $\sim P$ are used to get things going or glycogen in which case only 1 is used at the time (-- nothing was gotten for free -- recall from the last class that energy was required to synthesize the glycogen --we're just getting it back here). The other thing that matters is the enzyme **PFK** -- it is a regulated (non-equilibrium) enzyme and is the most important controller of the rate of glycolysis. **PFK is activated ("de-inhibited") by high [AMP] -- this stuff is produced when lots of ATP is broken down. PFK is inhibited by higher than "normal" [ATP].**

(ii) We're not going to sweat most of the details of what comes next -- we'll treat the rest of glycolysis as a black box and simply look at what goes in and what comes out. We need to consider the energy conserved and the waste products, just as with the mitochondrial reactions.

(a) **per hexose**, we get **two molecules of "waste"** at the bottom. Under aerobic conditions, this waste is **pyruvate** (the conjugate base of pyruvic acid -- pyruvic acid is normally dissociated at physiological pH). Under aerobic conditions, the pyruvate will go to the mitochondria and be completely oxidized in the "bridge reaction" and the Krebs cycle.

(b) **per hexose**, there are a total of **4 substrate level phosphorylations** (i.e., two per pyruvate).

(c) **per hexose**, there are two molecules of NADH produced from NAD^+ . Under aerobic conditions, the electrons on these NADH will eventually end up in the ETS (see below). So, here is the summary (next page):



(iii) Accounting:

(a) Energy Gains:

1. From substrate-level

phosphorylations -- a total of **4**.

2. We also got 2 NADH (two pairs of high energy electrons). What can we get from these? You might expect from the earlier diagram that we could get 3 from each NADH. In fact, the number varies between 2 and 3 depending on the cell type. In muscles it is usually 2 and in the liver it can be 3. We need not worry why, except to say that it has to do with the fact that NADH does not travel from the glycolytic reactions to the mitochondria. Instead, the electrons are attached to a carrier molecule that moves them. In the process some energy may be lost. **We will assume that we only get 2 ~P from oxidative phosphorylation for each NADH produced in glycolysis. That gives a total of 4 ~P from oxidative phosphorylation.**

3. Gross ~P yield = 4 (substrate level) + 4 (ox-phos) = **8 ~P total** . But wait -- unlike the Krebs cycle we had to pay in to get things started.

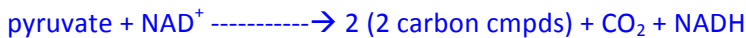
(b) **Energy costs:** we saw earlier that if our hexose was glucose, we paid 2 ~P and if it was glycogen our immediate cost was 1~P (we paid the other one earlier in synthesizing the glycogen). Thus, costs are 1 or 2 ~P.

(c) **Net Yield:** Gross - "cost": for **glucose, 8 - 2 = 6 ~P**, from **glycogen, 8 - 1 = 7 ~P**.

(d) **wastes:** two 3-carbon molecules (pyruvate).

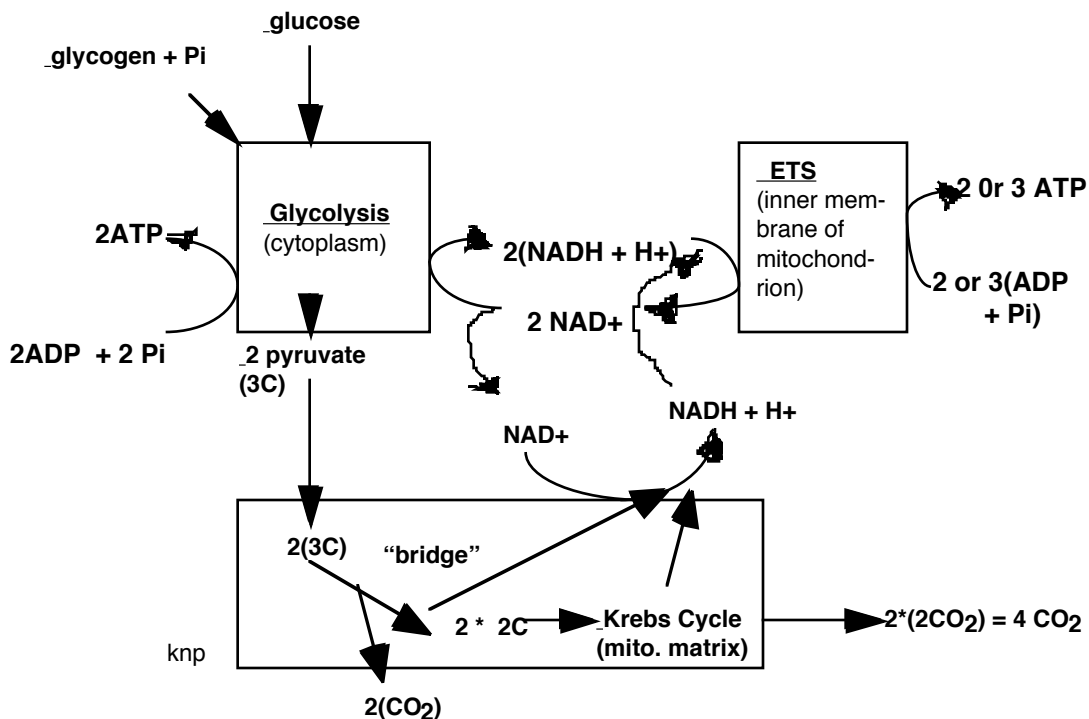
(iv) **Getting from Glycolysis to the Krebs Cycle -- the so-called "bridge reaction" (I prefer to call this the PYRUVATE DEHYDROGENASE COMPLEX REACTION OR THE PDH RX FOR SHORT)**

(a) If the Krebs cycle is going, and there is adequate NAD^+ and FAD, it will be able to accept more 2 C fragments. We have just seen that pyruvate, the "waste" product of aerobic glycolysis has 3 C. To use it in the Krebs cycle, we must remove one carbon. This is done by the "bridge reaction" -- more properly, the pyruvate dehydrogenase reaction. This occurs in the mitochondrion; here is a simplified version (we'll ignore the CoEnzyme A stuff which is important in terms of chemistry but not energetics):



(the CO_2 is released as nothing more than the result of a simple decarboxylation of pyruvate). The simplified overall scheme is given on the next page:

Simplified Overview of Aerobic Glycolysis



(b) Energetics of the "bridge reaction": the NADH molecules produced by the pyruvate kinase reaction will yield 3 ~P each since they are produced within the mitochondria. Since the pyruvate dehydrogenase (a.k.a. bridge) reaction will occur twice per hexose that enters glycolysis (since we get two pyruvates), then a total of 2 NADH are yielded which gives us a total of 6 ~P.

c. **How much ~P is yielded per hexose?**

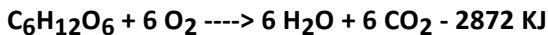
1. From glycolysis: 6 or 7
2. From the "bridge": 6
3. From the Krebs cycle and ETS: 24
4. TOTAL: 36 or 37 per hexose
5. waste products -- 6 CO₂ and 6 H₂O (see below).

IMPORTANT The 36 or 37 ~P, although it is a number given all of the time, is actually an over-estimate. It is what is theoretically possible with the steps of glycolysis, the ETS and Krebs cycle. The place where things fall apart has to do with H⁺ ions chemiosmosis across the inner membrane of the mitochondria. The previous calculation assumed that all H⁺ pumped out by the ETS came back via the ATP synthase and resulted in ATP synthesis. In fact, some H⁺ leaks through the membrane and this lowers the amount of ~P produced by oxidative-phosphorylation from 24 to something more like 20 (it varies) and so the typical production is more like around 32~P per mol of hexose that enters aerobic metabolism.

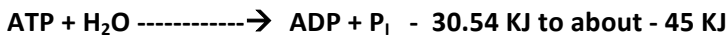
II. The efficiency of aerobic glycolysis

A. We have just seen that if we start with one mol of hexose, aerobic metabolism will conserve energy in the form of 36 or 37 ~P bonds. These can be used in other reactions in the cell; they represent the useful output of catabolic reactions. The question quickly arises as to how efficient the process was at conserving energy in a useful form (as ~P).

B. The theoretical yield of any aerobic reaction is obtained by taking a known amount of some fuel molecule and burning it completely with oxygen and measuring the total amount of energy released. Usually this is done with a **bomb calorimeter**. In the case of glucose or other hexose molecules:



So, a total of 2872 KJ of energy are liberated per mol of hexose totally oxidized. If we look at the free energy of hydrolysis of the ~P bond in ATP (hydrolysis is the essential feature of using a ~P from ATP or similar compounds), we find:



Why the range of energies? We learned earlier that the energy release just given is for the special condition where the concentrations of ATP, ADP and Pi are all 1 M. In the body there is actually far more ATP than ADP and so for a given set of conditions, more ATP molecules break down. This is tantamount to saying that under these conditions the bond energy is higher since it is more likely that one will get a given molecule of ATP to breakdown.

Now since in aerobic metabolism, a total of 36 or 37 ATP are synthesized, then the amount of energy conserved in ATP is between $36 * 30.54 \text{ KJ} = 1099 \text{ KJ}$ and $37 * 45 \text{ KJ} = 1665 \text{ KJ}$. For the moment, let's use the standard free energy change for hydrolysis of ATP (30.54KJ) and assume we started with glucose. Thus, 1099 KJ are conserved.

C. As we learned earlier, efficiency is simply the useful work (in this case the conserved energy) divided by the total available energy. In our example then:

$$\begin{aligned} \text{Efficiency} &= (\text{conserved energy}) / (\text{available energy}) * 100 \\ &= ((\text{Energy stored in ATP}) / (\text{total energy released in oxidation})) * 100 \\ &= (1099 \text{ KJ} / 2872 \text{ KJ}) * 100 \\ &= \mathbf{38\%} \end{aligned}$$

Notice that under actual cellular conditions, the efficiency is greater -- starting from hexose and under ideal conditions of no H^+ leakage (see above) $E = ((36 * 45)/2872) * 100 = 56\%$

One other way to look at this is to think about the amount of energy from that oxidation of glucose that is available to synthesize ATP from ADP and P_i :



where 2872 KJ is the available energy and 1773 KJ is the energy that is not conserved but instead is lost as heat. The remainder is stored in the newly minted ATP. However, remember that this $\sim\text{P}$ will also eventually be broken down and the energy stored in it released. Energy is conserved.

III. Conversation of \dot{V}_{O_2} or \dot{V}_{CO_2} to \dot{Q} : The Respiratory Quotient

A. For many comparisons, it is necessary to convert O_2 consumption or CO_2 production measurements of metabolism to power. A good example would be anytime a physiologist wants to know the efficiency with which an animal performs some activity. Since the power output of the animal doing the activity represents its useful work the scientist also needs to find the power input. Recall that \dot{V}_{O_2} and \dot{V}_{CO_2} are simply stand-ins for power.

B. It is not hard to see how to convert \dot{V}_{O_2} and \dot{V}_{CO_2} to power or energy **provided that we know the fuel being used**. This is because if we know the fuel, we know the stoichiometry and energy yield of particular reaction. Let's take the example of hexose as fuel. Here is the reaction:



1. First note that the amounts of O_2 used and CO_2 produced would represent \dot{M}_{O_2} and \dot{M}_{CO_2} (metabolism measured in mols of O_2 or CO_2 respectively per unit time). In this particular case, if one mol of glucose is burned in time t, then $\dot{M}_{\text{O}_2} = 6$ mols O_2 / t and $\dot{M}_{\text{CO}_2} = 6$ mols CO_2 / t .

2. Following this same logic, we can see that if we know that the fuel is glucose (or most any carb.; see below) then if we measure $\dot{M}_{O_2} = 15$ mols O_2 /t then 2.5 mols of hexose were burned and therefore a total of $-2872 \text{ kJ} * 2.5 = 7180 \text{ KJ}$ were released per time t. A similar calculation could be made using CO_2 .

3. Thus, we can see that it is easy to establish a relationship between a mol of O_2 consumed or a mol of CO_2 produced and the energy release rate if we know the fuel being used.

(a) for our particular example, we can see that the energy release per mol of O_2 consumed, when carbs. are the fuel, is $2872 \text{ kJ}/6 \text{ mols } O_2 = 478.7 \text{ KJ/mol } O_2$ -- we can make a similar calculation for CO_2 and we get the same magnitude answer.

(b) It is now an easy matter to go from molar amounts to volumes. Recall that at standard temperature and pressure, a mol o' gas occupies 22.4 L. Thus, if carb. is the fuel, then the energy equivalent of 1 L O_2 is:

$$2872 \text{ KJ} / 6 \text{ mols of } O_2 * 1 \text{ mol } O_2 / 22.4 \text{ L } O_2 = 21.37 \text{ KJ/L } O_2.$$

A similar calculation can be made for CO_2 .

Note: You might object that only part of this 2872 KJ of energy in one mol of glucose is immediately released since some is conserved in ATP. So is it correct to make calculations like this? Certainly so -- the energy that is conserved in ATP is only there briefly. It will soon be transferred or released.

C. All this is fine and good but how do we know what fuel we are using? Let's look at the equation for the oxidation of glucose again (hidden):



Notice that, practically speaking, certain factors in this equation are hidden from a physiologist who is studying the metabolic rate of some individual. Our physiologist can measure \dot{V}_{O_2} and \dot{V}_{CO_2} with comparative ease. However, she cannot directly measure the amount of fuel used. Moreover, she needs a way to figure out what fuel is actually being used. To repeat -- all she has access to are \dot{V}_{O_2} and \dot{V}_{CO_2} . She needs some way to find the type of fuel to complete calculations of energy and power. Fortunately, there is a way to discern the fuel simply based on the respiratory gas volumes.

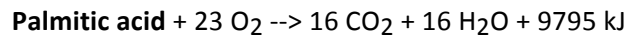
D. The Respiratory Quotient (RQ)

1. Defined:

$$RQ = \frac{\dot{V}_{CO_2}}{\dot{V}_{O_2}} = \frac{\dot{M}_{CO_2}}{\dot{M}_{O_2}}$$

2. How does this help? Each type of fuel or mix of fuels used in the body is accompanied by its own particular RQ. For instance, for any hexose, complete oxidation always requires 6 O₂ and releases 6 CO₂. The RQ is always 1.0 (for any type of carbohydrate that the body would use for fuel -- notice that if some unusual carbs. such as deoxyribose are burned you get a slightly different value, but then the body does not normally use deoxyribose as an energy source).

3. Let's look at a typical fatty acid, palmitic acid. It is a common energy storage molecule:



Notice that in this case $\text{RQ} = 16 \text{ CO}_2 / 23 \text{ O}_2 = 0.7$. For other fatty acids slightly different values are obtained but for fats in general the RQ averages at about 0.71. Thus, if we measure \dot{V}_{O_2} and \dot{V}_{CO_2} simultaneously on a particular individual and find the $\text{RQ} = 0.71$ we know that the fuel being burned is fat. Furthermore, we can calculate the amount of energy released per mol or liter of O₂ used or CO₂ released, just as we did with glucose. For instance, in the case of palmitic acid (a typical fat), the energy equivalent for oxygen is $9795 \text{ kJ} / 23 \text{ mols O}_2 = 425 \text{ kJ/mol O}_2$; for CO₂ the factor is $9795 / 16 = 612 \text{ kJ/mol CO}_2$ produced.

4. By running various types of fuels or mixes of fuels that animals commonly use, and then measuring the energy output, O₂ used and CO₂ consumed, it was possible to make up a table of energy equivalents of oxygen used or CO₂ consumed at different RQs. A complete RQ table can be found at the end of these notes and as a separate download with lab.

Some important things to notice: for different substances:

(i) The value of energy per L O₂ varies less than for CO₂ -- there is a maximum error of about 5% in \dot{Q} if one were to

1. measure \dot{V}_{O_2}
2. incorrectly assume an RQ for carb. when in reality fat was being burned.

(ii) If CO₂ were measured instead, the max. error in estimating \dot{Q} is 32%. Also note **THERE ARE OTHER EVEN WORSE ERRORS ASSOCIATED WITH \dot{V}_{CO_2} THAT WILL BE MENTIONED LATER.**

Thus, we can estimate \dot{Q} using \dot{V}_{O_2} with good accuracy. We can get especially accurate estimates of \dot{Q} if we know the RQ since we know the fuel being used.

SUMMARY:

1. \dot{V}_{O_2} and \dot{V}_{CO_2} are indicators of metabolism, but they are indirect measures and not as accurate as \dot{Q} .
2. \dot{V}_{CO_2} estimates are especially fickle.

3. In terms of fuels, **carbohydrates yield the most energy per amount of oxygen that the organism must take in.** Thus, *in situations where oxygen is limited (by the circulation, for instance) it is best to burn carbs.*

? What does it mean if an animal's RQ goes from 0.75 to 0.95?

Are there any other problems with indirect methods of estimating \dot{Q} ?

**Supplementary Table:
Energy Equivalents of Respiratory Gas Volumes for Different RQs
(Aerobic Respiration)**

RQ	KJ/LO₂	KJ/LCO₂	Kcal/LO₂	Kcal/LCO₂
0.71	19.62	27.64	4.69	6.61
0.72	19.67	27.32	4.70	6.53
0.73	19.72	27.02	4.71	6.46
0.74	19.78	26.73	4.73	6.39
0.75	19.83	26.44	4.74	6.32
0.76	19.87	26.15	4.75	6.25
0.77	19.93	25.89	4.76	6.19
0.78	19.98	25.62	4.78	6.12
0.79	20.03	25.36	4.79	6.06
0.80	20.09	25.11	4.80	6.00
0.81	20.14	24.86	4.81	5.94
0.82	20.19	24.62	4.83	5.88
0.83	20.24	24.39	4.84	5.83
0.84	20.29	24.16	4.85	5.77
0.85	20.34	23.93	4.86	5.72
0.86	20.40	23.72	4.88	5.67
0.87	20.45	23.50	4.89	5.62
0.88	20.50	23.29	4.90	5.57
0.89	20.55	23.09	4.91	5.52
0.90	20.60	22.89	4.92	5.47
0.91	20.65	22.69	4.94	5.42
0.92	20.70	22.50	4.95	5.38
0.93	20.76	22.32	4.96	5.33
0.94	20.81	22.14	4.97	5.29
0.95	20.86	21.95	4.99	5.25
0.96	20.91	21.78	5.00	5.21
0.97	20.96	21.61	5.01	5.16
0.98	21.01	21.44	5.02	5.12
0.99	21.07	21.28	5.04	5.09
1.00	21.12	21.12	5.05	5.05

Source: Zuntz N. 1901. Ueber die Bedeutung der verschiedenen Nahrstoffe als Erzeuger der Muskelkraft. Pflügers Arch 83: 557.

This table is based on the notion that all RQs between 0.71 (fats only energy substrate) and 1.0 (carbohydrates only substrate) are mixes of lipid and fat metabolism -- i.e., that no protein is being used for energy. This is probably approximately true in many species, especially in resting individuals who are not starving. However, in other conditions and in some species, intermediate RQs may indicate significant protein metabolism and the calculation of energy equivalents is a bit more complicated. Nevertheless, this table generally represents a good approximation for most purposes.

RQ	Kcal/LO ₂	Kcal/LCO ₂	Percent Contribution		Calculation	
			Carbs	Fats	Kcal/LO ₂	Kcal/LCO ₂
0.71	4.69	6.61	0	100	4.69	6.72
0.72	4.70	6.53	5	95	4.70	6.66
0.73	4.71	6.46	8	92	4.72	6.60
0.74	4.73	6.39	12	88	4.73	6.54
0.75	4.74	6.32	16	84	4.74	6.47
0.76	4.75	6.25	19	81	4.76	6.41
0.77	4.76	6.19	23	77	4.77	6.35
0.78	4.78	6.12	26	74	4.78	6.29
0.79	4.79	6.06	30	70	4.79	6.23
0.8	4.80	6.00	33	67	4.81	6.17
0.81	4.81	5.94	37	63	4.82	6.11
0.82	4.83	5.88	40	60	4.83	6.06
0.83	4.84	5.83	44	56	4.84	6.00
0.84	4.85	5.77	47	53	4.86	5.94
0.85	4.86	5.72	51	49	4.87	5.88
0.86	4.88	5.67	54	46	4.88	5.82
0.87	4.89	5.62	58	43	4.89	5.76
0.88	4.90	5.57	61	39	4.90	5.71
0.89	4.91	5.52	64	36	4.92	5.65
0.9	4.92	5.47	68	33	4.93	5.60
0.91	4.94	5.42	71	29	4.94	5.54
0.92	4.95	5.38	74	26	4.95	5.48
0.93	4.96	5.33	77	23	4.96	5.43
0.94	4.97	5.29	81	19	4.98	5.37
0.95	4.99	5.25	84	16	4.99	5.32
0.96	5.00	5.21	87	13	5.00	5.26
0.97	5.01	5.16	90	10	5.01	5.21
0.98	5.02	5.12	94	6	5.02	5.15
0.99	5.04	5.09	97	3	5.03	5.10
1	5.05	5.05	100	0	5.04	5.04

Example:

If we assume that the average energy equivalence for all carbohydrate metabolism is 678 Kcal/mol carb or about 5.045 Kcal/LO₂ and L CO₂ and if we assume that mixed fat metabolism yields about 2415 Kcal/mol fats or 4.688 Kcal/LO₂ and 6.74 Kcal / LCO₂, then, for RQ = 0.85 51% of energy is from carbs and 49% from lipids therefore for O₂:

$$0.51 * 5.045 \text{ Kcal/LO}_2 + 0.49 * 4.688 \text{ Kcal/LO}_2 = 4.87$$

(The slight discrepancy with the value given in the table is due to rounding errors for energy equivalents of a liter of O₂.)