10 October 2005 **Metabolism I** ® R. B.Huey

Goals for This Lecture:

- ♦ Understand the importance of "metabolism" and "metabolic rate
- ♦ Learn to measure metabolic rate in lab
- ♦ Appreciate some factors that alter an individual's metabolic rate

**I. What is metabolism and why is it important?** *(SN 169)*

A. Animals require energy for maintenance, growth, reproduction, and work. For almost all animals, energy is from food that is derived (directly or indirectly) from plants. Part of food is then oxidized to form ATP, the energy "currency" of cells (some food goes to waste or to "storage"). *Metabolism* is a general term that refers to the sum of all biological transformations of energy and matter.

B. Energy metabolism is a measure of the intensity of life, a summary statistic of the rate of energy use. Metabolic *rate* refers to energy metabolism per unit time. Thus if one animal has a relatively high metabolic rate, its overall physiology is working faster. ➔ So metabolic rate provides information on (i) overall activity of physiological machinery, (ii) resource needs (e.g., food, water, air), and (iii) even the production (new tissue, reproduction) of an animal. Not surprisingly, the study of metabolism is fundamental to physiologists and ecologists.

C. Before the end of the 18th Century, the source of "animal heat" was thought to be from a "inborn fire." The heat was thought to arise in the left ventricle of the heart, and breathing functioned to cool this internal fire!

1. But in 1783 the great French physiologist Lavoisier [1] showed that an animal's production of heat related to the amount of oxygen consumed and the amount of carbon dioxide released.
2. Thus "animal heat" is **a byproduct of chemical reactions** and thus of metabolism. Why? At each step in a biochemical (or metabolic) pathway, some chemical energy in fuel is necessarily lost as heat (2nd law thermodynamics).

**II. How can one measure an animal's metabolism?** *(SN 170-172)*

A. Most animals require molecular $0_2$ for cellular metabolism (hence called **aerobic** metabolism -- we will discuss **anaerobic** metabolism later) to produce ATP, the immediate energy source for physiological processes. Here is the fundamental relationship:

$$\text{fuel} + 0_2 \rightarrow CO_2 + H_20 + \text{heat} \ (+ \text{ATP})$$

B. So how can one measure (or compare) metabolic rates? The above relationship suggests that overall metabolic flux through this pathway can in fact be measured in several ways.

C. Two basic categories: measure metabolism **"directly"** (quantify heat production) or **"indirectly"** (quantify $O_2$ or fuel consumption, or $CO_2$ or $H_20$ production). [2]

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[1] For a fascinating history of metabolic studies, see E. Mendelsohn, 1964, *Heat and Life: The Development of the Theory of Animal Heat,* Harvard Univ. Press.

[2] This terminology is historical – because scientists in 18th and 19th centuries thought that animals literally burned food to liberate heat, and so they logically considered heat production to be the "direct" measure of metabolism.

D. **Direct measure** of heat production, calorimetry

Lavoisier & Laplace in France were the first to measure metabolism. They placed a guinea pig inside an ice jacketed chamber ("calorimeter"). The principle was ingenious – heat from the animal melted ice in the jacket, and so the heat lost (metabolism) could be quantified simply by measuring the amount of ice melted! [Because 335J is required to melt 1 g of ice, heat produced by the mouse simply equals the mass of water melted times 335J! Note: don't memorize these numbers!] Also, they discovered that the heat produced was <u>proportional</u> to the $O_2$ consumed and the $CO_2$ liberated.

Direct calorimetry is very accurate. Water-jacket versions now used, allowing control of ambient temperature. But technically difficult, and the animal is obviously confined!

➔ *Note: all live animals produce heat, even those that are cool to the touch.*

➔ ***Note: if you are unfamiliar with SI units (e.g., joules), see Appendix A in the text or the Appendix at the bottom of this file***

E. Main Indirect Measures

1. One can easily measure an animal's **$O_2$ consumption**, and this is the *usual* method of estimating metabolism. But can one convert $O_2$ consumption to heat production? Yes, because the $O_2$ consumed is directly related to the amount of heat produced:
   a. <u>Complete</u> oxidation of 1 mole glucose yields

   $$C_6H_{12}O_6 + \mathbf{6\ O_2} \rightarrow 6\ CO_2 + 6\ H_2O + \mathbf{2874\ kJ}$$

   b. Therefore **6** moles of $O_2$ consumed (or of $CO_2$ produced) yields **2874 kJ** of heat. Or 1 mole of gas is equivalent to 479 kJ of heat. This equivalence is true in metabolic pathyways or in a test tube (1$^{st}$ Law of Thermodynamics, Hess Law). THUS, if you measure $O_2$ consumed, you can easily estimate the heat the animal has produced!
   c. Thus one refers to the "energetic equivalence" of a given volume of gas.
2. The exact caloric equivalent (or conversion factor) depends somewhat on the fuels being metabolized by the cells *(SN Table 5.1)*. To see this, take a gram of different fuels, measure heat produced by oxidation in "bomb calorimeter", measure $O_2$ consumed, and $CO_2$ and heat generated. 1 g "fat" yields 39.3 kJ, consumes 2.0 l $O_2$ and produces 1.42 l $CO_2$. Thus, 1 l $0_2$ = 39.4/2.0 = 19.7 kJ and 1 l $CO_2$ = 39.4/1.42 = 27.7 kJ. "Caloric equivalents" of oxygen and of $CO_2$ are thus 19.7kJ and 27.7 kJ, respectively, for fat metabolism.
3. [When protein is fuel, caloric equivalents depend on whether animal producing ammonia, urea, or uric acid. *Note: these numbers differ slightly from those in the text*.]
4. By measuring <u>both</u> $CO_2$ and $O_2$, can improve the accuracy of the conversion to heat production. **R = respiratory exchange ratio** = ($CO_2$ formed/ $O_2$ used)
5. a. If R = 1, animal is metabolizing carbohydrate, and so use 20.9 as caloric equivalent.
   b. If R = 0.7 (1.42/2.0), the animal is metabolizing fat and so use 19.6.
   c. If intermediate R, use 20.1. *This is the conversion factor typically used.*
   d. Note: "R" refers to gas ratio at the <u>organismal</u> level, whereas "R.Q." (or respiratory quotient) refers to the <u>tissue</u> level. The text (p. 171) uses "RQ," which technically is incorrect.
6. Physiologists have validated these converstions by measuring gas exchange and heat production simultaneously. The error is usually < 1%, if fuel is known.
7. *Why is $O_2$ used more than other indirect measures ($CO_2$ or $H_2O$ produced)?*
   a. $H_2O$ production. Technical problems (e.g., frog in dry air would appear to have high metabolism). So not used often.
   b. $CO_2$ production. Easy to measure very accurately, but still potential errors because energetic equivalents for $CO_2$ are relatively sensitive to the food being metabolized. Nevertheless, is often used on small organisms, which have low metabolic rates.

8. One can measure an animal's oxygen consumption (or $CO_2$ production) via a mask (vertebrates) or in a chamber. Both are technically very easy.

## III. What factors cause the metabolic rate of an animal to change?

A. An animal's metabolic rate isn't fixed but changes dynamically. Physiologists study this variation either to understand the dynamics of physiology **or** because they need to "control" this variation when comparing the metabolism of animals for other purposes.

B. Temperature and activity level have **major** influences (to be detailed later). For present purposes, however, note that metabolism of "ectotherms" (e.g., fish) rises exponentially with ambient temperature; whereas that of "endotherms (e.g., birds) is more U-shaped.

C. **Digestion** ("Specific Dynamic Effect" or "Heat Increment of Feeding").

1. $O_2$ increases for a while after feeding -- c. 30% humans, 45 fold in burmese pythons!
2. Energy use is probably related to the mechanical and chemical "costs" of converting, transporting, and storing food molecules, as well as for overall cellular synthesis in response to nutrients. In pythons, which eat infrequently, the energy used to "resynthesize" digestive organs prior to digestion itself!
3. The increase in metabolism is proportional to the amount of food eaten.
4. Increase in metabolism also depends on the type of food being digested, especially high for proteins, low for carbohydrates. (High SDE of protein probably relate to cost of deamination and the formation of nitrogenous wastes).
5. "Basal" and "standard" metabolic measurements are done on fasting organisms.

D. Metabolic rate drops during **starvation**. In human, metabolism drops about 25% during a 30-day fast. [This is one reason why it is hard to lose weight on a diet! But who said physiology was fair?] Why might such a response be adaptive?

E. **Day vs. night**. Typically MR is higher in the active period (e.g., day for diurnal animals). In mammals and birds, metabolism during the active phase is 25-30% higher than that during the resting period.

F. **Reproduction** – has a major impact on metabolism

1. In human females, metabolic rate may increase 30% near term (cost of "making" fetus, satisfying fetal metabolic requirements, growth of mammary tissue)
2. Lactation is expensive. Female ground squirrels in Cascades expend 30% of their total energy budget for the entire year during one month (June), when lactating!

E. **Torpor, hibernation, and estivation** *(SN 277-284, but ignore details!)*

1. Many animals can lower their metabolic rates well below resting levels (dormant state). Promotes survival during harsh conditions.
2. Hibernation – is dormancy during winter. Bear ($33^{o}$C) metabolism is about 30% normal, bat only 1-4% normal. Tremendous energy saving.
3. Estivation – is dormancy during hot or dry periods. Land snail metabolism drops to 10-30% normal, desert toad 17-30% normal. Saves water as well as energy.
4. Torpor -- a daily drop in body temperature and thus metabolism in birds or mammals. Metabolism may drop to 5 - 75% of normal, depending on species.

**Homework Problem – Metabolism**

This example is designed to give you experience at converting $O_2$ consumption to heat production, and to getting a feel for the meaning of the numbers. Work through the numbers for practice, but don't hand this in. A 70 kg human at rest consumes 15 liters $O_2$ $h^{-1}$ but consumes 200 1 $0_2$ $h^{-1}$ when running at 15 km $h^{-1}$. Let's convert that to Joules.

a. How many joules are these? (Joules = volume $0_2$ x "energetic" equivalent; assume 1 l $O_2$ = 19.7 kJ) [**Ans**. 295.5 and 3940 kJ $h^{-1}$, respectively.]

b. Convert these measurements to watts. (recall 1 J $s^{-1}$ = 1 watt). [**Ans.** 82 watts and 1094 watts, respectively. *(Thus a 70-kg human at rest produces about the same amount of heat per time as a 75-watt light bulb).] Note: if your answer if off by several decimal point,* ***check your units*** *(kJ vs. J, etc.). Also,note that watts are in seconds, not hours – so you have to convert to seconds.*

c. Imagine Lavoisier had done this experiment with a human in a big calorimeter. In 1 h, how much ice would have been melted by the resting and by the exercising human? (Note: 334kJ melts 1 kg ice, and 3015 kJ vaporizes (i.e., melts, raises it to 100°C, and evaporates it) 1 kg ice.) [**Ans.** The heat from the human in one hour would melt 0.88 kg ice when at rest, and remarkably would vaporize 1.3 kg ice when running. Obviously, we produce a lot of heat while running!]

**Appendix: Some definitions and units used in physiology** *(SN Appendix A)*

A. Scale of measurements
   1. Physiologists now use "S.I." units (Système Internationale). Two types, "**base**" and "**derived**".
   2. **Base** units are all physically independent (e.g., length, m; mass, kg; time, s)
   3. **Derived** units **combine** two or more base units (e.g., force = ma = mass x length / time$^2$)

B. Heat (a form of energy)
   1. **Calorie** was the traditional unit -- defined arbitarily as the amount of heat necessary to raise 1 gm $H_20$ from 14.5°C to 15.5°C (1000 cal = 1 Kilocalories or kcal).
   2. The S.I. unit is, however, the **joule** (symbol = J), a derived* unit. (1000J = 1kJ). Conversion of calories to joules is simple, 1 cal = 4.19 joules or 1 joule = .24 cal
   3. *Rate* of heat production (power = energy/time): cal/h or now **watts** ( 1 J $s^{-1}$= 1 watt). *Thus is a watt a base or a derived unit?*

C. Temperature. The SI temperature scale is the Kelvin scale (K**). However, almost all physiological studies use the Celsius scale (°C).

* in terms of base units, the joule = $m^2$ kg $s^{-2}$. N.B. you are NOT responsible for knowing this!

** Note: do NOT place a " ° " symbol is used in front of "K".