Heat, Work, and Metabolism

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Throughout the 18th century and into the mid-19th century, physiologists believed that living organisms were controlled by a "vital force." In 1861 (*1*) Helmholtz suggested that the real causes of the processes which go on in the living body were not different from the chemical and mechanical processes which took place outside the body, provided the more complicated circumstances and conditions under which these bodily processes occurred were taken into account. Helmholtz further pointed out that experiments suggested by the conservation of energy law could be used to solve this dispute.

In the 1880's the German physiologist Max Rubner (*2*) demonstrated that the heat of oxidation of a food is the same whether the reaction takes place in the body or in a combustion calorimeter. Rubner made measurements on animals in calorimeters and combined these data with measurements of food consumed and feces passed. These and later experiments show that the body's energy is produced by combustion and spent through work or heat exchange to the surroundings.

Animal metabolism, the rate of conversion of chemical energy into forms necessary for maintaining the body, is generally studied by one of two procedures, material balance or energy balance. Only energy balance procedures will be considered in this work.[1]

Energy balance procedures require measurement of the intake and expenditure of energy (*3–5*). Food and oxygen provide energy intake. Catabolic processes combust the large organic molecules of foodstuffs to smaller molecules and energy. Three means of measuring energy balance can be utilized: 1) measurement of the quantity of food consumed, 2) measurement of the oxygen consumption, and 3) measurement of the heat transfer from the body. Food intake is the least reliable of the three approaches to energy balance because intermittant consumption and storage does not allow energy production at a given instant to be determined. In contrast to food, oxygen is not stored in the body, the total supply of oxygen in the body is utilized in about 3 min. Oxygen intake, known as indirect calorimetry, is one of the most used procedures to study metabolic rates.

Closed and open methods of indirect calorimetry are used to determine oxygen consumption. Closed methods usually involve absorption of CO_2 produced by the subject. Oxygen consumption may be measured directly by this technique or the amount of CO_2 absorbed together with a respiratory quotient[2] may be used to calculate oxygen consumption. Open methods utilize the analysis of expired air. Air, from which CO_2 and water have been removed, may be passed over a small animal in a chamber and the CO_2 and water again removed from the air after leaving the chamber. Because only CO_2 and water are lost by the animal, the animal may be weighed before and after an experiment and the oxygen consumption calculated. In the Douglas bag technique the subject breathes into a mouthpiece which directs the expired air into a bag. CO_2, oxygen, and total volume allow calculation of oxygen consumption.

Direct calorimetry measures the heat production of the body. The subject is placed inside a large calorimeter maintained such that it is possible to spend several days in the calorimeter. The Atwater-Benedict calorimeter has double walls with a heater between the walls so that no heat is lost by radiation from the inner wall. The heat produced by the subject is removed by a water circulation system and is measured by temperature changes in the water. A striking confirmation that the body is subject to the first law of thermodynamics was provided by an experiment conducted on an individual who lived for four days in the respiration chamber of the Atwater-Benedict calorimeter (*6*). The per-day (d^{-1}) average heat of combustion of food eaten was 2519 kcal, when this figure was corrected for the heat of combustion of feces (110 kcal d^{-1}) and urine (135 kcal d^{-1}), the estimated heats of combustion of protein and fat (−83 kcal d^{-1}), the estimated energy of material oxidized in the body was found to be 2357 kcal d^{-1}. The actual heat loss of the subject was measured as 2397 kcal d^{-1}.

This experiment and others establish that the law of conservation of energy applies to metabolism. Thus the first law of thermodynamics can be used to provide a quantitative description of the relationship between animal metabolism, work, and heat. The first law is usually written $dE = dQ - dW$. As applied to metabolic processes, dE is the change in the energy of the body, dQ is the heat transfer, which is taken to be negative if heat is produced, and dW is the work in the surroundings. The necessity for energy exchange with the surroundings can be made clear by the following analysis. The heat capacity of the human body is generally taken to be 0.83 kcal kg^{-1} K^{-1} (*7*), the same as the heat capacity of lean flesh. The heat capacity of fat is 0.45 kcal kg^{-1} K^{-1} and that of water is 1.0 kcal kg^{-1} K^{-1}, thus the heat capacity will be lower the higher the fat content of the body. For a lean, 65-kg professor, the metabolic rate while lecturing is 200 kcal h^{-1}. For a one-hour lecture, the professor's body temperature would rise by ($Q = 200 = (0.83)(65)\Delta T$) 3.7°C if no energy exchange with the surroundings occurred. Above a body temperature of 40°C hyperthermia results; if the lecture is particularly vigorous heat death could result. In order to maintain body temperature at around 37 ± 1°C, metabolic heat production must be compensated through heat exchange and by work.

Energy Dissipation

Heat loss may occur by evaporation of water from the skin, conduction, convection, and radiation. Under certain conditions conduction, convection, and radiation may contribute to heating of the body. At 23°C for a resting individual about 66% of the heat loss of the body is due to radiation (*8*).

Convective heat exchange depends on a number of factors including temperature differential between the body and surroundings and wind velocity. Convective cooling due to the intake of cooler air during breathing accounts for about 3% of the total heat loss. Further convective cooling can result when warm air in direct contact with the skin expands and is replaced by the cooler air of the surroundings.

Conductive heat exchange occurs when the body is in contact with external medium and is usually small. About 15% of heat loss is due to conduction and convection. If, however, the body is submersed in water heat exchange may be considerable due to the high thermal conductivity of water. Humans can survive only a few minutes in water at 0°C.

Evaporative heat loss occurs even at temperatures sufficiently low that sweating does not occur. Sweating begins at

[1] Additional readings on energy and exercise are given in the *Interface* series by Bent, H. A., J. CHEM. EDUC., **54**, 456, 526, 586, 659, 726, 796, (1978).

[2] The ratio of the volume CO_2 given off to the volume O_2 taken in.

an environmental temperature of about 31°C. Below this temperature evaporation of water from the skin, called insensible perspiration, still accounts for a significant percentage of heat loss. This loss is about 19% of the total at 23°C. The rate of loss of water through insensible perspiration is about 30 g h^{-1}. The maximum rate loss of water from the body is about 1 L h^{-1}. The sweating mechanism for heat loss can be highly efficient if the surrounding air is dry as shown by a described test (*9*) on two men who entered a chamber at 127°C taking with them an uncooked beef steak. The men maintained tolerable body temperatures while the steak was cooked. At temperatures above 31°C heat loss may be almost entirely determined by evaporation of sweat. If, however, rather than being evaporated sweat runs off the body no cooling benefits are realized.

Heat loss by sweating may be represented by

$$H_2O(l,T_1,P_1) \overset{(1)}{\rightleftharpoons} H_2O(g,T_1,P_1) \overset{(2)}{\rightarrow} H_2O(g,T_2,P_1) \overset{(3)}{\rightleftharpoons} H_2O(g,T_2P_2)$$

In the overall process, liquid water on the surface of the skin in equilibrium with its saturated vapor pressure, P_1, at the skin temperature is converted to gaseous water at the prevailing environmental temperature, T_2, and partial water vapor pressure of air, P_2. The steps of the cycle consist of: (1), a reversible vaporization at T_1 and P_1; (2), cooling of the water vapor to surrounding temperature, and, (3), a reversible isothermal expansion from P_1 to P_2. From these steps the heat change for the process may be calculated:

$$Q = Q_1 + Q_2 + Q_3$$

$$= \Delta H^{\text{vap}} + C_P(T_2 - T_1) + RT_2 \ln\frac{P_1}{P_2}$$

Environmental factors influence skin temperature, but under many conditions of exposure skin temperature may be taken to be 35°C (*10*), the vapor pressure of water at this temperature is 42 torr, (relative humidity = 100%) and the heat of vaporization of water at 35°C is taken to be 580 cal g^{-1}. Thus if the environmental temperature is 27°C and the relative humidity is 20%, Q is 629 cal g^{-1}.

Thermodynamic considerations give only the heat loss per quantity of water evaporated. What is important is the rate at which water is vaporized from the body. If the ambient temperature and skin temperature are the same, and if the vapor pressure of water over the skin and that in the surrounding air are equal, the entire process becomes one equilibrium step. Thus, when rates are considered, it is apparent that under the conditions just described no cooling can occur because the rates of evaporation and condensation are equal.

A simple model which expresses the general features of the evaporative process may be developed from kinetic molecular theory. In order for cooling to occur, the rate of evaporation must be greater than the rate of condensation. If it is assumed that all water molecules that strike the surface of the liquid water on the skin stick, the rate of evaporation dn_e/dt may be calculated from the frequency of collisions of water molecules with a unit area. This is given from kinetic molecular theory as

$$\frac{1}{4}\frac{P}{kT}\sqrt{\frac{8RT}{\pi M}}$$

At equilibrium the number of water molecules leaving the skin is equal to the number condensing, thus

$$\frac{dn_e}{dt} = \frac{1}{4}\frac{P_s}{kT_S}\sqrt{\frac{8RT_s}{\pi M}}$$

Suppose water molecules are removed from the area of the skin as they evaporate by wind or other processes. The number of water molecules evaporating is still that given above. The number of water molecules condensing per unit time will be

$$\frac{dn_c}{dt} = \frac{1}{4}\frac{P_a}{kT_a}\sqrt{\frac{8RT_a}{\pi M}}$$

where P_a and T_a refer to the vapor pressure of water and temperature in the surrounding atmosphere. The maximum heat loss per unit time, Q_L, due to sweating is then

$$Q_L = \left(\frac{dn_e}{dt} - \frac{dn_c}{dt}\right)\Delta H^{\text{vap}} = -K\left(\frac{P_s}{T_s^{1/2}} - \frac{P_a}{T_a^{1/2}}\right) \quad (1)$$

where K is a constant incorporating ΔH^{vap}, reflective factors which account for the fraction of molecules that stick, wind velocity, and other constants from the frequency equations. Q_L is maximal because it is assumed that the entire skin surface is moistened. If this is not the case, another factor relating the percentage skin moistened would be necessary. The negative sign is used to show that Q_L is a negative quantity. K may be evaluated from parameters developed by Hatch (*12*) or from data obtained under actual conditions. At a metabolic rate of 350 kcal h^{-1} the maximum tolerable conditions are 44.7°C and the water vapor pressure is 21.9 torr. Actual experiments confirmed these predictions (*12*). Substitution of these data into eqn. (1) gives $K = 500$.

Equation (1) shows that if skin temperature and environmental temperature are the same, heat loss can occur only if the surrounding air has a relative humidity less than 100%; i.e., the vapor pressure gradient is the driving force for evaporation. If the vapor pressure gradient is removed, $P_s = P_a$, and evaporation cannot occur because under these conditions T_a must be equal to or greater than T_s. At low temperatures $P_a/T_a^{1/2}$ will always be less than $P_s/T_s^{1/2}$ because the water vapor pressure falls more rapidly than does $T_a^{1/2}$. It is thus possible to evaporate water into air already saturated with water vapor if the air is cooler than the evaporating surface. However, in the poorly ventilated Black Hole of Calcutta, air and skin temperatures equilibrated, and the prisoners' breath and sweat produced saturation of the air with water. Body temperature rose and heat-death ensued.

The evaporation rate necessary to maintain thermal balance depends on the metabolic rate, M, the environmental conditions that determine the heat loss or gain by radiation, R, and convection, C, and work done.

$$Q_L - W = M + R + C \quad (2)$$

Equation (2) is a statement of the first law in which ΔE is replaced by the heat load M, R, and C. If work is done part of the heat load would not appear as heat to be lost by evaporation. In eqn. (2), Q_L and M are negative, W is positive, and R and C may be positive or negative.

The Stefan-Boltzmann law for radiant heat exchange depends on the fourth power of the temperature gradient. With small radiation load, as occurs in animals, a first-power relation has been shown to hold (*11*),

$$-R = 11(t_a - 35)\text{kcal h}^{-1} \quad (3)$$

Heat exchange by convection is a function of temperature gradient and wind velocity, V (*11*)

$$-C = V^{0.6}(t_a - 35)\text{kcal h}^{-1} \quad (4)$$

or, for $V = 90$ m min^{-1},

$$-C = 15(t_a - 35)$$

The equations for R and C assume the atmosphere is at 100% relative humidity.

If t_a is 35°C, no heat loss by radiation or convection can occur. At temperatures greater than 35°C, R and C will add to the heat load and thus are negative quantities. These equations find application in determining comfortable work conditions and can be used to determine survival limits.

Consider a soldier marching on level ground through a desert. If the rate of march is 3 mph, 260 kcal h^{-1} is the metabolic rate. The maximum sweating rate is about 1 L h^{-1} so

Table 1. Metabolic Rate for Various Activities [a]

Activity	Metabolic Rate [b] (kcal h^{-1})	Oxygen Consumption Rate [b] (mL min^{-1} kg^{-1})
Sleeping	65	3.5
Sitting	90	4.8
Standing	160	8.5
Walking (3 mph)	260	13.9
Housework	260	13.9
Bicycling (10 mph)	400	21.4
Basketball	600	32.0
Sawing wood	500–600	26.7–32.0
Swimming	600	32.0
Running	1100	58.7
Bicycling (27 mph)	1400	74.8

[a] Compiled from Refs. (*3*, *13*), and Eisenberg, D., and Crothers, D., "Physical Chemistry with Applications to the Life Sciences," Benjamin/Cummings Publishing Company, Inc., Menlo Park, CA, p. 209.
[b] 65-kg man, height 1.83 m, body area 1.84 m^2.

that evaporative cooling cannot exceed roughly 600 kcal h^{-1}. The soldier cannot endure radiative and convective heat gain of more than $600 - 260 = 340$ kcal h^{-1}. Equations (3) and (4) give the maximum allowable temperature as 48.1°C. From eqn. (1) the maximum endurable vapor pressure of water in the atmosphere can be found to be 21.5 torr, or a relative humidity of 24%.

Metabolic Rate

The metabolic rate is dependent on the rate of consumption of oxygen. The combustion of a typical carbohydrate, glucose, illustrates the role of oxygen in heat production by the body.

$$C_6H_{12}O_6(s) + 6O_2(g) = 6CO_2(g) + 6H_2O(g)$$

One mole of glucose requires 134.4 L of oxygen at STP and the combustion produces 686 kcal of heat. The calorific equivalent of oxygen is defined as the ratio of the energy produced to the volume of oxygen used. For carbohydrates this ratio is

$$\frac{686 \text{ kcal}}{134.4 \text{ L}} = 5.15 \text{ kcal L}^{-1}$$

For proteins and fats the calorific equivalent of oxygen is 4.46 and 4.74 kcal L^{-1}, respectively.

For metabolic processes the first law is most usefully given in terms of rates, i.e., the rate at which dE, dQ, and dW change with time,

$$\frac{dE}{dt} = \frac{dQ}{dt} - \frac{dW}{dt}$$

Oxygen consumption rates measured by a respirator may be used to establish an average metabolic rate (*13*):

$$\frac{dE}{dt} \text{ kcal s}^{-1} = 4.8 \frac{dO_2}{dt} \text{ L s}^{-1}$$

The greater the physical effort the greater the oxygen consumption rate, and the better the fitness level the greater the oxygen consumption rate. A poorly fit individual may consume about 30 mL min^{-1} per kg of body weight as compared to 70 mL min^{-1} for an individual in superior condition (*14*).

Table 1 lists oxygen consumption rates and metabolic rates for various forms of activity.

Basal Metabolism

The minimum possible metabolic rate is called the basal metabolic rate, BMR. The BMR is measured under comfortable conditions so that the subject is completely relaxed physically and mentally. Age, sex, nutrition, disease, and other less important factors influence the BMR (*15*). For the adult

Table 2. Total Body BMR Contribution by Organs [a]

Organ	BMR (kcal day^{-1}) [b]	% BMR	% Total Mass
muscle	306–340	18–20	34
liver	340	20	3.5
kidney	119–170	7–10	7.0
heart	119–187	7–11	0.9
brain	306–323	18–19	2–2.5
other	323	19	~50
spleen	119	7	3.2
total	1632–1802	96–106	

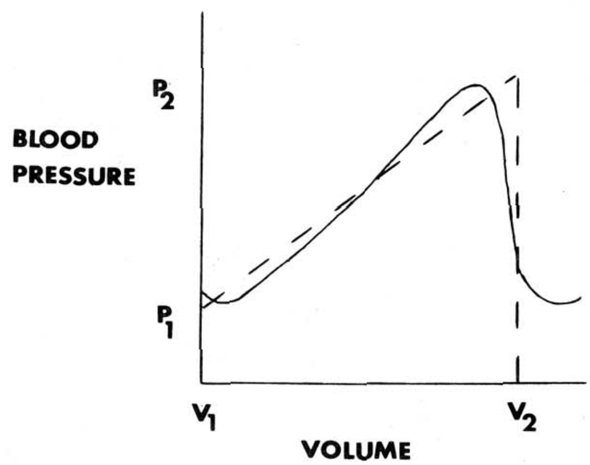
[a] Data compiled from Refs. (*3*, *5*, and *13*).
[b] Adult male, 65-kg body weight.

man the BMR is about 1700 kcal d^{-1} and for the adult woman about 1400 kcal d^{-1} (*16*). The basal metabolic rate of the whole body is determined by the BMR of each of the vital parts of the body. Table 2 gives the contribution to total BMR for several organs. With high levels of activity, the metabolic rate may increase to 10 times the BMR. In general, as the metabolic rate increases from the basal state the efficiency of the body increases. The maximum efficiency of the human body in conjunction with mechanical devices is about 20% (*17*). Efficiency as used in physiology is defined as the ratio of mechanical work to metabolic heat,

$$e = \frac{-dW/dt}{dE/dt}$$

The efficiency of certain parts of the body can be determined by measurements of oxygen consumption and work output. It is also possible in many cases to calculate the work of an organ at rest and determine the efficiency from the BMR of that organ, or, as the following example illustrates, it is also possible to calculate work theoretically and use the BMR to find the efficiency.

Blood enters the heart through the mitral valve, the pressure of the heart muscle increases to the systolic pressure of 120 torr, the blood flows out and the pressure then decreases to the diastolic pressure of 80 torr at the completion of the stroke. A typical plot of blood pressure versus blood volume leaving the heart is shown in the figure (*18*, *19*). The dotted line gives a crude approximation to the actual curve. Up to P_2 the stroke is approximated by the straight dotted line, at P_2 the pressure drops immediately to P_1. Thus the blood pressure can be given as $P = K(V - V_1) + P_0$, where K is the slope of the straight line portion of the heart stroke, $(P_2 - P_1)/(V_2 -$



Blood pressure as a function of the volume of blood leaving the heart. The solid line represents the pressure of the heart muscle during one beat. The dotted line approximates the actual stroke.

V_1). The work done by the heart in one stroke is

$$W = \int_{V_1}^{V_2} P\mathrm{d}V$$

or

$$W = \int_{V_1}^{V_2} (K(V - V_1) + P_0)\mathrm{d}V = \left(\frac{P_2 - P_1}{2} + P_0\right)(V_2 - V_1)$$

From ballistocardiographs ($V_2 - V_1$), the volume of blood forced from the heart in one contraction is 75 cm^3 (*20*). Then the work done by the heart in one stroke is 1.0 J. If heart beats about 60 times per minute the work done by the heart per second is 1.0 J s^{-1} (= 0.24 cal s^{-1}, = 1.0 w). Thus, about 250 resting human hearts are required to deliver one horsepower (*21*) (1×10^{-7} w = 1.34×10^{-10} hp).

The BMR of the heart is given in Table 2 as being in the range 119 to 187 kcal d^{-1}. The efficiency of the resting heart based on the calculated work is then 11 to 18%. This efficiency is slightly high due to the inaccuracies of the calculated work. The efficiency of the heart probably never exceeds 30%; usually it is about 10%.

On a daily basis, dQ may be found from $\mathrm{d}E = \mathrm{d}Q - \mathrm{d}W$ to be $\mathrm{d}Q = -153 + 21 = -132$ kcal. The efficiency equation may also be written

$$e = 1 - \frac{\mathrm{d}Q/\mathrm{d}t}{\mathrm{d}E/\mathrm{d}t}$$

If $\mathrm{d}Q = \mathrm{d}E$, no work is done and the efficiency is zero. If dQ is zero, the efficiency is one. If work is done, dQ decreases and the efficiency will depend on the rate at which the metabolism, dE, of the heart increases with increasing work. Experiment has shown that a doubling of the work of the heart increases the efficiency by about 4% (*22*). Thus, increased heart rate leads to an increase in metabolism, but this increase is not proportional to the increase in work, i.e., a doubling of work increases dE by a factor of about 1.4. Still, the maximum efficiency probably never exceeds 30%. There are some obvious reasons for the low efficiency of the heart.

First, arterial resistance to blood flow and the increase in kinetic energy of the blood leaving the heart add to the inefficiency (*23*). The kinetic energy term, which arises from the increased velocity of the blood ejected, is small unless considerable muscular work is being done. These factors play an analogous role to friction in heat engines. Secondly, if most of the heat goes to production of work the heart must beat more rapidly. There appears to be no change in the volume of blood delivered by each heart stroke with increasing work, but rather the burden is assumed by increased heart beating rate (*24*). When the beat rate reaches 160–170 beats/min, diastole is so shortened that filling of the ventricles and coronary flow are impaired.

There is, however, a more significant factor which determines the efficiency of the heart. If resting muscle is stretched it develops a tension. The efficiency may also be written $e = -\mathrm{d}W/\mathrm{d}Q - \mathrm{d}W$, where d$Q$ is the maintenance heat. This heat is proportional to the tension developed by the heart and the time the tension is maintained. This tension is analogous to that developed in isometric exercise; no work is actually done but increased consumption of oxygen results from this type of exercise. The mechanical work of the heart is small compared to the maintenance heat, and as a result the efficiency is low. However, as shown, the efficiency can increase considerably if work is increased. For cardiac patients the total load on the heart must be kept low. Due to the small effect the mechanical work has on the total load light exercise does not produce as much stress on the heart as does increased blood pressure which increases the tension of the heart and hence the maintenance heat.

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