

## BASICS OF METABOLISM

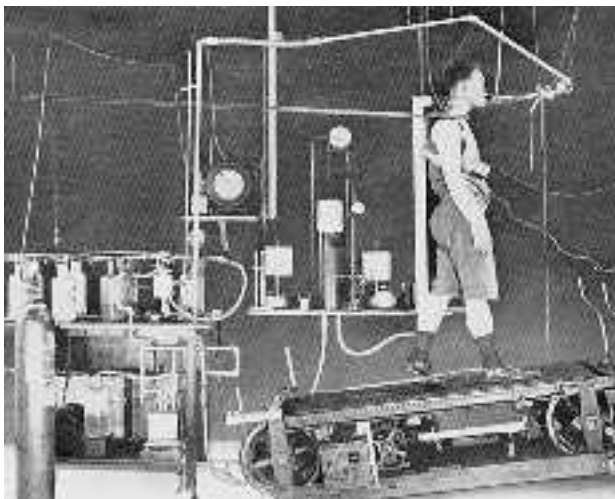
**M**etabolism can be defined as the sum total of processes occurring in a living organism. Because heat is produced by those processes, the *metabolic rate* is indicated by the rate of heat production. All processes of metabolism ultimately depend on biological oxidation, so measuring the rate of  $O_2$  consumption yields a good estimate of the rate of heat production, or metabolic rate. The maximum capability of an individual to consume oxygen ( $\dot{V}_{O_{2,max}}$ ) is highly related to that individual's ability to perform hard work over prolonged periods. A high capacity to consume and utilize  $O_2$  indicates a high metabolic capacity.

**Energy Transductions in the Biosphere**

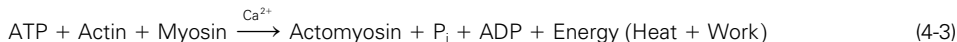
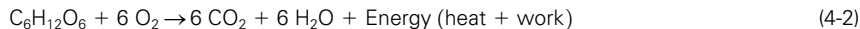
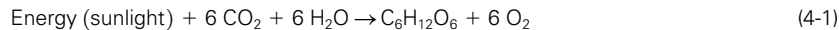
Our lives depend on conversions of chemical energy to other forms of energy. These conversions, or *transductions*, of energy are limited by the two laws of thermodynamics, which apply to physical as well as biological energy transductions.

In the biological world (the biosphere), there are three major stages of energy transduction: photosynthesis, cell respiration, and cell work.

The photosynthesis of sugars is illustrated by Equation 4-1. In photosynthesis, the  $\Delta G$  is positive in sign. Energy is put in.



**Figure 4-1** A photo from the classical study of human metabolic and cardioventilatory responses to exercise by H. M. Smith, 1922.



Cell respiration can be illustrated by Equation 4-2. In cell respiration, the  $\Delta G$  is negative in sign. Energy is given up and the process is associated with the production of the important high-energy intermediate compound, ATP.

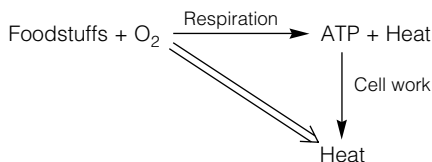
There are many types of cellular work, including mechanical, synthetic, chemical, osmotic, and electrical forms. Muscle contraction (a chemical-mechanical energy transduction) was described in Chapter 3 and is again illustrated by Equation 4-3. Here, actin and myosin are the contractile proteins and the release of  $\text{Ca}^{2+}$  within the muscle cell triggers the reaction.

Although it may appear that our functioning depends on only two of these three major energy transductions (respiration and cell work), in reality we are ultimately dependent on photosynthesis. The products of photosynthesis give us the oxygen we breathe and the food we eat. Cell respiration is a reversal of photosynthesis. Have you thanked a green plant today?

## Metabolism and Heat Production in Animals

One characteristic of living animals is that they give off heat. As illustrated in Figure 4-2, for a body at rest, life processes result in heat production.

Scientists have developed two definitions of metabolism. A functional definition is that metabolism

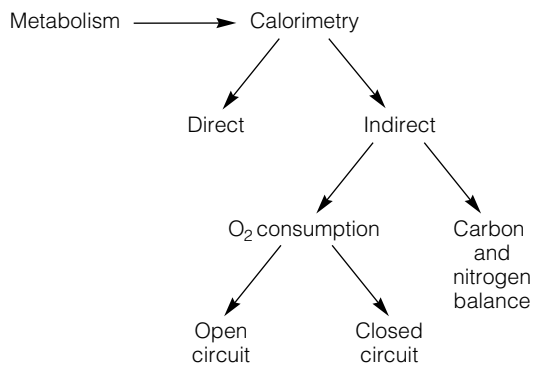


**Figure 4-2** Metabolism and heat production. In a body at rest, all metabolic processes eventually result in heat production. Measuring heat production (calorimetry) gives the metabolic rate.

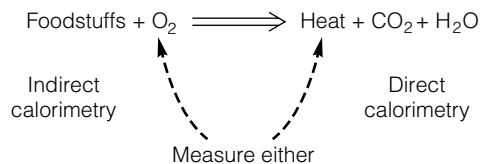
is the sum of all transformations of energy and matter that occur within an organism. In other words, by this definition, metabolism is everything going on. It is not possible to measure that. Therefore, another operational definition has been developed, stating that metabolism is the rate of heat production. This definition takes advantage of the fact that all the cellular events result in heat. By determining the heat produced, one can obtain a measure of metabolism.

The basic unit of heat measurement is the calorie. Simply defined, a *calorie* is the heat required to raise the temperature of 1 gram of water 1 degree Celsius. The calorie is a very small quantity, so the term *kilocalories* (kcal) is frequently used instead. A kilocalorie represents 1000 calories. Because heat must be measured to determine metabolic rate, this procedure is termed *calorimetry*. Several types of calorimetry are currently used. They are diagrammed in Figure 4-3.

*Direct calorimetry*, involving the direct measurement of heat, is technically very difficult. However,



**Figure 4-3** Relationship between metabolism and different methods of calorimetry. Because the processes of metabolism result in heat production, measuring heat production gives an estimate of the metabolic rate. Heat production can be measured directly (direct calorimetry), or it can be estimated from  $\text{O}_2$  consumption or from the carbon and nitrogen excreted (indirect calorimetry).



**Figure 4-4** The principle of indirect calorimetry (measuring  $\text{O}_2$  consumption) as a basis of estimating heat production. Instead of measuring the heat produced as the result of biological reactions, we measure the  $\text{O}_2$  used to support biological oxidations.

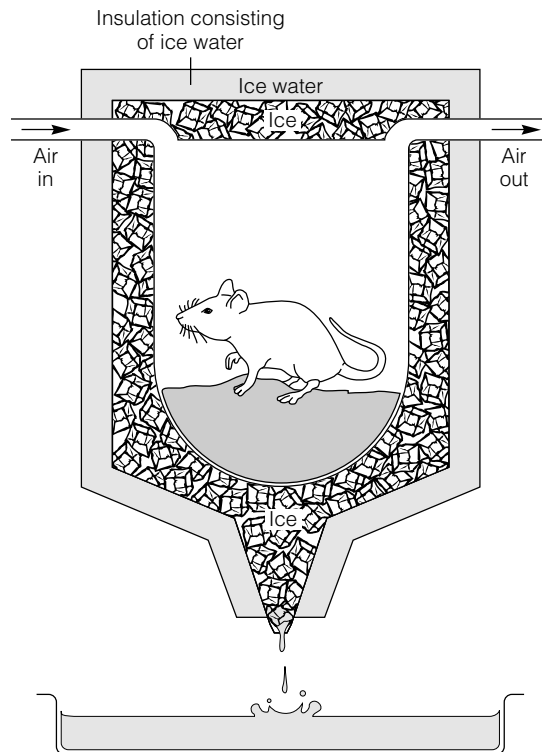
it has been determined that *indirect calorimetry*, the measurement of oxygen consumption, is also a valid and technically reliable procedure for measuring metabolic rate. The principle of indirect calorimetry is illustrated in Figure 4-4. Another form of indirect calorimetry involves determining the carbon and nitrogen content of excreted materials.

## ■ Early Attempts at Calorimetry

To understand the relationship between heat production and  $\text{O}_2$  consumption as alternative methods for determining metabolic rate, let us consider some of the work of the eighteenth-century genius, French chemist Antoine Lavoisier.

Because of his interest in studying living creatures, Lavoisier came to recognize certain characteristics of living animals: They give off heat and they breathe. Dead animals do not give off heat and do not breathe. Lavoisier's calorimeter, diagrammed in Figure 4-5, is simple but beautiful in its design. By allowing the animal's warmth to melt the ice, and knowing the quantity of heat required to melt a given quantity of ice, Lavoisier could calculate the heat produced by the animal by measuring the volume of water produced. Such a device is called a *direct calorimeter* because it determines metabolism by measuring heat produced.

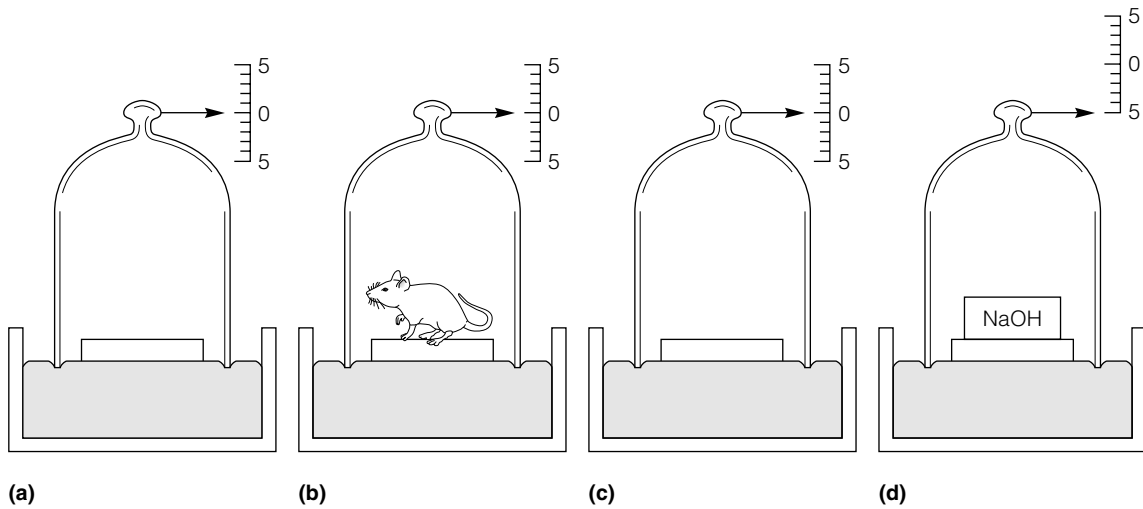
Lavoisier's respirometer (Figure 4-6) was another device that was novel for its time. With it Lavoisier could establish that something in the air ( $\text{O}_2$ ) was consumed by the animal and that something else ( $\text{CO}_2$ ) was produced in approximately



**Figure 4-5** Lavoisier's calorimeter of 1780. The animal's body heat melts the ice. Knowing that 80 kcal of heat melts 1000 grams of ice, we can measure the amount of water formed to estimate the heat produced. The ice water surrounding the calorimeter provides a perfect (adiabatic) insulation because it is at the same temperature as the ice in the inner jacket around the animal's chamber. The insulation will neither add heat to nor take heat from the calorimeter. Based on original sources and Kleiber, 1961. Used with permission.

equal amounts. Lavoisier also determined that matter gains weight when it burns. It had been thought previously that burning represented the loss of substance, sometimes called phlogiston.

With information obtained from his experiments, Lavoisier was able to interpret some earlier findings. For instance, Boyle had shown that air was necessary to have a flame, and Mayow had observed that a burning candle and an animal together in an airtight container expired at the same time. The fire of life and the fire of physical burning depended on the same substance in the air, which Lavoisier called *oxygène*.



**Figure 4-6** Lavoisier's respirometer of 1784. (a) A glass bell jar rests on a bed of mercury. (b) An animal is placed in the jar from beneath the mercury seal and is left there for several hours. The apparent respirometer volume increases when the animal enters, but then the volume decreases very slowly if at all because  $O_2$  is being replaced by  $CO_2$ . (c) The animal is removed, and the volume is observed to have decreased slightly. (d) Addition of NaOH (a  $CO_2$  absorber) into the jar results in a decrease in the measured volume. From these volume changes,  $O_2$  consumption ( $\dot{V}_{O_2}$ ) and carbon dioxide production ( $\dot{V}_{CO_2}$ ) can be measured:  $\dot{V}_{O_2} = V_a - V_d$ ;  $\dot{V}_{CO_2} = V_c - V_d$ . Based on original sources and Kleiber, 1961. Used with permission.

The belief of Lavoisier and others that biological oxidation took place in the lungs has led to some confusion. Although it is true that breathing, or ventilation, takes place in the lungs and associated organs, respiration, or biological oxidation, takes place in most of the body's cells. Therefore, in this text, we shall use the term *respiration* to denote cellular oxidations and *ventilation* to denote pulmonary gas exchange.

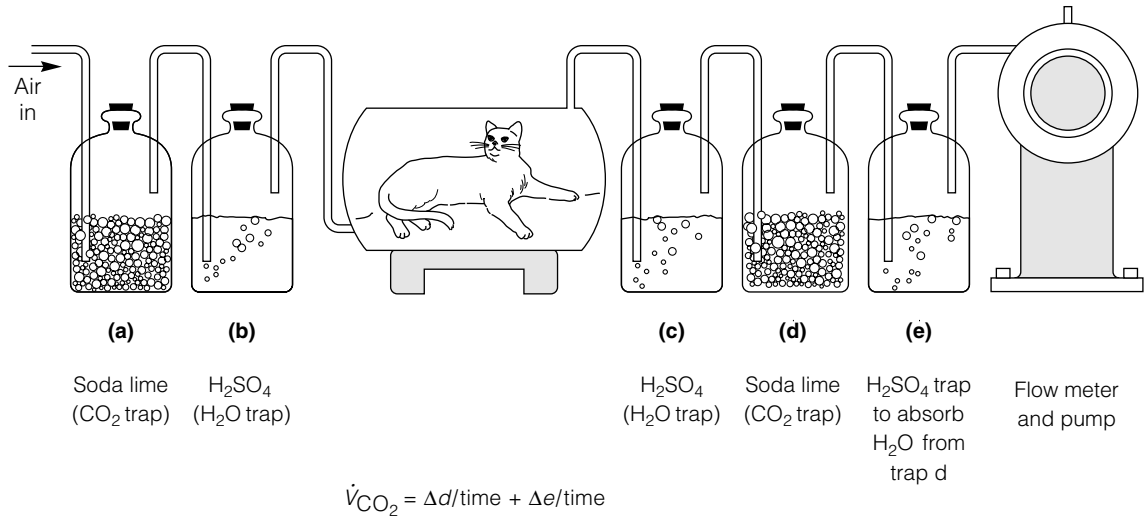
Devices such as Lavoisier's respirometer are called *indirect calorimeters* because they estimate heat production by determining  $O_2$  consumption or  $CO_2$  production. Lavoisier's device is also referred to as a closed-circuit indirect calorimeter because the animal breathes gas within a sealed system.

Haldane's respirometer (Figure 4-7) is an example of an open-circuit indirect calorimeter. This system is open to the atmosphere, and the animal breathes air. Today, the type of calorimeters most frequently used are open-circuit indirect designs.

The Atwater and Rosa device (Figure 4-8) is an important apparatus for the study of metabolism. Large enough to accommodate a person, it has the capability of determining heat production,  $O_2$  consumption, and  $CO_2$  production simultaneously. Through this device, the relationship between direct and indirect calorimetry was established. Thus, it is now possible to predict metabolic rate (heat production) on the basis of determinations of  $O_2$  consumption and  $CO_2$  production in resting individuals.

The calorimeter illustrated in Figure 4-9 is called a *bomb calorimeter*. In this device, foodstuffs are ignited and burned in  $O_2$  under pressure. Through this device, the heats of combustion ( $\Delta H$ ) of particular foods can be determined.

Table 4-1 presents the relationships among caloric equivalents for combustion of various foodstuffs as determined by indirect and direct calorimetry as well as by bomb calorimetry. Perhaps the



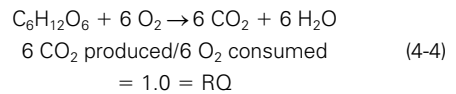
**Figure 4-7** Haldane's respirometer. This device is an open-circuit indirect calorimeter, in which carbon dioxide and water vapor in air entering the system are removed by traps (a) and (b), respectively. Trap (c) removes the animal's expired H<sub>2</sub>O vapor. Increase in weight of the soda lime CO<sub>2</sub> trap (d) gives the animal's CO<sub>2</sub> production. Based on original sources and Kleiber, 1961. Used with permission.

most interesting feature of this table is that, with a single exception, the caloric equivalents for the combustion of foodstuffs inside and outside the body are the same. Protein is the exception because nitrogen, an element unique to protein, is not oxidized within the body but is eliminated, chiefly in urine but also in sweat. Therefore, the caloric equivalent of protein metabolism is approximately 26% less than in a bomb calorimeter.

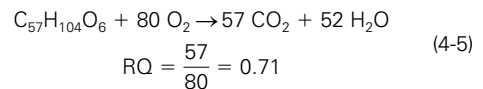
Table 4-1 also gives the caloric equivalents of foodstuffs in kilocalories per liter of O<sub>2</sub> consumed. Although fat, because of its relatively high carbon and hydrogen content (reduction), contains more potential chemical energy on a per-unit-weight basis, carbohydrates give more energy when combusted in a given volume of O<sub>2</sub>.

In addition to providing an estimate of metabolic rate, indirect calorimetry provides a means of estimating the composition of the fuels oxidized. Similarly, determining the ratio of CO<sub>2</sub> produced ( $\dot{V}_{\text{CO}_2}$ ) to O<sub>2</sub> consumed ( $\dot{V}_{\text{O}_2}$ ) gives an indication of the type of foodstuff being combusted. This ratio ( $\dot{V}_{\text{CO}_2} / \dot{V}_{\text{O}_2}$ ) is usually referred to as the *respiratory quotient* (RQ) and reflects cellular processes. Equa-

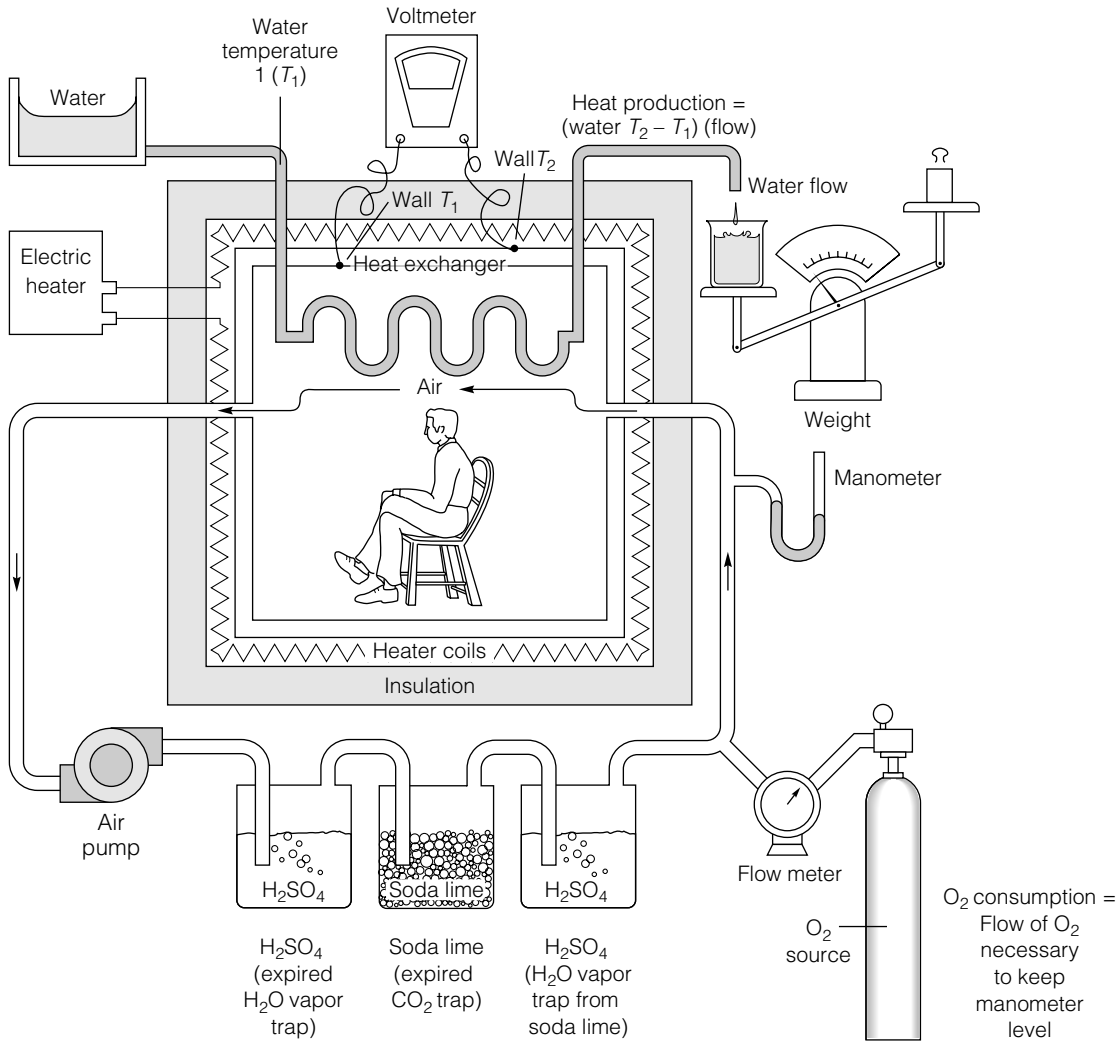
tion 4-4 shows why the RQ of glucose, a sugar carbohydrate, is unity:



For the neutral fat trioleate, the RQ approximates 0.7:



During hard exercise, an individual's respiratory gas exchange ratio [R, an estimate of RQ (see page 53)] approaches 1.0, whereas during prolonged exercise, the R may be somewhat lower, 0.9 or less. Figure 4-10 shows data on male subjects running a marathon on a treadmill where respiratory gas exchange could be measured. In one case, subjects ran at their race pace, whereas in the other case subjects ran more slowly. Note that subjects' race pace corresponds to an R of 0.95 to 1.0. Note also that in later stages, R declined, but then rose at the



**Figure 4-8** Atwater–Rosa calorimeter. A direct calorimeter suitable to accommodate a resting human and simultaneously determine that individual’s  $O_2$  consumption and  $CO_2$  production. Through this device, direct and indirect calorimetry were correlated.  $O_2$  consumption is equal to the volume of  $O_2$  added to keep the internal (manometer) pressure constant. In the calorimeter, heat loss through the walls is prevented by heating the middle wall (wall  $T_2$ ) to the temperature of the inner wall (wall  $T_1$ ). Metabolic heat production is then picked up in the water heat exchanger. Based on original sources and Kleiber, 1961.

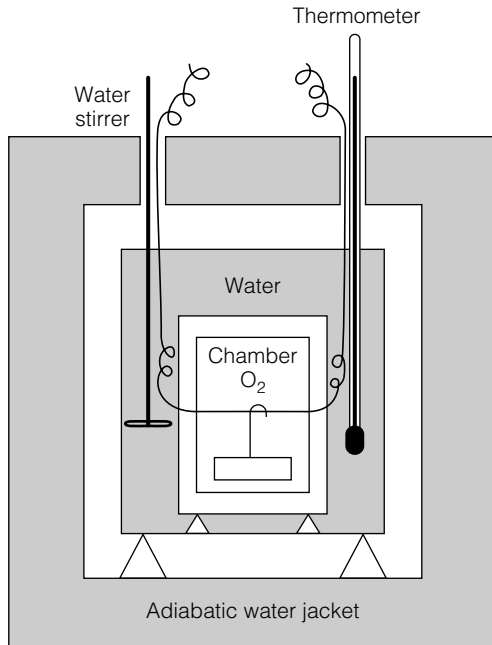
end. In the slower marathon runners,  $R$  was lower, indicating less carbohydrate and more lipid use than in the faster runners. The fuel mix was, however, still mostly carbohydrate.

Table 4-1 shows why it is an advantage for these changes in  $RQ$  to occur. During hard exercise,  $O_2$  consumption can be limiting. Therefore, as shown

in Equation 4-6, in oxidizing carbohydrate rather than fat the individual derives

$$\frac{5.0 - 4.7 \text{ kcal} \cdot \text{liter}^{-1} O_2}{4.7 \text{ kcal} \cdot \text{liter}^{-1} O_2} \quad (4-6)$$

or 6.4% more energy per unit  $O_2$  consumed. During prolonged exercise, however, it makes sense that



**Figure 4-9** Bomb calorimeter. A food substance is attached to the ignition wires and placed in the chamber under several atmospheres of  $O_2$  pressure. The sample is then ignited and burns explosively. The stirrer distributes the heat of combustion uniformly throughout the water surrounding the chamber. The thermometer detects the heat released. Based on Kleiber, 1961.

RQ decreases, indicating that more fat is combusted. In prolonged work, glycogen supply rather than  $O_2$  consumption can be limiting. Table 4-1 indicates that on a mass basis, fats provide about  $9.5/4.2 \text{ kcal} \cdot \text{g}^{-1}$ , or 2.3 times as much energy as carbohydrate. Given this large difference, we can also see why endurance training improves the ability to use fat as a fuel during prolonged mild to moderate intensity exercise (i.e.,  $40\text{--}60\% \dot{V}_{O_{2\max}}$ ).

The preceding type of discussion is sometimes referred to as a “teleological argument,” meaning that the purpose of something is assumed to explain its operation. In actuality, as will be shown, the reason why relatively more carbohydrate is used in hard exercise is related to the quantity of activity and regulation of glycolytic enzymes. There are also enzymatic explanations for the preponderance of fat used in prolonged exercise.

In order to obtain a precise estimate of metabolic rate and fuel used by means of indirect calorimetry, we must know a few other details besides the quantities of  $O_2$  consumed and  $CO_2$  produced. These additional parameters include the food ingested and the nitrogen excreted. To provide a relatively simple example of the utility of indirect calorimetry, let us consider a starving man, in whom there is no food input to account for and no large excretion of urinary nitrogen (Table 4-2).

**TABLE 4-1**

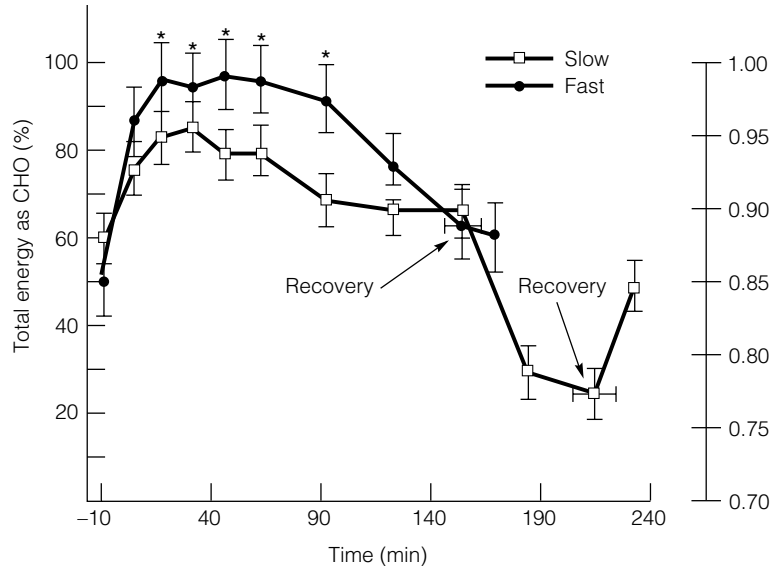
**Caloric Equivalents of Foodstuffs Combusted Inside and Outside the Body**

Food	$\text{kcal} \cdot \text{liter } O_2^{-1}$	RQ ( $\dot{V}_{CO_2}/\dot{V}_{O_2}$ )	Inside Body ( $\text{kcal} \cdot \text{g}^{-1}$ )	Outside Body ( $\text{kcal} \cdot \text{g}^{-1}$ )
Carbohydrate	5.05	1.00	4.2	4.2
Fat	4.70	0.70	9.5	9.5
Protein	4.50	0.80	4.2	5.7 <sup>a</sup>
Mixed diet	4.82	0.82		
Starving individual	4.70	0.70		

<sup>a</sup>The amount of protein combusted outside the body is greater than that combusted inside the body (see text):

$$\frac{5.7 - 4.2}{5.7} = 26\% \text{ difference}$$

**Figure 4-10** Calculated percentage of energy expenditure contributed by carbohydrates (CHO) before, during, and after a treadmill marathon in fast and slow groups. Values are means  $\pm$  SEM;  $N = 6$  per group. SOURCE: O'Brien et al., 1993. Used with permission.



**TABLE 4-2**

**Calculation of Nitrogen-Free RQ on a Resting Starving Man**

- Given:** (a) Protein is about 17% N by weight, or there is 1 g N  $\cdot$  5.9 g<sup>-1</sup> protein (1/5.9 = 0.17).  
 (b) For protein RQ = 4.9/5.9 = 0.83, or 4.9 liters CO<sub>2</sub> are derived from the catabolism of the protein associated with 1 g N, and 5.9 liters of O<sub>2</sub> are required to catabolize the protein.

The total O<sub>2</sub> consumption was 634 liters. The total CO<sub>2</sub> production was 461 liters, and urinary N losses were 14.7 g over 24 hours. We can use these data to calculate the nitrogen-free RQ.

Calculations	Total CO <sub>2</sub> (liters)	Total O <sub>2</sub> (liters)
	461	634
In the urine, there were 14.7 g N. The CO <sub>2</sub> produced by protein catabolism was (14.7) (4.9) = 72.0 liters CO <sub>2</sub> .	72	
The O <sub>2</sub> consumed associated with protein catabolism was (14.7) (5.9) = 86.7 liters O <sub>2</sub>	—	86.7
	389	547.3

$$\text{Nonprotein RQ} = \frac{389}{547.3} = 0.71$$

**Heat production**

From protein: (14.7 g N) (5.9 g protein  $\cdot$  g<sup>-1</sup> N) (4.2 kcal  $\cdot$  g<sup>-1</sup> protein) = 364.3 kcal

From fat: The nonprotein RQ was 0.71, so fat comprised the remaining fuel. Therefore, (547.3 liters O<sub>2</sub>) (4.7 kcal  $\cdot$  liter<sup>-1</sup> O<sub>2</sub>) = 2572.3 kcal.

$$\text{Total heat production} = 364.3 + 2572.3 \text{ kcal} = 2936.6 \text{ kcal}$$



In exercise physiology, current estimates of fuels combusted are usually simplified by assuming there is no increase in the basal amino acid and protein degradation during exercise. The ventilatory exchange ratio  $R$  is then used to represent the non-protein RQ. As we shall see later (Chapter 8), this assumption is not quite valid.

Although both RQ and  $R$  are given by the same formula ( $\dot{V}_{\text{CO}_2}/\dot{V}_{\text{O}_2}$ ), over any short period of measurement of gas exchange at the lungs, changes in  $\text{CO}_2$  storage may cause  $R$  not to equal RQ. Although RQ does not exceed 1.0,  $R$  can reach 1.5 or higher. For the present, let us consider RQ to be the ratio  $\dot{V}_{\text{CO}_2}/\dot{V}_{\text{O}_2}$  in the cell, where  $\text{O}_2$  is consumed and  $\text{CO}_2$  produced. Further, let us consider  $R$  to be the ratio  $\dot{V}_{\text{CO}_2}/\dot{V}_{\text{O}_2}$  measured at the mouth. Over time,  $R$  must equal RQ, but during the onset and offset of exercise, as well as during hard exercise,  $R \neq \text{RQ}$  because body  $\text{CO}_2$  storage changes (see Figure 4-14).

## ■ Indirect Calorimetry

For individuals at rest, indirect calorimetric determinations on the effects of body size, growth, disease, gender, drugs, nutrition, age, and environment on metabolism are very useful. The resting metabolic rate per unit body mass is greater in males than in females, greater in children than in the aged, greater in small individuals than in large ones, and greater under extremes of heat and cold than under normal conditions.

## ■ The Utility of Indirect Calorimetry During Exercise

Physical exercise represents a special metabolic situation. As Figure 4-2 indicates, for a body at rest, all the energy liberated within appears as heat. If metabolism is constant, the quantity of heat produced within the body over a period of time will be the same as that leaving the body. However, during exercise, some of the energy liberated within the body appears as physical work outside the body. There-



**Figure 4-11** Bicycle ergometers are convenient, stationary laboratory devices to control the external work rate (power output) while physiological responses to standardized or experimental protocols are observed. Courtesy of Monark, Inc., Varberg, Sweden.

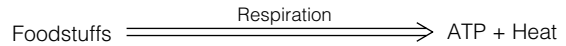
fore, devices to measure external work performed, such as bicycle ergometers (Figure 4-11) and treadmills (Figure 4-12), are used.

During exercise, direct calorimeters such as the Atwater–Rosa calorimeter (Figure 4-8) are of little use for several reasons. First, such devices are very expensive. Second, the heat generated by an ergometer, if it is electrically powered, may far exceed that of the subject. Third, body temperature increases during exercise because not all the heat produced is liberated from the body. Therefore, the sensors in the walls of the calorimeter do not pick up all the heat produced. Finally, the body sweats during exercise, which also affects the calorimeter and changes body mass. Changes in body mass and the unequal distribution of heat within the body make it very difficult to use direct calorimetry in exercise.

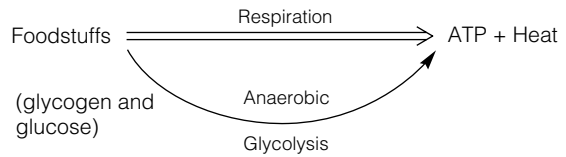


**Figure 4-12** Treadmills are frequently used in the laboratory to apply exercise stress and record physiological responses on relatively stationary subjects during exercise. Compared to the bicycle ergometer (Figure 4-11), it is difficult to quantify external work on the treadmill. However, the treadmill does allow subjects to walk or run, which are perhaps more common modes of locomotion than is bicycling. Photo: © David Madison.

As with direct calorimetry during exercise, techniques of indirect calorimetry have certain limitations. These are summarized in Figure 4-13a. In order for determinations of  $\dot{V}_{O_2}$  to reflect metabolism accurately, the situation in Figure 4-13a must hold. If another mechanism is used to supply energy, such as that shown in Figure 4-13b, then respiratory determinations do not completely reflect all metabolic processes. As will be seen, the body has the means to derive energy from the degradation of substances without the immediate use of  $O_2$ . These mechanisms include immediate sources and rapid glycogen (muscle carbohydrate) breakdown. Use of the  $\dot{V}_{CO_2}/\dot{V}_{O_2}$  ratio is also limited during exercise. Although over time the  $O_2$  consumed by and  $CO_2$  liberated at the lungs (the respiratory, or ventilatory exchange ratio) equals the respiratory quotient, the



(a)

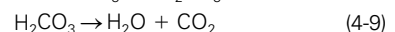


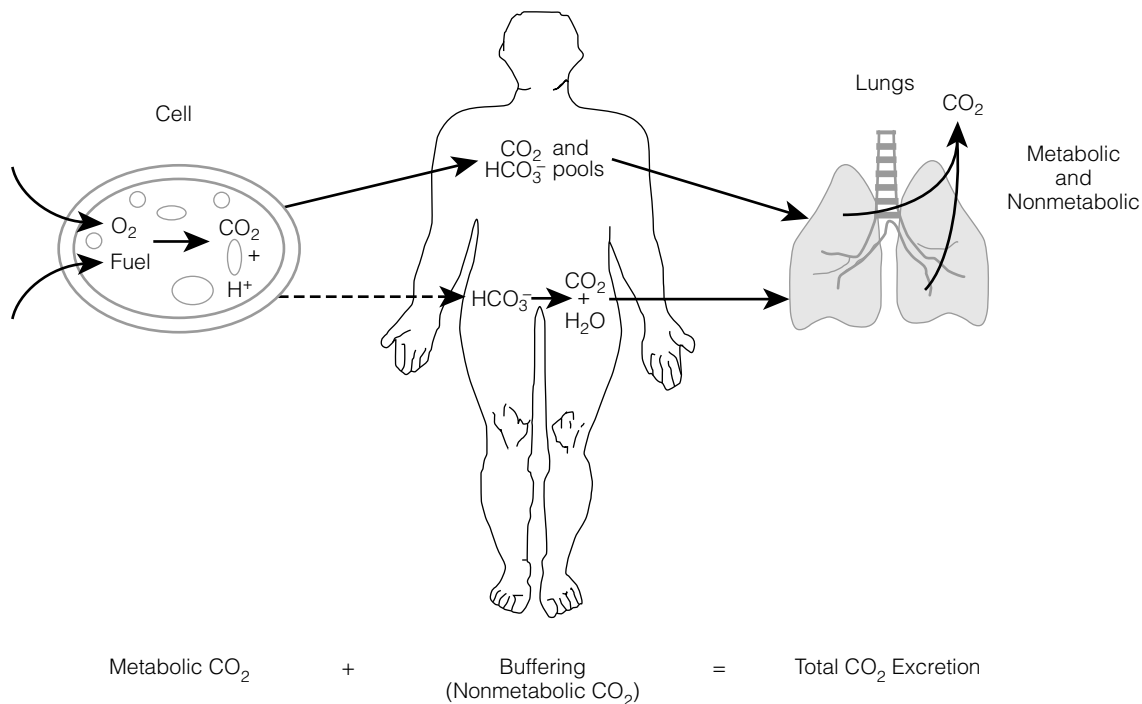
(b)

**Figure 4-13** Respiration and ATP production. The validity of indirect calorimetric measurements depends on the  $O_2$  consumption accurately representing the ATP formed. This is not always the case in exercise. In (a), the measurement is valid. In (b), it is invalid.

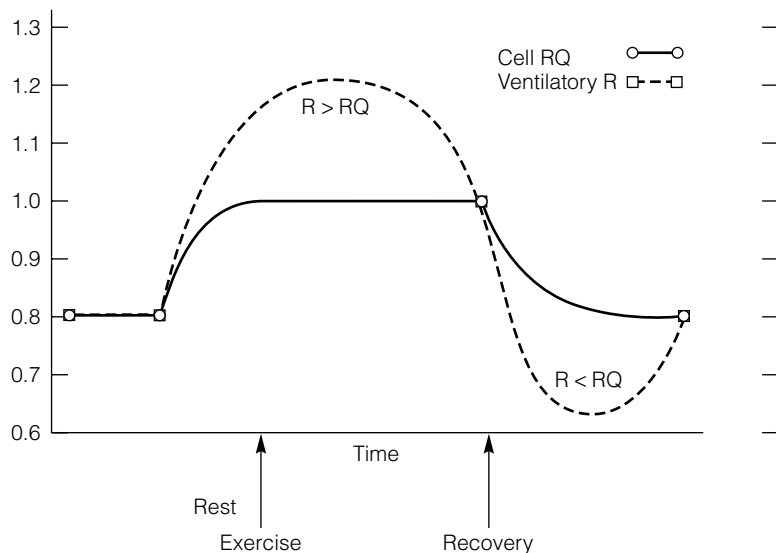
cellular events are not always immediately represented in expired air. This is because the cells are fluid systems, and they are surrounded by other fluid systems on both the arterial and venous sides. When exercise starts,  $CO_2$  is frequently stored in cells. When exercise is very difficult, the blood bicarbonate buffer system buffers lactic acid, and extra nonrespiratory  $CO_2$  is produced (Chapter 11).

As illustrated in Figure 4-14a, lactic acid (HLA) is a strong acid whose level in muscle and blood increases during heavy work. It is known as a strong acid in physiological systems because it can readily dissociate a proton ( $H^+$ ). To lessen the effect of protons generated from lactic acid during hard exercise, the body has a system of chemicals that lessen, or buffer, the effects of the acid. In the blood, the bicarbonate ( $HCO_3^-$ )–carbonic acid ( $H_2CO_3$ ) system is the main system by which the effects of lactic acid are buffered. As shown in Figure 4-14a and in Equations 4-7 to 4-9,  $HCO_3^-$  neutralizes the  $H^+$ , but  $CO_2$  is produced. This is eliminated at the lungs and appears in the breath. Consequently, during hard exercise,  $R \neq RQ$  (Figure 4-14b). After exercise, metabolic  $CO_2$  may be stored in cells, blood, and other body compartments to make up for that lost during exercise.





(a)



(b)

**Figure 4-14** Diagrammatic representations of the formation of metabolic  $\text{CO}_2$  (from fuel oxidation) and nonmetabolic  $\text{CO}_2$  (from the buffering of lactic acid) and their effects on  $\text{CO}_2$  excretion in the lungs and the whole-body respiratory exchange ratio (RER, or  $R = \dot{V}_{\text{CO}_2}/\dot{V}_{\text{O}_2}$ ). In panel a, body cells produce metabolic  $\text{CO}_2$  as well as protons ( $\text{H}^+$ ) from glycolysis. The effect of protons is lessened (buffered) by the bicarbonate ( $\text{HCO}_3^-$ ) buffering system. Metabolic and nonmetabolic  $\text{CO}_2$  from acid buffering are excreted in the lungs. In panel b, the transient effects of acid buffering at the onset of exercise and restoration of  $\text{HCO}_3^-$  reserves in recovery are illustrated. The initiation and cessation of exercise are conditions when  $R \neq \text{RQ}$ .

Furthermore, during and immediately after exercise, urine production by the kidney is inhibited. Also, during exercise considerable nitrogen can be lost as urea in sweat. Therefore, it is difficult to determine the nitrogen excreted during exercise.

Determinations of indirect calorimetry are somewhat limited in their use by the fact that the respiratory gases give no specific information on the fuels used. If, for example, RQ is 1.0, then although we know that carbohydrate was the fuel catabolized, we do not know specifically which carbohydrate was involved. The possibilities could include, among others, glycogen, glucose, lactic acid, and pyruvic acid. However, radioactive and nonradioactive tracers to study metabolism at rest and during exercise have come into use in conjunction with indirect calorimetry to provide more detailed information on specific fuels.

Exercise is also a special situation in that the metabolic responses persist long after the exercise itself may have been completed. Consequently, physical activity results in an excess postexercise  $O_2$  consumption (EPOC). This EPOC has sometimes in the past been called the " $O_2$  debt" and has been used as a measure of anaerobic metabolism during exercise. A more detailed explanation of the  $O_2$  debt is given later (Chapter 10); suffice it to say here that the mechanisms of the  $O_2$  debt are complex and cannot be used to estimate anaerobic metabolism during exercise.

Whereas the body does present certain problems in determining metabolic rate during exercise, careful consideration of those various factors allows us to obtain important information about metabolic responses to exercise. Estimations of  $\dot{V}_{O_2}$ , for example, provide information on the cardioventilatory response to exercise. The caloric cost of various exercises can be estimated (Table 4-3), and information about the fuels used to support the exercise can be obtained.

Knowing that part of the energy liberated during exercise appears as external work is useful. By measuring the respiratory response to graded, submaximal exercise at specific external work rates, we can determine the fraction of the energy liberated within the human machine that appears as external

TABLE 4-3

### Estimates of Caloric Expenditures of Sports Activities for a 70-kg Person

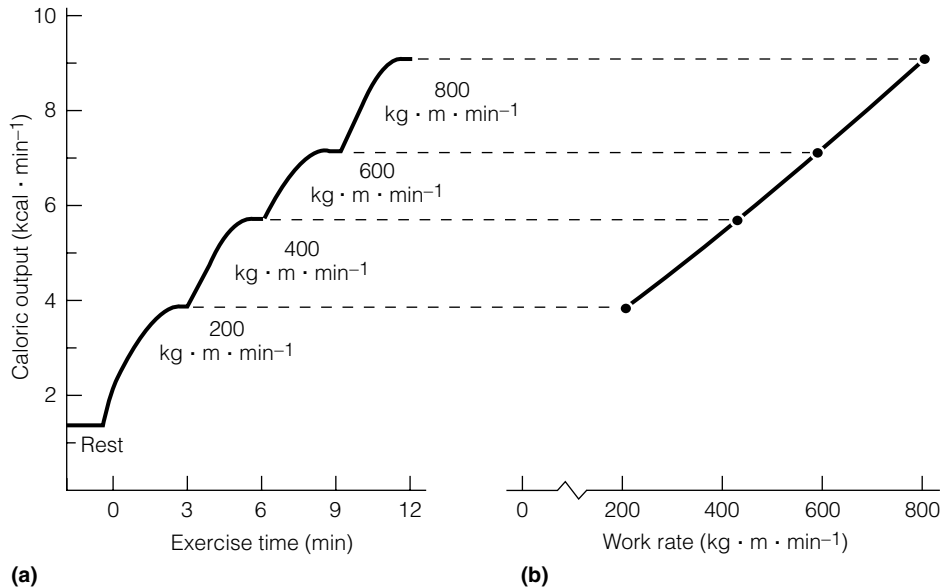
Activity	Caloric Expenditure (kcal · min <sup>-1</sup> )
Archery	4.6
Badminton	6.4
Basketball	9.8
Canoeing	7.3
Cycling	12.0
Field hockey	9.5
Fishing	4.4
Football	9.4
Golf	6.0
Gymnastics	4.7
Judo	13.8
Resting	1.2
Running	
8 min · mi <sup>-1</sup>	14.8
6 min · mi <sup>-1</sup>	17.9
Squash	15.1
Swimming	
Backstroke	12.0
Crawl	11.1
Tennis	7.7
Volleyball	3.6
Walking, easy	5.7

work. This fraction is frequently reported as a percentage and is called *efficiency*.

An example of how the efficiency of the human body is calculated during bicycle ergometer exercise is given in Equation 4-10. In Figure 4-15, we see that the  $O_2$  consumption of an individual increases in direct response to increments in work load while pedaling at constant speed. In this case, efficiency can be calculated as in Equation 4-10.

The plateau steps in Figure 4-15a are referred to as *steady-rate* exercise. During the steady rate, the oxygen consumption ( $\dot{V}_{O_2}$ ) is relatively constant and is directly proportional to the constant submaximal work load.

The calculation of body efficiency during bicycle exercise is given in Table 4-4. Here the calculated value of efficiency is 29.2%, which is close to a maximum value for bicycle ergometer work. Cycling at



**Figure 4-15** Respiratory response to graded submaximal bicycle ergometer work. Every 3 minutes the work rate is increased 200 kg · m · min<sup>-1</sup>. The observed O<sub>2</sub> consumption ( $\dot{V}_{O_2}$ ) is converted to kcal · min<sup>-1</sup>. These values are then plotted as (a) a function of time and (b) a function of the steady-rate work load. Note that a plot of the caloric cost of exercise against work rate (b) yields a straight line, or one that bends upward slightly.

**TABLE 4-4**

**Calculation of Body Efficiency  
During Cycling Exercise**

*Given:*

$$\dot{V}_{O_2} \text{ at } 200 \text{ kg} \cdot \text{m} \cdot \text{min}^{-1} = 0.76 \text{ liter} \cdot \text{min}^{-1}$$

$$\dot{V}_{O_2} \text{ at } 400 \text{ kg} \cdot \text{m} \cdot \text{min}^{-1} = 1.08 \text{ liters} \cdot \text{min}^{-1}$$

$$R = RQ = 1.0$$

$$\text{When } RQ = 1.0, 1 \text{ liter } O_2 = 5 \text{ kcal}$$

$$1 \text{ kg} \cdot \text{m} = 0.00234 \text{ kcal}$$

$$\text{Efficiency} = \frac{\text{Change in work output}}{\text{Change in } \dot{V}_{O_2}}$$

Efficiency

$$\begin{aligned} &= \frac{400 - 200 \text{ kg} \cdot \text{m} \cdot \text{min}^{-1}}{1.08 - 0.76 \text{ liter} \cdot \text{min}^{-1}} \\ &= \frac{200 \text{ kg} \cdot \text{m} \cdot \text{min}^{-1} \times 0.00234 \text{ kcal} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}}{0.32 \text{ liter} \cdot \text{min}^{-1} \times 5 \text{ kcal} \cdot \text{liter}^{-1} O_2} \\ &= 0.292 \text{ or } 29.2\% \end{aligned}$$

greater speeds and working at greater loads results in decrements in calculated efficiency. The efficiency of walking is slightly higher than that of cycling, but responds similarly to increments in speed and resistance. The reason it is usually easier to cycle from one place to another than to walk is that the rolling and wind resistance to cycling at a particular speed are far less than the work done in accelerating and decelerating the limbs during walking—that is, less work is done in cycling. Attempting to bicycle in soft sand will reveal that the work done in covering a given distance is far greater; yet measurements of the efficiency of movement would reveal no change or only a relatively small decrement.

In contrast to the bicycle ergometer, where the work done is the product of the pedaling speed and the resistance, the calculation of work done in walking is more involved. This is because the body walking on a level treadmill does no external work. Estimates of the work done in walking, therefore, depend on applying an external work load that can

$$\text{Efficiency} = \frac{\text{Caloric equivalent of change in external work}}{\text{Caloric equivalent of change in } O_2 \text{ consumption}} \quad (4-10)$$

$$\text{External work rate} = [\text{Body weight (kg)}][\text{Speed (m} \cdot \text{min}^{-1})][\% \text{ grade}/100] \quad (4-11)$$

$$\text{External work rate} = [\text{Body weight (kg)}][\text{Speed (m} \cdot \text{min}^{-1})][\sin \Theta] \quad (4-12)$$

be measured, or by estimating the work done internally in the body as a result of accelerating and decelerating the limbs.

The most common way to apply external work during walking is to have a subject go up an incline. In Figure 4-16, the vertical external work performed is in lifting the body mass the distance  $B-D$ . The work done is calculated according to either of two formulas as seen in Equations 4-11 and 4-12.

Where  $\sin \Theta$  is the angle  $ACB = BD/CB$ . Recently, external work has been applied in studies of energetics by having subjects walk against a horizontal impeding force (Figure 4-17). The work done against the horizontal impeding force is calculated in Equation 4-13.

$$\text{External work} = [\text{Speed (m} \cdot \text{min}^{-1})][\text{Weight pulled (kg)}] \quad (4-13)$$

An example of how to calculate the efficiency of performing external work during incline walking is given in Table 4-5.

Another innovation for estimating the work involved in horizontal walking has been established

by Ralston, Zarrugh, and other mechanical engineers at the University of California. They attached sensitive transducers to the joints so that their movements during walking could be recorded; these recordings, coupled with estimates of the masses of different body parts, made it possible to calculate on a computer the work done in moving the body parts and the entire body. Because the various techniques of estimating work done in walking give similar results, it appears that the efficiencies with which the body does internal, horizontal, and lifting work during walking are similar.

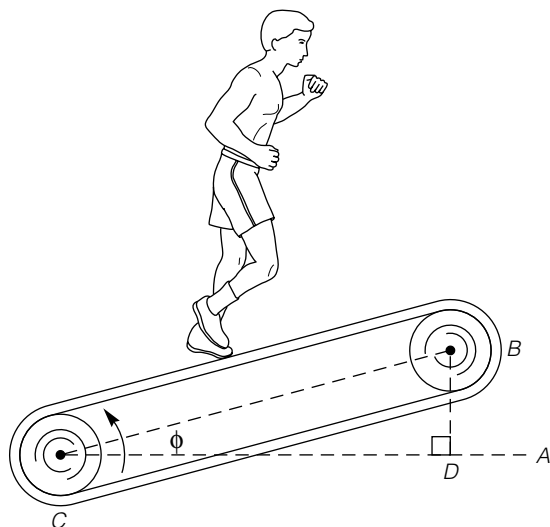
Although the efficiency of the body during easy cycling and walking may be as high as 30%, it can only be surmised that the efficiency of running is somewhat lower. Evidence concerning the efficiency of running is lacking because running is not a true steady-rate situation. During running, the metabolic rate is so high that both situations a and b in Figure 4-13 occur. Because  $\dot{V}_{O_2}$  does not account for all the ATP supplied during running, a proper estimation of efficiency during running awaits development of the technical ability to estimate non-oxidative ATP supply during exercise.

**TABLE 4-5**

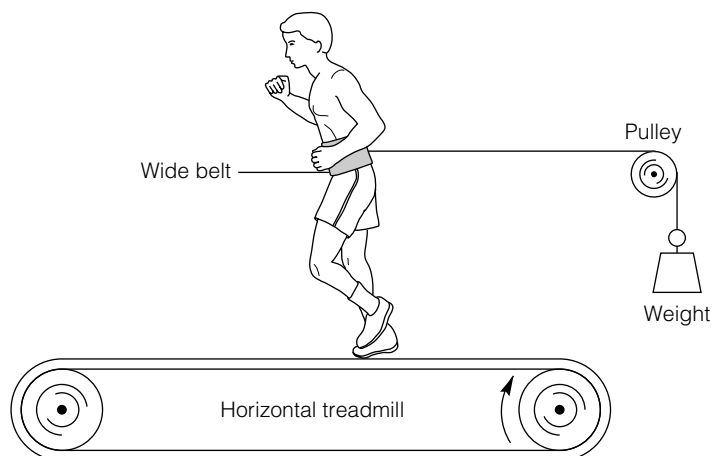
**Estimation of the Whole-Body Efficiency of Doing Vertical Work  
During Steady-Rate Treadmill Walking at  $3.0 \text{ km} \cdot \text{h}^{-1}$**

- Given:* (a) Steady-rate caloric equivalent of  $\dot{V}_{O_2}$  during horizontal, ungraded walking (i.e., zero vertical work) at  $3.0 \text{ km} \cdot \text{h}^{-1} = 5 \text{ kcal} \cdot \text{min}^{-1}$   
 (b) Steady-rate caloric equivalent of  $\dot{V}_{O_2}$  while performing  $375 \text{ kg} \cdot \text{m} \cdot \text{min}^{-1}$  of vertical work at  $3.0 \text{ km} \cdot \text{h}^{-1} = 7.9 \text{ kcal} \cdot \text{min}^{-1}$   
 (c)  $1.0 \text{ kg} \cdot \text{m} = 0.00234 \text{ kcal}$

$$\begin{aligned} \text{Efficiency} &= \frac{\text{Caloric equivalent of change in vertical work}}{\text{Caloric equivalent of change in respiration}} \\ &= \frac{(375 \text{ kg} \cdot \text{m} \cdot \text{min}^{-1} - 0 \text{ kg} \cdot \text{m} \cdot \text{min}^{-1})(0.00234 \text{ kcal} \cdot \text{kg}^{-1} \cdot \text{m}^{-1})}{7.9 - 5 \text{ kcal} \cdot \text{min}^{-1}} \\ &= 0.30 \text{ or } 30\% \end{aligned}$$



**Figure 4-16** During horizontal treadmill walking, no external work is done; therefore, it is impossible to calculate a value for body efficiency. However, a way to determine external work is to measure the work done in lifting the body up a hill. Refer to Equations 4-11 and 4-12 in the text for details of work rate calculation.



**Figure 4-17** External work can be determined during horizontal treadmill walking by having subjects pull a training weight. Refer to Equation 4-13 in the text for work rate calculation.

## SUMMARY

Metabolism can be estimated in two ways: by direct determinations of heat production and by determinations of  $O_2$  consumption. Determinations of metabolic rate provide valuable information about the status of an individual. In resting individuals, both methods provide similar results. During exercise, direct calorimetry is not feasible; therefore, in-

direct calorimetry must be used. However, during hard and prolonged exercise, indirect calorimetry may not provide a precise estimate of metabolic rate. Under these conditions, determinations of  $O_2$  consumption still provide important information about the cardioventilatory systems.

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