Energy Balance 3

3.1 Introduction

The heat produced by an animal is the result of exothermic biochemical reactions in its tissues, the energy for which is derived ultimately from food. Living systems obey the *First Law of Thermodynamics* (the 'Law of Conservation of Energy'), which can therefore be applied to the energy balance of the body. Thus:

TOTAL ENERGY INTAKE = HEAT PRODUCTION + WORK OUTPUT + ENERGY STORAGE (3.1)

Note: In a mammal in a neutral thermal environment, *total energy intake* means, in effect, *food intake*. However, in certain circumstances, e.g., a lizard in the hot sun, other forms of energy can contribute to the total energy intake. It should also be noted that some of the chemical energy of the food is not used by the animal and is lost in the urine and faeces (see p. 21).

It is technically impossible to measure all the four variables accurately, so the equation is simplified by measuring heat production in a resting subject who has been starved for at least 18 h. Thus:

Total energy intake = 0 (the last meal will have been digested within 18 h)

Work output = 0 (the subject is resting)

and the equation becomes: (3.2)

HEAT PRODUCTION = − ENERGY STORAGE (the subject is burning up his energy stores)

The measurement of heat production under these conditions indicates the *Basal Metabolic Rate* (B.M.R.).

The B.M.R. gives a measure of the heat production of the body when it is 'ticking-over': it is a valuable clinical tool and it provides a base-line from which factors influencing heat production can be assessed.

3.2 Calorimetry

DIRECT CALORIMETRY It is technically very difficult to measure accurately the heat production of an experimental subject. Such measurements are made in special, well-insulated chambers called *calorimeters* (Fig. 3–1). Water flows through coils of copper pipes within the calorimeter and absorbs the heat produced by the subject. If the temperature increase of the water is measured, together with the rate of flow, the heat production in kilojoules (kJ) or kilocalories (kcal) can be calculated. To this must be added the latent heat present in the water vapour of the perspiration and expired air. The water vapour produced is measured from its absorption in sulphuric acid: each gram of water accounts for 2.451 kJ (0.585 kcal) (the latent heat of vaporization of water at 20 °C).

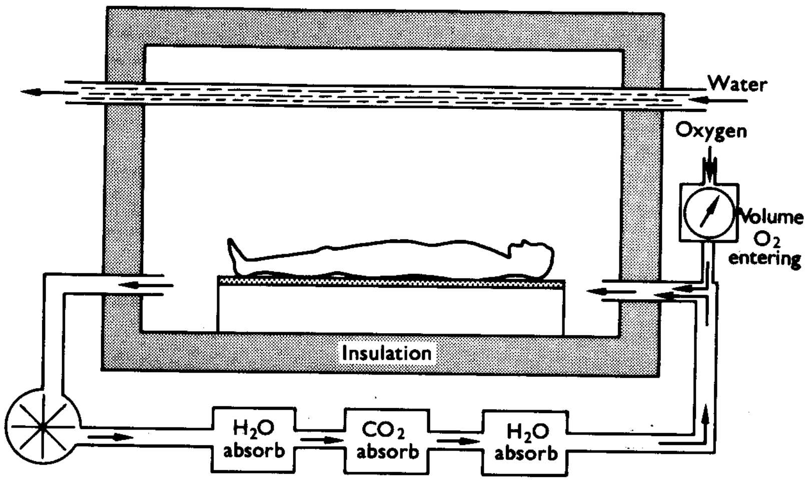

Fig. 3–1 The human calorimeter. In a resting subject the total energy output is the sum of (i) the heat evolved (measured from the temperature rise of the water flowing in coils through the chamber) (ii) the latent heat of vaporization (measured from the amount of water vapour extracted from the circulating air by the first H_2O absorber). CO_2 must be absorbed to prevent its accumulation within the chamber; this process evolves water, so a second H_2O absorber is needed. Oxygen consumption can be measured by noting the rate at which O_2 must be added to keep the chamber in a steady state. (From BROWN, A. C., and BRENGELMANN, G. (1965). Temperature regulation and energy metabolism, in RUCH, T. C. and PATTON, H. D., (Eds.). *Physiology and Biophysics*, 19th Edn, W. B. Saunders, Philadelphia and London).

Calorimeters, although simple in principle, are very expensive and complex in operation and there are very few in existence. Fortunately, however, it is possible to calculate heat production indirectly from simple measurements of O_2 consumption, CO_2 production and nitrogen excreted into the urine.

INDIRECT CALORIMETRY The expression $\dfrac{CO_2 \text{ production}}{O_2 \text{ consumption}}$ is known as the *respiratory quotient* (R.Q.) and it can be related to the composition of the diet and thus to the proportions of carbohydrate, fat and protein being oxidized.

When carbohydrate is oxidized, the consumption of O_2 by volume is exactly equal to the CO_2 production, thus the R.Q. = 1.

For example: GLUCOSE

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

1 gram molecule of glucose (180 g) requires 6×22.4 l (134.4 l) of O_2 and produces $\cancel{2}6 \times 22.4$ l (134.4 l) of CO_2 and 2820 kJ (673 kcal) of heat.

Thus the R.Q. $= \dfrac{134.4}{134.4} = 1$ and the *calorific value* of 1 l of O_2 when glucose is oxidized is $\dfrac{2820}{134.4}\text{kJ} = 20.9\text{kJ}\left(\dfrac{673}{134.4}\text{kcal} = 5.0\text{kcal}\right)$.

When fat is oxidized the volume of O_2 used exceeds the volume of CO_2 produced.

For example: TRIPALMITIN

$$C_{51}H_{98}O_6 + 72.5\ O_2 \rightarrow 51\ CO_2 + 49\ H_2O$$

1 gram molecule of tripalmitin (806 g) requires 72.5×22.4 l (1624 l) of O_2 and produces 51×22.4 l (1142 l) of CO_2 and 32 083 kJ (7657 kcal).

Thus the R.Q. $= \dfrac{1142}{1624} = 0.703$ and the calorific value of 1 l of O_2 is $\dfrac{32\,083}{1624}\text{kJ} = 19.7\text{kJ}\left(\dfrac{7657}{1624}\text{kcal} = 4.7\text{kcal}\right)$.

It is more difficult to calculate the R.Q. for protein, because some of the oxygen and carbon of the constituent amino acids remain combined with nitrogen and are excreted as nitrogeneous compounds in the urine and faeces. However, it has been found that a reasonably accurate estimate of protein metabolized can be derived from knowledge of the nitrogen excreted in the urine. Thus 1 g of urinary nitrogen indicates the catabolism of 6.25 g of protein. It has also been shown that 1 g urinary nitrogen signifies that:—

$$\left.\begin{array}{l} 5.94\text{ l } O_2 \text{ have been consumed} \\ 4.76\text{ l } CO_2 \text{ have been produced} \end{array}\right\} \text{(R.Q. 0.801)} \qquad \begin{array}{r}(3.3)\\(3.4)\end{array}$$

$$111.1\text{ kJ (26.51 kcal) have been produced} \qquad (3.5)$$

Armed with these facts, it is possible to calculate the heat production of a subject by making 3 relatively simple measurements.

$$\left.\begin{array}{l} \text{(a) } CO_2 \text{ produced} \\ \text{(b) } O_2 \text{ consumed} \\ \text{(c) N in the urine} \end{array}\right\} \text{during the experimental period}$$

This method of *indirect calorimetry* will be explained by reference to the following example:

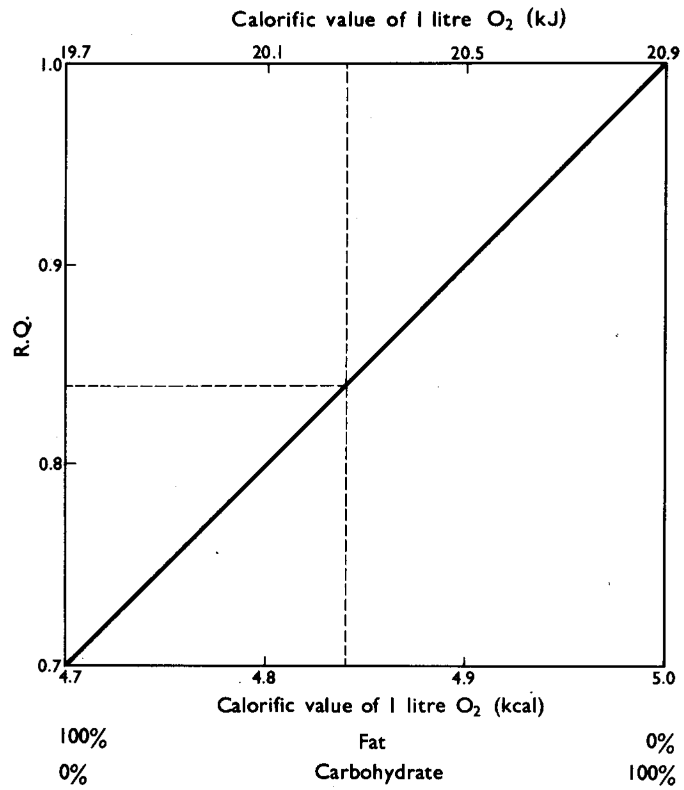

Fig. 3–2 Relation between respiratory quotient and the calorific value of oxygen. (At a Respiratory Quotient of 0.84 the calorific value of 1 litre of oxygen is 4.84).

Urinary nitrogen/h $= 0.37$ g
Total CO_2 produced/h $= 9.48$ l
Total O_2 consumed/h $= 11.40$ l

Proportion of the total O_2 used in protein oxidation (see equation **3.3** above)
$= 0.37 \times 5.94 = 2.20$ l
Proportion of the total CO_2 resulting from protein oxidation (see equation **3.4** above) $= 0.37 \times 4.76 = 1.76$ l
Heat produced by oxidation of protein (see equation **3.5** above)
$= 0.37 \times 111.10 = 41.10$ kJ (9.81 kcal)

Subtraction of the CO_2 produced and O_2 consumed in protein oxidation from the total CO_2 production and O_2 consumption reveals the CO_2 produced and O_2 consumed in oxidizing fat and carbohydrate.

protein RQ $= \frac{1.76}{2.20} = .80$

Thus:

CO_2 from fat and carbohydrate $= 9.48 - 1.76 = 7.72$ l
O_2 consumed by fat and carbohydrate $= 11.40 - 2.20 = 9.20$ l

The *Non-protein respiratory quotient* (N.P.R.Q.)

is thus $\frac{7.72}{9.20} = 0.84$.

Knowing the N.P.R.Q. it is simple to read off from Fig. 3–2 the calorific value of each litre of oxygen used in the oxidation of the fat and carbohydrate by the subject.
Calorific value of 1 l O_2 when R.Q. $= 0.84 = 20.28$ kJ (4.84 kcal), see Fig. 3–2.
Thus the heat produced from the oxidation of fat and carbohydrate

$= 20.28 \times 9.20 = 186.58$ kJ (44.53 kcal)

Heat from protein oxidation $= 41.10$ kJ (9.81 kcal), (see above)

Total heat production/h $= 227.68$ kJ (54.33 kcal).

Estimates of heat production made by Indirect Calorimetry agree extremely well with those obtained by the more laborious means of Direct Calorimetry.

3.3 Basal metabolic rate

Once the B.M.R. in kJ or kcal/24 h has been estimated by either direct or indirect calorimetry, the size of the individual must be taken into account. Table 1 shows a comparison of B.M.R. in kcal/24 h expressed in terms of body weight, surface area and (body weight, W)$^{0.73}$ for four different species. It can be seen that a comparison in terms of body weight is unsatisfactory and yields higher values for smaller subjects. Comparison in terms of surface area gives some improvement, but it is difficult to estimate accurately the surface area of an individual. It has been found, however, that the heat production, divided by the weight raised to the power of 0.73, yields an answer of about 70 kcal/24 h or 293 kJ/24 h irrespective of the size and species of the subject.

Table 1 Comparison of B.M.R. in four different species (kcal/24 h)

	Body Weight (kg)	B.M.R./kg	B.M.R./M²	B.M.R./W$^{0.73}$
Pig	128	19.1	1078	70.8
Man	64.3	32.1	1042	70.5
Dog	15.2	51.5	1039	70.9
Mouse	0.018	654.0	1188	71.6

CONDITIONS WHICH INFLUENCE B.M.R. B.M.R. in man depends on the age and sex of the individual; it is highest in infants and declines progressively with age and at any age tends to be slightly higher in males than females. Under-nutrition or starvation and underactivity of the thyroid gland lower the B.M.R., whereas overactivity of the thyroid gland and fever tend to elevate the B.M.R.

The calorie intake in the diet necessary to support basal metabolism is about 2000 kcal/24 h for an average sized male subject. This is approximately equivalent to 8400 kJ/24 h. (From equation **3.1** on p. 15 it follows that if the dietary intake of calories is less than 2000 kcal/24 h, the subject loses weight; conversely if the dietary intake exceeds the energy requirement, weight is gained.

FACTORS WHICH RAISE THE HEAT PRODUCTION ABOVE THE BASAL LEVEL

(*a*) *Muscular effort* Physical exercise requires fuel so that, as is well known, people employed as labourers or lumberjacks need to eat more than people in sedentary occupations. A lumberjack, for example, requires in his daily diet 13 000 kJ (3000 kcal) in addition to the 8400 kJ (2000 kcal) needed for his basal metabolism, while a sedentary student requires only an extra 2100 kJ (500 kcal).

(*b*) *Mental effort* Thought processes require negligible dietary energy. As a result of experiments where subjects were required to perform difficult mental arithmetic, it has been calculated that the extra energy required for this would be met by one-half of a salted peanut per hour!

(*c*) *Feeding* The ingestion of food increases heat production. This increase is known as the *Specific Dynamic Action* (S.D.A.) or the calorigenic action of food. Heat production begins to rise about 1 h after feeding, reaches a peak after about 3 h and then remains above the basal level for several more hours. Protein has a high S.D.A.: 30% of the calorific value is lost as heat. Therefore, if an animal required, for example, 100 kJ/day in its diet to maintain its energy balance, it would have to be given 130 J/day if its diet were pure protein. Corresponding figures for carbohydrate and fat are 106 and 104 kJ/day.

The mechanism of the S.D.A. is not known, but it is clear that it does not derive from events within the digestive tract, because amino acids infused intravenously produce the same S.D.A. as when they are fed orally. The S.D.A. must therefore be a consequence of metabolic events after the food products have been absorbed into the circulation and distributed to peripheral tissues. The heat produced contributes to the maintenance of body temperature.

(d) thermoregulation

3·4 The efficiency of feeding

During digestion not all the energy of the diet is made available for the production of work or the storage of energy by the body. The efficiency of utilization of the diet can be computed as shown below:

Gross energy = heat of combustion of the food as measured in a bomb calorimeter.

Digestible energy = Gross energy − heat of combustion of faeces.

Digestible energy gives a measure of the calorific value of the food absorbed from the digestive tract. However, not all this food is completely oxidized in the body: protein forms urea and other nitrogenous compounds excreted in the urine.

Thus the energy available for metabolism is:

Available (metabolizable) *Energy* = Digestible energy − heat of combustion of the urine.

In man, on a typical mixed diet, the ***available energy*** is about 85% of the ***gross energy***.

A proportion of the available energy is expanded as the S.D.A., so the ***net energy*** (that which can contribute to work or energy storage) is less than the available energy. In practice, about 20% of the available energy is lost as S.D.A. so that the overall efficiency of feeding $\frac{\text{net energy}}{\text{gross energy}} \times 100$ is about 68%.

There is considerable variation between human subjects in the efficiency of feeding which can in part be explained by genetic differences.