Chapter 15

Metabolic Energy Expenditure of Activity (Work and Exercise)

Muscle is well recognized as an energy-conversion device because of its ability to convert energy from one form to another. Yet as demonstrated in previous chapters, energy demands also are imposed by the orderly transfer of energy and materials along an operating metabolic pathway. The energy-exchange devices of muscular contraction and metabolism are coupled: (1) chemo-chemical energy conversion and transfer via the metabolic pathways – from the chemical bonds of the food we eat to the chemical bonds of ATP and (2) chemo-mechanical energy conversion and transfer via muscle displacement – from the chemical bonds of ATP to physical force. In addition to contraction, there are other expenditures – ion pumps and protein turnover too – but here, primary focus is on the collective result of muscle contraction and the estimate of whole-body energy expenditure.

15.1 Rate vs. Capacity vs. METs

Energy expenditure is represented in a variety of formats that include measurements of rate, capacity, and metabolic equivalents (METs).

Rate measurements are ideally suited for aerobic energy expenditure because a volume (V) of oxygen uptake can be recorded per minute $(\mathrm{VO_2\,min^{-1}})$ and subsequently so too can energy expenditure $(\mathrm{kJ\,min^{-1}})$. For example, if oxygen is consumed at a steady rate of $1\,\mathrm{L\,min^{-1}}$ at an RER of 0.70, then energy expenditure is estimated as:

$$1\,\mathrm{L\ VO_2\,min^{-1}} = 19.6\,\mathrm{kJ\,min^{-1}}(4.7\,\mathrm{kcal\,min^{-1}})$$

At rest or with steady-state light to moderate exercise, a measurement of steady-state oxygen uptake provides a *valid* means of estimating energy expenditure (Fig. 15.1). Anaerobic energy expenditure is, unfortunately, difficult to quantify as a

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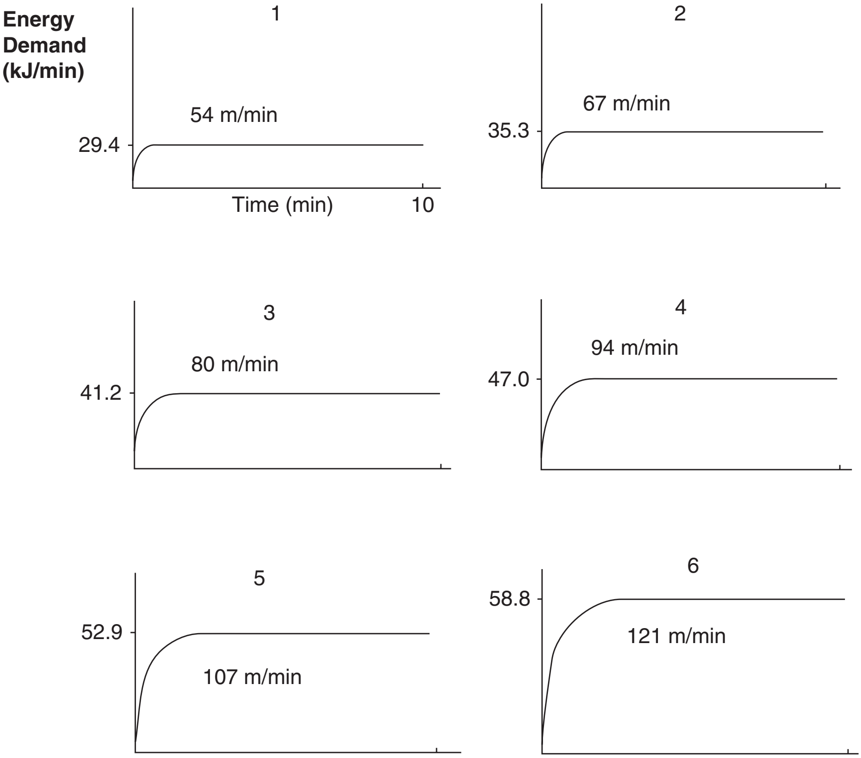

Fig. 15.1 Energy demand $(\mathrm{kJ\,min^{-1}})$ and treadmill speed $(\mathrm{m\,min^{-1}})$ are shown for six separate 10-min exercise periods. A single individual performed all six exercise trials. The grade of the treadmill was 10% for all six trials. Notice that steady-state oxygen uptake was achieved for all workloads signifying easy to moderate intensity exercise

rate function measure. Anaerobic activities are known to be brief and intense, conditions that preclude the ability to obtain a steady-state estimate of energy expenditure. This is certainly a limitation.

Anaerobic energy expenditure, in fact all energy expenditure, can be estimated in the context of a capacity. A capacity measurement portrays an aliquot of energy expenditure for a complete time period; that is, a single bout of exercise, from start to finish. Based on the physiology of longer, slower, distance-type exercise for example, walking at a pace where oxygen is consumed for 30 min and at a rate of $1\,\mathrm{L\,min^{-1}}$ (RER = 0.70), the total amount of energy expended is estimated at:

$$30\,\mathrm{min} \times 19.6\,\mathrm{kJ\,min^{-1}} = 588\,\mathrm{kJ}(141\,\mathrm{kcal})$$

Figure 15.2 demonstrates the hypothetical relationship between work performed during three separate bouts of brief, intense, resistance-type training (e.g., push-ups)

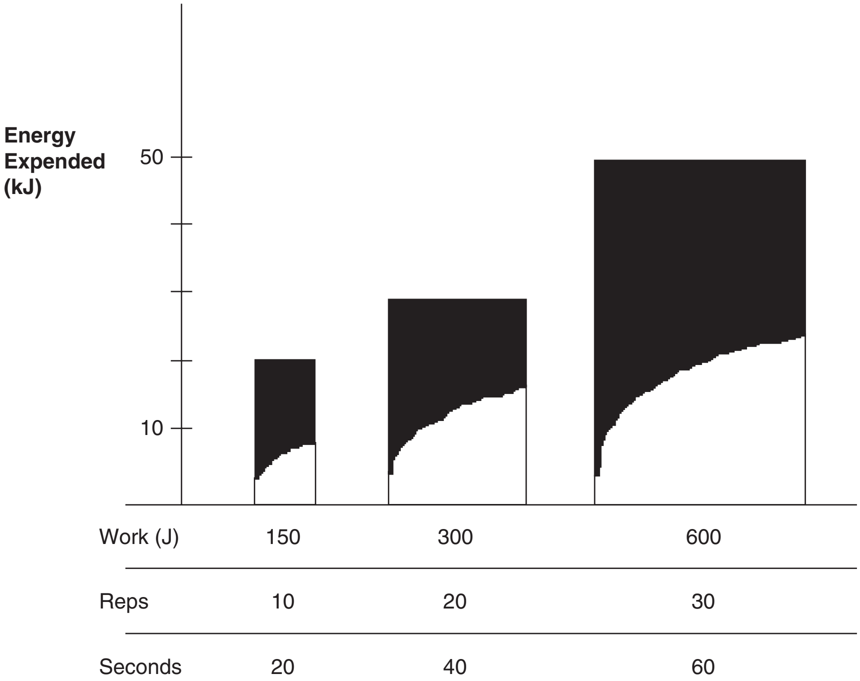

Fig. 15.2 Hypothetical energy expenditure and work load are shown for three separate bouts of the push-up exercise. Each bout contains an anaerobic (*in black*) and an aerobic (*in white*) energy-expenditure component

and the estimated anaerobic and aerobic energy expenditure throughout each bout. In this example a steady rate of Oxygen update is never achieved (an oxygen deficit is apparent). These data are also reported in a capacity format.

METs are strictly a representation of aerobic energy expenditure where 1 MET represents the oxygen uptake of a "typical" person resting in a reclining position; the value associated with this is:

$$3.5\ \text{mL}\ \text{O}_2\ \text{min}^{-1} = 1\ \text{MET}$$

This universally accepted MET value was obtained decades ago by testing a single subject ($N = 1$). Nowadays, such a case study (data from a single person) would never be accepted as representing the energy expenditure of an entire population. Yet with decades of human bias behind this MET equivalent, the number is here to stay. Data obtained from a much larger population ($N = 769$) revealed resting oxygen uptake to be about 30% lower than $3.5\,\text{mL}\ \text{O}_2\,\text{min}^{-1}$ (at $2.6 \pm 0.4\,\text{mL}\ \text{O}_2\,\text{min}^{-1}$) (1).

Table 15.1 METs for a few selected activities

Activity	METs
Guitar playing (rock & roll)	3.0
Weight training (light)	3.0
Calisthenics (no weight)	4.0
Gymnastics	4.0
Golf (no cart)	4.3
Outside painting	5.0
Walking (4 mph)	5.0

MET values provide a reasonable estimate of aerobic energy expenditure. Upon closer examination of the above data, however, is it to be believed that playing a guitar is energetically equivalent to a light-weight training work-out? Does painting outside really expend more energy than calisthenics (push-ups, sit-ups, and the like)? Does golfing "burn more calories" than gymnastics (floor exercise, high bar, rings, balance beam, etc.) or are semantics to be blamed? For aerobic activity the table appears fine, for anaerobic activity it does not. If Table 15.1 also were to include a reasonable estimate of anaerobic exercise energy expenditure, then the MET values would most likely be higher for heavy to severe exercise and activity that contains an anaerobic component (i.e., weight training, calisthenics, gymnastics). Information from (2)

METs also describe exercise energy expenditure as multiples of resting metabolic rate, being especially used in clinical rehabilitation programs: 1 MET is resting energy expenditure, 2 METs is 2× resting energy expenditure, 3 METs is 3× resting energy expenditure, and so on. It also has been suggested that the numerical MET value can be extended to caloric expenditure as:

$$1\,\mathrm{kcal\,kg^{-1}\,h^{-1}}$$

Thus, a 70-kg person working at 3 METs for 2 h expends 420 kcal (1,758 kJ) (1):

$$70\,\mathrm{kg} \times 3\mathrm{METs} \times 2\,\mathrm{h} = 420\,\mathrm{kcal}(1,758\,\mathrm{kJ})$$

It is important to recognize that MET values do not contain an anaerobic energy-expenditure component and this can be problematic when estimating the energy demands of heavy to severe but not light to moderate exercise and activity (Table 15.1).

Imagine the physical intensity of pushing a broken down car to the side of a road, a tug-of-war contest or shoveling wet, heavy snow. Powerful isotonic and isometric muscle contractions often constrict blood vessels, reducing blood flow or stopping it altogether. Under these conditions, anaerobic metabolism rather than aerobic metabolism may contribute most to a muscles' energy expenditure. The muscles' use of oxygen is usually not at a physiological maximum (i.e., VO_2 max) during brief intense activity but it may certainly reach a peak value. Figure 15.3 demonstrates how the use of both anaerobic and aerobic components may more reasonably portray energy expenditure as METs for brief periods of heavy to severe exercise, work, and activity.

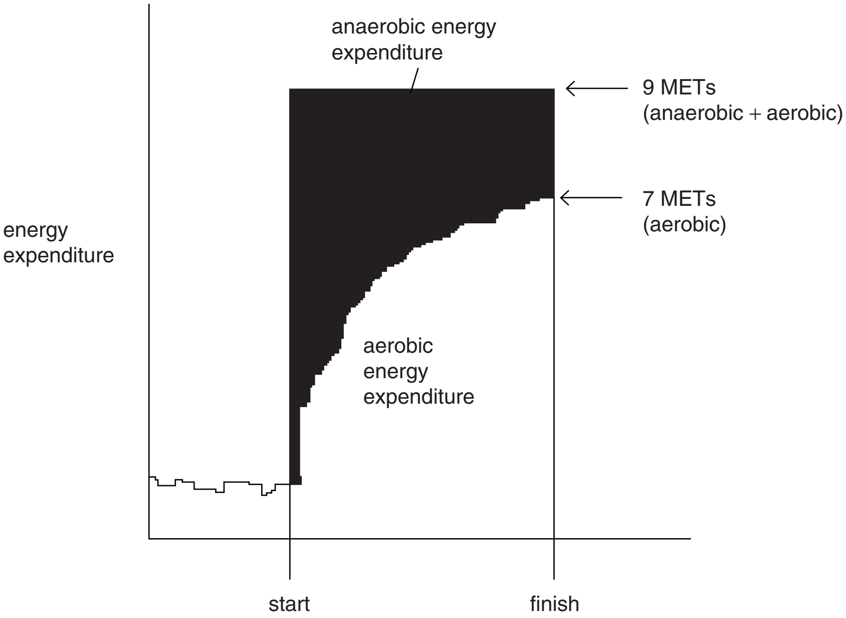

Fig. 15.3 MET tables typically profile exercise and activity in terms of multiples of resting oxygen uptake (i.e., aerobic energy expenditure). To the contrary, this figure reveals METs as comprised of aerobic (*white*) and anaerobic (*black*) energy expenditure. A peak in VO_2 is found at 7× resting oxygen uptake (7 METs). But in terms of both aerobic and anaerobic energy expenditure the metabolic rate is actually 9 METs

15.2 Muscle

Muscle is a chemo-mechanical converter, the energy within ATP being converted into mechanical force. Contraction proceeds when the energy of ATP hydrolysis is large enough to promote movement within muscles molecules.

The molecular aspects of muscle contraction occur at the level of the actin–myosin protein interface. The spread of calcium (Ca^{2+}) throughout the muscles' many sarcomeres initiates muscle contraction (Fig. 15.4).

The actin–myosin motor has been described as both a catalyst and a mechanical ratchet (3). Myosin is in fact an ATPase, catalyzing ATP hydrolysis. In the resting state, myosin and actin are unattached with myosin, tightly binding the products of ATP hydrolysis, ADP, and Pi (until the ADP and Pi are allowed to disperse (repulse) no conversion of chemical to mechanical energy takes place). When muscle is stimulated to contract myosin and actin bind, then the Pi and ADP are released (in that order). Myosin attaches to actin perpendicularly, but upon the release of Pi and ADP, the head of the myosin protein tilts at a sharper angle; this is the power stroke, contraction – the mechanical part of chemo-mechanical conversion.

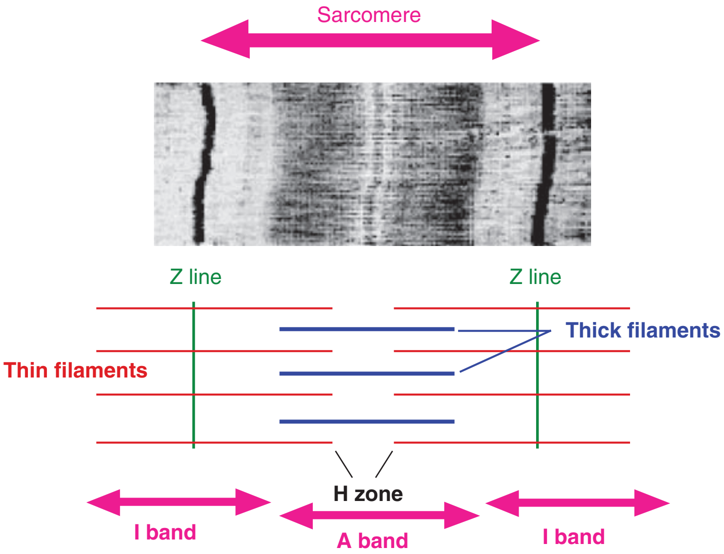

Fig. 15.4 A muscle sarcomere, the contractile component of muscle. A single muscle cell may contain several thousand sarcomeres. The molecules of contraction are shown as actin (*thin filaments in red*) and myosin (*thick filaments in blue*) (from http://commons.wikimedia.org/wiki/Image:Sarcomere.gif)

The conformational change in the head of the myosin molecule represents a lower energy state (upon death and the absence of energy supply, rigor mortis sets in, the state of uninterrupted contraction). The subsequent binding of ATP by myosin causes dissociation of the actin–myosin interface (the so-called resting state). ATP subsequently undergoes hydrolysis to form ADP and Pi and the Gibbs energy change of this reaction is stored within the myosin protein molecule; the myosin head resumes its higher energy state "resting" position, being prepared for the next cycle of binding-and-dissociation with actin. The complete cycle is known as the power stroke.

Under high loads it appears that one ATP molecule is responsible for one power stroke (supplied by the actin–myosin interface) (3, 4). At lighter and perhaps moderate workloads, the energy of one ATP molecule may promote several power strokes at an efficiency of 40% or more (4). The power stroke however represents only one aspect of muscular ATP utilization. ATP is also required to maintain the resting electro-chemical potential of the sarcomere membrane (via the Na^+-K^+ ATPase) and the Ca^{2+} storage facilities (via the Ca^{2+}-ATPase). The energy expended by muscle contraction is considered primarily the result of chemo-mechanical conversion by actomyosin, the orderly movement of energy and materials along the metabolic pathways, and the supporting ion movement within and without the muscle cell.

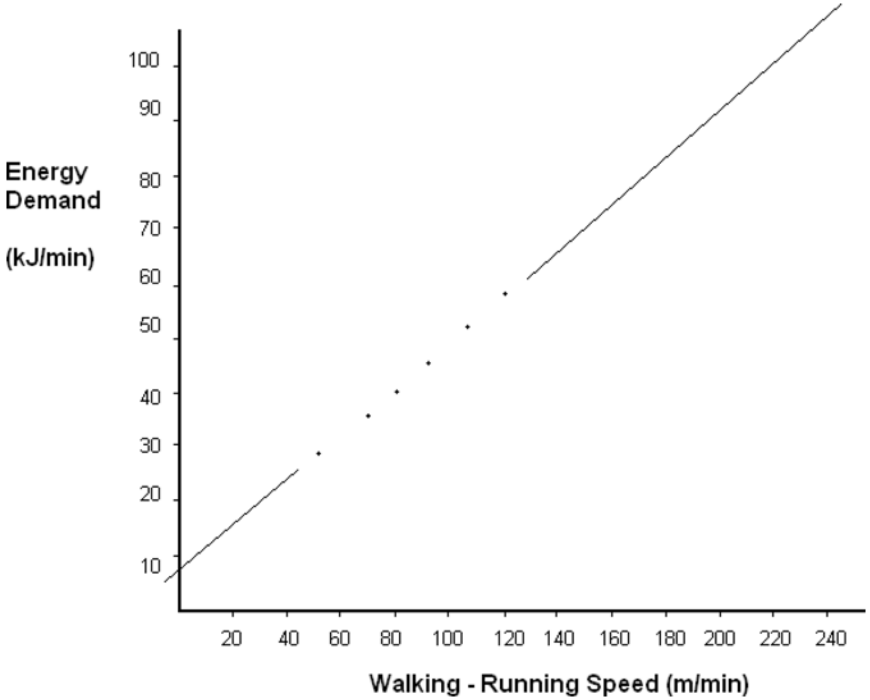

Fig. 15.5 The energy demand and treadmill speed for the six exercise trials in Fig. 15.1 are portrayed here by six dots. Note the linear extrapolations that can be made above and below this power output-to-energy-expenditure relationship. These data have limitations in that they only represent the energy expenditure of longer duration, easy to moderately easy, steady-state exercise. Energy demand can however be *predicted* for treadmill speeds where subjects never achieve a steady rate of oxygen uptake.

15.3 Work and Energy Expenditure Relationships

At steady-state power outputs, a steady rate of oxygen uptake provides an estimate of energy expenditure for that particular workload. In Fig. 15.1, the energy demand, based on oxygen uptake for a single individual, is recorded for six 10-min bouts of treadmill exercise at six different treadmill speeds. The treadmill grade was held at 10% for all six exercise periods.

If the energy demand of the six exercise periods in Fig. 15.1 were plotted on a single graph, a rather remarkable relationship with work is demonstrated. As can be seen in Fig. 15.5, energy demand has a linear relationship with steady-state power output during easy to moderately-easy longer duration exercise. Thus, the modeling of energy expenditure is rather simple for long, slow distance-related exercise; there is a direct correlation between the rate of work and the rate of energy expenditure.

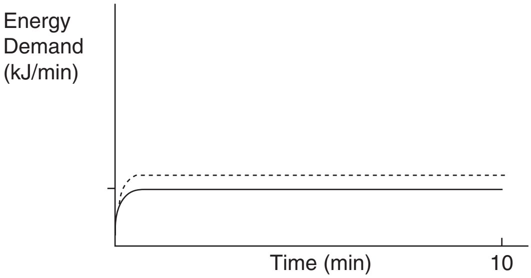

Fig. 15.6 Two identical twins of equal body mass and composition take a leisurely stroll at $54\,\mathrm{m\,min^{-1}}$ (2.0 mph). The *bottom solid line* reveals lower energy expenditure at this work load, indicating a better exercise economy for one of the twins, the *dotted line* reveals greater energy expenditure and thus a worse economy. Economical athletes are often at a distinct advantage during competition because they expend less energy at a given race pace

Based on steady-state linear relationships between less-intense exercise and its associated energy expenditure, the energy demand for brief, and/or intense, heavy to severe exercise may also be predicted. But there are shortcomings here. In fact, when work rates take place well above measured rates of oxygen uptake (i.e., above VO_2 max, VO_2 peak or during an oxygen deficit phase at the start of exercise), the relationship between work and energy expenditure may not be linear at all. Moreover, the energy expenditure of a single work rate often varies among people, for a variety of reasons.

Estimates of aerobic energy expenditure for a given individual are ideal for that specific person but may only portray a rough approximation of energy expenditure for another person (or peoples). For example, as a "rule of thumb," a $100\,\mathrm{kcal}(418\,\mathrm{kJ})\,\mathrm{mile}^{-1}$ estimate of energy expenditure has been used for walking, running, or jogging. Yet some people require more then 100 kcal, some less during a 1-mile jog; body weight and power output figure heavily into this (heavier people and faster running speeds increase energy demands). Under recognized limitations, however, a *reasonable estimate* of energy expenditure – a $100\,\mathrm{kcal\,mile}^{-1}$ approximation – can be useful, as depicted by the electronic display on exercise equipment for example. At other times greater accuracy is required; for example, as part of the detailed training and eating regimen of an elite athlete. Likewise the precise knowledge of an athlete's energy expenditure at a given workload, such as at racing pace, can provide valuable performance-related information.

The relationship between energy expenditure and workload among individuals is known as exercise economy and it is almost always expressed as a measure of oxygen uptake (Fig. 15.6). Using 25 tests per subject to model the energy demand-power output relationship for each, Medbo et al found a 16% range in oxygen uptake among treadmill runners working at identical power outputs (5). A measure or estimate of economy can serve as a useful tool to help predict performance outcomes because economical athletes utilize less energy to perform a given amount of work, placing themselves at a distinct advantage during competition (6, 7) (it can only be wondered as to how anaerobic energy expenditure would fit into the description

Fig. 15.7 The two lines provide a dramatic demonstration of differences in economy for two subjects during participation of an identical ramp-type work test lasting 20 min or more (11). As heavy exercise is approached and fatigue ensues, additional muscle is recruited and energy demand does not remain linear for the subject whose data is shown in the *top line*. A departure from linearity makes predicting the energy expenditure of heavy to severe exercise problematic because most models of energy expenditure are based on linear not curvilinear relationships. See also Fig. 13.4

of exercise economy when extreme energy demands are greatly supplemented with anaerobic energy exchange).

During heavy to severe exercise the workload–energy-expenditure relationship may not remain linear (see Figs. 13.4 and 15.7). In accordance with traditional oxygen-only views of energy expenditure, increases in energy expenditure that creep above linearity have only been identified using oxygen-uptake measurements. These increases have been termed "extra energy expenditure" (8). Again, following traditional oxygen-only descriptions of energy expenditure, the "extra" demand for energy expenditure during heavy to severe exercise is termed the *slow component of* O_2 *uptake* (8). However, heavy to severe work rates likely invokes an anaerobic component to this so-called "extra" energy expenditure (9). "Extra" nonlinear energy demands are found during both steady-state power output (10) (Fig. 13.4) and ramp-type work where power output steadily increases (11) (Fig. 15.7). Evidence suggests that the potential for "extra" energy expenditure results from the additional recruitment of muscle as intense work progresses and fatigue sets in (10). The presence of nonlinearity in energy expenditure during heavy to severe exercise represents a real problem for the reasonable estimation (extrapolation) of both aerobic and anaerobic energy expenditure. But all is not lost; reasonable estimates of energy expenditure, while controversial, are available (Figure 15.3). The issue of what is and is not a reasonable estimate continues to be debated in the scientific literature (12–14).

15.4 Glycolytic vs. Respiratory Efficiency

In a world that often focuses on aerobic metabolism (i.e., oxygen uptake), inefficient is the usual description of anaerobic metabolism. To the contrary aerobic

Table 15.2 In-series energy-exchange efficiency

Krebs cycle						
84%						
Krebs cycle		Electron transfer		Efficiency		
84%	×	97%	=	81%		
Krebs cycle		Electron transfer		H^+ gradient		Efficiency
84%	×	97%	×	80%	=	65%
Aerobic metabolism		Chemo-mechanical conversion		Efficiency		
65%	×	45%	=	29%		
Anaerobic metabolism		Chemo-mechanical conversion		Efficiency		
65%	×	45%	=	29%		

The three independent energy-exchange gradients are shown for aerobic metabolism: Krebs cycle, electron transfer, H^+ gradient. In going from top to bottom, notice the more exchange devices placed in-series, the lower the overall efficiency. The coupling of aerobic or anaerobic energy exchange (65%) to muscle contraction (45% efficiency) suggests a whole-body efficiency of running or cycling at 29%. These numbers are hypothetical (demonstration purposes only)

metabolism is thought to be a rather efficient process. Are these statements true? Only 2 ATPs are resynthesized during net anaerobic glycolysis (3 ATPs if glycogen is the starting point). Compared with aerobic (mitochondrial) metabolism, where ~32 ATPs are resynthesized from a molecule of glucose, it indeed looks as if glycolysis is woefully inefficient in terms of the *amount* of ATP resynthesized. Because there is no evidence to suggest that the ATP resynthesized from anaerobic metabolism is of lower quality (less $-\Delta G$) than that of aerobically resynthesized ATP, an interesting question arises: Why do cells retain glycolysis as a limited anaerobic energy-exchange device?

There are several ways to compare and thus interpret aerobic and anaerobic efficiency (although efficiency is defined strictly as the ratio of output to input). To begin, anaerobic glycolysis *is* inefficient in terms of the amount of ATP resynthesized per glucose moiety; 2 ATPs as compared with the 32 additonal ATPs involving mitochondrial respiration. Moreover, a good deal of available energy is still contained within lactate, an end product of glycolysis.

Another method of interpretation is to examine the overall efficiency of coupled energy-exchange devices. As an in-series compilation of efficiency, the metabolic and work-related devices of energy exchange are suggested in Table 15.2. As a generalization, the more exchange devices placed in-series, the lower the overall efficiency. In Table 15.2 the two metabolic pathways are comparable in efficiency (even though aerobic respiration involves additional in-series energy-exchange devices as compared with anaerobic metabolism; krebs cycle × electron transfer × H^+ gradient versus substrate level phosphorylation.).

Another way to compare aerobic vs. anaerobic efficiency is to rationalize both phosphorylation potential (i.e., efficiency of the actual process of ATP resynthesis) and the energy content of the substrate being utilized during metabolism (15, 16). With this interpretation there is evidence to suggest that anaerobic substrate-level (glycolytic) phosphorylation is as much or more an efficient energy-exchange device than is aerobic respiratory (mitochondrial) phosphorylation (17, 18). Per unit, fat also contains much more energy than does glucose. Using the parameters of phosphorylation potential and substrate energy content, the greater amount of energy contained within fat may be purposely coupled to a less-efficient aerobic means of ATP resynthesis. On the other hand, a molecule or mole of glucose contains less energy than fat, but at heavy to severe work rates, working muscle may switch to a greater rate of anaerobic glycolysis for its "as much or more" efficiency of ATP resynthesis (15, 16).

Efficiency can be further viewed as a lower heat loss during the conversion of energy to work output. Heat-only measurements of muscle contraction (i.e., complete ATP turnover) suggest that anaerobic glycolytic metabolism may be more efficient as compared with aerobic metabolism (17). A thermal rationale also can be applied to the use of the ATP, PC stores during intense exercise, representing only one-half of ATP turnover and thus "incomplete" heat loss interpreted as "improved" efficiency during contraction; the metabolic resynthesis of these stores, the other-half of ATP turnover and its associated aerobic heat production, takes place in recovery (18) (it must be kept in mind however that heat production, not ATP resynthesis, can be a metabolic goal (19, 20); also heat and entropy are both expenditures, but only the former is actually measured in the consideration of efficiency (21) (see Fig. 9.3).

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