EXERCISE PHYSIOLOGY

SHEPHARD

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ROY J. SHEPHARD, M.D. (Lond), Ph.D.
Director
School of Physical and Health Education
Professor of Applied Physiology
Faculty of Medicine
University of Toronto
Toronto, Ontario

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PREFACE

Exercise physiology might be thought a crowded market for another textbook. When B. C. Decker first proposed that I write such a volume, I shared this opinion. However, after some discussion, I agreed that the majority of currently available offerings were in reality low level physiology texts. Moreover, by attempting to treat both physiology and exercise physiology within a limit of 300 to 400 pages, the available texts failed to do even elementary justice to the exciting progress that has been made in this latter topic over the past decade.

The present text, although written with the undergraduate in mind, is unashamedly directed to exercise physiology. It is based upon nearly 20 years of experience in a third year honors course at the University of Toronto, and it assumes that students have already completed university level courses in the basics of anatomy and physiology. The starting point is thus motion, which is a central characteristic of the animal kingdom. The demand for energy to induce the various forms of human movement is discussed, and identified are the prime bottlenecks in the translation of food stores into external work. Methods of measuring human activity in the laboratory and in the field are compared, and the optimum choice of fuel for physical activity is debated. Chapters 4 through 7 examine the hormonal and neural regulation of the various body systems under the stress of physical exercise. Consideration is then given to methods of measuring fitness, the modification of physical condition by various types of training regimens, and the influences of age and sex upon human working capacity. The following two chapters look at physical performance under conditions of environmental stress—extremes of ambient pressure and temperature. The last two chapters review such important topics as the interactions between exercise and cardiovascular health and potential modification of physical performance by various drugs (ergogenic aids, air pollutants, cigarette smoke, and alcohol).

Although it is often undertaken lightly, in many respects, exercise is a matter of life and death. When prescribed judiciously, an increase of physical activity can add much to the quality of daily life, and in some instances, it may even extend lifespan. On the other hand, sudden bursts of exercise for which an individual is ill-prepared can be life-threatening, and such dangers are substantially increased when the exercise must be carried out under harsh environmental conditions. This book is perhaps the first to acknowledge that physical educators face vital decisions about such issues in their daily practice, and it offers sound physiological reasoning for the recommendations which must be made.

Specific references have been avoided because they date quickly and add unnecessarily to the cost of a text. Those wishing to read further may pursue selected topics via the Cumulative Index Medicus and recent issues of the various international journals of sports science. A detailed bibliography of some 5,000 entries is also available in the author's graduate level text *Physiology and Biochemistry of Exercise* (New York: Praeger, 1982).

Although this book has been written primarily for the undergraduate in physical and health education, the author has deliberately avoided unnecessary and unexplained technical jargon. It is thus hoped that the material presented will appeal to sports physicians, exercise physiotherapists, coaches, trainers, and the growing group of professionals who advise either athletes or the general public on programs of training and physical activity.

R. J. Shephard

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BASIC CONCEPTS

HUMAN MOTION AND ENVIRONMENTAL CHALLENGE

CHAPTER 1

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- Principle of Homeostasis
- Contribution of Movement to Homeostasis

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CENTRALITY OF MOTION TO LIFE

Movement as a Characteristic of Life

What is the academic importance of exercise science? Whereas classical physiology describes the characteristics of body function in a person who is living under resting or basal conditions, the exercise scientist is concerned with the woman or man on the move. The resting state has traditionally been considered a convenient frame of reference, both for reporting the functional behavior of the various body systems and for observing their responses to various types of experimental intervention. However, motion is such a fundamental feature of life that classical physiology provides a very incomplete description of human phenomena; a complementary study of reactions to vigorous exercise in average and in athletic subjects is necessary to understand the full range of human responses.

Principle of Homeostasis

One interesting aspect of human functional design noted by the French physiologist Claude Bernard was the principle of homeostasis—an innate ability to maintain the constancy of the body's internal environment or milieu interieur in the face of various challenges. While it is quite remarkable how the concentrations of cellular constituents, acidity, oxygen pressure, and temperature are held within closely specified limits under resting conditions, the process of self-regulation or Selbsteuerung becomes yet more fascinating when the constancy of these same variables is challenged by a 10- to 20-fold increase of metabolic rate, as an athlete moves at high speed through such challenging environments as extremes of heat, cold, or high or low ambient pressures.

Contribution of Movement to Homeostasis

Except in the most artificial of laboratory situations, movement makes an essential contribution to the process of homeostasis. As body food reserves are depleted, the individual must move in search of fresh nutrients to replenish internal stores. Likewise, by moving from a challenging to a more comfortable environment, the cost of maintaining the constancy of internal conditions can be greatly reduced, and if a person is confronted by an excessive environmental challenge, movement away from the problem may be essential to survival.

The central theme of this book is thus the way in which the milieu interieur is held constant in the face of dual challenges from vigorous exercise and an adverse environment. In the present chapter, we shall look briefly at the value of animal versus human studies. We shall then examine the energy needs of motion, the available energy resources, and the efficiency of their translation into external work.

ANIMAL VERSUS HUMAN STUDIES

Value of Animal Research

Although the most striking characteristic of the classical physiologist is a preoccupation with descriptions of the basal state, many classical physiologists also show a preference for animal rather than human experimentation. The classical physiologist has argued that the mind has a striking power over human responses and that such problems can be circumvented by studies of the anesthetized or the decerebrate animal.

In fact, the advantages of such preparations are somewhat illusory, particularly in the context of physical activity. Anesthetics often modify systemic blood pressure and various autonomic reflexes. The level of decerebration may vary through continued bleeding or recovery of traumatized brain tissue, and usually the decerebrate animal shows an abnormal increase of muscle tone. Moreover, the only possible form of exercise in an unconscious preparation is the atypical situation of electrical stimulation of a muscle or a nerve.

The main advantages of animal experiments are that biological specimens of blood and muscle can be collected without concern about causing permanent damage, and aging processes can be studied within a fairly brief lifespan, sometimes only 2 to 3 years.

Exercise in Animals

Exercise is sometimes performed on trained, conscious animals. Horses, sheep, dogs, and rats have all been persuaded to exercise on a treadmill, while rats and mice have been forced to swim to exhaustion in a tank, sometimes with weighted tails. Mice have been put in activity wheels, and various species have been trained to perform isometric exercise (the operation of weighted levers), using food pellets as a reward. In such circumstances it is difficult to be certain that there is less emotional disturbance than in human experiments. A rat which is persuaded to run by a repeated electrical shock or a mouse on the verge of drowning is hardly in a relaxed emotional state! A second problem is that between experiments the animal is usually confined to a small cage. It thus begins exercise in very poor physical condition and bears little resemblance to its free-living namesake. In theory, the daily amount of exercise can be controlled more closely than in humans, but in practice many animals run on the treadmill in a very clumsy fashion. The amount of oxygen consumed by small mammals is also quite limited, and measurements of gas exchange thus becomes subject to substantial experimental error. There are finally difficulties of scaling both immediate results and lifespan to an equivalent human value.

Emotional Disturbances in Humans

The scientist who chooses to examine the phenomenon of exercise nevertheless has several advantages over colleagues who study resting responses. Vigorous exercise is a major physiological disturbance, inducing a 10- to 20-fold increase of metabolism, and equally large changes in many other body systems. Minor disturbances of the resting state induced by the emotions thus pale into insignificance before such a major influence. It has also been argued that emotional disturbances become smaller or even disappear as a person becomes involved in an exercise task. Certainly, the relative importance of an emotional increase in heart rate (tachycardia) of 10 beats per minute is much smaller if vigorous exercise has increased the heart rate to 180 beats per minute than if it has remained at a typical resting value of 60 beats per minute. Nevertheless, emotional factors can still be an important source of error when interpreting data; for example, if the heart rate response to a given work-rate decreases from 180 beats per minute to 170 beats per minute with test repetition, this may be attributed to cardiovascular training, when in reality it reflects no more than a decrease of anxiety.

Several simple techniques minimize the effects of anxiety; (1) all experiments must be fully explained to the subjects, and must be conducted with a minimum of fuss and disturbance; (2) if the resting heart rate remains high despite a prolonged initial rest, or if it is thought important to eliminate emotional overlay, the subject should be allowed several preliminary exposures to both the investigator and the laboratory—such "habituation," or negative conditioning, is an important element of a well-designed human experiment; (3) an alternative approach is to examine exercise responses relative to values for loadless pedalling of a cycle ergometer, rather than relative to data for rest or a hypothetical basal state.

Most of the findings to be discussed in this book have been obtained by human research, with all of its advantages and shortcomings. Recourse made to animal research will be clearly indicated.

ENERGY NEEDS OF MOTION

Range of Energy Expenditures

How much energy is consumed by human movement? An old lady who spends most of her day sitting in an armchair at a nursing home has an energy expenditure of approximately 6.3 megajoules per day (MJ per day).[1] However, this energy expenditure may be doubled for individuals involved in hard physical employment, and in exceptional circumstances, such as a 24-hour road race, energy expenditures of 30 to 40 MJ per day are conceivable.

[1] Standard international (SI) units and abbreviations have been adopted throughout this book (Table 1–1). This system of measurement has now been accepted by most international journals. However, older books express energy expenditure in calories (1 calorie = 4.186 joules).

TABLE 1–1 The Standard International (SI) Units of Scientific Measurement, with Conversion Factors for Previously Used Units*

Variable	*Dimensions*	*Current Unit and Abbreviations*	*Previously Used Units*
Mass	kg	kilogram (kg)	pound (= 0.454 kg)
Distance	m	meter(m)	foot (= 0.305m) mile (= 1.606km)
Time	s	second(s)	
Speed	m/s	m/s km/hour	foot/min (= 0.508 cm/s) mile/hour (= 0.446 m/s) (= (1.606 km/h)
Force	kgm/s^2	newton (N)	kg-force (= 9.81N) kilopond (= 9.81N)
Work	kgm^2/s^2	joule (J)	calorie (= 4.186J)
Power	kgm^2/s^3	watt (W)	kgm/min (= 0.164W)
Pressure	$kg/m\ s^2$	pascal (Pa)	mm Hg (= 133Pa) torr (= 133Pa)
Molality	mol/kg	mol/kg	g/kg
Concentration	mol/dm^3	mol/dm^3	mol/ℓ (= mol/dm^3) g/ℓ, g/dℓ

* Advanced texts generally use negative exponents, e.g., speed is shown as ms^{-1} rather than m/s; however, to simplify typesetting and the writing of equations, the more familiar format of numerator and denominator has been used here.

Resting Energy Usage

Let us look first at the energy used under resting conditions. A variety of homeostatic processes contribute to resting energy usage (Table 1–2). Continued operation of the respiratory pump maintains the constancy of alveolar and thus arterial gas consumption, but energy is used by the chest muscles. Cellular homeostasis depends in turn on the steady pumping of blood by the heart, again an energy-using process. Within individual cells, other pumps transfer food from the gut to the blood stream, and waste products from the blood to the renal tubules. Cell membranes suffer a steady inward leakage of sodium ions and an outward movement of potassium ions, and this tendency must be corrected by operation of a "sodium pump." Likewise, the cycle of muscular contraction and relaxation depends on the pumping of calcium ions. All of these intracellular pumps also consume energy.

The basic cell consituents—protein, fat, and carbohydrate—seem relatively permanent, but are in fact broken down and reformed every few days, again at the cost of a substantial energy expenditure. The energy demands of synthesizing cell constituents are further increased by such processes as growth, tissue hypertrophy, pregnancy, and lactation.

If the environment is cool, the resting rate of metabolism may be deliberately increased (for example, by an increase of muscle tone or a deliberate breakdown and resynthesis of fat) in order to sustain body temperature. Lastly, unless a subject is lying completely relaxed upon a couch, some energy is expended in maintaining body posture against the force of gravity.

Exercise increases many of the sources of resting energy expenditure noted above. The work of the chest muscles and the heart is greatly augmented by the increase of ventilation and cardiac output, the pumping of sodium and calcium ions is increased to compensate for greater leakage of ions, more food must be absorbed, and more waste products excreted. A substantial hypertrophy of muscle may also be induced by a regular exercise program, and postural demands generally rise as a person moves from sitting or lying to an upright position.

TABLE 1–2 Factors Contributing to Resting Energy Usage

Food turnover of protein, fat, and carbohydrate
Pump mechanisms, e.g., respiratory, cardiac, gastrointestinal, renal, sodium, and calcium
Growth and hypertrophy
Pregnancy and lactation (women only)
Temperature regulation
Maintenance of posture

Specific Costs of Movement

Movement adds several new specific sources of energy expenditure as the body is displaced against gravitational acceleration and other opposing forces such as wind and friction. Let us consider a young woman with a 55-kg body mass who is cycling up a 1 percent gradient (Table 1-3). She is very conscious of a stiff headwind, and although she crouches low over the handlebars, the silhouette of cycle plus rider presents an area of perhaps $0.3m^2$ to the wind; at the particular wind-speed, this generates an opposing force of 43.3 newtons per square meter (13N).[2] There is always a small amount of friction in the chain and pedal bearings, but assuming that these have been well oiled, the main frictional resistance is between the tires and the road. If the tires are narrow and well inflated, the coefficient of sliding friction is about 0.05; this implies that the force opposing forward movement is one-twentieth of the mass of body plus rider, perhaps 3.75 kg force, or about 37N. There is also some air resistance, but since this is proportional to the third power of speed, it can be neglected when riding up hill. Let us assume that speed drops to 4.4 m per second (10 miles per hour). The rate of working against the wind and ground friction is then (13+37) 4.4 or 220 newton-meters per second (220 watts).[3] At the same time, potential energy is being accumulated by lifting the 55-kg woman and a 20-kg bicycle up the 1 percent gradient. The height climbed is (4.4) 0.01 meters per second; thus this element of energy expenditure amounts to a power output of 9.81 (55+20) 0.044 newton-meters per second or about 32 watts. In some sports, much further energy is lost in accelerating and decelerating the limbs or the entire body mass; however, the constant-speed rotary motion of the legs largely overcomes this particular problem for the cyclist.

In our example of the cyclist, it is instructive to notice the substantial power output demanded by a barely perceptible rise in the road. With a 10 percent gradient, the rate of accumulation of potential energy would in itself impose a load of 320 watts. Most individuals could only sustain this load for a fraction of a minute. When climbing a long hill, it is therefore essential to gear down and adopt a much slower rate of climbing.

Conservation of Energy

One of the important biochemical discoveries of the mid-nineteenth century was that the Newtonian

[2] See Table 1–1 Many older texts and gauges are calibrated in pounds or kilograms. 2.2 pounds = 1 kilogram = 9.81 newtons in a standard gravitational field (981 cm per square second). The older units become completely erroneous if the force of gravity changes (for example, during space exploration).

[3] Notice that calculations are greatly simplified when using SI units of newtons, meters and seconds; for instance, 1 watt = 1 J per second = 1 N·m per second.

TABLE 1–3 Work Involved in Cycling Up Grades of 1 Percent and 10 Percent at a Speed of 4.4 m/sec

Component	Elements	Work Calculation
Headwind	Force × projected area × speed	$43.3 N/m^2 (0.3 m^2)\ 4.4 = 58$
Ground friction	Mass × gravity × friction × speed	$75 \times 9.81(0.05)\ 4.4 = 162$
Air friction	Constant × projected area × $speed^3$	Neglected
Vertical ascent	Mass × gravity × speed × slope	$75 \times 9.81(0.01)\ 4.4 = 32$ $75 \times 9.81(0.1)\ 4.4 = 320$

principle of the conservation of energy applied to the human organism. People can neither create nor destroy energy. Whether homeostasis is being maintained or external work is being performed, the impact of these activities upon body reserves of energy can be determined by thermodynamic principles; in the long term, input must match output. Moreover, as with most machines of human invention, the body is mechanically inefficient. At best, some 25 percent of the stored energy is translated into "useful" work, with the remaining 75 percent appearing as heat. In a cool environment, the increase of heat production in an active person contributes to homeostasis, but under warmer conditions, elimination of metabolic heat poses a serious problem to continuing exercise.

SOURCES OF ENERGY

The Role of Adenosine Triphosphate

The immediate source of energy in the body is the chemical adenosine triphosphate (ATP). This molecule contains a terminal high energy phosphate bond. Thus, when it is broken down to adenosine diphosphate (ADP) and phosphate, the reaction is exothermal, i.e., energy is released by rupture of the phosphate bond and this energy can be used to perform the functions discussed above (muscular work, metabolic synthesis, or membrane pumping). The precise energy liberated from a single gram molecule of ATP varies somewhat with local conditions of temperature and pH, but is normally approximately 46 kJ:

$$\text{ATP} \rightarrow \text{ADP} + 46 \text{ kJ}$$

Unfortunately, the total intracellular stores of ATP are extremely small. For example, skeletal muscle contains only 5×10^{-6} moles per gram. Thus, even if 20 kg of muscle are called into play by vigorous exercise, the effective store of ATP energy is no more than $(20 \times 10^3)(5 \times 10^{-6})$, or one-tenth mole. The corresponding energy yield is only 4.5 kJ, and at least in theory this reserve could be exhausted by 0.5 seconds of all-out effort.

The Role of Creatine Phosphate

The next energy resource is a small store of creatine phosphate (Fig. 1–1). Creatine phosphate also has a terminal high energy phosphate bond, and the energy liberated by rupture of this bond can be applied to the resynthesis of ATP with an efficiency of close to 100 percent. The total reserve of creatine phosphate is approximately 15×10^{-6} mol per gram of wet muscle, so that in theory, both forms of "phosphagen" (ATP + creatine phosphate) could be depleted by approximately 2 seconds of maximum effort.

The two reactions are biochemically linked in such a way that creatine phosphate is depleted first, and only as exhaustion is approached do reserves of ATP decrease.

The Role of Glycogen

Once phosphagen reserves have been depleted, resynthesis must occur if exercise is to continue. The processes of resynthesis use the energy stored in glycogen and other foods. Glycogen can be broken down to pyruvate in the sarcoplasm of an active muscle. Under anaerobic conditions, pyruvate is converted to lactate, which accumulates in both the muscle and the blood stream. However, if the cardiac pump is bringing an adequate amount of oxygen to the working tissues, pyruvate is further metabolized to carbon dioxide and water within the mitochondria. Each glucose mole that is derived from glycogen[4] provides sufficient energy for resynthesis of 37 moles of ATP (a 63 percent efficiency in the transfer of energy from carbohydrate to ATP). Given that approximately 49 percent of the ATP energy can be applied in turn to the task of muscle contraction, the overall efficiency of energy transformation is 0.63×0.49 or approximately 31 percent, with the remaining 69 percent of the initial energy store being dissipated as heat.

Anaerobic Glycolysis

If oxygen is not available to the working muscle, the glycolytic reaction proceeds from pyruvate to lactate, and the latter accumulates within the sarcoplasm. The yield is then no more than 3 moles of ATP for each mole of glucose derived from glycogen, one-thirteenth of the efficiency calculated for aerobic metabolism.

[4] If glucose itself is the fuel, it must first be phosphorylated to glucose-6-phosphate, at the cost of one "priming" mole of ATP.

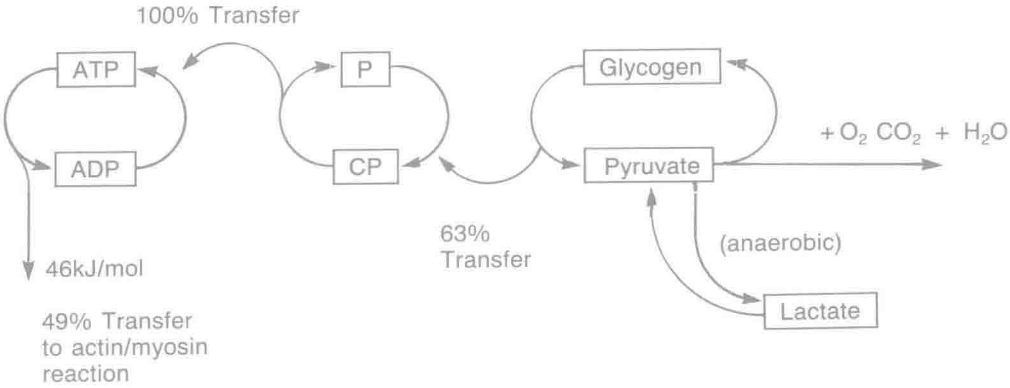

Figure 1–1 Diagram of energy flow in working muscle. ATP = adenosine triphosphate; ADP = adenosine diphosphate; P = phosphate; CP = creatine phosphate.

During the recovery period, a part of the lactate is oxidized to carbon dioxide and water, and the remainder is reconverted to glucose or glycogen, using energy derived from the oxidative reaction. In essence, each mole of glycogen can undergo approximately 10 cycles of anaerobic breakdown and resynthesis before its energy content has been exhausted. From a long-term perspective, the efficiency of anaerobic work may thus rise to ten-thirteenths of that for aerobic exercise.

Anaerobic energy release is limited by the intramuscular accumulation of lactate and associated changes of intracellular pH. When the intramuscular lactate concentration reaches approximately 30 mmol per cubic decimeter, key enzymes needed for the breakdown of glycogen (phosphorylase, phosphofructokinase) are inhibited, and anaerobic metabolism stops. Again assuming an active muscle mass of 20 kg, the total potential build-up of lactate is 600 mmol, equivalent to a yield of 1.8 moles of ATP, or about 87 kJ of energy. The speed of the anaerobic reactions is such (Table 1–4) that phosphagen breakdown may generate a power of more than 9 kilowatts for 2 seconds, while the build-up of lactate over a period of 40 seconds is equivalent to a power output of more than 2 kilowatts. By way of comparison, a sedentary woman with an aerobic power of 40 mℓ per kilogram per minute and a body mass of 55 kg can probably sustain an aerobic energy release of some 770 watts for 10 minutes (a total yield of 460 kJ); if the intensity of activity is decreased to 50 percent of aerobic power, this level of energy release can be sustained for 4 hours (a total yield of 5.39 MJ).

SUBSTRATE RESERVES

Muscle Glycogen

The main immediate reserve of energy is intramuscular glycogen. Local concentrations vary with diet, habitual activity and type of muscle fiber (fast or slow-twitch), but a typical figure is 15 g per kilogram of wet tissue. With 20 kg of active muscle, the total intramuscular glycogen store is thus 300 g, equivalent to 1.67 moles of glucose. Combustion of any type of carbohydrate in a heat-measuring "bomb calorimeter" shows an energy yield of about 16 kJ per gram or 2.9 MJ per mole of glucose equivalent, so that the total glycogen reserve can contribute approximately 4.8 MJ of energy. Typically, this is depleted over the course of 2 hours of exhausting activity.

Hepatic Resources

The liver also stores approximately 100 g of glycogen. During vigorous exercise, this is released into the blood stream as glucose at a rate of about 1 g per minute (5 to 6 mmol per minute). The total contribution amounts to 1.6 to 2.0 MJ over a bout of sustained exercise.

As physical activity continues, there is also some potential for the hepatic synthesis of glucose ("gluconeogenesis") from circulating glycerol, lactate, and amino acids. Glucose formation does not proceed fast enough to satisfy the full needs of the skeletal muscles once sarcoplasmic glycogen has been exhausted, but it does help to service tissues which can only metabolize carbohydrates (e.g., the brain and the red

TABLE 1–4 Energy Release in the Human Body

Source	*Rate of Yield (Watts)*	*Duration (sec)*	*Capacity of System (kJ)*
Anaerobic power	9200	2*	18.4
Anaerobic capacity	2175	40	87
Aerobic power			
100% loading	770	600	460
50% loading	385	14×10^3	5390

* In practice, ATP, creatine phosphate, and other immediate energy stores are usually depleted less rapidly than the theoretical 2 seconds.

cells). After 40 minutes of exercise, Wahren found that the percentage of freshly synthesized glucose in the hepatic vein was 16 percent at a cycle ergometer loading of 65 watts, 11 percent at a loading of 135 watts and 6 percent at a loading of 200 watts. After 4 hours of moderate activity, however, 45 percent of hepatic glucose output was attributable to gluconeogenesis.

Depot Fat

There are small amounts of fat stored within the muscle fibres. However, if activity is very prolonged, most of the necessary energy is derived from a mobilization of depot fat. The body carries a small amount of essential fat (larger in women than in men), but most sedentary adults have 10 to 15 kg of adipose reserves which can be exploited in any sustained athletic feat. Each gram of fat yields approximately 29 kJ of energy,[5] so that 10 kg of disposable body fat provides a total resource of some 290 MJ, sufficient for 3 to 4 weeks of strenuous exercise. The main drawback to fat as a source of fuel is that it can only be metabolized aerobically. During moderate exercise it provides approximately half of the required energy, but with more intense effort many muscle fibers become short of oxygen, and in such circumstances the limited reserves of glycogen must meet 75 percent or more of total energy needs. One interesting feature of a well-trained athlete is the ability to burn a higher proportion of fat during vigorous submaximal exercise; this conserves glycogen reserves for tasks that can only be performed anaerobically.

Tissue Proteins

If food intake is inadequate (e.g., an athlete attempting to make a specific "weight category," or a ballet dancer who is unduly concerned about her figure), the body may also draw upon protein reserves. The normal process of catabolism (breakdown) continues, or is accelerated, but resynthesis does not occur. The muscle mass is thus steadily depleted. The energy yield from protein is similar to that from carbohydrate, approximately 16 kJ per gram.

Alcohol

Alcohol can serve as an immediate energy source, with a yield of some 27 kJ per gram. A sedentary person who consumes 100 g per day (less than a liter of wine) thus satisfies a substantial proportion of energy needs from alcohol alone. Given that most alcoholic beverages contain few vitamins, a combination of regular drinking and a sedentary lifestyle can lead to the development of serious dietary deficiencies. The most common disorder in a chronic alcoholic is the mental disturbance (psychosis) with peripheral nerve inflammation that is associated with a lack of vitamin B_1.

[5] This figure is the energy yield of *body fat*. The heat yielded by dietary fat is somewhat greater (approximately 38 kJ per gram).

LIMITATIONS OF GAS TRANSPORT

If all-out physical activity continues for more than 30 to 40 seconds, the build-up of lactate forces a reliance on aerobic metabolism. A further important key to local homeostasis, and thus persistent functioning of the working muscles is therefore the transport of oxygen to and carbon dioxide from the exercising tissues.

Oxygen

The relative barriers to movement of oxygen and carbon dioxide can be gauged from the respective partial pressure gradients between the atmosphere and the working tissues. The total gradient for oxygen is some 20 kilopascals (kPa).[6] During a large muscle task such as treadmill running, approximately one-third of this barrier (or impedance, to think in electrical terms) arises in the ventilatory system, and the remaining two-thirds in the cardiovascular system. The partial pressure in the capillaries of the active muscle drops to near zero. We may thus conclude that the major bottleneck for oxygen flow during this type of exercise is the ability of the heart to pump oxygenated blood from the pulmonary capillaries to the vascular bed of the active muscles. Local tissue factors do not become important until less than 20 percent of the total muscle mass is involved in the exercise.

Carbon Dioxide

The total pressure gradient for carbon dioxide is less than 10 kPa, partly because its effective blood solubility is five times greater than that of oxygen, and partly because CO_2 is more readily transported across the pulmonary membrane. During large muscle work, more than one-half of the barrier of CO_2 elimination arises in the thoracic pump, and in some older individuals performance is limited by an accumulation of carbon dioxide in the blood stream (chronic obstructive lung disease). In younger individuals, the smaller total pressure gradient does not necessarily exonerate carbon dioxide as a factor limiting performance; the key issue is whether the observed tissue pressure of 10 kPa reduces muscle pH to the point that glycolysis is being slowed through an inhibition of phosphorylase and phosphofructokinase. This does not generally seem to be the case.

[6] Older books have expressed partial pressure gradients in mm Hg. 100 mm Hg is equal to some 13.3 kPa (Table 1–1).

EXTERNAL EFFICIENCY

Measures of Efficiency

The mechanical efficiency of any system can be expressed very simply as the ratio of the output of useful work to the energy expended. The top athlete is commonly marked by not only a large power output, but also an efficient use of energy. The exercise physiologist usually distinguishes gross efficiency (total work output: total energy expenditure) from net efficiency (the latter being the ratio of total work output to total minus basal energy expenditure). Because of considerable difficulties in establishing a true basal reading, the resting energy expenditure is often substituted in the latter calculation. If the intensity of effort is high, the discrepancy between resting and basal values does not have a major influence upon the estimate of net efficiency. Even the resting energy expenditure can be quite variable in an anxious subject. A third possibility is thus to calculate efficiency (the increase of work output for a given increase of energy expenditure).

Typical Net Efficiency

The net efficiency is the most commonly used of these statistics, at least in exercise science. As noted in the section, The Role of Glycogen, there are sound biochemical reasons why efficiency should not exceed 31 percent, even under optimal conditions of aerobic work. In practice, somewhat lower net efficiencies are usually observed because (1) there is an incomplete coupling of biochemical resources to any external machine such as a cycle ergometer, and (2) the body work-rate is boosted above the assumed basal or resting figure by the increased demands on the cardiac and respiratory pumps, together with an increased need for postural activity while the body is moving. Some machines such as a modern cycle ergometer (average efficiency of operation in a young adult approximately 23 percent) come fairly close to the theoretical figure. In other activities such as stepping, the efficiency of upward displacement of the body mass is of a similar order to that seen in cycling. However, in the usual design of step test, the subject not only climbs up, but also descends. The total energy cost of the task is then increased by approximately one-third in assuring a controlled descent from the bench. In some sports, quite low efficiencies have been observed. Thus typical figures for a swimmer are only 1 to 2 percent. In such activities there is substantial opportunity for a coach to improve performance through an increase in the skill of the performer, even if energy output cannot be increased.

Efficiency on the Treadmill

Authors interested in treadmill exercise (particularly Rodolfo Margaria) have quoted mechanical efficiencies ranging from +30 percent to −120 percent, depending upon the slope. When a person is running on the flat, there is no ultimate upward displacement of the body mass. The "useful" work and the mechanical efficiency (at least in the terms of a physicist) are thus both zero. When running downhill the entire potential energy associated with descent of the body mass is lost (an efficiency of −100 percent), and a further 20 percent of energy is expended controlling this descent (a total net efficiency of −120 percent). During uphill running, efficiency reaches or may even exceed the theoretical maximum of 31 percent. A probable reason for this surprisingly satisfactory performance is that some of the potential energy liberated during descent of the leg becomes stored in stretched tendons (see Chapter 2).

FURTHER READING

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MEASURING ACTIVITY IN LABORATORY AND FIELD

CHAPTER 2

EXERCISE IN THE LABORATORY
- Cycle Ergometer
  - Mechanical Ergometers
  - Electrical Ergometers
  - Advantages and Disadvantages
  - Maximum Testing
- Treadmill
  - Work Efficiency and Oxygen Cost
  - Maximum Tests
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- Step Tests
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MEASUREMENTS OF HABITUAL ACTIVITY
- Dietary Records
- Questionnaires
- Direct Observation
- Mechanical Impulses
- Heart Rate
- Ventilation
- Oxygen Consumption
- Biochemical Correlates
- Other Measurements

The exercise physiologist needs well-standardized laboratory forms of exercise in order to determine current levels of fitness, to examine human reactions to graded exercise, and to provide known training stimuli. Field measurements of habitual activity are an important foil to this approach. They can indicate whether the fitness level observed in the laboratory is below the individual's potential, because of a sedentary lifestyle. Moreover, measurement of total daily energy usage provides guidance to nutritional requirements in various situations. Finally, determination of individual costs of selected activities is needed for accurate exercise prescription in work and leisure.

Before delving more deeply into exercise physiology and biochemistry, it is thus important to review how standard exercise is performed in the laboratory, and how energy expenditures are assessed in the field.

EXERCISE IN THE LABORATORY

Cycle Ergometer

The cycle ergometer provides a readily standardized work task. In the mechanical type, subjects crank a flywheel against the friction imposed by a loaded leather belt or the air resistance of a series of vanes, while in the electrical type effort is developed against the impedance of a dynamo or an electro-magnet.

Mechanical Ergometers. The mechanical device of a loaded belt is the simplest type of arrangement, although unfortunately the indicated work-rate ignores a frictional energy loss of 8 to 10 percent in the chain and pedal bearings. The coefficient of friction on the main flywheel decreases as the belt becomes hot, so that a frequent adjustment of tension is needed in order to ensure a constant work-rate. The work performed by the subject also depends on the pedalling rate, so that power output may drop below the intended value as a person becomes fatigued (Table 2–1); it is always important to use a counter to determine the precise number of flywheel revolutions per minute.

Electrical Ergometers. The loading of many electrically-braked ergometers can be modified by adjusting the current flowing through the field coils of the dynamo or electromagnet. Given a suitable type of feedback device, compensation can be made for small variations in the speed of pedalling. Unfortunately, the mechanical efficiency of the subject changes with speed. Thus, if there is any great departure from the optimum 50 to 60 pedal revolutions per minute, the subject must work harder in order to sustain a given output of electrical energy. The main drawbacks of the electrical type of ergometer are a high capital cost and a need for periodic calibration by bolting a known source of power (a torque generator) to the pedal crank shaft.

Advantages and Disadvantages. The main advantages claimed for the cycle ergometer (Table 2–2) are a seated subject (facilitating ancillary measurements of oxygen consumption, cardiac output, and blood pressure) and a relatively constant mechanical efficiency (Table 2-3) of approximately 23 percent (facilitating the conversion of external work-rate into an approximate power demand on the body). The main disadvantages are (1) a need to adjust loadings for inter-individual differences of body mass and thus the likely working capacity of the subject, (2) overloading of the quadriceps muscle at high intensities of effort (so that maximum effort is often halted by local muscular fatigue rather than a general exhaustion of the cardiorespiratory system), and (3) some difficulty in dismounting should an emergency arise.

Maximum Testing. Experienced cyclists sometimes complain that the usually required cadence of 50 to 60 revolutions per minute is less than they adopt in vigorous cycling. By fitting toe clips, drop handlebars, and a very high racing saddle, while allowing the subject to stand for a final "sprint", it is possible to attain the maximum oxygen intake seen on a treadmill. However, with more usual cycle ergometer techniques, the limiting oxygen consumption falls 7 to 8 percent short of a true maximum value, due to local muscular fatigue.

TABLE 2–1 Energy Cost of Three Common Modes of Laboratory Exercise

Measurement Factor	*Cycle Ergometer*	*Treadmill*	*Step*
Force	Pendulum or belt loading (e.g., 20 N)	Weight of body + clothes (e.g., 600 N)	Weight of body + clothes (e.g., 600 N)
Distance	2π (radius of flywheel) (e.g., 2 m)	(e.g., 1 m)	Step height (e.g., 0.45 m)
Work	40 J	600 J	270 J
Speed	2π (radius) pedal revs per second (gear rate) (e.g., (2)1(2.5) = 5 m/s)	Belt speed (slope) (e.g., (2)0.05 = 0.1 m/s)	Ascents per second (e.g., 0.33)
Power output	(20)5 = 100 W	600(0.1) = 60 W	270(0.33) = 90 W

TABLE 2–2 Comparison of the Advantages and Disadvantages of Various Laboratory Forms of Exercise

Cycle Ergometer	*Treadmill*	*Step Test*
Advantages		
Seated subject	Effort limited by central factors	Low cost
		Simplicity
Relatively constant mechanical efficiency	Effort machine-paced	Portability
	Natural exercise (moderate walking)	No need for calibration
		Familiar exercise
		No need for electricity
Disadvantages		
Inter-individual differences of loading	Cost	Ancillary measurements difficult
	Noise	
Quadriceps overloaded	Need for special wiring	Danger of stumbling (high speeds)
Difficult to dismount in an emergency	Bulk	
	Causes anxiety (uphill running)	Step too tall for young children
Power output varies with pedalling rate		
	Danger of injury	Self-paced
Cost	Ancillary measurements difficult	
Calibration		
Peak effort submaximal		

Treadmill

Work Efficiency and Oxygen Cost. Some work is performed while walking or running on the level, since the center of mass of the body is raised and lowered repeatedly. However, the body does not accumulate any potential energy and there is no readily measured external power output; convention thus ascribes a mechanical efficiency of zero to this activity (see Chapter 1). As in cycling (see Chapter 1), the energy cost of moving increases sharply if an uphill gradient is introduced. The vertical component of the total work is calculated quite readily as the product of body weight (expressed in Newtons), the treadmill speed (expressed in m per second) and slope (expressed in decimal format, for example, 5 percent = 0.05). The mechanical efficiency of uphill running (up to 30 percent in terms of vertical work, as much as 40 to 45 percent when account is taken of oscillations in the center of mass) is higher than would be anticipated from the biomechanical reactions involved (see Chapter 1). The explanation is that when the foot hits the track, the tendo-Achilles is stretched and stores some of the potential energy released by descent of the body's center of mass; this resource is used to lift the body when the next stride is taken. At low speeds, walking is more efficient than running, but as the speed of the treadmill is increased, the oxygen cost of walking rises more sharply than that of running (Fig. 2–3). Thus, depending somewhat on the individual's leg length, running becomes the more economical mode of progression at a speed of approximately 2 m per second (7.2 km per hour).

Maximum Tests. As the speed of the treadmill is increased, the oxygen cost of running at first shows a proportional rise, but eventually a point is reached where a further increase of speed or slope augments oxygen consumption by less than 2 mℓ per kilogram per minute (1.5 mmol per kilogram per second). This is the generally accepted definition of a "centrally-limited" maximum oxygen intake (Fig. 2–1, also see Chapter 8); it is thought that the maximum cardiac output, and thus the maximum oxygen intake of the individual has been attained.

Because a high proportion (approximately 70 percent) of the body muscles are already involved in uphill treadmill running, it is not possible to increase either cardiac output or oxygen consumption more than marginally by performing simultaneous arm work (for instance, manipulating some form of ski pole while continuing to run on the treadmill).

Downhill Runners. If the treadmill is arranged for downhill walking or running, the body absorbs and releases as heat an amount of potential energy equiva-

TABLE 2–3 The Approximate Oxygen Cost of Common Forms of Laboratory Exercise*

Type of Exercise	*Mechanical Efficiency (%)*	*Oxygen Cost (ℓ/min)*	*Coefficient of Variation (%)*
Cycle ergometer	23	10.5(W) + 300	4–5
Treadmill	25	11.4(W) + 300	5
Step	16	7.3(W) + 300	7

* Assuming a resting oxygen consumption of 300 mℓ/min and a power output of W (watts)

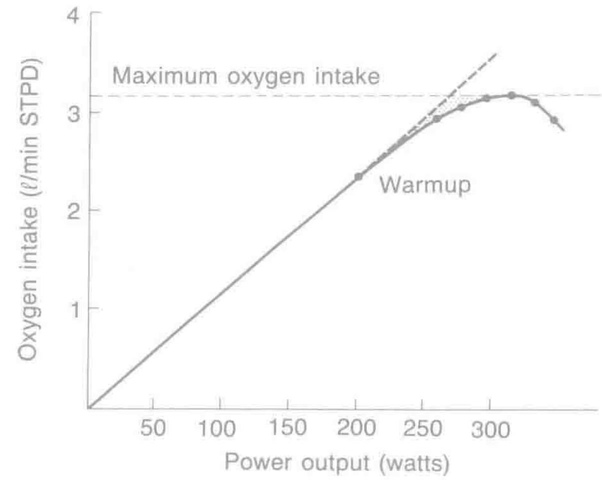

Figure 2–1 Concept of the measurement of maximum oxygen intake. The test begins with a 3-minute warmup at about 70 percent of maximum power output. Loading is then increased to an estimated 95 percent of maximum oxygen intake and is further increased by 5 percent at 2-minute intervals until a plateau has been identified or there are other indications to halt the test. The shaded area indicates a growing component of anaerobic activity. STPD = Standard temperature and pressure, dry gas

lent to the cumulative descent of the body's center of mass. Additional energy must be spent to control the descent (Fig. 2–2). If the cost of control amounts to 20 percent of the lost potential energy, the convention is to express mechanical efficiency as −120 percent (−100 percent, −20 percent). The gastrocnemius muscle must contract vigorously as it is being stretched by the impact of the foot (a process described as "eccentric work"), and the loading can sometimes be sufficient to cause local muscle damage with delayed soreness and a leakage of intramuscular enzymes into the blood stream (see Chapter 9).

Advantages and Disadvantages. The main advantages of treadmill exercise are (1) a central (cardiovascular) rather than a peripheral (muscular) limitation of maximum effort, (2) an exercise task where the subject cannot slow down as fatigue develops, and (3) a fairly natural pattern of activity (most people have some experience of both walking and running, although in practice there is at least a 10 percent inter-individual variation in the oxygen cost of both walking and running (Fig. 2–3) on a treadmill; moreover, many people show a substantial decrease of oxygen cost as they learn the technique of maintaining a constant position

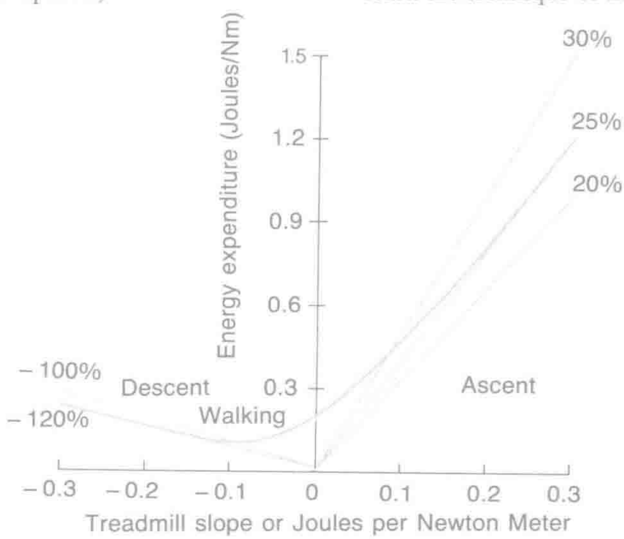

Figure 2–2 Energy cost of treadmill walking in relation to slope, showing isoefficiency lines for ascent (20 to 30 percent efficiency) and descent (– 100 to – 120 percent). Based on a concept of Margaria.