Don MacLaren • James Morton

Biochemistry for Sport and Exercise Metabolism

Second Edition

WILEY

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Preface

My goodness, it has been 13 years since we published the first edition of this text – in essence, based on lectures we provide for our undergraduate and postgraduate sport and exercise science and the sports/performance nutrition students at Liverpool John Moores University. Guess it is time for an update! The world does not stand still and certainly, neither does scientific endeavour. As Isaac Newton stated, 'To me there has never been a higher source of earthly honour or distinction than that connected with advances in science'. This is so true of the significant developments in techniques over the past 13 years or so – notably in the understanding of not only cellular and molecular control mechanisms but also cell structures. It is the technical developments that have enabled scientists to get a greater understanding of research into human metabolism. Tools such as magnetic resonance imaging and spectroscopy, mass spectrometry, more sophisticated ergometers and improvements in some biochemical testing apparatuses have contributed to the plethora of scientific investigations reported in peer-reviewed journals. To this end, we have updated our original text to that which you are ready to explore. Of course, there is a limit to what we can change since most of the biochemistry is in essence the same. To this end, we have made some subtle modifications. We have included a chapter on biochemical techniques in order to furnish you with some background as to how the reported metabolic changes during exercise have been achieved and have made a few additions in the three chapters on metabolism.

As sport and exercise scientists, ultimately, we are left with the task of critically evaluating research (both our own and those of others) concerning exercise metabolism in the hope of integrating training and nutritional strategies which maximize performance. Underpinning all of this demands a knowledge and understanding of some biochemical principles associated with the macronutrients involved in energy production and the likely mechanisms controlling these events. We hope that after completing this text of *Biochemistry for Sport and Exercise Metabolism*, you will possess the appropriate platform for which to do so! Furthermore, we hope you will have been stimulated sufficiently to further engage in a deeper understanding of your chosen area of interest. Best wishes and good luck!

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1

Energy Sources for Muscular Activity

Learning Outcomes

After studying this chapter, you should be able to:

- outline the key energy sources for exercise;
- distinguish between anaerobic and aerobic sources of energy;
- describe the essential structure of ATP;
- draw and explain the components of the energy continuum;
- describe the role of PCr in ATP synthesis;
- explain how PCr is resynthesized;
- describe the involvement of carbohydrates and fats as energy sources for exercise;
- explain reasons why an athlete is unable to sprint a marathon;
- describe the amounts and sources of energy in the body and their rates of energy formation;
- show how and where the main energy sources are derived and utilized;
- discuss how amino acids can be used as an energy source during exercise.

This chapter presents a brief overview of the energy sources used by muscles in order to engage in various activities. It is a 'taster' that will (hopefully) encourage you to delve a bit more deeply into the basic biochemistry of the macronutrients which provide energy, as well as to gain an understanding of the likely regulation of the processes which produce energy. From this perspective, this chapter examines the energy-yielding processes from a superficial level in addressing issues of energy for sprinting and for more prolonged events.

Key words

energy continuum
energy sources for exercise
aerobic energy sources
anaerobic energy sources
protein synthesis
protein degradation

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1.1 Adenosine Triphosphate: The Energy Currency

In order for muscles to contract and provide movement, energy is required. Such energy is provided by adenosine triphosphate (ATP) and is the only energy capable of being used for muscle contraction in humans. Figure 1.1 provides the structure of an ATP molecule. As you can see from this diagram, ATP consists of a base (adenine) attached to a sugar (ribose), to which is attached three phosphate molecules. The phosphates are attached by 'high energy' bonds which, when removed, provide energy.

$$\text{ATP} \leftrightarrow \text{ADP} + \text{P}_i + \text{Energy} \quad (7.3 \text{ kcal or } 30.5 \text{ kJ})$$

The process is reversible, which means that ATP may be re-formed from adenosine diphosphate (ADP) as long as there is sufficient energy to restore the missing phosphate molecule on to the ADP. The latter can be achieved by phosphocreatine (PCr) or by processes such as anaerobic glycolysis, and aerobic processes.

The stores of ATP in muscle tissue are rather limited, so there is a constant need to resynthesize it for survival, let alone movement. The amount of ATP in a muscle cell amounts to 25 mM/kg dry muscle or about 40–50 g in total, which is sufficient to enable high intense activity for around 2–4 seconds if it is the only useable source of energy available. This is not a great amount – hence the importance of resynthesis of ATP at rates sufficient to enable appropriate levels of exercise to ensue, i.e. fast rates of resynthesis for sprinting and slower rates for prolonged exercise.

1.2 Energy Continuum

The major energy sources for exercise are dependent on the intensity and duration of the activity. Examination of Figure 1.2 highlights that there appears to be three such sources, i.e. PCr, glycolytic and aerobic. These energy-producing processes predominate exercise from 1 to 10 seconds, 10 to 60 seconds and beyond 60 seconds respectively.

Another way of expressing the energy continuum is represented in Figure 1.3, which shows the major energy sources for running events of varying distances. Note that short, highly intense sprinting bouts lasting 1–10 seconds use PCr predominantly, while events such as the 400 m mainly use anaerobic glycolysis, and thereafter aerobic metabolism predominates.

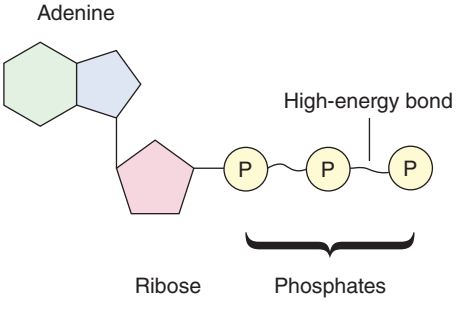

Figure 1.1 Adenosine triphosphate (ATP).

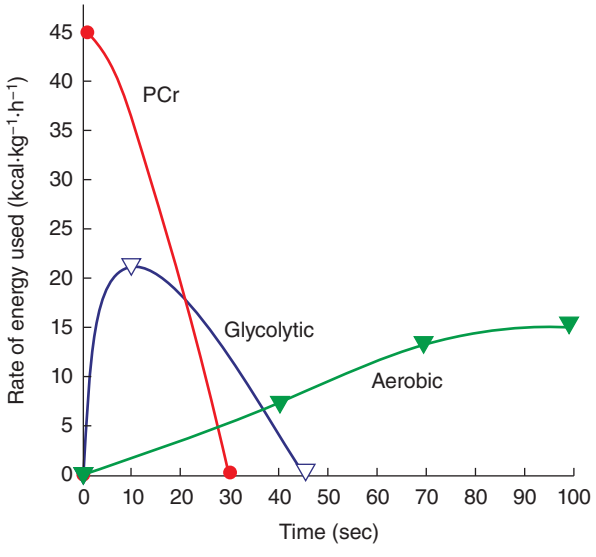

Figure 1.2 Energy continuum.

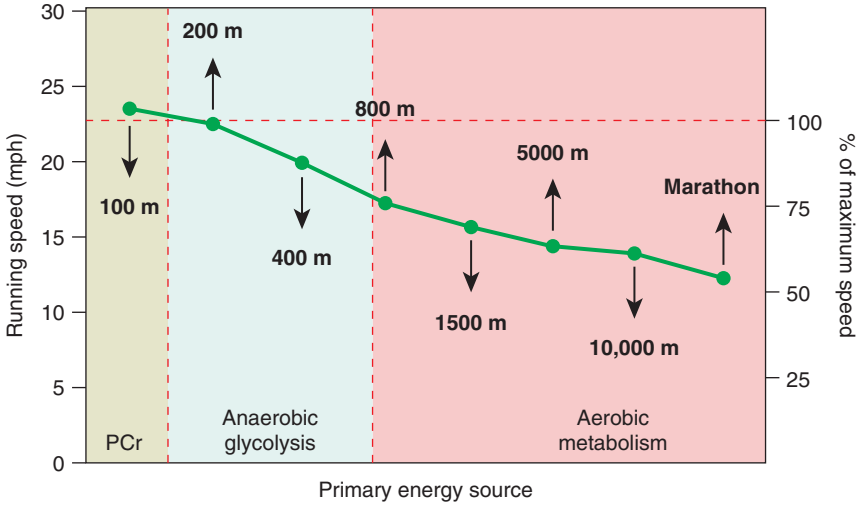

Figure 1.3 Primary energy sources for different running distances.

1.3 Energy Supply for Muscle Contraction

ATP is not stored to a great degree in muscle cells. Therefore, once muscle contraction starts, the regeneration of ATP must occur rapidly. There are three primary sources of ATP; these, in order of their utilization, are PCr, anaerobic glycolysis and aerobic processes.

Energy from ATP derives from cleaving the terminal phosphate of the ATP molecule. The resulting molecule is ADP. PCr converts ADP back to ATP by donating its phosphate in

the presence of the enzyme creatine kinase (CK), and in turn the PCr forms creatine (Cr), i.e. the dephosphorylated form of PCr.

$$ADP + PCr \underset{CK}{\Leftrightarrow} ATP + Cr$$

The reaction of PCr with ADP to form ATP is very rapid, but is short-lived since the cell does not store high amounts of PCr (the muscle concentration of PCr is about 80 mM/kg dry muscle or 120 g in total). However, during short, high-intensity contractions, PCr serves as the major source of energy. This form of energy generation is sometimes referred to as anaerobic alactic, because it neither produces lactic acid nor requires oxygen. It is of paramount importance in sports requiring bursts of speed or power, such as sprints of 1 to10 seconds, lifting weights, engaging in a high/long jump or a throw in an athletics field event.

Figure 1.4 provides a schematic to show the synthesis of ATP from ADP using PCr at the muscle crossbridge, as well as the regeneration of PCr from Cr by ATP at the mitochondria. This is known as the 'PCr shuttle'.

Thus, Cr is produced from PCr during intense bouts of exercise, while Cr is re-phosphorylated to PCr by ATP produced in the mitochondria during an aerobic recovery phase. Oxygen is needed for recovery of PCr, as can be seen in Figure 1.5, which clearly demonstrates that recovery of exercise-depleted PCr only happens when the blood supply to the exercising muscle is not occluded, i.e. there is an intact blood supply taking oxygen to the cells. If the blood supply is occluded (e.g. via a tourniquet), then PCr resynthesis fails. As a consequence, there is the need for a low level (so-called active) recovery in between bouts of intense exercise.

The enzyme CK, which regulates PCr activity, exists in a number of forms known as isoforms (this will be dealt with later). Note that not only is there a CK which favours the formation of ATP from PCr, but there is also another form, CK_{mito}, which is present at the mitochondria and favours the synthesis of PCr from Cr using ATP. In effect, the same enzyme (CK) but in different isoforms which results in either the breakdown or synthesis of PCr.

You should also note from Figure 1.5 that there is a rapid loss of PCr during intense exercise and that it is rapidly recovered (PCr stores may even be depleted if the exercise is sufficiently intense or prolonged). Nearly 75% of PCr is resynthesized within the first

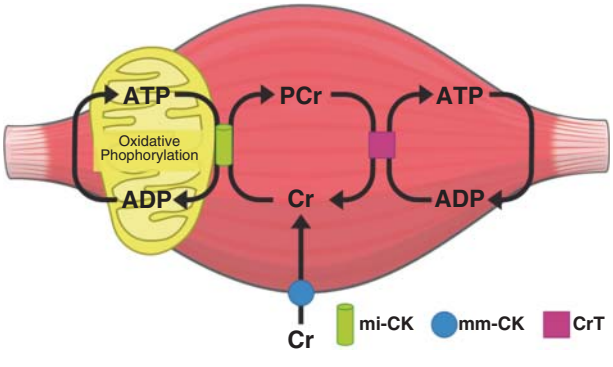

Figure 1.4 PCr shuttle (mi-CK is mitochondrial CK; mm-CK is skeletal muscle CK; CrT is creatine transporter).

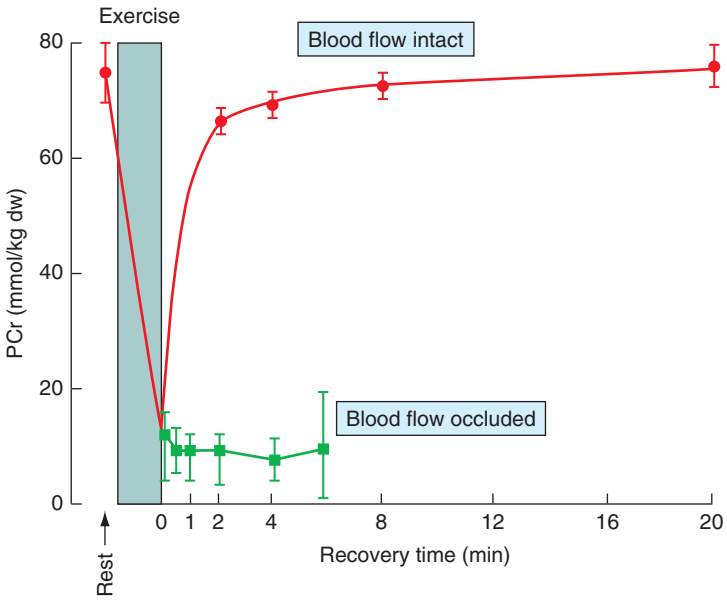

Figure 1.5 Resynthesis of PCr after exercise with and without an occluded blood supply (adapted from Hultman *et al.*, 1990).

minute of recovery and the rest over the next 3–5 minutes. The graph is biphasic, i.e. rapid restoration at first, then a second, slower phase.

As soon as muscle contraction starts, the process of anaerobic glycolysis also begins. Anaerobic glycolysis does not contribute as large an amount of energy as PCr in the short term, but its contribution is likely to predominate from 10 to 60 seconds.

During glycolysis, locally stored muscle glycogen, and possibly some blood-borne glucose, supply the substrate for energy generation. Glycolysis takes place in the cytoplasm, where no oxygen is required, so the process is called anaerobic. It has been referred to as 'anaerobic lactic', since lactic acid is formed as the end product. Sufficient lactic acid formation can lower the pH of the cell (i.e. make it more acid) to the extent that further energy production may be reduced.

The major substrate for anaerobic glycolysis (see equation below) is glycogen stored within the muscle, so prior hard exercise without adequate repletion of glycogen will limit further high-intensity short-term work.

$$\text{Glycogen} \rightarrow \text{Glucose-1-P} \rightarrow \text{Lactic acid} + \text{ATP}$$

Exercise beyond 60 seconds requires mainly aerobic energy sources, such as the complete oxidation of glucose or fatty acids to carbon dioxide and water. These processes necessitate oxygen and take place in the mitochondria of the cells. The equations below illustrate the essence of aerobic metabolic reactions:

$$\text{Glucose} + \text{Oxygen} \rightarrow \text{Carbon dioxide} + \text{Water} + \text{ATP}$$

$$\text{Fatty acid} + \text{Oxygen} \rightarrow \text{Carbon dioxide} + \text{Water} + \text{ATP}$$

More detail about these processes are presented in Chapters 5 and 6.

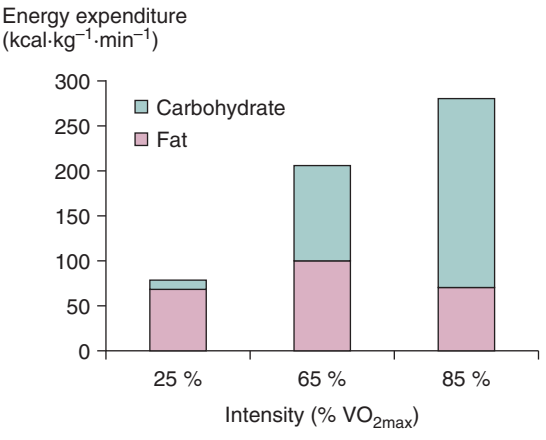

Figure 1.6 Carbohydrate and fat use at three exercise intensities (adapted from Romijn *et al.*, 1993).

Aerobic activities invariably occur at lower exercise intensities (which are those lasting longer than one minute), and the contributions of carbohydrate and fat at these levels of intensity can be realized in Figure 1.6. Note that fats contribute a greater percentage (and amount) of energy at 25% VO_{2max} (i.e. walking pace) than carbohydrate, around 50% of the energy at 65% VO_{2max} (i.e. steady state pace), and around 25% of the energy at 85% VO_{2max} (i.e. an intense aerobic bout with some significant anaerobic energy involved).

1.4 Energy Systems and Running Speed

Based on world record times, humans can maintain maximum sprinting speed for approximately 200 m. The average speeds for the 100 and 200 m world records are similar, at 22.4 and 21.6 mph, respectively. However, with increasing distances, average speeds decline. The average speed for the marathon world record is about 12 mph, which is 55% of the world sprint record. This is quite a remarkable pace, since the marathon distance is more than 200 times the length of a 200 m race.

Although natural selection plays a crucial role in elite sprinting and marathon performance, the energy systems must also be highly trained and exercise-specific to be successful. For example, the energy needed to maintain an average sprinting speed of 22 mph for 200 m or less, and that required for an average running speed of 12 mph for the marathon, are acquired by two very different systems (the predominant energy systems required for running at different speeds can be seen in Figure 1.3). The primary energy source for sprinting distances up to 100 m is PCr. From 100 to 400 m, anaerobic glycolysis is the primary energy source. For distances longer than 800 m, athletes rely primarily on aerobic metabolism.

The rate of glycogen and fat utilization varies according to the relative running speed. Although the rate of glycogen utilization is low while running a marathon, the duration of the event increases the possibility of depleting glycogen stores. In contrast, the rate of glycogen utilization is substantially higher during a 5000 m run, but glycogen depletion is not a concern because of the shorter duration of the event.

Maximum maintainable speed decreases by approximately 7 mph as running distance increases from 200 to 1500 m. However, as the distance increases from 1500 m to 42.2 km,

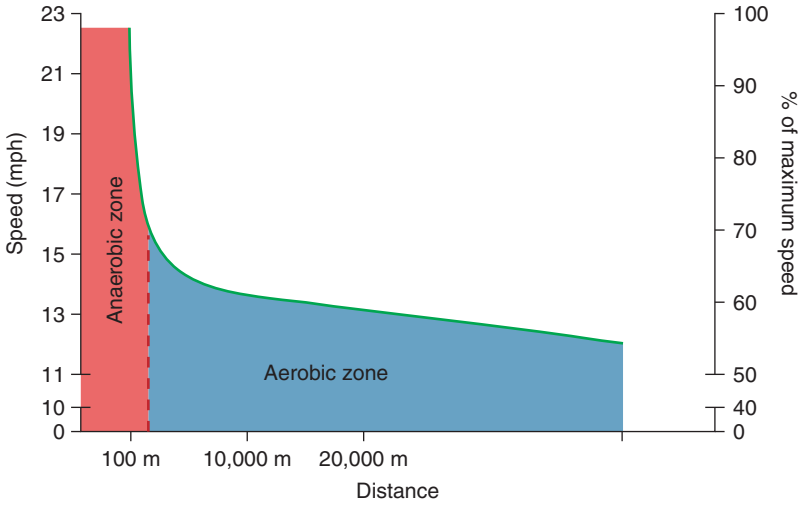

Figure 1.7 Sustainable running speed and distance run.

maximum maintainable speed only drops by an additional 3.5 mph. On average, a healthy, fit, non-elite, male athlete can be expected to sprint at an average speed of 16–18 mph for 100–200 m and at approximately 6–8 mph for a marathon (see Figure 1.7).

1.5 Why Can't a Marathon be Sprinted?

Figure 1.7 clearly demonstrates the inability to sustain high running velocities for a protracted duration. So why is an athlete unable to keep up higher running speeds over a marathon distance? The different energy sources have already been noted above, but what it is necessary to understand is that each of these energy sources resynthesizes ATP at varying rates. Table 1.1 highlights the likely rates of ATP production, and you should note the hierarchy.

The PCr system is the most rapid of these ATP-producing systems. A calculated rate of 9 $mM \cdot kg^{-1} \cdot s^{-1}$ dry muscle is more than twice as fast as ATP generation from anaerobic glycolysis which in turn is twice as fast as aerobic oxidation of carbohydrates. Furthermore,

Table 1.1 Maximum rates of energy production.

Metabolic process	Maximum power ($mM \cdot kg^{-1} \cdot s^{-1}$)
PCr → ATP	9
CHO → lactate + ATP	4
CHO → $CO_2 + H_2O$ + ATP	2
Fat → $CO_2 + H_2O$ + ATP	1

the aerobic breakdown of carbohydrates produces ATP at twice the rate of fats (i.e. 2 vs. 1 mM·kg^{-1}·s^{-1}). It thus seems that energy processes in the cytoplasm produce ATP at a faster rate than those which require oxidation via the mitochondria, and that carbohydrates produce ATP quicker than fats.

In Chapters 5 and 6, we will see that whereas PCr generation of ATP is a single reaction, anaerobic glycolysis entails 10 reactions, aerobic breakdown of glucose necessitates around 26 reactions (if the TCA cycle is used twice), and somewhere in the region of 90–100 reactions are required for complete fatty acid oxidation. No wonder, there are varying rates for ATP production.

Since the muscle stores of PCr are rather limited, and the end product of the rapid ATP generation from anaerobic glycolysis produces lactic acid, it would appear that it is not possible for an athlete to keep running at a sprint pace when undertaking a marathon – either they would run out of PCr, or the pH of their muscles would be significantly reduced due to lactic acid production. In addition, there are also limited stores of muscle and liver carbohydrate (glycogen) which would seem to be problematic as a source of energy for a complete marathon, so the need to employ fatty acids is important in energy production. Fatty acids produce the slowest rates of ATP synthesis – hence the fact that when these stores are engaged, running speeds are lowered.

1.6 Energy Sources and Muscle

Figure 1.8 provides an important overall schema as to how carbohydrates and lipids contribute as the major energy sources for muscle activity – the relevance of amino acids will

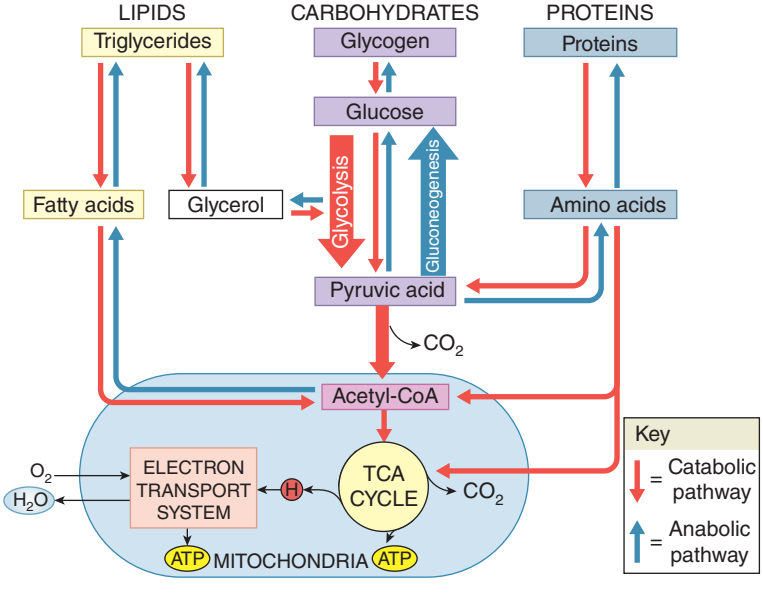

Figure 1.8 Schema of key sources and processes for skeletal muscle to derive energy during exercise.

Table 1.2 Energy sources available to working muscle including amounts and likely duration before depletion.

	ATP	PCr	Anaerobic glycolysis	Carbohydrate oxidation	Fatty acid oxidation
Total amount	40 g	120 g	350 g of CHO	500 g of CHO	15,000 g of fatty acids
Duration of exercise before depleted stores		4–6 sec	1–2 min	1–2 h	>6 h
Max rate of ATP synthesis ($mM \cdot kg^{-1} \cdot s^{-1}$)		9	4	2	1

be described in Chapter 4. It is a figure that we shall return to, albeit in greater detail, throughout the text. In summary, you will note that the so-called anaerobic energy processes from ATP, PCr and anaerobic glycolysis occur in the cytoplasm, whereas the aerobic energy processes from muscle glycogen, blood-borne glucose, intramuscular triacylglycerol and blood-borne free fatty acids take place in the mitochondria. The blood-borne glucose arises from the liver due to both the breakdown of liver glycogen and the ability of the liver to produce glucose from glycerol (in essence the breakdown of triacylglycerol) as well as amino acids such as leucine and glutamine. Furthermore, it is clear that in order for blood-borne sources to enter a muscle there is a need for some form of membrane transport mechanism for each of the extramuscular energy sources to enter a muscle cell as rapidly as possible. In Chapters 5 and 6 we will explore, in more detail, the nature of these transporters as well as examine the production of energy in skeletal muscle.

A final consideration is to deliberate as to how much energy these sources contain and how quickly a muscle can utilize them. Table 1.2 highlights a number of key points in relation to energy sources for muscle. These include:

1. the total amount of the energy source, from which it is quite apparent that the faster ATP-producing sources normally present within the muscle are limited (notably PCr and intramuscular glycogen for anaerobic glycolysis) whereas the slower ATP-producing and essentially extramuscular sources are more plentiful;
2. the likely duration for which these energy sources will last if they are the only source of ATP production, from which it is apparent that extramuscular sources provide longer lasting energy compared with intramuscular sources;
3. the maximal rates by which they can produce ATP from which it is apparent that intramuscular sources which do not require oxygen (anaerobic processes) rapidly generate ATP, whereas those requiring oxygen (aerobic processes) generate ATP more slowly.

1.7 Can Muscle Use Protein for Energy?

So far there has been little mention of using proteins for energy. Muscles are made of proteins in the main, but can muscle protein provide energy? The answer is, to a limited extent,

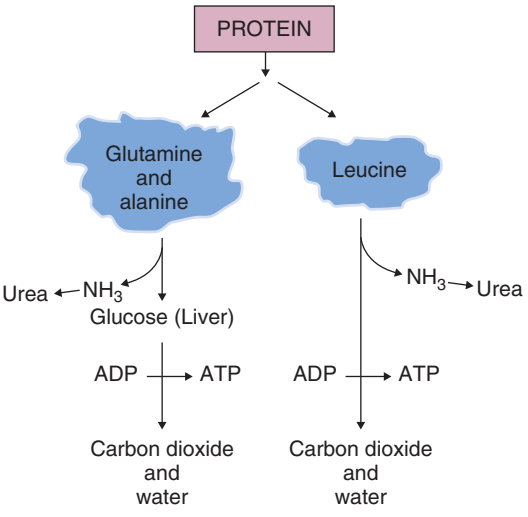

Figure 1.9 Likely use of amino acids for energy.

yes. A major difference between carbohydrates and fats is that they are essentially made up of carbon, hydrogen and oxygen only, whereas protein molecules also contain an amino group (i.e. a nitrogen). The end result of carbohydrate and fat oxidation is the generation of carbon dioxide and water, whereas oxidation of proteins requires the removal of nitrogen.

Figure 1.9 illustrates the fact that amino acids (the basic structural component of proteins) can, after the removal of the nitrogen (which ends up as urea), be converted to carbohydrates, which can then be oxidized. During prolonged exercise, the amino acids alanine and glutamine are converted to glucose in the liver, and the glucose is then oxidized by muscle. In addition, the muscle also has a limited capacity to oxidize the amino acid leucine. In total, amino acids usually accounts for 5% of the energy needed by muscle.

1.8 Key Points

- Adenosine triphosphate (ATP) is the useable form of energy for muscle contraction.
- Phosphocreatine (PCr), anaerobic glycolysis and aerobic processes enable ATP to be resynthesized during exercise.
- High intensity bouts of exercise demand a faster rate of ATP generation if the activity is to proceed and this is achieved by the faster 'anaerobic' sources, i.e. PCr and anaerobic glycolysis.
- Low to moderate bouts of exercise use aerobic energy processes such as complete oxidation of carbohydrates and fats.
- ATP and PCr content are limited in muscle and hence the reduced capability to engage in very intense levels of activity for prolonged periods.
- Anaerobic glycolysis results in lactic acid formation which is considered by some research to contribute to fatigue.
- Aerobic energy sources can be present within muscle (intramuscular glycogen and intramuscular triacyglycerol) or brought to the muscle as exogenous sources (glucose, acids and amino acids).

- Carbohydrate sources of energy (glycogen) are limited in comparison with fat sources.
- Amino acids from protein breakdown can contribute to energy production in a limited manner.

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2

Skeletal Muscle Structure and Function

Learning Outcomes

After studying this chapter, you should be able to:

- describe the gross anatomical structure of skeletal muscle;
- list the main sub-cellular components of the muscle fibre and outline their location and function;
- draw and label the sarcomere including the A-band, I-band, M-line and H-zone;
- describe the structure of the thick and thin filaments;
- define the term motor unit;
- explain the structure and function of the neuromuscular junction;
- explain and outline the main stages involved in the process of muscle contraction;
- compare and contrast the structural, biochemical and functional properties of type I, type IIa and type IIx muscle fibres;
- explain how muscle fibres are recruited with varying exercise intensities;
- define what is meant by lengthening, shortening and isometric muscle contractions;
- highlight and explain the phases of a twitch contraction;
- describe how stimulation frequency affects contractile force and define the term tetanus;
- explain the length–tension and force–velocity relationships;
- define the terms fatigue, central fatigue and peripheral fatigue.

Key words

skeletal muscle structure	muscle relaxation	muscle fibre types
muscle contraction	sliding filament mechanism	central and peripheral fatigue

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2.1 Skeletal Muscle Structure

In Chapter 1, we provided an introductory overview of the energy sources and systems involved in producing energy for muscular activity. Given that our focus is on the provision of energy for working *skeletal muscle*, it follows that we should now develop a sound understanding of both the structure and function of muscle itself. These topics are therefore the central theme of this chapter. Much of what will be discussed herein relates to the combined interplay between a variety of sub-cellular components and proteins involved in co-ordinating muscle contraction. For this reason, readers not familiar with general cell structure or protein function may wish to initially read sections of Chapter 4 prior to reading this chapter.

Skeletal muscle can be considered an organ as it is composed of cells from multiple tissues, i.e. nervous tissue, connective tissue, etc. and, of course, cells from muscle tissue itself. In this context, skeletal muscle is the largest organ in the human body, comprising 40–50% of total body weight.

There are over 600 muscles in our bodies, all performing common functions:

1. producing body movements;
2. maintaining posture;
3. storing and moving substances within the body; and
4. generating heat.

Skeletal muscle is so called because it primarily functions to move bones of the skeleton and as such, muscle tissue is connected to bones by connective tissue known as tendons. Each end of a specific skeletal muscle is attached to a bone that is essentially stationary (termed the *point of origin*) or to a bone that is moved (termed the *point of insertion*) during the specific muscle contraction. For example, the *biceps brachii* muscle has its points of origin and insertion in the scapula and radius bones, respectively.

2.1.1 Gross Anatomical Structure

The gross anatomical structure of skeletal muscle is shown in Figure 2.1. Surrounding the entire whole muscle is a strong sheet of fibrous connective tissue known as *fascia*. Three separate layers of connective tissue then extend from the outermost layer of fascia to strengthen and protect the muscle further.

The initial layer encompassing the whole muscle is known as the *epimysium*. If we were to cut through the epimysium, we would then encounter the *perimysium*. The perimysium encloses groups of 10–100 muscle cells and essentially separates them into muscle cell bundles known as *fascicles*. In turn, each muscle cell within this bundle is also separated from one another by a layer of connective tissue known as the *endomysium*.

2.1.2 The Muscle Fibre

Skeletal muscle cells are more commonly referred to as *muscle fibres* and they differ from many other cells in the body for a number of reasons. Muscle fibres have a unique shape