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Biochemistry for Sport and Exercise Metabolism

Don MacLaren
James Morton

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Preface

Ever since I started lecturing, firstly as a biologist (1973–1980) and then as a sport scientist (1980–2010), I always encouraged my students to keep in mind the questions 'how' and 'why' – in other words, how does that happen and why does that happen? In essence, I wanted them to possess an enquiring mind and not to be satisfied with a superficial understanding of the subject matter if possible – especially if the subject is one in which they wish to specialize.

As a young lecturer in exercise physiology in 1980, I was fortunate enough to possess the wonderful '*Textbook of Work Physiology*' by Astrand and Rodahl, and so get my teeth into a new subject area. As a biologist with a passion for sport, this really was exciting and novel to me. Having an opportunity to lecture in this field with my world-renown colleague, Tom Reilly, I couldn't have wished for a better start. However, there was a problem. In order to understand the 'how' and the 'why' of energy production for muscle contraction and exercise, it was imperative to have a knowledge and understanding of biochemistry.

I was fortunate enough to have undertaken some modules in biochemistry as an undergraduate at Liverpool University, but the sports science students also required this knowledge. In the early years, this was achieved by placing them with the biology and biochemistry students. Unfortunately, it didn't really work out, because the emphasis was not (at least initially) on relating to sport and exercise. The same was said of the statistics modules – too pure, too detailed and not applied enough.

So what did I do? I decided to run the biochemistry modules myself for our own students. The end result was greater satisfaction from the student cohorts and a greater interest by myself in what was necessary and to what depth. I was not intent on producing biochemists, but rather enabling sport science (physiology) students to gain a better grasp on aspects of biochemistry and metabolism as relating to sport and exercise.

Did I (and thereby my students) have recourse to any useful biochemistry texts for support? The answer was a qualified 'yes'. I was also fortunate enough to buy another wonderful textbook, '*Biochemistry for the Medical Sciences*' by Newsholme and Leech. This was a rather large tome to get through, but it did present much of the material I felt was needed for our students and, because the *late* Eric Newsholme had a passion for running, it related to aspects of sport. To gain further understanding, I encouraged my students to read other biochemistry textbooks (which were for students on biochemistry degree courses) that were available in the library. Over the years, I presented my adapted versions from such texts, since nothing else was suitable. Of course, more recently, a number of biochemistry textbooks have been written for sport and exercise science students, and what is interesting to note, in general, is how traditional black and white texts have become more colourful (and perhaps more interesting).

In May 2002, a young, eager second year student came to see me about getting on my level 3 'Muscle Metabolism' module. A prerequisite for this module was to undertake my level 2 'Biochemistry for Sport' modules. Being a science and football student and not a sports science (physiology) student, he had not had the opportunity to take this module. I tried to put him off, but he was quite insistent. So I gave him a biochemistry text to read over the next four weeks and to come back and see me. I had hoped it would turn him off. Fortunately, he kept coming back for tutorials to get a clear grasp of various concepts. I realised that this guy was not for turning and I allowed him to enrol on my level 3 module. He completed the module with a clear first class mark, obtained a first class degree overall, and went on to successfully undertake a PhD (with myself on his supervisory team) in exercise metabolism. His name? Dr James Morton – my co-author.

Since first arriving in Liverpool ten years ago, James has developed a passion for research and teaching exercise biochemistry and metabolism. He has helped me enormously. When I was asked to write this book, I agreed to do so on the basis that he would help me. Thankfully he agreed. We both feel that we needed to provide a textbook dedicated to sport and exercise science students who want to gain a solid (not necessarily comprehensive) understanding of key aspects in biochemistry – particularly those relating to energy metabolism. That is our mission in this text. We hope that the way we have approached and organized the work is interesting and makes you want to continue. Although not a superficial text, this book is not a comprehensive biochemistry treatise, but rather one which should 'tickle your fancy' and want you to read more and develop yourself.

We have organised the book into three parts. The first part encompasses some rather basic information for you to get to grips with. This includes an overview of energy metabolism (hopefully to gain your interest), some key aspects of skeletal muscle structure and function and some simple (but necessarily basic) biochemical concepts. The second part of the book really gets to grips with the three macromolecules which provide energy and structure to skeletal muscle – carbohydrates, lipids, and protein. The third and final part moves beyond biochemistry to examine key aspects of metabolism, i.e. the regulation of energy production and storage. To this end, we have a chapter on basic principles of regulation of metabolism, followed by three chapters exploring how metabolism is influenced during high-intensity, prolonged and intermittent exercise by intensity, duration, and nutrition. We also provide some pointers towards an understanding of fatigue when undergoing these activities. This is, after all, how we teach and progress our biochemistry and metabolism modules, and so we want to share this with you.

Dear reader, I hope you enjoy the journey into biochemistry and muscle metabolism as much as I have over many years. Sadly, I have come to the end of my career, but am fortunate enough to pass on the mantle to my dedicated and enthusiastic colleague, James Morton. Remember to always ask the questions 'how' and 'why'.

Don MacLaren, PhD

Exercise metabolism is undoubtedly an essential component of sport and exercise science degree programmes. While many students are fascinated by this topic, they often have difficulty in grasping the underpinning biochemistry that regulates how our muscles produce energy for exercise. Students tend to focus on learning the essential facts, chemical structures and the major metabolic pathways, often neglecting the understanding of how these factors respond to the stress of exercise.

A focus on factual recall without understanding of application is, of course, not representative of a deep approach to learning. To this end, we have sought to develop a text which combines a traditional approach to biochemistry teaching but with a focus on sport, by ensuring that the material is always dominated by exercise-related questions. In our experience, students of sport and exercise science learn better when their real interest of sport and exercise dominates the conversation. If by the end of this text, you now understand how exercise mode, intensity, duration, training status and nutritional status, etc. can all affect the regulation of energy-producing pathways, then I believe we will have achieved our aim. Additionally, if you can apply this material in the real world, perhaps to develop training and nutritional programmes to maximise athletic performance, then you have successfully acquired the deep approach to learning that we strive to achieve every time we enter a lecture theatre.

In writing this text, I must acknowledge the support of several people who have played a significant role in these early years of my academic career. Firstly, I will be forever grateful to my co-author, Professor Don MacLaren. It was Don who first fuelled my passion for exercise metabolism as an undergraduate student, and who continued to provide much valued support both as a postgraduate student and as an academic member of staff. His open door approach and his ability to motivate students to ask ‘how’ and ‘why’ are just two of many traits that I have tried to replicate in my own teaching.

Liverpool John Moores University is a wonderful institution. In addition to outstanding facilities, it is really through the collective hard work of many talented people which makes it such a special place. In particular, I must thank the late Professor Tom Reilly, Professor Tim Cable and Dr Barry Drust, all of whom have been instrumental in providing me with the platform that allows me to study something I love.

With the increasing time pressures of balancing the demands of teaching, research and applied practice, much of the writing of this text was written outside of office hours. For this, I must acknowledge the understanding and patience of my partner, Natalie. Thank you for understanding that exercise science is more than just my profession, it is my hobby. Finally, I extend my sincere appreciation to my Dad, Mum, Lisa and Julie for teaching me my most important lesson – that is, when all things else are considered, it is family that really gives meaning to life.

James Morton, PhD

Part One

Basic Muscle Physiology and Energetics

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;
- 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

adenosine diphosphate (ADP)	fatty acid
aerobic	glycogen
anaerobic	glycogenolysis
anaerobic alactic	glycolysis
anaerobic glycolytic	lipid
anaerobic glycolysis	lipolysis
anaerobic lactic	mitochondria
adenosine triphosphate (ATP)	oxidation
carbohydrate	PCr (phosphocreatine)
CK (creatine kinase)	phosphorylation
creatine	protein
dephosphorylation	protein degradation
energy continuum	protein synthesis

1.1 Adenosine triphosphate: the energy currency

In order for our muscles to contract and provide movement, energy is required. Such energy is

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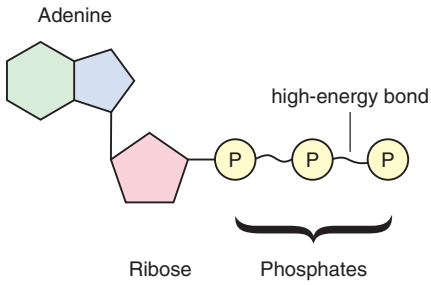

Figure 1.1 Adenosine triphosphate (ATP)

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.

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

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 1–10 seconds, 10–60 seconds and beyond 60 seconds respectively.

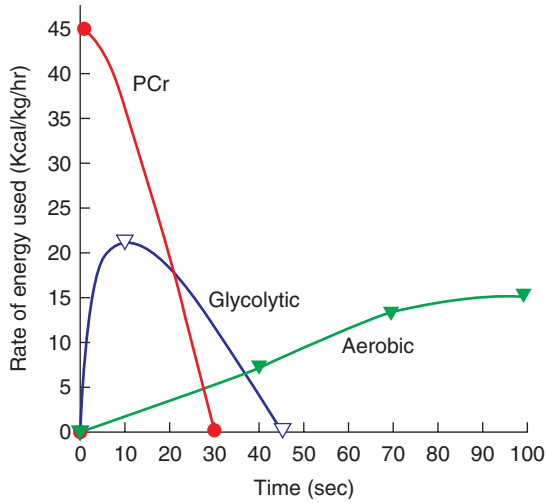

Figure 1.2 Energy continuum

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 metres mainly use anaerobic glycolysis, and thereafter aerobic metabolism predominates.

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 adenosine diphosphate (ADP). Phosphocreatine converts ADP back to ATP by donating its phosphate in the presence of the enzyme **creatine kinase** (CK), and

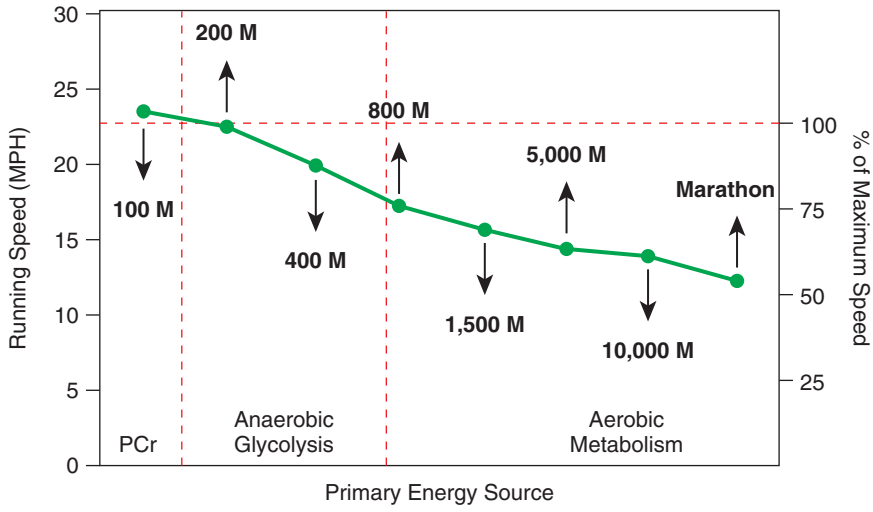

Figure 1.3 Primary energy sources for different running distances

in turn the PCr forms **creatine** (Cr), i.e. the **dephosphorylated** form of PCr.

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

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 often called **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 1–10 seconds.

Figure 1.4 provides a schematic to show the synthesis of ATP from ADP using PCr at the muscle crossbridge, and also the regeneration of PCr from Cr by ATP at the mitochondria.

Thus, Cr is formed from PCr during intense bouts of exercise, while Cr is re-phosphorylated to PCr by ATP produced in the mitochondria during aerobic recovery. 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

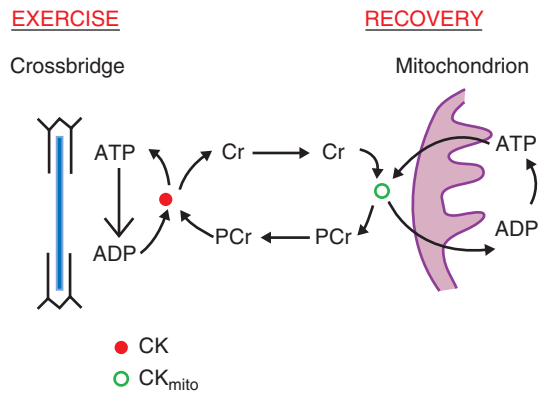

Figure 1.4 PCr shuttle

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, you should appreciate 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.

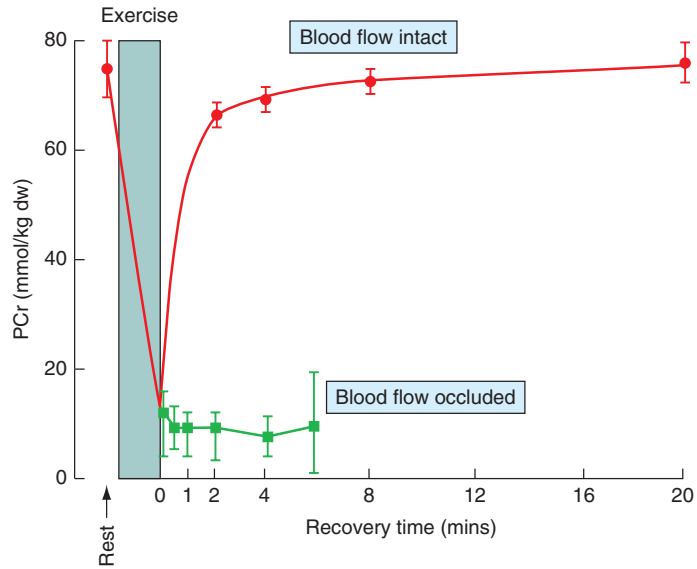

Figure 1.5 Resynthesis of PCr after exercise with and without an occluded blood supply (adapted from Hultman *et al.*, 1990)

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 (this may even be depleted if the exercise is sufficiently intense or prolonged). Indeed, nearly 75% of PCr is resynthesized within the first 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 10–60 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 may also be called '**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 below equation) is glycogen, 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:

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

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

We shall see more detail about these processes in Chapters 5 and 6.

Aerobic activities invariably occur at lower exercise intensities (which are those lasting

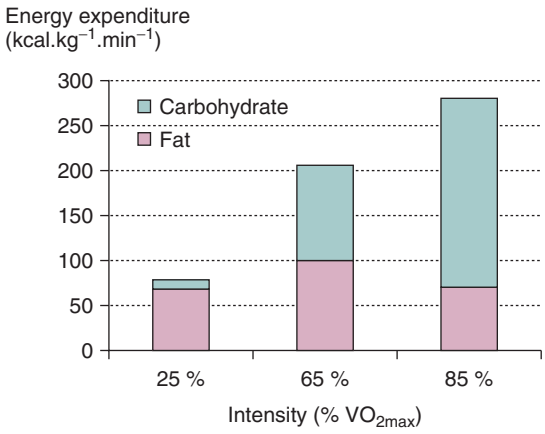

Figure 1.6 Carbohydrate and fat use at three exercise intensities (adapted from Romijn *et al.*, 1993)

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), 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 m and 200 m world records are similar, at 22.4 mph and 21.6 mph respectively. However, with increasing distances, average speeds decline. The average speed for the marathon world record is 12.1 mph, which is 55% of the world sprint record. This is remarkable, 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 12.1 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 m 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 5,000 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 m to 1500 m. However, as the distance increases from 1500 m to 42.2 km, 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.

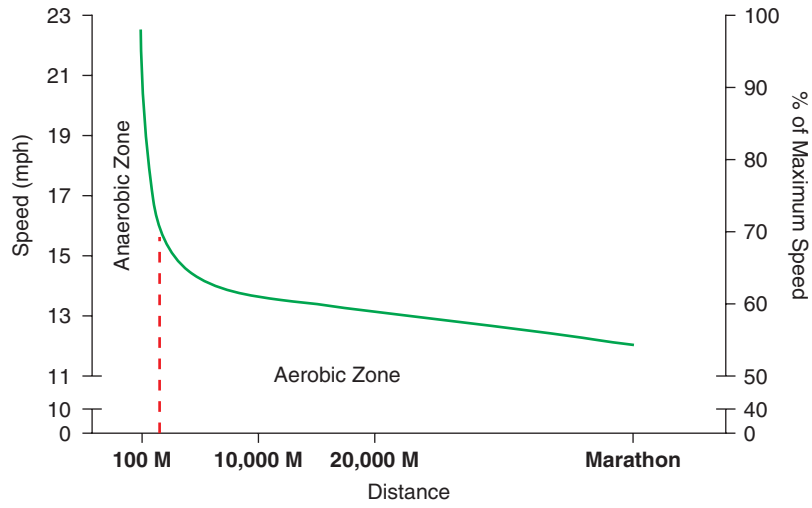

Figure 1.7 Sustainable running speed and distance run

Table 1.1 Maximum rates of energy production

Process	Maximum power
PCr → ATP	9 mM/kg/s
CHO → lactate + ATP	4 mM/kg/s
CHO → CO_2+ H_2O + ATP	2 mM/kg/s
Fat → CO_2+ H_2O + ATP	1 mM/kg/s

The PCr system is the most rapid of these ATP-producing systems. A calculated rate of 9 mM/kg dry muscle/s 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, the aerobic breakdown of carbohydrates produces ATP at twice the rate of fats (i.e. 2 mM/kg/s vs. 1 mM/kg/s). 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 later chapters, we will see that whereas PCr generation of ATP is a single reaction, anaerobic glycolysis entails ten 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, that 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 – they would either 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

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 are limited (notably PCr and glycogen for anaerobic glycolysis);
2. the likely duration for which these energy sources will last if they are the only source of ATP production;
3. the maximal rates by which they can produce ATP.

1.7 Can muscle use protein for energy?

So far there has been little or no mention of using **proteins** for energy. Muscles are made of protein in the main, but can muscle protein provide energy? The answer is, to a limited extent, 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 1.8 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.

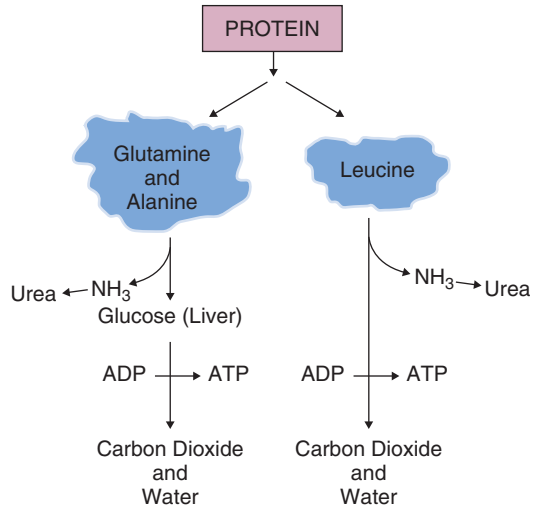

Figure 1.8 Likely use of amino acids for energy

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

	ATP	PCr	Anaerobic glycolysis	Carbohydrte 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 s	1–2 min	1–2 h	>6 h
Max rate of ATP synthesis (mM/kg/s)		9	4	2	1

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.
- 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.

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

A-band	force-velocity relationship
actin	frequency
α-actinin	I-band
acetylcholine	isometric
ACh receptors	isotonic
ATPase	H-zone
central fatigue	latent period
concentric	length-tension
contraction phase	M-line
crossbridges	motor end plate
desmin	motor neurons
dihydropyridine receptor	motor unit
eccentric	M protein
endomysium	multinucleated
epimysium	muscle fibre
fascia	muscle glycogen
fascicles	muscle triglyceride
fast twitch	myofibrils
fatigue resistant	myoglobin

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