Exercise Physiology

A Thematic Approach

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WILEY

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To my wife, Nan, for her love and steadfastness, to Nicola, Tim and Gavin for their unconditional love, and to our beautiful grandchildren, Kimberley, Eleanor, Tamsin, Lucy, Megan, Jonathan and Cameron, for the joy they bring every day –

and to my parents

Mary Ceridwen Hale (1914–1950)

Samuel Thomas Hale (1910–1977)

without whom none of this would have been possible.

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Series Preface

One of the most astonishing cultural phenomena of the twentieth century has been the exponential growth in our knowledge and understanding of the importance of sport and exercise to humankind. At the beginning of that century, sport was principally a force for moral development, whilst strenuous exercise, though necessary to ensure military personnel were fit to engage in combat, was medically proscribed. The academic study of sport – what there was of it – was restricted largely to the history of the Olympic Games and philosophical arguments for the moral case for team games. A hundred years later, the picture is very different. Four hundred million people turn on their television sets to watch the Opening Ceremony of the Olympic Games and soccer's World Cup Final; millions of people jog, go to the gym, or work out in front of the television; and the academic study of sport embraces physics, chemistry, biology, biomechanics, physiology, psychology, politics, sociology, social anthropology and business studies, as well as history and philosophy. Over the last twenty years the number of degree courses in the academic study of sport and exercise has grown phenomenally, attracting students from a wide range of backgrounds. It is against this background that the new series *Wiley SportTexts* was conceived.

This new series provides a collection of textbooks in Sport and Exercise Science that is rooted in the student's practical experience of sport. Each book covers the theoretical foundations of the contributing disciplines from the natural, human, behavioural, and social sciences, and provides the theoretical, practical and conceptual tools needed for the rigorous academic study of sport. Individual texts focus on a specific learning stage from the various levels of undergraduate to postgraduate study.

The series adopts a student-centred, interactive, problem-solving approach to key issues, and encourages the student to develop autonomous learning strategies through self-assessment exercises. Each chapter begins with clear learning objectives and a concise summary of the key concepts covered. A glossary of important terms and symbols familiarizes students with the language and conventions of the various academic communities studying sport. Worked examples and solutions to exercises, together with a variety of formative and summative self-assessment tasks, are also included, supported by key references in book, journal and electronic forms. The series will also have a dedicated web site with specific information on individual titles, supplementary information for lecturers, important developments in the academic study of sport, and links to other sites of interest.

It is intended that the series will eventually provide a complete coverage of the mainstream elements of taught undergraduate and postgraduate degrees in the study of sport.

Tudor Hale, Jim Parry and **Roger Bartlett**
April 2003

Acknowledgements

It is not possible to write a book like this without the help of others. The major source of inspiration for my interest in exercise physiology is Professor Rainer Goldsmith, who not only taught me about maximal oxygen uptake but also how to write. The late Dr Ernest Hamley supervised my masters degree at Loughborough, and the late Professor Gordon Cumming made the facilities of the Midhurst Medical Research Institute available for my doctoral studies. The former gave me a sound grounding in human biology, the latter, with his colleague Dr Keith Horsfield, told me more about the lung than I knew existed. Two heads of departments, Henry Uren at Aberdeen and Dennis Drinkwater at Bishop Otter College, and three College Principals, Gordon McGregor, John Wyatt and Philip Robinson at Chichester, gave practical and psychological support and encouragement throughout my career in higher education. I enjoyed the benefits of very good colleagues and undergraduates over 30 years spent at Chichester. My postgraduate students almost certainly taught me more than I taught them.

During the gestation of the book, I re-learned much of what I thought I knew. Most of this occurred through existing published material in book or journal form, but some came out of the aether via the Internet; the main sources are listed under 'Further reading'. My thanks go to the librarians at University College Chichester who have continued to provide their customary speedy and efficient services. However, it is impossible to acknowledge the unconscious use of the material in the public domain that has been absorbed over 30 years of teaching.

Alan Rees (Portsmouth), John Sproule (Edinburgh), Rob James (Coventry), and Simon Northcott (Chichester) read every chapter and made very useful suggestions for improving the material. David Bishop (Western Australia) provided similar service, from reading Chapters 2 and 9, and my long-time colleague and good friend Craig Sharp tidied up my efforts at a glossary of terms. None of the above is responsible for the errors that remain.

Andy Slade of Wiley gave sage advice at the outset of the project and at intervals thereafter. Celia Carden, Wiley's Development Editor, led me calmly through the intricacies of the publishing world, always offered sound advice, and maintained a good sense of humour and determined cheerfulness at all times. Special thanks go to Robert Hambrook for his skill at turning my illustrations into intelligible material. Finally, I have had the renewed pleasure of the company and good sense of my friends and Series Co-editors Roger Bartlett and Jim Parry.

Tudor Hale

Prologue

Introduction

Molecular oxygen is a diatomic, colourless, odourless gas. Discovered independently in 1772 by an English cleric, Joseph Priestley, and a Swedish chemist, Karl Scheele, but given its name in 1777 by the French chemist, Antoine Lavoisier, it is vital for human life. We can survive for weeks on a diet of bread and water, and for several days without water, providing we keep still and in the shade. But, without oxygen, we can survive for minutes only before irreversible brain damage and then death occurs. Molecular oxygen is essential because it is necessary for the production of a high-energy compound – adenosine triphosphate (ATP) – that drives all of our cellular activity. However, our stores of oxygen and adenosine triphosphate are very limited, so we need physiological mechanisms to provide both continuously.

At rest, our oxygen demands are quite modest – depending on our size and body composition, we consume about a quarter of a litre of oxygen each minute. During exercise, the position changes dramatically, and the oxygen needed to maintain sufficient adenosine triphosphate increases as much as twentyfold. Our early ancestors evolved a three-stage energy-producing system that ensured their survival. It enabled them to gather fruits, hunt for meat, and escape from predators; it also enables us to engage in a range of sport and exercise activities.

The first stage provides an initial burst of maximum speed, allowing them a quick dash to the nearest tree or cave. The same process enables some of us – Carl Lewis, Linford Christie, Dwain Chambers and Tim Montgomery for example – to run a 100 metres in under 10 seconds. The second stage gives a

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slightly better chance of survival by providing energy for a sustained burst of speed over about a quarter of a mile. This process allowed two of us – Butch Reynolds and Michael Johnston – to run the 400-metres in less than 43.3 seconds. The third stage was necessary for the hunt with bows and curare-tipped arrows. When hit, the prey runs off, but dies slowly and quietly through progressive muscle paralysis. The hunter jogs after the animal until it collapses, kills it and gathers its meat. The chase requires large amounts of oxygen. It enables some of us – Steve Ovett, Seb Coe and Steve Cram – to run a mile (1.609 km) in well under 4 minutes, and Paula Radcliffe to run more than 26 miles (42.195 km) faster then most men.

The most interesting feature of the first two stages is the fact that we can achieve such high speeds without using very much oxygen during the actual events. In the 100-m, we use another high-energy compound called creatine phosphate (CrP) to maintain the adenosine triphosphate (ATP) availability needed for muscle contraction. In the 400-m, the process requires the breakdown – technically called catabolism – of glucose to deliver a limited supply of adenosine triphosphate and producing lactic acid. The process that allows these astonishing achievements without oxygen is *anaerobic* metabolism. The third, oxygen-dependent, stage of the system is *aerobic* metabolism. It underpins all of our everyday activities – working, sleeping, playing, eating, thinking and exercising, and breaks down carbohydrate (glycogen) and fat (lipids) into carbon dioxide and water.

Maximal oxygen uptake

Maximal oxygen uptake ($\dot{V}_{O_2max}$) describes our ability to transport and consume the greatest amount of oxygen breathing air at sea level. A laboratory-based maximal oxygen uptake test is a measure of our cardiovascular, respiratory, and skeletal muscle biochemical capabilities and is a feature of almost all sport and exercise science courses. During maximal exercise the average sport and exercise science student consumes between three and four litres of oxygen a minute, or about 45 to 55 millilitres for each kilogram of body mass. An elite endurance athlete doubles this to around six litres of oxygen each minute, roughly 24 times resting oxygen consumption. The process allows some of us to run 1500 m in under 3.5 min, and a marathon in just over 2 hours at an average speed of nearly 21 $km \cdot hr^{-1}$ (12 $mi \cdot hr^{-1}$). At the other end of the scale, patients with heart or lung disease struggle to reach symptom-limited oxygen uptake values of 1–1.5 litres of oxygen per minute. The need to understand the physiological processes that take oxygen from the atmosphere to the muscle cell is a key feature of all exercise physiology texts and provides the central theme for this book. There are innumerable ways of doing this, but in this book we shall be using a fairly simple equation – the Fick equation for oxygen – as the framework around which to introduce key physiological processes that underpin much of sport and exercise physiology.

The Fick equation

In 1870, a German physiologist, Adolf Fick, was interested in measuring cardiac output – the amount of blood pumped out of the heart in one minute. This is what he said to one of his contemporaries.

> *It is astonishing that no one has arrived at the following method by which it [the measurement of cardiac output] may be determined, at least in animals. One measures how much oxygen an animal absorbs from air in a given time, and how much carbon dioxide it gives off. During the experiment one obtains a sample of arterial and venous blood; in both the oxygen and carbon dioxide content are measured. The difference in oxygen content tells us how much oxygen each cubic centimetre of blood takes up in its passage through the lungs. As one knows the total quantity of oxygen absorbed in a given time one can calculate how many cubic centimetres of blood passed through the lungs in this time.*

Put more simply, Fick was saying: 'Cardiac output ($\dot{Q}_{\mathrm{C}}$) is oxygen consumption ($\dot{V}_{\mathrm{O_2}}$) divided by the difference in the oxygen content ($C_{\mathrm{O_2}}$) of arterial and mixed venous blood (a-$\bar{\mathrm{v}}$)' – i.e.

$$\dot{Q}_{\mathrm{C}} = \frac{\dot{V}_{\mathrm{O_2}}}{C_{\mathrm{a\text{-}\bar{v}O_2}}}$$

However, Fick's idea was ahead of its time. The process he described in 1870 was not testable on humans because no one had invented the methods for sampling mixed venous and arterial blood. Consequently, it took another 60 years, when arterial catheters were developed and arterial blood sampling became possible, to confirm his prediction. In 1956 Verner Forssman, Andre Cournand and Dickson W. Richards received a Nobel Prize for developing the technique.

Now, it doesn't take much to rearrange the Fick principle to read: 'Oxygen uptake equals cardiac output multiplied by the difference in oxygen content of arterial and mixed venous blood' – i.e.

$$\dot{V}_{O_2} = \dot{Q}_C \cdot C_{a\text{-}\bar{v}O_2}$$

This simple equation, the Fick equation for oxygen, provides us with a framework for investigating the physiology that underpins maximal oxygen uptake. However, to understand the logical chain of events that governs oxygen uptake, we need to re-arrange the equation and consider the *sequential* order of the physiological mechanisms involved. The logic behind this rearrangement is quite straightforward. We breathe in oxygen molecules from the atmosphere which then combine with the blood passing through the lungs to give us oxygenated blood – so first we consider the oxygen content of arterial blood (C_{aO_2}). The heart then pumps this oxygenated blood around the body to the cells; this is our whole body flow ($\dot{Q}_C$) or cardiac output. The oxygen delivered to the muscle cells enables them to contract and us to exercise in a variety of ways and at different speeds. These cells extract oxygen from the blood as it passes through the capillaries of muscle groups. The aerobic breakdown of glycogen and fats consumes oxygen and produces carbon dioxide and water, and the oxygen content of the venous blood (C_{vO_2}) falls. The oxygen content of this systemic venous blood tells us how effective the muscle cells are at oxygen extraction. The venous blood returns to the right side of the heart and then the lungs where the carbon dioxide produced from the breakdown of glucose and fats is excreted and oxygen picked up to start the whole process again. This sequential approach to understanding the physiology of maximal oxygen uptake provides the general structure of this book.

At this point it is important to say that what is set out in this book is a summary of what we *think* we know about the cascade of oxygen from atmosphere to muscle cell. However, all scientific knowledge is *provisional*, and what we now think of as facts may well turn out to be false in the future. This is how science has progressed from the fifteenth century. It was then that Nicolaus Copernicus, a Polish priest, astronomer and doctor, first showed that the earth travelled around the sun, thus refuting the second century geocentric universe theory of Egyptian astronomer and geographer, Ptolemy. So, do not be lulled into thinking that we are dealing with irrefutable facts; even Einstein thought that some of his findings could not be true.

Equally important are the findings from research into learning strategies. These indicate that if the sole strategy is simply *reading* the text, learners retain only about 10 per cent of the information. *Discussion* improves retention to about 50 per cent; but the greatest retention level occurs when *explaining* what you have learned to others. Experience shows that students learn a great deal by talking to tutors, even more from their postgraduate peers, and most by working in small friendship groups by talking through difficulties and discussing possible solutions.

General structure of the book

Each chapter begins with a list of things you should be able to do if you

(a) read the chapter carefully,

(b) attempt the exercises and questions, and

(c) clear away any uncertainties by discussion amongst your peers or with your tutors.

An objective test follows to assess your current level of knowledge. Attempt these tests before reading the subsequent chapter; photocopy the page and file the answers in your notes. After all, if you know most of the answers you may wish to skip that particular chapter. Thirty-three per cent or more ‘Don’t know’ responses suggest that the chapter should form part of further private study.

The exercises and questions within the text have been designed to achieve two things. First, they reinforce the material; second, they provide a respite from the periods of intense concentration needed for careful reading. Research shows that learning is most effective in short bursts, interspersed with rest periods of a few minutes, or a change of activity. If you are not sure of the answer, read on a little further and come back to the question. The answers to the exercises and questions, with explanations, are at the end of the each chapter. Don’t look at the answers until you have finished the chapter.

Before moving on to the next chapter, take the objective test again to monitor your progress. You can check your answers from the lists provided at the end of the book, but you will only get ‘right’ or ‘wrong’ responses here. You will find additional information on the *Wiley SportTexts series* website. A success rate of less than 40 per cent – i.e. a fail grade in most institutions – suggests that you have not understood the material sufficiently. This has two consequences: the first is failure in examinations, and the second is that you may find subsequent material difficult to grasp. The least you should do is seek tutorial advice. A success rate of 50–55 per cent is adequate, but only just; more than 65 per cent augurs well for the future. If you file your answers, they can act as a useful reminder of the areas where additional revision is necessary around examination time.

Each chapter also includes a list of the symbols and abbreviations in current use in journal articles and textbooks. Become comfortable with them, and use them whenever you can in your written work – it saves time and paper, and confirms to your tutors that you are becoming familiar with the everyday conventions of exercise physiology. It is important to recognize that the dots over volume data ($\dot{V}$) carry precise information – namely, that time, usually minutes, is involved; any symbol carrying a bar above it ($\bar{v}$) indicates that the figure is a mean (average) value.

Some material – abbreviations, symbols and units for example – appears in several places in the text. This is deliberate. Firstly, repetition in itself is a good learning strategy; secondly putting material into slightly different contexts can aid understanding; thirdly, repetition helps those who only read selected chapters rather than the whole book. At the end of each chapter, a short summary acts as a quick revision aid.

Chapter 1 introduces an important piece of practical work that underpins the rest of the book, namely the maximal oxygen uptake test. All sport and exercise science courses use this laboratory practical to introduce the concept of the oxygen cascade and to give students some experience of collecting and analysing raw data. Chapters 2 to 9 cover sequentially the specific physiological systems involved in oxygen delivery and consumption. The chapters are built around the concept of levels. Each one contains typical data that might be recorded during one of your practical sessions; this is an attempt to link practice and theory, a link too often ignored by many students. Try not to treat lectures and practical laboratory exercises as separate entities. Study the data carefully, and see how they fit in with the lectures. After the practical examples, there is a basic outline of the physiological mechanisms at work during a particular part of the oxygen uptake chain; this aims to provide a foundational account of the information needed to pass the course. A fuller account follows giving more detailed information on the theoretical underpinning of the mechanisms at work; if the theories are understood and applied appropriately to examination questions, laboratory reports and assessed coursework assignments, higher grades should result.

The final two chapters (10 and 11) are slightly different and take the form of coursework essays that try to critically evaluate current theories on particular topics. They deal with two important issues that are likely to confront sport and exercise science students during their study of exercise physiology. The first examines the factors likely to limit maximal oxygen uptake, a topic that has been the subject of debate, sometimes heated, since the 1920s. Understanding of such physiological limitations is important in grasping the fundamentals of exercise physiology.

The second deals with the complex relationships between exercise, fitness and health. This topic has become the concern in many of the rich, industrialized countries worried about the cost of diseases of affluent societies, where the physical labour that once fuelled the industrial revolution of the nineteenth century has all but disappeared. No sport and exercise science student can ignore these issues and claim to be adequately educated.

The four appendices contain supplementary material that may help knowledge and understanding. The first offers suggestions for additional reading material that can be found in encyclopaedias, key textbooks, journal articles and websites. Two words of caution are necessary here. The first relates to the referencing of material, and the second to the use of websites.

The Editors of the *Wiley SportTexts series* made a conscious decision to place all reference material at the end of the book rather than within the text or at the end of each chapter. The decision was taken to facilitate ease of reading and to maintain the continuity of the text and flow of ideas. *However, this is not conventional academic practice and students should not follow this example in their written work. Each sport and exercise department will have specific guidelines for referencing written work. Students would be foolish to ignore these guidelines.*

Web sites can provide some very interesting and useful material, not only in the form of text but with diagrams and animations. However, the quality is very variable ranging from the very basic to PhD level and users should be selective in what they choose to use. *Whatever that is, be sure you acknowledge the source of the material.*

The second appendix provides a glossary that may help clarify some of the technical terms used. The third gives the roots of some of the words we use, and demonstrates how much we owe to the Greeks and Romans for our present-day language. These roots may help in understanding and memory. Finally, there is the appendix containing the answers to the objective tests.

1 The Maximal Oxygen Uptake Test

Learning Objectives

By the end of this chapter, you should be able to

- distinguish between aerobic and anaerobic metabolism
- define maximal oxygen uptake
- give the Fick equation for maximal oxygen uptake
- outline the procedures entailed in the indirect calculation of oxygen uptake
- list the physiological characteristics indicating the achievement of maximal oxygen uptake
- describe the safety procedures to be undertaken before a maximal oxygen uptake test
- explain the differences between discontinuous and continuous exercise test protocols
- describe three commonly used ergometers along with their strengths and weaknesses
- outline the calibration procedures for gas analysers and gas meters
- calculate values for oxygen uptake, carbon dioxide excretion and the respiratory exchange ratio

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Objective test

Say whether the following answers are true (T) or false (F). If you do not know, say so (D) – not knowing is not an academic crime, but not finding out is. Try not to look at the answers until you have worked your way through the chapter and completed the test a second time. In this way, you can monitor your progress.

	Pre-test			Post-test		
	T	F	D	T	F	D
1. A. V. Hill first reported the O_2 plateau during maximal exercise						
2. $\dot{V}_{O_2max}$ is defined as a plateau in an O_2 uptake–power graph						
3. $\dot{V}_{O_2max}$ is the greatest $\dot{V}_{O_2}$ consumed breathing air at altitude						
4. Aerobic exercise requires increased oxygen consumption						
5. The $\dot{V}_{O_2max}$ test is the best measure of anaerobic performance						
6. Large quantities of oxygen are consumed during the 100-m						
7. At rest about 0.25 L of oxygen is consumed each minute						
8. Elite endurance athletes have reached $\dot{V}_{O_2max}$ of $6\ L \cdot \text{min}^{-1}$						
9. The Fick equation for oxygen is $\dot{V}_{O_2} = \dot{Q} \cdot C_{a-\bar{v}O_2}$						
10. The indirect calculation of $\dot{V}_{O_2}$ requires $\dot{V}_I$ measurement						
11. Pure inspired air contains 3% CO_2						
12. Expired air contains 20.93% O_2						
13. Calculation of $\dot{V}_{O_2}$ assumes that nitrogen is metabolically inert						

	Pre-test T	Pre-test F	Pre-test D	Post-test T	Post-test F	Post-test D
14. Various forms of ergometer can regulate exercise intensity						
15. A set of steps, and a treadmill can be used to measure power output						
16. An infrared gas analyser measures the O_2 fraction in expired air						
17. A paramagnetic analyser measures the CO_2 fraction in expired air						
18. 'White spot' N_2 sets the baselines of both O_2 and CO_2 analysers						
19. Fresh air is used to set the upper limits of the CO_2 analyser						
20. 15% O_2–5% CO_2 in N_2 is used to check analyser accuracy						
21. Expired air is measured by a dry gas meter						
22. Inspired and expired air volumes are always the same						
23. The volume of O_2 consumed = $\dot{V}_{O_2}$ inspired + $\dot{V}_{O_2}$ expired						
24. $\dot{V}_{O_2} = \dot{V}_E \cdot \{[(1 - F_{EO_2} - F_{ECO_2}) \cdot 0.265] - F_{EO_2}\}$						
25. $\dot{V}_{CO_2} = \dot{V}_E \cdot (F_{ECO_2} - 0.0003)$						
26. $\dot{V}_{CO_2}/\dot{V}_{O_2}$ is called the respiratory exchange ratio (RER)						
27. RER is affected by the energy source – fat or carbohydrate – used						
28. RER is always <1						
29. Maximum heart rates can be estimated from 220 + subject's age						
30. A 20–50 mL blood sample is needed for lactate analysis						

Symbols, abbreviations and units of measurement

ambient pressure	P_{amb}	Pa; kPa; mmHg
arterio-venous	a-v	
barometer, barometric	B	
barometric pressure	P_B	Pa; kPa; mmHg
breathing rate, respiratory frequency	f_R	$br \cdot min^{-1}$
carbon dioxide fraction	F_{CO_2}	
cardiac output/whole body blood flow	$\dot{Q}_C$	$L \cdot min^{-1}$
expiratory	E; exp	
frequency	f	min^{-1}; s^{-1}
gas fraction	F_{GAS}	
gas fraction expired	F_{EGAS}	
gas fraction inspired	F_{IGAS}	
heart rate, cardiac frequency	f_C	$bt \cdot min^{-1}$
inspiratory	I; insp	
kilogram	kg	
lactate concentration of blood	$[La_{bl}]$	mM; $mmol \cdot L^{-1}$
litre	L	
mass	m	kg
maximum	max	
maximum oxygen uptake	$\dot{V}_{O_2max}$	$L \cdot min^{-1}$
oxygen fraction	F_{O_2}	
pascal; kilopascal	Pa; kPa	
pressure	P	Pa; kPa; mmHg
standard temperature and pressure dry	STPD	0°C; 101.1 kPa; 760 mmHg
volume	V	L
volume of gas flow in unit time	$\dot{V}$	$L \cdot min^{-1}$
volume expired in unit time	$\dot{V}_E$	$L \cdot min^{-1}$
volume inspired in unit time	$\dot{V}_I$	$L \cdot min^{-1}$
venous	v	
venous (mixed)	$\bar{v}$	

Introduction

With modern equipment and techniques, it is quite possible to calculate oxygen consumption in the way Fick described, i.e.

$$\dot{V}_{O_2max} = \dot{Q}_{Cmax} \cdot C_{a\text{-}\bar{v}O_2max}$$

It occurs routinely in certain medical investigations requiring cardio-respiratory information. However, it is an invasive process and entirely unsuitable for the everyday testing of athletes and sport and exercise science students. This is especially so when we can obtain a perfectly good estimate from analysing the gases in the breath we exhale. If we do this whilst undertaking progressive exercise, we get a relationship that looks like that shown in Figure 1.1. This indirect calculation of oxygen consumption merely requires a note of

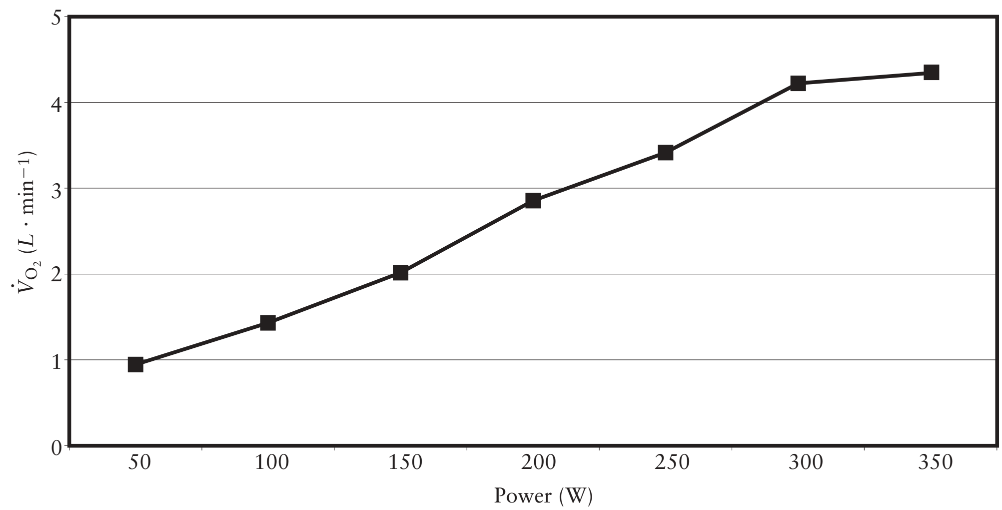

Figure 1.1 A schematic representation of the systematic increase in oxygen uptake as exercise intensity increases until the point at which no further increase in oxygen uptake occurs in spite of an increase in exercise demand

(a) the prevailing barometric pressure (P_B), and ambient temperature;

(b) a collection of expired gas and a record of the fractions of oxygen and carbon dioxide in it;

(c) a note of its volume and temperature.

It is not clear who first discovered the method, but it appears that someone measured oxygen consumption in some form even earlier than 1888.

Question 1.1 *How do we know this?*

An English physiologist, John Scott Haldane, is widely credited with devising the method for calculating oxygen consumption from expired air only, and it has carried his name – the Haldane Transformation – ever since. This is how he described the process in 1912 in his book, *Methods of Air Analysis*.

> *Let us suppose, for instance, that the volume of air expired in exactly ten minutes was 70.4 litres, and that the temperature of the gas meter was 18.5°, and the barometric pressure 748 millimetres. From the table the factor for correction* [given earlier] *is evidently about 0.902, and the reduced volume is therefore 70.4 × 0.902 = 63.5 litres.*

> *Let us now suppose that the inspired air was pure, and contained 20.93 per cent of oxygen, 0.03 of carbon dioxide, and 79.04 of nitrogen; and that the sample of expired air contained 16.41 per cent of oxygen, 3.62 of carbon dioxide, and 79.97 of nitrogen. It is clear that the volume (at 0° and 760 mm dry) of carbon dioxide given off was*

$$\frac{3.62 - 0.03}{100} \times 63.5 = 2.280 \text{ litres.}$$

> *The volume of oxygen absorbed is less easy to calculate, however, as the volume of dry air has diminished in the process of respiration, because more oxygen has been taken up than carbon dioxide has been given off. Since nitrogen is neither taken up nor given off in respiration it is evident that for every 100 volumes of air there corresponded in the air not 20.93 volumes of oxygen but*

$$20.93 - \frac{79.97}{79.04} = 21.18 \text{ volumes.}$$

> *Hence the oxygen which disappeared was*

$$\frac{21.18 - 16.41}{100} \times 63.5 = 3.029 \ litres;$$

and the respiratory quotient was 2.280/3.029 = 0.753.

However, it is uncertain whether Haldane thought of this method independently in 1912, or whether he knew of it from the work of two German physiologists, J. Geppert and N. Zuntz, who, 24 years earlier, had reported it as follows.

> *The content of oxygen in expired air does not say how much oxygen has disappeared from inspired air, because the quantity of expired air is not the same as inspired air when both gases are thought to be free of water. Normally the volume of expired air will be smaller because more oxygen is used than carbon dioxide acid is given off. Only the amount of nitrogen remains unchanged. We can, under the assumption of a constant relation between oxygen and nitrogen in atmospheric air, calculate the amount of inspired oxygen from the nitrogen of the expired air. We just have to multiply the latter by the constant 20.93/79.07.*

Although Haldane's description is easier to follow, scientific convention indicates that the least we must do is to describe the method as the Geppert–Zuntz–Haldane (GZH) Transformation. However, Haldane invented a very precise chemical method of analysing the oxygen and carbon dioxide fractions in expired air, and his work has been a critical factor in developing our understanding of oxygen consumption at rest and during exercise.

Using the Haldane gas analyser and the GZH Transformation, an English physiologist, Archibald Hill, examined the effects of exercise on oxygen consumption. In a series of experiments on himself and other colleagues in the 1920s, he measured the amount of oxygen consumed during running around a grass track at different speeds. The concept that underpinned the experiments was very imaginative, but by today's standards the process was rather crude. The subjects ran with a wooden, A-shaped frame tied to their back. Attached to this frame was a tube connecting a one-way mouthpiece to a large rubberized canvas bag – called the Douglas bag after one of Hill's colleagues – that was used to collect the runners' expired air. The subjects ran at a constant speed for about five minutes and the expired air collection occurred during the last minute. Hill analysed the contents of the bag for oxygen and carbon dioxide concentrations, and measured the total volume of the expired gas in the bag. He repeated the process on separate occasions at higher speeds until the subjects were unable to run any faster.

On the basis of these data, Hill and his colleagues claimed that oxygen uptake increased with increasing speed up to a point at which, no matter how much faster the subject was able to run, oxygen uptake did not increase any further. He showed this phenomenon quite clearly in one of his subjects (Subject J), a particularly skilled runner who was able to run faster than any other subject. This gave rise to the term 'the oxygen plateau', which is still regarded as the main criterion for determining an individual's maximal oxygen uptake ($\dot{V}_{O_2max}$) by most practising exercise physiologists. However, there are also other physiological indicators including maximum heart rates, the respiratory exchange ratio, and the level of lactic acid in the blood. Often, in the absence of the plateau, we use these second-level indicators to determine the maximal level. Some people would argue that this is an unjustified step and that the term 'peak oxygen uptake' is the more appropriate term to use.

If we repeat Hill's intermittent exercise experiment and plot oxygen uptake against running speed the outcome is the classical graph as shown in Figure 1.2. Oxygen uptake rises linearly with growing oxygen demand until the final increase in speed results in a levelling off in oxygen consumption. An immediate question that arises is 'What is the energy source for completing that final increment in exercise intensity?' The obvious answer is that subjects complete the final stage with the aid of supplementary anaerobic breakdown of glucose

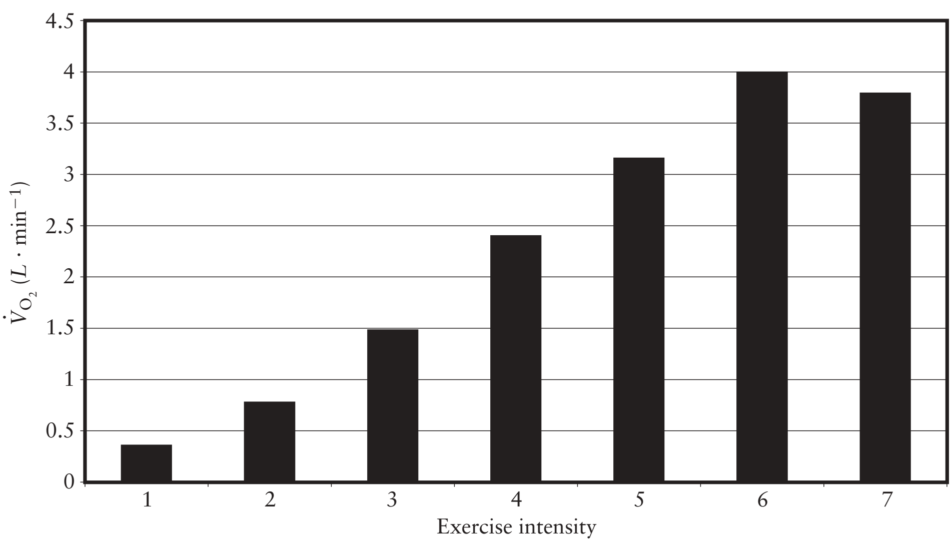

Figure 1.2 A typical A. V. Hill graph obtained from a discontinuous progressive exercise test

to lactic acid. High levels of blood lactate recorded after a maximal test support this view.

Intuitively, that explanation seems to make some kind of sense. Several chemical reactions follow a similar pattern. Our own experience of running at maximum effort shows speed increasing up to our maximum rate, being maintained for a time before the effects of fatigue become too great and we stop. So for now, the notion of a plateau in oxygen uptake at maximal levels is a useful starting point for trying to understand the processes involved in oxygen consumption when we exercise. However, not everyone believes that this classical graph gives an entirely satisfactory picture of what really happens, and that is an issue we will return to in which Chapter 10 deals with factors limiting oxygen uptake.

Collecting data

The most effective way of starting to understand the physiology underpinning maximal oxygen uptake is to take part in a laboratory test to measure it in two roles – as a subject, and then as a data recorder. The procedures are now routine and relatively easy to perform, but if the test is to be useful, it must be done very carefully and with as much precision as possible.

Informed consent

There is an ethical, and perhaps even legal, obligation to take every precaution to ensure the safety and well-being of every subject. Thus, the most important pieces of preliminary information required of subjects are their willingness to undertake the test, and their state of health. The test procedures need to be explained carefully and fully so that the subjects are in no doubt about what is going to happen to them and can give their informed consent. This means that they fully understand the kinds of discomforts they are likely to experience in a test to exhaustion, and that they can withdraw from the test at any time. After signing an informed consent form, subjects complete a health questionnaire. This attempts to identify three main things: the likelihood of exercise-induced asthma; the familial risks of cardiovascular insufficiency, particularly important in older subjects prone to erratic heart rhythms; and that subjects are not suffering from the presence, or after-effects, of musculo-skeletal problems,