

OXFORD

THE **BIOCHEMICAL**
BASIS OF

SPORTS
PERFORMANCE

SECOND EDITION

RON MAUGHAN ■ MICHAEL GLEESON



The Biochemical Basis of Sports Performance

SECOND EDITION

Ron Maughan & Michael Gleeson



OXFORD
UNIVERSITY PRESS

OXFORD

UNIVERSITY PRESS

Great Clarendon Street, Oxford OX2 6DP

Oxford University Press is a department of the University of Oxford.
It furthers the University's objective of excellence in research, scholarship,
and education by publishing worldwide in

Oxford New York

Auckland Cape Town Dar es Salaam Hong Kong Karachi
Kuala Lumpur Madrid Melbourne Mexico City Nairobi
New Delhi Shanghai Taipei Toronto

With offices in

Argentina Austria Brazil Chile Czech Republic France Greece
Guatemala Hungary Italy Japan Poland Portugal Singapore
South Korea Switzerland Thailand Turkey Ukraine Vietnam

Oxford is a registered trade mark of Oxford University Press
in the UK and in certain other countries

Published in the United States
by Oxford University Press Inc., New York

© Ron Maughan and Michael Gleeson, 2010

The moral rights of the authors have been asserted
Database right Oxford University Press (maker)

First edition published 2004

Second edition published 2010

All rights reserved. No part of this publication may be reproduced,
stored in a retrieval system, or transmitted, in any form or by any means,
without the prior permission in writing of Oxford University Press,
or as expressly permitted by law, or under terms agreed with the appropriate
reprographics rights organization. Enquiries concerning reproduction
outside the scope of the above should be sent to the Rights Department,
Oxford University Press, at the address above

You must not circulate this book in any other binding or cover
and you must impose the same condition on any acquirer

British Library Cataloguing in Publication Data

Data available

Library of Congress Cataloging in Publication Data

Data available

Typeset by MPS Limited, A Macmillan Company

Printed in Italy on acid-free paper by
L.E.G.O. S.p.A.

ISBN 978-0-19-920828-9

1 3 5 7 9 10 8 6 4 2

Preface to the Second Edition

It seems only a short time since the first edition of this book appeared. In reality, it is six years. In that time, there have been many major advances in the field of exercise biochemistry, and there have also been a few retreats. Many of these have come from the application of new techniques to the study of old problems, and from the cross-fertilization of ideas from different areas of specialization. Molecular biology continues to develop rapidly and to provide insights into the mechanisms operating at the sub-cellular level that underpin many of the responses and adaptations to different types of exercise stress. The cytokines, for example, are now recognized as having a wide range of roles in intracellular signalling pathways. Likewise, free radicals, formerly thought of as being exclusively harmful to cells, are seen to play important roles in a range of cellular processes. The rapid developments in gene therapy, with their implications for abuse in sport, offer the prospect of tissue engineering in ways that did not seem possible even a few years ago.

In revising the text, we have tried to take account of the new information that has emerged, and some substantial new sections have been added. At the same time though, we have tried not to lose sight of our original aim, which was 'to introduce students of sports science or exercise physiology to the biochemical processes that underpin exercise performance and the adaptations that occur with training.' As pointed out in the preface to the first edition, we have tried to maintain the focus on physiological chemistry—the processes that occur in the living body under physiological conditions rather than those that can occur in the test tube.

We have added many new references to the further reading lists at the end of each chapter to illustrate recent advances in knowledge. We have, however, also retained, and even added, many older references. We have done this as we believe that students should not lose sight of the development of the subject: many of these older references highlight major developments as they occurred and they are still relevant today.

This second edition has benefited from the many comments made by colleagues and former students. The fact that these have been generally positive has encouraged us in the preparation of a new edition.

Ron Maughan

Mike Gleeson

Loughborough University, 2010

Preface to the First Edition

Some understanding of the biochemistry of exercise is fundamental to any study of the factors that contribute to sports performance. It is the physical, chemical and biochemical properties of cells and tissues that determine the physiological responses to exercise, and yet the teaching of exercise biochemistry is poorly developed compared with exercise physiology. Where the subject is taught at all, the student often finds the approach somewhat daunting, with its focus on thermodynamics, chemical structures and metabolic pathways. Many students find the subject difficult, when it should not be so.

The aim of this book is to introduce the student of sports science or exercise physiology to the biochemical processes that underpin exercise performance and the adaptations that occur with training. The focus is on skeletal muscle metabolism and the provision of energy for working muscles. This is strictly physiological chemistry—the study of the biochemical or metabolic processes that occur in the whole organism—as opposed to those that might occur in the test-tube under non-physiological conditions. Although the factors that cause fatigue during exercise are not well understood, it seems likely that they have a biochemical rather than a physiological basis. Students of sport and exercise science do not require a deep understanding of biochemistry, but do need to be familiar with the main concepts.

We have tried in this book to introduce the principles of exercise biochemistry in a context that is immediately relevant to the student of sports science. This has meant abandoning the traditional approach of working through the main classes of biomolecules and the major metabolic pathways. Instead, we have tackled the subject by considering the biochemical processes involved in energy provision for different sports events and the way in which limitations in the energy supply can cause fatigue and thus limit performance. Recovery from exercise is important for athletes who train and compete with only a limited rest period, and the biochemical processes that influence recovery and restoration of performance capacity are also addressed in this book.

The subject matter lends itself well to this approach. The weightlifter is concerned only with force production, but the sprinter needs to sustain high-power outputs, albeit only for short periods of time. The endurance athlete must produce only a moderate power output, but this rate of work must be sustained for long periods. The biochemical processes that fuel the different activities that contribute to sport are the focus of this book, together with the changes that occur with training and the role of diet in providing the necessary fuels. Sporting

talent is a rare gift inherited by the elite athlete from his or her parents, and a brief description of the basis of heredity is included.

The authors both teach undergraduate courses in exercise biochemistry, physiology and nutrition and bring their experience of research and teaching to this book in the hope that it will stimulate the interested student to pursue this fascinating subject.

Ron Maughan

Mike Gleeson

Contents

1 Introduction: The biochemical basis of exercise and sport

Learning objectives	1
Introduction	2
Historical perspective	3
Evolution of records	3
The appliance of science	11
The abuse of science	12
Key points	13

2 The weightlifter

Learning objectives	14
Introduction	15
Muscle structure and function	16
Types of muscle	16
Structure of skeletal muscle	16
Muscle fibre ultrastructure	18
Molecular composition of the thick and thin myofilaments	20
The contractile mechanism	21
Control of contraction	25
Motor units	27
Fibre types	29
Types of contraction	36
Eccentric exercise-induced muscle damage	36
Adaptive capacity of skeletal muscle	38
Proteins: structural and functional characteristics	39
Amino acids	39

Protein structure	44
Protein turnover	48
Anabolic hormones	50
Proteins as enzymes	51
Mechanisms of enzyme action and enzyme kinetics	51
Control of enzyme activity	57
Enzyme isoforms	58
Energy for muscle contraction	59
The role of ATP	59
Burning fuel to resynthesize ATP	62
Nutritional effects on strength training and performance	64
Protein needs	64
Supplements	66
Steroids	68
Key points	69
Selected further reading	72

3 The sprinter

Learning objectives	73
Introduction	74
Anaerobic metabolism	74
Phosphagen system	75
Metabolic response to very high-intensity exercise	83
ATP resynthesis from phosphocreatine breakdown	83
ATP resynthesis from glycogen metabolism	84
Phosphocreatine and glycogen breakdown in Type-I and Type-II fibres	86
Myokinase reaction	87
Loss of adenine nucleotides	88
The cellular energy charge and the adenylate pool	89
Causes of fatigue in sprinting	90
Post-exercise recovery: the resynthesis of phosphocreatine	91
Nutritional effects on sprint performance	93
Key points	95
Selected further reading	97

4 Middle-distance events

Learning objectives	99
Introduction	100
Energy and oxygen cost of middle-distance running	101
Glycolysis	103
Fuels for glycolysis	103
The glycolytic pathway	105
Regulation of glycolysis	108
Regeneration of NAD	111
Oxidative metabolism of carbohydrate	112
Fatigue mechanisms in middle-distance events	113
Recovery after exercise	117
Nutritional effects on the performance of the middle-distance athlete	119
Carbohydrate	119
Increasing buffer capacity	121
Key points	125
Selected further reading	126

5 The endurance athlete

Learning objectives	127
Introduction	128
Energy supply	129
Aerobic power	130
Fractional utilization of aerobic capacity	131
Energy metabolism	133
Oxidation of carbohydrate	136
Fat as a fuel	137
Fat metabolism	138
β -Oxidation of fatty acids	143
The tricarboxylic acid cycle	144
The terminal respiratory system	145
Amino acids as a fuel source for exercise	147

Integration and regulation of fuel use	148
Factors affecting key enzymes	149
Hormonal responses to exercise	151
Regulation of energy metabolism by hormones	154
Fatigue in prolonged exercise	161
The role of the brain in fatigue	163
Nutrition and endurance exercise performance	165
Carbohydrate and protein	166
Caffeine and carnitine	168
Key points	170
Selected further reading	173
6 The games player	
Learning objectives	174
Introduction	175
Activity patterns and work rate in games play	175
Metabolic responses to intermittent high-intensity exercise	178
Resynthesis of phosphocreatine	182
Why does the rate of lactate production fall with repeated sprints?	184
Fatigue in multiple-sprint sports	186
Nutritional strategies for team sports athletes	191
Energy and carbohydrate needs	191
Creatine supplements and performance of multiple sprints	193
Key points	196
Selected further reading	197
7 Sporting talent: the genetic basis of athletic capability	
Learning objectives	199
Introduction: factors determining success in sport	200
The nature of the genetic material	201

Nucleic acids and control of protein synthesis	202
Mutations	214
Principles of heredity	215
Inheritance of traits	215
Muscle fibre-type composition: determined by nature or nurture?	219
Gene doping: a realistic prospect?	221
Key points	223
Selected further reading	225

8 Adaptations to training

Learning objectives	226
Introduction	227
Training strategies and the associated adaptations	229
Training for strength	231
Training for speed	235
Training for middle distance: increasing anaerobic capacity	237
Training for endurance: increasing aerobic capacity	238
Mechanisms and limitations to adaptation	242
Overreaching and overtraining	253
Exercise training, immune function, and susceptibility to infection	255
Acute effects of exercise on immune function	256
Chronic effects of exercise training on immune function	257
Effects of detraining	258
Nutritional effects on training adaptation	259
Training and diet	259
Nutrient–gene interactions	260
Free radicals and antioxidants	263
Key points	278
Selected further reading	279

**Appendix 1 Key concepts in physical,
organic, and biological chemistry**

Introduction	283
Matter, energy, and atomic structure	283
Chemical bonds, free energy, and ATP	286
Hydrogen ion concentration and buffers	289
Membrane structure and transport	291
Cells and organelles	295

**Appendix 2 Glossary of abbreviations
and biochemical terminology**

Abbreviations	297
Biochemical terminology	301

**Appendix 3 Units commonly used in biochemistry
and physiology**

Système International d'Unités (SI units)	306
Derived SI units and non-SI units allowed or likely to be met	307
SI fractions and multiples	307
<i>Index</i>	309

Introduction: The biochemical basis of exercise and sport



Historical perspective	3
Evolution of records	3
The appliince of science	11
The abuse of science	12

Learning objectives

After studying this chapter, you should be able to . . .

1. appreciate why knowledge of biochemistry is important to our understanding of the factors that determine success in sport;
2. describe some of the factors that have contributed to the improvement of world records in sports events over the last century;
3. understand the limitations of extrapolating from the changes in previous world records to predict the pace of future improvements;
4. describe some of the factors that limit exercise performance and determine success in sport;
5. describe the concept of failure of ATP supply as a biochemical cause of fatigue.

Introduction



The innate level of ability and the ability to respond to training with an improvement in performance are the keys to success in sport

All sports activities involve muscular activity, and for each one of us there is an upper limit to our ability to perform any task involving muscular effort. When we try to do more, fatigue intervenes: when this happens, we have to slow down or stop, and skill and coordination deteriorate. This applies to all activities involving strength, speed, stamina, and skill. It is these differences in physical capacity between individuals that form the basis of sporting contests as each competitor strives to reach those limits. The limitations to exercise performance are many and varied, but no matter what our event or our level of performance, we can improve with appropriate training. These two factors, the innate level of ability and the ability to respond to training with an improvement in performance, are the keys to success in sport.



The genetic material dictates the formation of proteins and these in turn control metabolism

Both of these factors are essentially determined by our body's biochemical make-up. Our genetic material, which is made up of deoxyribonucleic acid (DNA), dictates the formation of proteins and these in turn control the metabolism of all the other chemical elements and compounds that make up our cells and tissues. The human body is nothing more than a collection of biochemicals that interact with each other to provide both structure and function. The structure is important: it determines our height, weight, external appearance, and all our other physical characteristics. Function is even more important as this determines strength, speed, stamina, and skill. The nature of the mind, of thought processes or even of simpler human attributes such as memory, is not well understood, but all of these phenomena must also have a biochemical basis. Physiology and medicine are no more than the physical manifestations of the underlying biochemistry. Some would argue that psychology falls into the same category.



Understanding the body's responses to exercise is important for the athlete who seeks to perform well

Sport takes many different forms, and offers as many opportunities for those who simply want to participate in a pleasurable recreational or social activity as it does for those who want to compete at the highest level. The recreational participant can benefit from long-term improvements in physical and mental well-being

and in functional capacity as well as the immediate pleasure of participation. Understanding the body's responses to exercise is important for the athlete who seeks to perform well, but it is also a crucial element in the development of successful physical activity programmes that can tackle the growing prevalence of the diseases that accompany a sedentary lifestyle.

An understanding of biochemistry—the chemistry of life—is fundamental to all of these aspects and it will become even more so as science progresses from simple descriptions of phenomena based on observation to a detailed understanding of the mechanisms that control bodily function.

Historical perspective

In team sports, there are few opportunities to set records, and the standards by which participants are judged are relative rather than absolute. The aim is simply to beat the opposition. Even in these sports, however, meticulous records of team and individual performances are kept, and the exceptional ability of outstanding individual players is recognized. Baseball players such as Joe DiMaggio, cricketers such as Don Bradman, and Pele from the world of soccer are remembered for the statistics they generated, but much more for their individual brilliance. To the younger generation this is seen only from film or television recordings, but memories of earlier days, before film records were kept, still persist. The great cricketer WG Grace, who was at his peak in the 1870s and 1880s, was filmed only in his declining years, and the few photographs available can convey little of his skills. We know, however, that Walter George set a world record for the mile in 1886 and that his time was recorded as 4 min 12.75 s. That may sound slow compared with today's performances, but it remains a creditable performance, given the state of the tracks on which he ran, the shoes he wore, and the limited training that he undertook.

Evolution of records

In some sports, the rules or the equipment have changed, making historical comparisons inappropriate



In sports where performance can be measured, it is possible to record the evolution of records, and the world record is a measure of the limit of what was achieved at any particular time in the history of sport. In some sports, the rules have changed or the equipment has changed, making historical comparisons inappropriate. The length and weight of the javelin, for example, were changed when the distances achieved by the top throwers became so great that they could not be contained within the confines of an athletics stadium. Likewise, the

introduction of aluminium and then fibreglass poles in the pole vault has made historical comparisons inappropriate. Most events, however, have not undergone fundamental changes, although it could be argued that the introduction of synthetic running tracks and improved shoe design have altered even the simple activity of running from A to B as fast as possible.



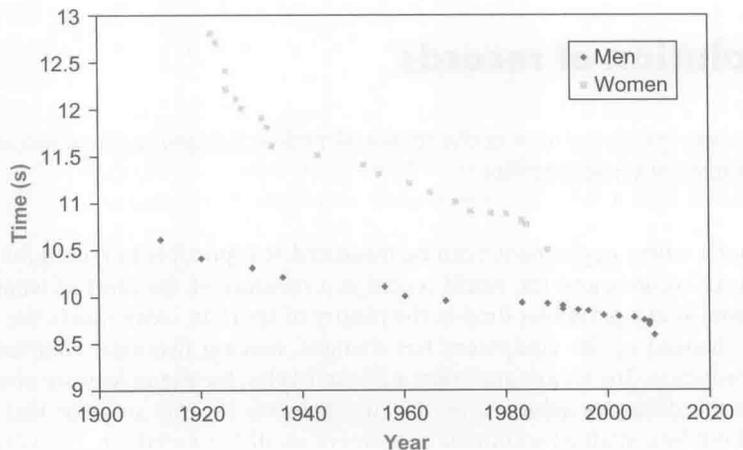
In the 100-m sprint, the men's record has always been better than the women's record

In an event such as the 100-m sprint on the track, successful performers must react rapidly to the starter's gun and generate high power to accelerate from the blocks. They must then maintain peak speed for as long as possible and slow down as little as possible in the later stages of the race. Improvements in performance may come from faster reaction times, better ability to generate power in the active muscles, improved resistance to fatigue, or some combination of these. Figure 1.1 shows how performances in the 100-m sprint have improved for men and women since records were first officially recognized in 1912. A number of factors are apparent from these graphs:

- there has been a steady improvement in performances for as long as records have been kept;
- there is no obvious indication that the rate of improvement has slowed—progress has been more or less linear at a rate of about 0.1 s per decade;
- the men's record has always been better than the women's record and even though the gap has narrowed somewhat, there is still a large (about 10%) difference.

Figure 1.1

Evolution of world record times for the 100-m sprint for men and women since official record keeping began.



There must be a limit to performance and at some point in the future there will be no further improvement



Although much can be learned from looking at a simple graph such as Figure 1.1, it is easy to over-interpret or misinterpret the information and to reach inappropriate conclusions. It is clear that there must be a limit to performance and at some point in the future there will be no further improvement. If we consider only the data for men, we can apply a linear regression analysis, which shows that there is no sign of the rate of progress falling off; the correlation coefficient is 0.948. This predicts that the world record will be 9.62 s in 2020 and 8.99 s in 2100 (Figure 1.2a). Clearly, however, the equation is not quite right as the World Record already exceeds that time—Usain Bolt having run a time of 9.58 s in 2009. That is the trouble with this type of analysis—progression is not linear, with periods of rapid improvement and other times when performances seem to stagnate. The women's record has not improved since 1988, a period of more than 20 years. It is clear that this time will be broken at some stage, but there is no way of knowing when this will happen. Another problem with the linear analysis model is the assumption that performances will continue to improve. A time of 8.99 s for the men's 100 m seems possible, but extending this extrapolation further suggests that at some stage in the future (in fact in the year 3276) the world record will be 0.00 s. The year after it will be negative—i.e. the runner who wants to break this record must finish before he has started. This is clearly absurd and will not happen, illustrating some of the difficulties with projections based on linear analyses. However, if we analyse these data differently and apply a non-linear equation to fit the best line, this fits just as well and indicates a gradual slowing of the rate of improvement. This analysis of the same information predicts that the ultimate limit will lie somewhere around 9.2 s, (Figure 1.2b) but it fails because it does not allow for an athlete like Usain Bolt, who was responsible for lowering the record by 0.16 s in less than 2 years. Only time will tell where the limit lies, and we cannot predict what impact new developments in track surfaces, shoes, and other factors may have on performance. Most predictions have been proved wrong by subsequent developments, but it seems safe to say that no man or woman will ever run 100 m in under 8 s. If that is accepted, then the ultimate limit must lie somewhere between the current record and the 8-s mark.

It is common to read that performance improvements will become progressively smaller, but there is no sign of that in some events. Even if the rate of progress does slow, measurement methods are becoming more precise, and performance can be measured to hundredths or even thousandths of a second. This can be seen with the 100-m world record mark. When times were recorded to 0.1 s, the record was broken only five times between 1912 and 1960: with the advent of electrical timing systems and the recording of times to 0.01 s, the record has been broken 14 times since 1960. Another example of this can be seen in the results of the Oxford–Cambridge University boat race, which has been contested