Thinking quantitatively about physiology is something many students find difficult. However, it is fundamentally important to a proper understanding of many of the concepts involved. In this enlarged second edition of his popular textbook, Richard Burton gives the reader the opportunity to develop a feel for values such as ion concentrations, lung and fluid volumes, blood pressures, etc. through the use of calculations that require little more than simple arithmetic for their solution. Much guidance is given on how to avoid errors and the usefulness of approximation and 'back-of-envelope sums'. Energy metabolism, nerve and muscle, blood and the cardiovascular system, respiration, renal function, body fluids and acid–base balance are all covered, making this book essential reading for students (and teachers) of physiology everywhere, both those who shy away from numbers and those who revel in them.

RICHARD F BURTON is Senior Lecturer in the Institute of Biomedical and Life Sciences at the University of Glasgow, Scotland, UK. *Biology by Numbers* by the same author is also published by Cambridge University Press.

Physiology by Numbers

An Encouragement to Quantitative Thinking

SECOND EDITION

RICHARD F. BURTON University of Glasgow, Glasgow



Cambridge University Press	
0521772001 - Physiology by Numbers: An Encouragement to Quantitative Think	ting,
Second Edition	
Richard F. Burton	
Frontmatter	
More information	

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS The Edinburgh Building, Cambridge, CB2 2RU, UK 40West 20th Street, New York, NY 10011–4211, USA 10 Stamford Road, Oakleigh, Melbourne 3166, Australia Ruiz de Alarcón 13, 28014 Madrid, Spain

http://www.cup.cam.ac.uk http://www.cup.org

© Cambridge University Press 1994, 2000

This book is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published 1994 Second edition published 2000

Printed in the United Kingdom at the University Press, Cambridge

Typeface Utopia 9.25/13.5 and Meta Plus. System QuarkXPress® [SE]

A catalogue record for this book is available from the British Library

 ${\it Library} of Congress \, Cataloguing \, in \, Publication \, Data$

Burton, R. F. (Richard F.)
Physiology by numbers: an encouragement to quantitative thinking / Richard F. Burton.
p. cm.
Includes bibliographical references and index.
ISBN 0 521 77200 1 (hb.). – ISBN 0 521 77703 8 (pbk.)
1. Human physiology – Mathematics Problems, exercises, etc.
I. Title.
QP40.B98 2000
612'.001'51–dc21 99-16237 CIP

ISBN 0 521 77200 1 hardback ISBN 0 521 77703 8 paperback

Cambridge University Press
0521772001 - Physiology by Numbers: An Encouragement to Quantitative Thinking,
Second Edition
Richard F. Burton
Frontmatter
More information

CONTENTS

	Preface to the second edition	ix
	Preface to the first edition	xi
	How to use this book	xv
1	Introduction to physiological calculation: approximation and unit	s 1
1.1	Arithmetic – speed, approximation and error	1
1.2	Units	3
1.3	How attention to units can ease calculations, prevent mistakes and	
	provide a check on formulae	5
1.4	Analysis of units in expressions involving exponents (indices)	13
1.5	Logarithms	15
_		
2	Quantifying the body: Interrelationships amongst representative	10
		10
3	Energy and metabolism	27
3 3.1	Energy and metabolism Measures of energy	27 27
3 3.1 3.2	Energy and metabolism Measures of energy Energy in food and food reserves; relationships between energy	27 27
3 3.1 3.2	Energy and metabolism Measures of energy Energy in food and food reserves; relationships between energy and oxygen consumption	27 27 28
3 3.1 3.2 3.3	Energy and metabolism Measures of energy Energy in food and food reserves; relationships between energy and oxygen consumption Basal metabolic rate	27 27 28 30
3 3.1 3.2 3.3 3.4	Energy and metabolism Measures of energy Energy in food and food reserves; relationships between energy and oxygen consumption Basal metabolic rate Oxygen in a small dark cell	27 27 28 30 31
 3.1 3.2 3.3 3.4 3.5 	Energy and metabolism Measures of energy Energy in food and food reserves; relationships between energy and oxygen consumption Basal metabolic rate Oxygen in a small dark cell Energy costs of walking, and of being a student	27 27 28 30 31 32
 3.1 3.2 3.3 3.4 3.5 3.6 	Energy and metabolism Measures of energy Energy in food and food reserves; relationships between energy and oxygen consumption Basal metabolic rate Oxygen in a small dark cell Energy costs of walking, and of being a student Fat storage and the control of appetite	27 27 28 30 31 32 33
 3.1 3.2 3.3 3.4 3.5 3.6 3.7 	Energy and metabolism Measures of energy Energy in food and food reserves; relationships between energy and oxygen consumption Basal metabolic rate Oxygen in a small dark cell Energy costs of walking, and of being a student Fat storage and the control of appetite Cold drinks, hot drinks, temperature regulation	27 27 28 30 31 32 33 34
 3.1 3.2 3.3 3.4 3.5 3.6 3.7 3.8 	Energy and metabolism Measures of energy Energy in food and food reserves; relationships between energy and oxygen consumption Basal metabolic rate Oxygen in a small dark cell Energy costs of walking, and of being a student Fat storage and the control of appetite Cold drinks, hot drinks, temperature regulation Oxygen and glucose in blood	27 27 28 30 31 32 33 34 36
 3.1 3.2 3.3 3.4 3.5 3.6 3.7 3.8 3.9 	Energy and metabolism Measures of energy Energy in food and food reserves; relationships between energy and oxygen consumption Basal metabolic rate Oxygen in a small dark cell Energy costs of walking, and of being a student Fat storage and the control of appetite Cold drinks, hot drinks, temperature regulation Oxygen and glucose in blood Adenosine triphosphate and metabolic efficiency	27 27 28 30 31 32 33 34 36 37
 3 3.1 3.2 3.3 3.4 3.5 3.6 3.7 3.8 3.9 3.10 	Energy and metabolismMeasures of energyEnergy in food and food reserves; relationships between energyand oxygen consumptionBasal metabolic rateOxygen in a small dark cellEnergy costs of walking, and of being a studentFat storage and the control of appetiteCold drinks, hot drinks, temperature regulationOxygen and glucose in bloodAdenosine triphosphate and metabolic efficiencyBasal metabolic rate in relation to body size	27 27 28 30 31 32 33 34 36 37 40
 3.1 3.2 3.3 3.4 3.5 3.6 3.7 3.8 3.9 3.10 3.11 	Energy and metabolismMeasures of energyEnergy in food and food reserves; relationships between energyand oxygen consumptionBasal metabolic rateOxygen in a small dark cellEnergy costs of walking, and of being a studentFat storage and the control of appetiteCold drinks, hot drinks, temperature regulationOxygen and glucose in bloodAdenosine triphosphate and metabolic efficiencyBasal metabolic rate in relation to body sizeDrug dosage and body size	27 27 28 30 31 32 33 34 36 37 40 43
 3.3 3.3 3.4 3.5 3.6 3.7 3.8 3.9 3.10 3.11 3.12 	Energy and metabolismMeasures of energyEnergy in food and food reserves; relationships between energyand oxygen consumptionBasal metabolic rateOxygen in a small dark cellEnergy costs of walking, and of being a studentFat storage and the control of appetiteCold drinks, hot drinks, temperature regulationOxygen and glucose in bloodAdenosine triphosphate and metabolic efficiencyBasal metabolic rate in relation to body sizeDrug dosage and body sizeFurther aspects of allometry-life span and the heart	27 27 28 30 31 32 33 34 36 37 40 43 44

Cambridge University Press	
0521772001 - Physiology by Numbers: Ar	n Encouragement to Quantitative Thinking,
Second Edition	
Richard F. Burton	
Frontmatter	
Moreinformation	

vi Contents

3.14	Production of metabolic water in human and mouse	46
4	The cardiovascular system	48
4.1	Erythrocytes and haematocrit (packed cell volume)	48
4.2	Optimum haematocrit – the viscosity of blood	53
4.3	Peripheral resistance	55
4.4	Blood flow and gas exchange	57
4.5	Arteriolar smooth muscle – the law of Laplace	58
4.6	Extending William Harvey's argument: 'what goes in must come out'	60
4.7	The work of the heart	61
5	Respiration	65
5.1	Correcting gas volumes for temperature, pressure, humidity and	
	respiratory exchange ratio	65
5.2	Dissolved O ₂ and CO ₂ in blood plasma	70
5.3	<i>P</i> co ₂ inside cells	70
5.4	Gas tensions at sea level and at altitude	72
5.5	Why are alveolar and arterial P_{Co_2} close to 40 mmHg?	74
5.6	Water loss in expired air	77
5.7	Renewal of alveolar gas	78
5.8	Variations in lung dimensions during breathing	82
5.9	The number of alveoli in a pair of lungs	82
5.10	Surface tensions in the lungs	84
5.11	Pulmonary lymph formation and oedema	85
5.12	The pleural space	89
6	Renal function	92
6.1	The composition of the glomerular filtrate	92
6.2	The influence of colloid osmotic pressure on glomerular filtration rate	95
6.3	Glomerular filtration rate and renal plasma flow; clearances of	
	inulin, para-aminohippurate and drugs	97
6.4	The concentrating of tubular fluid by reabsorption of water	100
6.5	Urea: clearance and reabsorption	101
6.6	Sodium and $\operatorname{bicarbonate}$ – rates of filtration and reabsorption	104
6.7	Is fluid reabsorption in the proximal convoluted tubule really	
	isosmotic?	106
6.8	Work performed by the kidneys in sodium reabsorption	107
6.9	Mechanisms of renal sodium reabsorption	109
6.10	Autoregulation of glomerular filtration rate; glomerulotubular	
	balance	112

Cambridge University Press
0521772001 - Physiology by Numbers: An Encouragement to Quantitative Thinking,
Second Edition
Richard F. Burton
Frontmatter
More information

	Contents	vii
6.11	Renal regulation of extracellular fluid volume and blood pressure	113
6.12	Daily output of solute in urine	114
6.13	The flow and concentration of urine	116
6.14	Beer drinker's hyponatraemia	119
6.15	The medullary countercurrent mechanism in antidiuresis –	
	applying the principle of mass balance	120
6.16	Renal mitochondria: an exercise involving allometry	128
7	Body fluids	132
7.1	The sensitivity of hypothalamic osmoreceptors	132
7.2	Cells as 'buffers' of extracellular potassium	133
7.3	Assessing movements of sodium between body compartments - a	
	practical difficulty	134
7.4	The role of bone mineral in the regulation of extracellular calcium	
	andphosphate	136
7.5	The amounts of calcium and bone in the body	138
7.6	The principle of electroneutrality	140
7.7	Donnan equilibrium	143
7.8	Colloid osmotic pressure	145
7.9	Molar and molal concentrations	148
7.10	Osmolarity and osmolality	150
7.11	Gradients of sodium across cell membranes	151
7.12	Membrane potentials - simplifying the Goldman equation	155
8	Acid-base balance	159
8.1	pH and hydrogen ion activity	160
8.2	$The CO_2-HCO_3equilibrium: theHenderson-Hasselbalchequation$	162
8.3	Intracellular pH and bicarbonate	166
8.4	Mitochondrial pH	169
8.5	Why bicarbonate concentration does <i>not</i> vary with P_{Co_2} in simple	
	solutions lacking non-bicarbonate buffers	172
8.6	Carbonate ions in body fluids	174
8.7	Buffering of lactic acid	176
8.8	The role of intracellular buffers in the regulation of extracellular pH	178
8.9	The role of bone mineral in acid–base balance	182
8.10	Is there a postprandial alkaline tide?	183
9	Nerve and muscle	185
9.1	Myelinated axons-saltatory conduction	185
9.2	Non-myelinated fibres	187

Cambridge University Press
0521772001 - Physiology by Numbers: An Encouragement to Quantitative Thinking
Second Edition
Richard F. Burton
Frontmatter
More information

viii Contents

9.3	Musical interlude – a feel for time	188
9.4	Muscular work – chinning the bar, saltatory bushbabies	190
9.5	Creatine phosphate in muscular contraction	193
9.6	Calcium ions and protein filaments in skeletal muscle	194
	Appendix A: Some useful quantities	198
	Appendix B: Exponents and logarithms	200
	References	205
	Notes and Answers	209
	Index	232

PREFACE TO THE SECOND EDITION

When I started to write the first edition of this book, I particularly had in mind readers somewhat like myself, not necessarily skilled in mathematics, but interested in a quantitative approach and appreciative of simple calculations that throw light on physiology. In the end I also wrote, as I explain more fully in my original Preface, for those many students who are ill at ease with applied arithmetic. I confess now that, until I had the subsequent experience of teaching a course in 'quantitative physiology', I was not fully aware of the huge problems so many present-day students have with this, for so many are reluctant to reveal them. Part of my response to this revelation was Biology by Numbers (Burton 1998), a book which develops various simple ideas in quantitative thinking while illustrating them with biological examples. In revising Physiology by Numbers, I have retained the systematic approach of the first edition, but have tried to make it more accessible to the number-shy student. This has entailed, amongst other things, considerable expansion of the first chapter and the writing of a new chapter to follow it. In particular, I have emphasized the value of including units at all stages of a calculation, both to aid reasoning and to avoid mistakes. I should like to think that the only prior mathematics required by the reader is simple arithmetic, plus enough algebra to understand and manipulate simple equations. Logarithms and exponents appear occasionally, but guidance on these is given in Appendix B. Again I thank Dr J. D. Morrison for commenting on parts of the manuscript.

R.F. Burton

PREFACE TO THE FIRST EDITION

Let us therefore take it that in a man the amount of blood pushed forward in the individual heartbeats is half an ounce, or three drams, or one dram, this being hindered by valves from re-entering the heart. In half an hour the heart makes more than a thousand beats, indeed in some people and on occasion, two, three or four thousand. Now multiply the drams and you will see that in one half hour a thousand times three drams or two drams, or five hundred ounces, or else some such similar quantity of blood, is transfused through the heart into the arteries – always a greater quantity than is to be found in the whole of the body.

But indeed, if even the smallest amounts of blood pass through the lungs and heart, far more is distributed to the arteries and whole body than can possibly be supplied by the ingestion of food, or generally, unless it returns around a circuit.

William Harvey, De Motu Cordis, 1628 (from the Latin)

In more familiar terms, if the heart beats, say, 70 times a minute, ejecting 70 ml of blood into the aorta each time, then more fluid is put out in half an hour (1471) than is either ingested in that time or contained in the whole of the body. Therefore the blood must circulate. Thus may the simplest calculation bring understanding. I invite the reader to join me in putting two and two together likewise, hoping that my collection of simple calculations will also bring enlightenment.

Although my main aim is to share some insights into physiology obtained through calculation, I have written also for those many students who seem to rest just on the wrong side of an educational threshold – knowing calculators and calculus, but shy of arithmetic; drilled in accuracy and unable to approximate; unsure what to make of all those physiological concentrations, volumes and pressures that are as meaningless as telephone numbers until toyed with,

xii Preface to the first edition

combined, or re-expressed. As 'an encouragement to quantitative thinking' I also offer, for those ill at ease with arithmetic, guidance on how to cheat at it, cut corners, and not be too concerned for spurious accuracy. Harvey's calculations illustrate very well that a correct conclusion may be reached in spite of considerable inaccuracy. In his case it was the estimate of cardiac output that was wrong; it is now known to be about two and a half ounces per beat. (There are eight drams to the ounce.)

Much of physiology requires precise computation, so I must not appear too much the champion of error and slapdash. There are, however, situations where even the roughest of calculations may suffice. Consider the generalization (see Section 3.10) that small mammals have higher metabolic rates per unit body mass than do large ones: taking the case of a hypothetical mouse with the relative metabolic rate of a steer, Max Kleiber (1961) calculated that to keep in heat balance in an environment at 3°C its surface covering, if like that of the steer, would need to be at least 20 cm thick! Arguments of this kind appear below. Be warned, however, that improbable answers are not always wrong, as exemplified by Rudolph Heidenhain's calculation of glomerular filtration rate in 1883 (Section 6.5).

The book is based on an assortment of questions to be answered by calculation, together with some introductory and background information and comment on the answers. (The answers are given at the back of the book, together with notes and references.) Such a quantitative approach is more suited to some areas of physiology than to others and the coverage of the book naturally reflects this. The book is neither a general guide to basic physiology, nor a collection of brain-teasers or practice calculations. It rarely strays from shopkeeper's arithmetic and it is not a primer of mathematical physiology or of mathematics for physiologists. Rather, it is supplementary thinking for those who have done, or are still doing, at least an elementary course in Physiology. I have learned much myself from the calculations and hope that other mature students may learn from them too.

Except where otherwise stated, the calculations refer to the human body. This is often taken as that of the physiologist's standard 70-kg adult man and many 'standard', textbook quantities are used here. This is partly to reinforce them in the reader's memory and build bridges from one to another, but such standard values are also a natural starting point for back-of-envelope calculations. Indeed, if there is any virtue to learning these quantities, it is surely helpful to exercise them and put them to use. Thus may one hope to bring life to numbers – and not just numbers to Life.

Preface to the first edition

The link between the learning and usefulness of quantities may be viewed the other way round. A student may memorize many of them for examinations and for future clinical application, but which are most profitably learnt for the better understanding of the body? Those with most uses? In how many elementary contexts is it helpful to know the concentration of sodium in extracellular fluid? Is that of magnesium as useful? Or manganese? Such questions of priority are as important for those inclined to overtax their memories unreasonably as for the lazy. This book may help both with these decisions and with the learning process itself.

Partly for reasons just indicated, many of my 'numbers' come from textbooks. Working on this text, however, I came increasingly to realize how hard it may be to find what one supposes to be well-known quantities. Textbooks have less and less room for these as other knowledge accumulates, of course, and there is a laudable tendency for concepts to displace quantitative detail. So do not disdain the older books! Diem (1962) has been a very useful source. Sometimes when a quantitative argument seems frustrated through lack of reliable figures, the solution is to turn it on its head, depart from the natural sequence of calculations, and defer the uncertainties to the end. The reader may spot where I was able to rescue items that way. Only once have I resorted to original data; I am very grateful to Dr Andrew Chappell for dissecting and weighing human muscles for me (Section 9.4).

I thank also all my colleagues who read portions of draft manuscript or otherwise gave of their time and wisdom, and in particular Dr F. L. Burton, Professor J. V. G. A. Durnin, Dr M. Holmes, Dr O. Holmes, Professor S. Jennett, Dr D. J. Miller, Dr J. D. Morrison, Dr G. L. Smith and Dr N. C. Spurway.

R. F. Burton

xiii

HOW TO USE THIS BOOK

Understand the objectives as stated in the Preface to the first edition; be clear what the book is – and what it is not. Since it is written for readers of widely varying physiological knowledge and numerical skills, read selectively. Chapters 3–9, and their individual subsections, need not be read in sequence.

Although the book is primarily about physiology, another objective is to encourage and facilitate quantitative thinking in that area. If such thinking does not come easily to you, pay particular attention to Chapter 1. Note too that the calculations are not intended to be challenging. Indeed, many are designed for easymental, or back-of-envelope, arithmetic – and help is always to hand at the back of the book, in 'Notes and Answers'. The notes often deal with points considered either too elementary or too specialized for the main text.

Consider carefully the validity of all assumptions and simplifications. If you try guessing answers before calculating them, you are more likely to be rewarded, in some cases, with a surprise.

If you are unfamiliar with exponents or logarithms, note the guidance given in Appendix B. The mathematics of exponential time courses are not dealt with in a single place, but most of the essentials are covered incidentally (see pages 13–16, 80–81, 98–100, 210–211, 219).