Amino Acids in Human Nutrition and Health

EDITED BY
J.P.F. D'MELLO

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Formerly of SAC, University of Edinburgh King's Buildings Campus, Edinburgh, UK

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A catalogue record for this book is available from the British Library, London, UK.

Library of Congress Cataloging-in-Publication Data

Amino acids in human nutrition and health / edited by J.P.F. D'Mello.
p. cm.
Includes bibliographical references and index.
ISBN 978-1-84593-798-0 (alk. paper)
1. Amino acids in human nutrition. 2. Amino acids--Metabolism. I. D'Mello, J. P. Felix. II. C.A.B. International.
[DNLM: 1. Amino Acids--metabolism. 2. Amino Acids--therapeutic use. 3. Enzymes--metabolism. 4. Enzymes--therapeutic use. 5. Nutritional Physiological Phenomena. QU 60]

QP561.A4845 2011
612'.015756--dc22

2011010103

ISBN-13: 978 1 84593 798 0

Commissioning editor: Rachel Cutts
Editorial assistant: Alexandra Lainsbury
Production editor: Fiona Chippendale

Typeset by SPi, Pondicherry, India.
Printed and bound by CPI Group (UK) Ltd, Croydon, CR0 4YY.

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Preface

Rationale

Research interest in the biochemistry of amino acids continues apace, generating significant dividends for nutritional support and the elucidation of mechanisms underlying a variety of disorders in humans. The remarkable scale of recent developments has provided the impetus for publication of this first edition of *Amino Acids in Human Nutrition and Health*. It was deemed appropriate to formally acknowledge these advances within a comprehensive volume. The recruitment of authors with exceptional merit constituted an integral part of my strategy.

There appears to be a demand for a book which integrates recent advances relating to amino acids within the two disciplines of nutrition and health. Various symposia have been convened on certain aspects covered in this book, but the published proceedings are distributed in different issues of journals, thereby compromising convenience for consultation by students and research staff. It is an unfortunate reflection of our time that university libraries cannot afford to stock some of the primary journals that have, in the recent past, been judged to be essential reading for advanced students. The publication of *Amino Acids in Human Nutrition and Health* might be viewed as an attempt to rectify this deficiency. Furthermore, the symposia have focused on restricted themes, whereas this volume is designed to address a comprehensive range of issues. The reviews in published proceedings of symposia have also been restricted to a few pages per article, but there is a need for in-depth coverage to more appropriately reflect current developments.

This volume is designed for academic, research, and corporate establishments worldwide, particularly in Europe, the United States, Canada, Japan, and Australia, but generally in all countries where English is a primary medium for education and research. This book should appeal to final year undergraduate and graduate students as well as to research staff. It is anticipated that it will be recommended reading for courses in general and clinical biochemistry, medicine, nursing, human nutrition and food science. The text is also designed with the commercial sector in mind, particularly pharmaceutical companies with extensive R&D laboratories.

Overview

The chapters in *Amino Acids in Human Nutrition and Health* are arranged within a thematic structure as indicated in the sections below. The nature of the subject and the need for

interlinking chapters have meant that a limited amount of overlap was inevitable. This is not necessarily a detraction, as individual chapters are now self-contained to ensure continuity for readers, with cross-referencing kept to the minimum. This strategy has also allowed authors increased flexibility in terms of emphasis and interpretation.

Part I Enzymes and metabolism

This section pursues the theme of amino acid metabolism through the driving actions of the principal enzymes, emphasizing recent developments particularly with reference to localization, molecular genetics, biophysical characterization and regulation. Subsequent chapters will also demonstrate the changing facets of amino acid biochemistry. The competing actions of enzymes for critical substrates are also features of relevance in this section. A number of the enzymes under review here catalyse rate-limiting steps in important metabolic pathways, leading to synthesis of physiologically active intermediates and end products. There is scope for elaboration of the important pathways initiated by enzymes under review in this section. Part I has also been developed with the aim of underpinning subsequent chapters in this volume.

Part II Dynamics

This section deals with important issues relating to whole-body amino acid dynamics, with a particular objective of supporting the chapters on nutrition and health that will follow. In this chapter, authors were encouraged to adopt an integrative approach to include their own expertise and that of others in their respective fields. A basic outline of metabolic pathways appears in Part I. The theme in this section centres around kinetics and regulation in broad-spectrum reviews incorporating innovative aspects of the relevant research. In other words, the concept of metabolic networking forms an underlying theme in this series of chapters.

Part III Nutrition

Since the publication of *Mammalian Protein Metabolism* (Munro and Allison, 1964), there has been a steady but perceptible shift in focus towards individual or distinct groups of amino acids, and this change is most clearly seen in nutritional developments. The move away from protein to amino acid considerations is a deliberate theme in the development of the rationale for this section. However, even traditional issues, such as protein-energy malnutrition, are being investigated in the light of kinetics of specific amino acids, with reduced emphasis on whole-body protein dynamics. Against such a background, it was considered appropriate to secure reviews that would reflect a modernizing and progressive agenda in amino acid research.

The chapters cover a number of topical research investigations employing existing technologies to develop novel concepts or to underpin contemporary practices. Methods previously developed and validated with animal models are now being applied to human physiology and nutrition with significant results worthy of publication in this volume.

Part IV Health

The earlier sections have provided the biochemical basis of several of the conditions to be reviewed here. It is now clear that the metabolism of amino acids is associated with or

modulated by a diverse array of disorders and, in certain instances, may provide markers for risk assessment. At least four of the chapters in this section will focus on different amino acids associated with neurological issues and cognitive performance measures. The approach here is designed to reflect developments in epidemiology, monitoring, and clinical interventions in the various conditions under consideration in this section.

Part V Conclusions

The final section contains a plenary review designed to summarize the main findings in the foregoing chapters within an integrated account. The main theme centres around the concept of the emergence of a new momentum driving forward a progressive agenda in further elucidating the biochemical and health implications of amino acids.

Acknowledgements

I am indebted to my team of distinguished authors who have made publication of this volume possible despite the constraints imposed by their normal schedules. Their cooperation in submitting manuscripts promptly has ensured that the book remains up-to-date and relevant in an ever-changing scenario. Their lucid chapters have inspired me to enquire further and to challenge existing hypotheses; I trust that my readers will be similarly motivated. I am heartened by responses I have received from a number of my authors. The following words of Professor Deniz Kirik (Chapter 26, with Professor Sahin) encapsulates these sentiments: 'It has been an interesting exercise for us to write this text as it provoked many interesting discussions in areas we thought we knew well but noticed gaps in our knowledge. We will follow on some of these points to inquire more and think that some of them could even become topics for experimentation in the next period. So it has been very valuable and pleasant for us as well.'

Disclaimer

This book necessarily contains references to commercial products. However, authors were asked to refrain from excessive usage of any trade names unless there were compelling reasons for doing so. No endorsement of these products is implied or should be attributed to the editor or to CAB International.

The information set out within *Amino Acids in Human Nutrition and Health* is presented in good faith and in accordance with 'best practice'. Although every effort has been made to verify the facts and figures, neither the editor nor CAB International can accept responsibility for the data presented in individual chapters or for any consequences of their use.

At the time of preparation, I was aware of articles in the popular press extolling the virtues of citrulline and the branched-chain amino acids in the context of health and longevity. However, the publication of this book should not be interpreted as a recommendation for individuals to use these or any other amino acids for whatever purpose. *Amino Acids in Human Nutrition and Health* is intended exclusively for use as a text in education and in R&D establishments.

J.P.F. D'Mello
Editor

Glossary

Introduction

Evaluation of issues underlying the role of amino acids in human nutrition and health inevitably entails an appreciation of specific nomenclature and technical descriptors. Although many of the terms and acronyms used are now in common usage outside scientific circles, it was deemed important to provide as comprehensive a list as possible to assist those readers who are new to this field. Further definitions are available in appropriate scientific dictionaries, for example in the compilations of Hodgson *et al.* (1998), Marcovitch (2005), Parish *et al.* (2006), Martin (2010) and the MedlinePlus (2010) website. Handbooks such as those by D'Mello (1997) and Longmore *et al.* (2010) and current textbooks in medical sciences (Bear *et al.*, 2007; Barker *et al.*, 2008; Baynes and Dominiczak, 2009; Naish *et al.*, 2009) are also recommended as sources of relevant information.

Definition of Terms and Acronyms

The important terms and acronyms are defined in Table 1. This compilation includes standard conventions as well as unique chapter-specific terms. Cross-referencing to individual chapters in this volume is provided in order to permit a greater appreciation of the context of usage of selected terms.

Table 1. Explanation of relevant terms and acronyms used in *Amino Acids in Human Nutrition and Health*.

Abbreviation or Term	Definition
AA	amino acid(s)
AAA	aromatic amino acid(s)
AAAH	aromatic amino acid hydroxylase (Chapter 9)
AADC	aromatic amino acid decarboxylase (Chapters 9 and 26)
AARE	amino acid regulatory element (Chapter 13)
Ac-CoA	acetyl coenzyme A
Acute toxicity	severe adverse effects occurring within a relatively short period of exposure to a potentially harmful substance

Continued

Table 1. Continued.

Abbreviation or Term	Definition
AD	Alzheimer's disease (Chapters 21, 22, 25, and 28)
Adduct	covalent product of a compound or metabolite to large biomolecules such as proteins and DNA (Chapter 28)
ADHD	attention deficit hyperactivity disorder (Chapter 9)
ADI	acceptable daily intake(s)
ADMA	asymmetrical dimethylarginine (Chapter 4)
ADP	adenosine diphosphate (Chapter 1)
AGE	advanced glycation end-product(s) (Chapters 19, 22, and 28)
Agonist	a compound eliciting a biological response by interacting with specific cell receptors, enzymes or metabolites
Akt	protein kinase B (Chapter 17)
ALE	advanced lipoxidation end-product(s) (Chapters 22 and 28)
Allosteric	multi-site enzyme modulation of structure and activity (Chapter 10)
ALP	alkaline phosphatase (Chapter 2)
ALS	amyotrophic lateral sclerosis (Chapter 25)
ALS/PDC	amyotrophic lateral sclerosis/Parkinsonism dementia complex (Chapter 19)
ALT	alanine aminotransferase (Chapter 2)
AMD	age-related macular degeneration (Chapter 22)
Aminoacidergic	relating to amino acids as neurotransmitters (Chapter 28)
AminoIndex	amino acid profiles for diagnostic applications (Chapter 27)
AMP	adenosine monophosphate (Chapter 9)
AMPA	α-amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid (Chapters 8, 25, and 28)
AMPAR	AMPA receptor (Chapter 25)
AMPK	AMP-activated protein kinase (Chapter 10)
ANF	anti-nutritional factor(s) (Chapter 14)
Antagonist	a compound acting as an inhibitor by virtue of structural analogy with nutrients or other intermediates (Chapter 19)
AOAA	aminooxyacetic acid (Chapter 2)
APEX	apurinic/apyrimidinic endonuclease (Chapter 10)
ARA	arachidonic acid (20:4n-6) (Chapter 23)
Arg	arginine
ASNS	asparagine synthetase (Chapter 13)
ASCT	alanine, serine, and cysteine transport system (Chapter 8)
Asn	asparagine
Asp	aspartate
ASS	argininosuccinate synthase (Chapter 3)
AST	aspartate aminotransferase (Chapter 2)
ATA	aurintricarboxylic acid (Chapter 1)
ATF	activating transcription factor (Chapter 13)
ATP	adenosine 5'-triphosphate (Chapters 1, 11, 20, and 28)
AUC	area under the curve (Chapter 27)
BBB	blood–brain barrier (Chapters 9 and 11)
BBMV	brush border membrane vesicles
BCAA	branched-chain amino acids (Chapters 2, 11, 16, 17, 19, and 28)
BCAT	branched-chain aminotransferase (Chapters 2 and 28)
BCH	2-aminobicyclo(2,2,1)-heptane-2-carboxylic acid (Chapter 11)
BCKA	branched-chain keto acids (Chapters 2 and 19)
BCKDH	branched-chain α-keto acid dehydrogenase (Chapter 2)
BH_4	tetrahydrobiopterin (Chapters 4, 9, and 23)
BLMV	basolateral membrane vesicles
BMAA	β-*N*-methylamino-L-alanine (Chapter 19)
BMI	body mass index (Chapter 23)

Table 1. Continued.

Abbreviation or Term	Definition
BOAA	β-*N*-oxalylamino-L-alanine (Chapter 19)
CAA	cationic amino acids (Chapter 11)
Carcinogenic	causing cancer
CAT	cationic amino acid transport
CBS	cystathionine β-synthase (Chapter 10)
cDNA	complementary DNA (Chapter 7)
CEL	N^{ε} -(carboxyethyl) lysine (Chapter 22)
cGMP	cyclic guanosine monophosphate
ChAT	choline acetyltransferase (Chapter 8)
CHD	coronary heart disease (Chapter 21)
CHOP	C/EBP homologous protein (Chapter 13)
Chronic toxicity	adverse effects resulting from prolonged and repeated exposure to relatively small quantities of a potentially harmful substance
Cit	citrulline
CML	N^{ε} -(carboxymethyl) lysine (Chapters 22 and 28)
cNOS	constitutive nitric oxide synthase (Chapter 28)
CNS	central nervous system (Chapters 1, 7, 8, and 28)
CoA	coenzyme A
COMT	catechol-*O*-methyltransferase (Chapter 26)
COPD	chronic obstructive pulmonary disease (Chapters 22 and 28)
CPS	carbamoyl phosphate synthase (Chapter 3)
CPu	caudate-putamen (Chapter 25)
CSA	cross-sectional area (of skeletal muscle fibre) (Chapter 17)
CSF	cerebrospinal fluid (Chapter 11)
CVD	cardiovascular disease (Chapter 21)
Cys	cysteine
d	day
DA	dopamine
DAA	dispensable amino acid(s) (see also NEAA) (Chapter 19)
DAAB	direct amino acid balance (Chapter 16)
DAAO	direct measurement of amino acid oxidation (Chapter 16)
DCAM	decarboxylated 5-adenosyl-methionine
DDC	DOPA decarboxylase (Chapter 6)
DFMO	α-difluoromethylornithine (Chapter 3)
DHA	docosahexaenoic acid (22:6n-3) (Chapter 23)
DHF	dihydrofolate (Chapter 10)
DMD	Duchenne muscular dystrophy (Chapter 18)
DMI	dry matter intake
$DMPH_4$	6,7-dimethyltetrahydropterin (Chapter 9)
DNA	deoxyribonucleic acid (Chapters 1, 5, 10, 19, and 28)
DOPA	3,4-dihdroxyphenylalanine (Chapters 26 and 28)
DOPAC	3,4-dihydroxyphenylacetate (Chapters 5, 6, and 26)
dUMP	deoxyuridine monophosphate (Chapter 10)
EAA	essential amino acid(s) (see also IAA) (Chapter 17)
EAAT	excitatory amino acid transport (Chapter 11)
EC	epicatechin (Chapter 1)
ECF	extracellular fluid (Chapter 11)
ECG	epicatechin gallate (Chapter 1)
EDTA	ethylendiamine tetraacetic acid (Chapter 27)
EEG	electroencephalogram (Chapter 25)
eEPSC	evoked excitatory postsynaptic current(s) (Chapter 25)
EGC	epigallocatechin (Chapter 1)
EGCG	epigallocatechin gallate (Chapters 1 and 22)

Continued

Table 1. Continued.

Abbreviation or Term	Definition
ELISA	enzyme-linked immunosorbent assay (Chapter 6)
EMG	electromyography (Chapter 25)
EOG	electrooculography (Chapter 25)
EU	European Union
FA	fatty acid(s)
FAD	flavin adenine dinucleotide
FAO	Food and Agriculture Organization (United Nations)
FDA	Food and Drug Administration (USA)
fEPSP	field excitatory postsynaptic potential(s) (Chapter 25)
FMN	flavin mononucleotide (Chapter 4)
fMRI	functional magnetic resonance imaging (Chapter 20)
Fol	folic acid (Chapter 21)
FSR	fractional synthetic rate
GA	glutaminase (Chapter 7)
GAB	glutaminase B (Chapter 7)
GABA	γ-amino butyrate (Chapters 1, 5, 6, 7, 25, and 28)
GABAR	GABA receptor (Chapter 25)
GAC	glutaminase C (Chapter 7)
GAD	glutamic acid decarboxylase (Chapters 6 and 28)
GCH	GTP cyclohydrolase (Chapter 26)
GCN	general control non-derepressive (Chapter 13)
GDH	glutamate dehydrogenase (Chapter 1, 2, and 28)
GDS	gut-derived serotonin (Chapter 9)
GGT	γ-glutamyl transpeptidase (Chapter 11)
GH	growth hormone
Glc-6P	glucose-6 phosphate
Gln	glutamine
Glu	glutamate
Glutamatergic	relating to glutamate neurotransmission (Chapter 28)
Gly	glycine
GMP	guanosine-5′-monophosphate (Chapter 20)
GNMT	glycine *N*-methyltransferase (Chapter 10)
GPCR	G protein-coupled receptors (Chapter 20)
GS	glutamine synthetase (2 and 28)
GSH	glutathione (Chapter 10)
GTP	guanosine triphosphate (Chapters 1, 4, and 26)
h	hour(s)
HCC	hepatocellular carcinoma (Chapter 10)
HCP	hexachlorophene (Chapter 1)
Hcy	homocysteine (Chapter 21)
HD	Huntington's disease (Chapter 25)
HDC	histidine decarboxylase (Chapters 6 and 28)
HDL	high density lipoproteins (Chapter 22)
Hepatotoxic	toxic to the liver
HHS	hyperinsulinism/hyperammonaemia syndrome (Chapter 1)
His	histidine
HO2	haem-oxygenase-2
HPLC	high-performance liquid chromatography (Chapter 26)
HRI	haem-regulated translational inhibitor (Chapter 13)
5-HT	5-hydroxytryptamine (serotonin) (Chapter 24)
HuR	human antigen R (Chapter 10)
HVA	homovanillic acid (Chapter 26)
hVps34	human vacuolar protein sorting-34 (Chapter 17)
IAA	indispensable amino acid(s) (see also EAA) (Chapters 16 and 19)

Table 1. Continued.

Abbreviation or Term	Definition
IAAB	indicator amino acid balance (Chapter 16)
IAAO	indicator amino acid oxidation (Chapters 15 and 16)
IGF-I	insulin-like growth factor-I (Chapter 13)
IGFBP-1	insulin-like growth factor binding protein-1 (Chapter 13)
ILAE	International League Against Epilepsy (Chapter 25)
Ile	isoleucine
IMP	inosine-5′-monophosphate (inosinate) (Chapter 20)
iNOS	inducible nitric oxide synthase (Chapter 28)
KA	kainate (Chapter 25)
KAR	kainate type glutamate receptor (Chapter 25)
KGA	kidney GA (Chapter 7)
KO	knockout (Chapter 9)
LCMT	leucine carboxyl methyltransferase
LCPUFA	long-chain polyunsaturated fatty acids (Chapter 23)
LDH	lactate dehydrogenase
LDL	low-density lipoprotein(s) (Chapters 3 and 4)
LDR	long-duration response (Chapter 26)
Leu	leucine
LFT	liver function tests (Chapter 2)
LGA	liver GA (Chapter 7)
LKB	liver kinase B (Chapter 10)
LNAA	large neutral amino acid(s) (Chapters 11, 23, and 24)
LTP	long-term potentation (Chapter 25)
Lys	lysine
MA	metabolic availability (Chapters 9 and 15)
MAO	monoamine oxidase (Chapters 9 and 26)
MAP4K3	mitogen activated protein kinase-3 (Chapter 17)
MAT	methionine adenosyltransferase (Chapters 10 and 28)
MDH	malate dehydrogenase (Chapter 2)
ME	malic enzyme (Chapter 2)
MeAIB	*N*-(methylamino)-isobutyric acid (Chapter 11)
Met	methionine
mGluR	metabotropic G protein-coupled glutamate receptor (Chapter 25)
MMP	mitochondrial membrane potential (Chapter 7)
Monoaminergic	relating to neurotransmission by biogenic amines (Chapter 28)
MPB	muscle protein breakdown (Chapter 17)
MPS	muscle protein synthesis (Chapter 17)
MPTP	1, methyl-4-phenyl-1,2,3,6-tetrahydropyridine (Chapter 26)
M_r	relative molecular mass (Chapter 7)
mRNA	messenger RNA
MSG	monosodium glutamate (Chapters 19, 20, and 28)
MSUD	maple syrup urine disease (Chapter 2)
MT	methyltransferases (Chapter 10)
MTHFR	methylene-tetrahydrofolate reductase (Chapter 21)
mTOR	mammalian target of rapamycin (Chapters 10, 13, 17, and 28)
Mutagenic	causing mutations
N	nitrogen
NAA	neutral amino acids (Chapter 11)
NAcc	nucleus accumbens (Chapter 25)
NAD^+	nicotinamide adenine dinucleotide (oxidized) (Chapter 1)
$NADP^+$	nicotinamide adenine dinucleotide phosphate (oxidized) (Chapter 1)
NADPH	nicotinamide adenine dinucleotide phosphate (reduced) (Chapters 1, 3, and 4)
NAFLD	non-alcoholic fatty liver disease (Chapters 2, 10, and 22)

Continued

Table 1. Continued.

Abbreviation or Term	Definition
NASH	non-alcoholic steatohepatitis (Chapters 10 and 22)
NCHS	National Center for Health Statistics (USA) (Chapter 23)
NDF	neutral detergent fibre (Chapter 14)
NEAA	non-essential amino acid(s)
Nephrotoxic	toxic to the kidney
NIH	National Institutes of Health
NMDA	*N*-methyl D-aspartate (Chapters 8, 25, and 28)
NMDAR	NMDA receptor(s) (Chapters 8 and 25)
NMMA	N^G-monomethyl arginine (Chapter 4)
NO	nitric oxide (Chapters 3, 4, 11, 12, 19, and 28)
NOHA	N^{ω}-hydroxy-L-arginine (Chapter 3)
nor-NOHA	N^{ω}-hydroxy-nor-L-arginine (Chapter 3)
NOS	nitric oxide synthase (Chapters 3, 4, 11, 12, 19, and 28)
NPB	net protein balance (Chapter 17)
NRC	National Research Council (USA)
NSRE	nutrient-sensing response element (Chapter 13)
NTD	neural tube defects (Chapter 21)
OAA	oxaloacetate (Chapters 2 and 7)
OAAL	obligatory amino acid loss (Chapter 16)
OAT	ornithine aminotransferase (Chapter 3)
OCT	ornithine carbamoyltransferase (Chapter 3)
ODC	ornithine decarboxylase (Chapters 3 and 28)
6-OHDA	6-hydroxydopamine (Chapter 26)
3-OMD	3-*O*-methyl-DOPA (Chapter 26)
Orn	ornithine
Outbreak	two or more incidents of disease attributed to a common cause
PAH	phenylalanine hydroxylase (Chapters 9 and 23)
PCPA	*p*-chlorophenylalanine (Chapter 9)
PCR	polymerase chain reaction (Chapter 6)
PD	Parkinson's disease (Chapters 25 and 26)
PDCAAS	protein digestibility-corrected amino acid score (Chapters 14 and 15)
PERK	PKR-like endoplasmic reticulum kinase (Chapter 13)
PET	positron emission tomography (Chapter 24)
PFC	prefrontal cortex (Chapter 25)
PHB	prohibitin (Chapter 10)
Phe	phenylalanine
PKR	double-stranded RNA (dsRNA)-dependent protein kinase (Chapter 13)
PKU	phenylketonuria (Chapters 19, 23, and 28)
PLP	pyridoxal phosphate (Chapters 2 and 6)
PMP	pyridoxamine phosphate (Chapter 2)
PPU	post-prandial protein utilization (Chapters 15 and 16)
Pro	proline
Proteomes	total complement of proteins within a cell
PRP	proline-rich proteins (Chapter 28)
PRPP	5-phosphoribosyl-1-pyrophosphate
PRT	protein (Chapter 17)
PTZ	pentylenetetrazole (Chapter 25)
Pyr	pyruvate
rAAV	recombinant-adeno-associated virus (Chapter 26)
R&D	research and development
RAGE	receptor for AGE (Chapter 22)
RBC	red blood cell(s) (Chapter 3)