

## An Introduction to Neuroendocrinology

### Second Edition

How does the brain regulate sexual behavior, or control our body weight? How do we cope with stress? Addressing these questions and many more besides, this thoroughly revised new edition reflects the significant advances that have been made in the study of neuroendocrinology over the last 20 years.

The text examines the importance of the hypothalamus in regulating hormone secretion from the endocrine glands, describing novel sites of hormone release, including bone, heart, skeletal muscle, and liver. The role of steroid hormone, neurotransmitter and peptide receptors, and the molecular responses of target tissues, is integrated into the discussion of the neuroendocrine brain, especially through changes in gene expression. Particular attention is attached to neuropeptides, including their profound influence on behavior.

Complete with new full-color figures throughout, along with review and essay questions for each chapter, this is an ideal resource for undergraduate and graduate students of neuroscience, psychology, biology, and physiology.

**Michael Wilkinson** has 40 years of experience in teaching neuroscience and neuroendocrinology to undergraduate and graduate students as a Professor in the Department of Obstetrics and Gynaecology and IWK Health Centre, Dalhousie University, Halifax, Canada. His research laboratory has focused on neurodevelopmental aspects of female reproduction with a specific interest in the neuroendocrine regulation of hypothalamic function, including the impact of sex hormones on sleep.

**Richard E. Brown** is a University Research Professor in the Department of Psychology and Neuroscience at Dalhousie University. He has taught courses on hormones and behavior, measuring behavior, and the neurobiology of learning and memory for more than 35 years. His research is on mouse models of Alzheimer's Disease, Fragile X Syndrome, ADHD, and other neurological disorders. He is currently examining the age-related hormonal changes in transgenic Alzheimer's mice.

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# An Introduction to

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# Neuroendocrinology

**Second Edition**

**Michael Wilkinson**

Professor of Obstetrics & Gynaecology  
Professor of Physiology & Biophysics  
Dalhousie University Faculty of Medicine, Halifax, Nova Scotia, Canada

**Richard E. Brown**

Professor of Psychology  
Dalhousie University, Halifax, Nova Scotia, Canada



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This book is dedicated, first, to the more than 2,000 Dalhousie University students who were enrolled in the “Hormones and Behavior” undergraduate course and who were the original inspiration for writing the book. Many of them provided critical comments on early drafts of the first edition.

Second, one of us (M. W.) acknowledges the mentorship of the late Professor Kurt B. Ruf, a neuroendocrinologist and friend.

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## PREFACE TO THE SECOND EDITION

In this second edition of *An Introduction to Neuroendocrinology*, we have rewritten and greatly extended the original content. The revised text includes entirely new reference lists and a complete new set of illustrations. The book reflects the many advances that have occurred in the study of neuroendocrinology during the past 20 years. Nevertheless, and although the text is based largely on modern references, our primary aim is to provide an introductory description of mammalian neuroendocrine control systems. Several books are available that cover this topical and clinically relevant field, but, although valuable, these tend to be advanced texts of the edited, multi-author type. Our book is designed to provide the basic principles necessary to understand how the brain controls, and responds to, the endocrine hormones. It will be suitable for a variety of different students and especially those who might not have been previously exposed to a focused course in neuroendocrinology. Thus, students in psychology, biology and science should be able to master much of the basic material. However, the book is also highly appropriate for honors students and first-year graduate students in physiology, anatomy, neuroscience and medicine. This book is therefore designed for students in two levels of classes: introductory classes, in which all of the material will be new to the student, and more advanced classes, in which the students will be familiar with many of the terms and concepts through courses in biology, physiology, psychology or neuroscience, but who have not studied neuroendocrinology as an integrated discipline.

This book offers an overall outline of the neuroendocrine system and will provide the vocabulary necessary to understand the interaction between hormones and the brain. In addition, we provide a concise description of those topics that must underpin any attempt to learn, and to teach, neuroendocrinology. For example, there are chapters on basic neuroscience (neurotransmitters and neuropeptides), the physiology of the endocrine glands (hormones), receptors and receptor signaling mechanisms (e.g. G proteins; nuclear receptors), hormone assay and gene expression techniques (e.g. ELISA; *in situ* hybridization) and a description of the immune system, with particular emphasis on the integration of immune and neuroendocrine pathways. This basic information is also essential to understand the profound effects of hormones on behavior, described in Chapter 14. Once this material is mastered, the study of how hormones influence developmental neural processes and behavior will be easier. Moreover, we have included throughout the book references to the clinical relevance of many topics; for example, the influence of neuropeptides in the control of body weight and obesity. However, this book focuses primarily on the neural actions of hormones, and many of the peripheral physiological actions of hormones, such as regulation of metabolism, water balance, growth, and the regulation of calcium, sodium and potassium levels, which are the focus of traditional endocrinology texts, are referred to only in reference to their importance in the neuroendocrine system.

The introductory (second- or third-year undergraduate) student can be expected to follow the material in this book at the level presented. To help in this, review/study

questions are given at the end of each chapter. These should be treated as practice examination questions and answered after each chapter is completed. For further detailed information on the topics covered in each chapter, all students can consult selected references provided in the text. Additional references under “Further reading” are also included at the end of each chapter and these will be particularly useful to the more advanced student. The book will be especially relevant for more advanced (honors and graduate) students who can use this book as an introductory account of the subject matter covered in each chapter. These students may then take advantage of the many references cited in each chapter to provide current and relevant information on each topic. The essay questions at the end of each chapter also serve to provide topics for discussion, analysis and directed research papers for the advanced student.

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The authors are indebted to friends and colleagues who offered generous and invaluable assistance in the writing of this book. Paul Wilkinson, Ms. Alex Pincock and Ms. Diane Wilkinson created several figures; Alex Pincock and Dr. Jim Pincock carefully read, and made useful suggestions for improvement of, several early chapters. Special thanks are due to Diane Wilkinson, who typed all the tables and assisted in compiling the extensive reference lists. The following scientists unselfishly provided illustrations from their published material: Dr. O. Almeida, Dr. A. Armario, Dr. R. Bridges, Dr. R. Goyal, Dr. L. De Groot, Dr. L. Hale, Dr. J. Herman, Drs. T. Horvath and M. Dietrich, Ms. A. Rain, Dr. T. Smith, Dr. J. Ström, Dr. J. Wakerley, Dr. A. Winokur and Dr. S. Winters. As far as we are aware, all sources of the illustrations used have been acknowledged. Permission to use previously published figures was obtained either from the original authors or via *RightsLink* (Copyright Clearance Centre).

Finally, thanks are due to Megan Waddington of Cambridge University Press for her patience in awaiting the delivery of this manuscript.

## ABBREVIATIONS

IIIv	third ventricle	CART	cocaine- and amphetamine-regulated transcript
2-AG	2-arachidinoyl glycerol	cGMP	cyclic guanosine monophosphate
5-HIAA	5-hydroxyindoleacetic acid	CB1	cannabinoid receptor 1
5-HT	5-hydroxytryptamine (serotonin)	CBG	corticosteroid binding globulin (transcortin)
5-HTP	5-hydroxytryptophan	CCK	cholecystokinin
6-OHDA	6-hydroxy-dopamine	CCK-KO	CCK knockouts
AC	adenyl cyclase	CGRP	calcitonin gene related peptide
ACh	acetylcholine	ChAT	choline acetyltransferase
ACTH	adrenocorticotrophic hormone	CL	centrolateral thalamus
ADH	antidiuretic hormone (vasopressin)	Cl <sup>-</sup>	chloride ion
ADHD	attention deficit hyperactivity disorder	CLIP	corticotropin-like intermediate lobe peptide
AEA	anandamide	CM	centromedial thalamus
AgRP	agouti-related protein	CNS	central nervous system
AH	anterior hypothalamus	COMT	catechol o-methyl transferase
AHA	anterior hypothalamic area	CP	caudate/putamen
AMPA	$\alpha$ -amino-3-hydroxy-5-methyl-4-isoxazole propionic acid	CREB	cAMP responsive element binding protein
AMYG	amygdala	CRF	corticotropin-releasing factor (also called CRH)
ANP	atrial natriuretic peptide	CRH	corticotropin-releasing hormone (also called CRF)
ANS	autonomic nervous system	CSF	cerebrospinal fluid
AP	area postrema	CVO	circumventricular organs
APC	antigen presenting cell	D	diestrus
APUD	amine precursor uptake and decarboxylation	D2R	dopamine 2 receptor
AR	androgen receptor	D3	diestrus 3
ARC	arcuate nucleus	DA	dopamine
AT	angiotensin	DAG	diacylglycerol
ATP	adenosine triphosphate	DBD	DNA binding domain
AVP	arginine vasopressin	DBH	dopamine beta-hydroxylase
AVPV	anteroventral periventricular nucleus	DG	dentate gyrus
$\beta$ 2-AR	$\beta$ 2-adrenergic receptor	DHEA	dehydroepiandrosterone
$\beta$ -END	$\beta$ -endorphin	DHT	dihydrotestosterone
$\beta$ -Gal-ir	$\beta$ -Galactosidase immunoreactivity	dISON	dorsolateral supraoptic nucleus
BBB	blood-brain barrier	DMN	dorsomedial hypothalamic nucleus
BDNF	brain-derived neurotrophic factor	DMT	dimethyltryptamine
BLA	basolateral amygdala	DNA	deoxyribonucleic acid
BNP	B-type natriuretic peptide		
Ca <sup>2+</sup>	calcium ion		
CAH	congenital adrenal hyperplasia		
cAMP	cyclic adenosine monophosphate		



## LIST OF ABBREVIATIONS

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DNES	Diffuse Neuroendocrine System	GnIH	gonadotropin inhibitory hormone
DYN	dynorphin	GnRH	gonadotropin-releasing hormone
E	estradiol	GPR54	G-protein-coupled receptor 54
EDC	endocrine disrupting chemicals	GR	glucocorticoid receptor
EGF	epidermal growth factor	GRE	glucocorticoid response element
EGL	external granule cell layer	G <sub>s</sub>	stimulatory G protein
EL	ejaculation latency	GTF	general transcription factor
ELISA	enzyme-linked immunosorbent assay	GTP	guanosine triphosphate
ENK	enkephalin	HBD	hormone binding domain
ENS	enteric nervous system	HCG	human chorionic gonadotropin
EOP	endogenous opioid peptide	HCS	human chorionic somatomammotropin
EPO	erythropoietin	HDC	histidine decarboxylase
ER	endoplasmic reticulum	HFD	high fat diet
ER	estrogen receptor	HGP	hepatic glucose production
ERE	estrogen response element	H-P-A	hypothalamic-pituitary-adrenal
FGF	fibroblast growth factor	HPL	human placental lactogen
fMRI	functional magnetic resonance imaging	HPLC	high performance liquid chromatography
FS	folliculostellate	HRE	hormone response element
FSH	follicle-stimulating hormone	HRT	hormone replacement therapy
FSH-RH	follicle-stimulating hormone-releasing hormone	HSP	heat shock protein
FX	fornix	HVA	homovanillic acid
G	granule cells	ICo	nucleus intercollicularis
G-CSF	granulocyte colony stimulating factor	IF	intromission frequency
GABA	gamma-aminobutyric acid	IFN $\gamma$	interferon $\gamma$
GABA-T	GABA transaminase	I <sub>g</sub>	immunoglobulin
GAD	glutamic acid decarboxylase	IGF	insulin-like growth factor; somatomedin
GDNF	glial-derived neurotrophic factor	IGFBP	insulin-like growth factor binding protein
GDP	guanosine diphosphate	IGL	internal granule cell layer
GFP	green fluorescent protein	III	inter-intromission interval
GH	growth hormone	IL	interleukin
GHRH	growth hormone releasing hormone	IL	intromission latency
GH-RIH	growth hormone release inhibiting hormone (see SOM)	IMAN	lateral magnocellular nucleus of the anterior midopallium
GI	gastrointestinal	IP3	inositol triphosphate
G <sub>i</sub>	inhibitory G protein	iR	ion channel
GIP	gastrin inhibitory peptide	IRS-1	insulin receptor substrate 1
GLP-1	glucagon-like peptide-1	JAK	janus kinase
GLP-2	glucagon-like peptide-2	K <sup>+</sup>	potassium ion
Glu	glutamate	K <sub>p</sub>	kisspeptin
GM-CSF	granulocyte-macrophage colony stimulating factor	LH	luteinizing hormone (also lateral hypothalamus)

LHRH	luteinizing hormone releasing hormone	NMDA	N-methyl-D-aspartate
LPH	lipotropic hormone (also $\beta$ -lipotropin)	NO	nitric oxide
LSD	lysergic acid diethylamide	NOS	nitric oxide synthase
M	muscarinic	NP	neurophysin
MAO	monoamine oxidase	NPY	neuropeptide Y
MBH	mediobasal hypothalamus	NSF	N-ethylmaleimide sensitive factor
MC	melanocortin	NT	neurotransmitter
M-CSF	macrophage colony stimulating factor	NTD	amino terminal domain
MD	dorsomedial thalamus	NTS	nucleus tractus solitarius
ME	median eminence	nXIIIts	tracheosyringeal portion of the nucleus hypoglossus
MET	metestrus	OB	olfactory bulb
mf	mossy fibers	OT	oxytocin
MF	mount frequency	ORL1	opioid receptor-like receptor
mGluR	metabotropic glutamate receptor	OTR	oxytocin receptor
MHC	major histocompatibility complex	OVLT	organum vasculosum of the lamina(e) terminalis
MHPG	3-methoxy-4-hydroxyphenylglycol	OXM	oxyntomodulin
mIU	milli international units	OXY	oxytocin
ML	mount latency	P	progesterone (also Purkinje cells)
ML	molecular layer	PACAP	pituitary adenylate cyclase-activating polypeptide
MMGB	medial geniculate body	PC	proprotein convertase
MOE	main olfactory epithelium	PCP	phencyclidine
MPOA	medial preoptic area	PCR	polymerase chain reaction
mR	metabotropic membrane receptor	pCREB	phosphorylated CREB
MR	mineralocorticoid receptor	PEI	post-ejaculatory interval
MRF	midbrain reticular formation	PeN	anterior periventricular nucleus
MRI	magnetic resonance imaging	PENK	preproenkephalin
mRNA	messenger ribonucleic acid	PET	positron emission tomography
$\alpha$ -MSH	$\alpha$ -melanocyte-stimulating hormone	pf	parallel fibers
MSH-RF	melanocyte-stimulating hormone – releasing factor	PFA	perifornical area
MSH-RH	melanocyte-stimulating hormone – releasing hormone	PGE2	prostaglandin E2
MSH-RIF	melanocyte-stimulating hormone – release-inhibiting factor	PH	posterior hypothalamus
MSH-RIH	melanocyte-stimulating hormone – release-inhibiting hormone	PI3K	phosphoinositide 3 kinase
MT	melatonin	PIF	prolactin releasing inhibiting factor
MUA	multiple unit activity	PIP2	phosphatidylinositol diphosphate
NA	noradrenaline (also norepinephrine, NE)	PIR	piriform cortex
Na <sup>+</sup>	sodium ion	PKA	protein kinase A
NE	norepinephrine (also noradrenaline, NA)	PL	placental lactogen
NGF	nerve growth factor	PLC	phospholipase C
NK	natural killer cell	PNS	parasympathetic nervous system
NKT	natural killer T cell	POA	preoptic area
		POL	RNA polymerase
		POMC	pro-opiomelanocortin

## LIST OF ABBREVIATIONS

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PP	pancreatic polypeptide	TIDA	tuberoinfundibular DA
PR	progesterone receptor	TNF $\alpha$	tumor necrosis factor $\alpha$
PRF	prolactin releasing factor	TR	thyroid hormone receptors
PRH	prolactin-releasing hormone	TRF	thyrotropin (TSH) releasing factor (also TRH)
PRL	prolactin	TRH	thyroid hormone releasing hormone
PRO	proestrus	trk	tyrosine receptor kinase
PrRP	prolactin-releasing peptide	T <sub>s</sub>	suppressor T cell
PTH	parathyroid hormone	TSH	thyroid-stimulating hormone
PTSD	post-traumatic stress disorder	TSHR	TSH receptor
PV	periventricular nucleus	TSH-RH	thyroid-stimulating hormone- releasing hormone (TRH)
PVN	paraventricular nucleus	VEGF	vascular endothelial growth factor
PYY	peptide YY	VIP	vasoactive intestinal polypeptide
RA	robust nucleus of the arcopallium	vmSON	ventromedial supraoptic nucleus
RER	rough endoplasmic reticulum	VMH	ventromedial hypothalamic nucleus
RSP	retrosplenial cortex	VMN	ventromedial nucleus of hypothalamus
SC	subcutaneous	VNO	vomeronasal organ
SCN	suprachiasmatic nucleus	VP	vasopressin
SDN	sexually dimorphic nucleus	WAT	white adipose tissue (fat)
SEM	standard error of the mean		
SHBG	sex hormone binding globulin		
SNAP	soluble SNF attachment proteins		
SNARE	SNAP receptor protein		
SNB	spinal nucleus of the bulbocavernosus		
SNS	sympathetic nervous system		
SOCS	suppressor of cytokine signaling		
SOM	somatostatin		
SON	supraoptic nucleus		
SP	Substance P		
SS	somatosensory cortex		
SST	somatostatin receptor		
STAT	signal transducer and activator of transcription / signal transduction and transcription		
T	testosterone		
T3	triiodothyronine		
T4	thyroxine		
TBG	thyroid hormone binding globulin		
T <sub>C</sub>	cytotoxic T cell		
TF5	thymosin fraction 5		
TGF $\alpha$	transforming growth factor $\alpha$		
TGF $\beta$ 1	transforming growth factor $\beta$ 1		
TH	tyrosine hydroxylase		
T <sub>H</sub>	helper T cell		
THC	tetrahydrocannabinol		