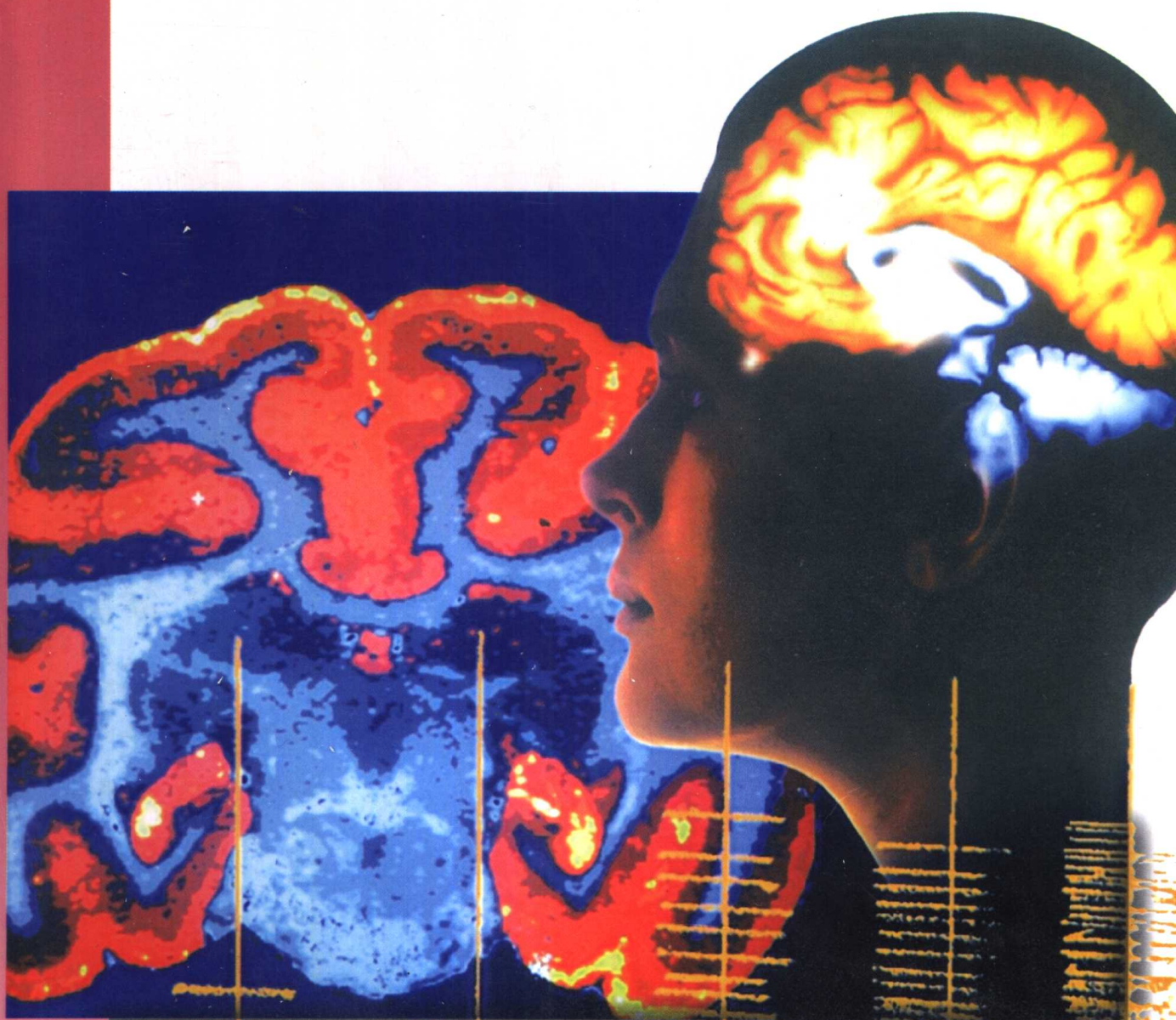


精要速览系列 (影印版)

*Instant Notes*

NEUROSCIENCE

# 神经科学



A. Longstaff

科学出版社

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**A. Longstaff**

*Science writer and freelance lecturer in neuroscience*



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## 内 容 简 介

本书是国外优秀教材畅销榜的上榜教材,面向大学本科生,由著名的神经科学撰稿人 A. Longstaff 编写,英国著名大学具有丰富教学经验的一流教授审阅。它以一种风格独特的方式,全面、系统地概括了神经科学的核心内容和前沿动态,并以一种便于学习、利于复习的编写形式,使学生能快速、准确的掌握知识,很好地指导学习和考试。本书配有全新绘制和编写的插图与表格,非常有指导性,是其他教材无法比拟的。本书的简明和扼要也为大学教师备课提供了最好的参考。书中英文使用最为自然、易懂的语句,是提高专业外语的最佳用书。

A. Longstaff

Instant Notes in Neuroscience

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# ABBREVIATIONS

ACh	acetylcholine	CVLM	caudal ventrolateral medulla
AChE	acetylcholinesterase	CVO	circumventricular organ
ACTH	adrenocorticotrophic hormone	DAG	diacylglycerol
AD	Alzheimer's disease	DBL	dorsal blastopore lip
Ang	angiotensin II	DCML	dorsal column-medial lemniscal system
AMPA	$\alpha$ -amino-3-hydroxy-5-methyl-4-isoxazole-propionic acid	DCN	dorsal column nuclei
ANS	autonomic nervous system	2-DG	2-deoxyglucose
AP	action potential	DHC	dorsal horn cell
apoE	apolipoprotein E	DI	diabetes insipidus
APP	amyloid precursor protein	DLPN	dorsolateral pontine nucleus
APV	D-2-amino-5-phosphonovalerate	DOPAC	dihydroxyphenyl acetic acid
ATN	anterior thalamic nuclei	DRG	dorsal root ganglion
ATP	adenosine 5'-triphosphate	DYN	dynorphin
AVP	arginine vasopressin	ECT	electroconvulsive therapy
$\beta$ A	$\beta$ -amyloid	EEG	electroencephalography
$\beta$ AR	$\beta$ adrenoceptors	EGF	epidermal growth factor
BAT	brown adipose tissue	EGL	external granular layer
BDNF	brain derived neurotrophic factor	EMG	electromyography
bl	basal lamina	ENK	enkephalin
BMP	bone morphogenetic protein	ENS	enteric nervous system
$\alpha$ -BTX	$\alpha$ -bungarotoxin	epp	endplate potential
CA	cornu ammonis	epsp	excitatory postsynaptic potential
CaM	calmodulin	ER	endoplasmic reticulum
CAM	cell adhesion molecule	F-actin	filamentous actin
CaMKII	calcium-calmodulin-dependent protein kinase II	FEF	frontal eye field
cAMP	cyclic adenosine monophosphate	FF	fast fatiguing
CAT	computer assisted tomography	FM	frequency modulation
cbf	cerebral blood flow	fMRI	functional magnetic resonance imaging
CC	cingulate cortex	FR	fatigue resistant
CCK	cholecystokinin	FRA	flexor reflex afferents
CF	characteristic frequency	FSH	follicle stimulating hormone
cGMP	3',5'-cyclic guanosine monophosphate	G <sub>i</sub>	inhibitory G protein
ChAT	choline acetyltransferase	G <sub>q</sub>	G protein coupled to phospholipase
CL	central laminar nucleus (of thalamus)	G <sub>s</sub>	stimulatory G protein
CNG	cyclic-nucleotide-gated channel	GABA	$\gamma$ -aminobutyrate
CNS	central nervous system	GC	guanylyl cyclase
CoA	coenzyme A	GDP	guanosine 5'-diphosphate
CPG	central pattern generators	GFAP	glial fibrillary acidic protein
CRH	corticotrophin releasing hormone	GH	growth hormone
CRO	cathode ray oscilloscope	GHRH	growth hormone releasing hormone
CS	conditioned stimulus	GnRH	gonadotrophin releasing hormone
CSF	cerebrospinal fluid	GPe	globus pallidus pars externa
CVA	cerebrovascular accident	GPI	globus pallidus pars interna

GR	glucocorticoid receptor	MI	primary motor cortex
GTO	Golgi tendon organs	MII	secondary motor cortex
GTP	guanosine 5'-triphosphate	MLCK	myosin light chain kinase
5-HIAA	5-hydroxyindoleacetic acid	MLR	mesencephalic locomotor region
HPA	hypothalamic-pituitary-adrenal (axis)	MOPEG	3-methoxy,4-hydroxy phenylglycol
HPG	hypothalamic-pituitary-gonadal (axis)	MPOA	medial preoptic area
HPT	hypothalamic-pituitary-thyroid (axis)	MPP <sup>+</sup>	1-methyl-4-phenyl pyridinium
HRP	horseradish peroxidase	mpsp	miniature postsynaptic potential
5-HT	5-hydroxytryptamine (serotonin)	MPTP	1-methyl-4-phenyl-1,2,3,6-tetrahydropyridin
5-HTP	5-hydroxytryptophan	MR	mineralocorticoid receptor
HVA	high voltage activated	MRI	magnetic resonance imaging
IaIN	Ia inhibitory interneurons	MSO	medial superior olivary complex
IbIN	Ib inhibitory neurons	MST	medial superior temporal cortex
IC	inferior colliculus	NA	noradrenaline
ICSS	intracranial self-stimulation	nAChR	nicotinic cholinergic receptor
Ig	immunoglobulin	NGF	nerve growth factor
IGF-1	insulin-like growth factor 1	NMDA	N-methyl-D-aspartate
IGL	internal granular layer	NMDAR	N-methyl-D-aspartate receptor
iGluR	ionotropic glutamate receptor	nmj	neuromuscular junction
ILD	interaural level differences	NMR	nuclear magnetic resonance
IP <sub>3</sub>	inositol 1,4,5-trisphosphate	NPY	neuropeptide Y
ipsp	inhibitory postsynaptic potential	NREM	nonrapid eye movement sleep
IT	inferotemporal cortex	NRM	nucleus raphe magnus
JGA	juxtaglomerular apparatus	NST	nucleus of the solitary tract
L-DOPA	L-3,4-dihydroxyphenylalanine	NT3-6	neurotrophins 3-6
LC	locus cerulus	OC	olivocochlear
LCN	lateral cervical nucleus	OCD	obsessive-compulsive disorder
LDCV	large dense-core vesicle	OHC	outer hair cells
LGN	lateral geniculate nucleus	6-OHDA	6-hydroxydopamine
LH	luteinizing hormone	ORN	olfactory receptor neurons
LSO	lateral superior olivary nucleus	OVLT	vascular organ of the lamina terminalis
LTD	long-term depression	P	parvocellular pathway
LTM	long-term memory	PAD	primary afferent depolarization
LTN	lateral tegmental nucleus	PAG	periaqueductal gray matter
LTP	long-term potentiation	Pc	Purkinje cells
LVA	low voltage activated	PD	Parkinson's disease
M	magnocellular pathway	PDE	phosphodiesterase
M/T	mitral/tufted cells	PDS	paroxysmal depolarizing shifts
mAChR	muscarinic cholinergic receptor	PET	positron emission tomography
MAO	monoamine oxidase	pf	parallel fibers
MAP	mean arterial (blood) pressure	PFC	prefrontal cortex
MB	mammillary bodies	PGO	pontine-geniculate-occipital spikes
mepp	miniature endplate potential	PHF	paired helical filaments
MFB	medial forebrain bundle	PIP <sub>2</sub>	phosphatidyl inositol-4,5-bisphosphate
MFS	mossy fiber sprouting	PKA	protein kinase A
mGluR1	type 1 metabotropic glutamate receptor	PM	premotor cortex
MGN	medial geniculate nucleus		

PNS	peripheral nervous system	STN	subthalamic nucleus
POA	preoptic area	STT	spinothalamic tract
POM	posterior complex (medial nucleus) of thalamus	TB	trapezoid body
POMC	pro-opiomelanocortin	TCA	tricyclic antidepressants
PP	posterior parietal complex	TEA	tetraethylammonium
PRL	prolactin	TENS	transcutaneous electrical nerve stimulation
PSNS	parasympathetic nervous system	TH	tyrosine hydroxylase
psp	postsynaptic potential	TM	transmembrane
PVN	paraventricular nucleus	TRH	thyrotropin releasing hormone
RA	retinoic acid	trk	tyrosine kinase receptors
REM	rapid eye movement sleep	TSH	thyroid releasing hormone
RF	receptive field	TTX	tetrodotoxin
RHT	retinohypothalamic tract	UR	unconditioned response
S	slow twitch fiber	US	unconditioned stimulus
SCG	superior cervical ganglion	VDCC	voltage-dependent calcium channel
SCN	suprachiasmatic nucleus	VDKC	voltage-dependent potassium channel
Sc	Schaffer collateral	VDSC	voltage-dependent sodium channel
SDN-POA	sexually dimorphic nucleus of the preoptic area	VIP	vasoactive intestinal peptide
SER	smooth endoplasmic reticulum	VLH	ventrolateral hypothalamus
SH2	src homology domain 2	VLPO	ventrolateral preoptic area
SHH	sonic hedgehog protein	VMAT	vesicular monoamine transporter
SMA	supplementary motor area	VMH	ventromedial hypothalamus
SNpc	substantia nigra pars compacta	VOR	vestibulo-ocular reflexes
SNzc	substantia nigra zona compacta	VPL	ventroposterolateral nucleus (of thalamus)
SNS	sympathetic nervous system	VPM	ventroposteromedial nucleus (of thalamus)
SON	supraoptic nucleus	VRG	ventral respiratory group
SP	substance P	VST	ventral spinocerebellar tract
SPL	sound pressure level	VZ	ventricular zone
SR	sarcoplasmic reticulum		
SSRI	selective serotonin reuptake inhibitors		
SSV	small clear synaptic vesicle		
STM	short-term memory		

# PREFACE

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Neuroscience is one of the most rapidly advancing areas of science and, as a consequence, spawns a literature which is growing dramatically. At one level it attempts to provide a mechanistic account of the most complex 'device' in the known Universe, the human brain. Moreover, neuroscience is multidisciplinary, having contributions from biochemistry and molecular biology, physiology, anatomy, psychology and clinical medicine, to name the most obvious. For these reasons, it is becoming increasingly difficult for lecturers and textbook authors to present neuroscience in a way that manages to be comprehensive, up-to-date and accessible, while still being sufficiently rigorous to prepare students to be successful explorers of the literature for themselves. *Instant Notes Neuroscience* is not intended as a replacement for lectures or the standard textbooks, but as an affordable text to supplement them, which is of a manageable size and in a format which aids learning.

The text is designed to provide the core of the subject in 18 sections containing 93 topics. When coming to a new subject, it is my experience that students commonly express two concerns: first, how to sort out the important ideas and facts from the wealth of detail, and second, how to get to grips with the unfamiliar terminology. Lecturers, in addition, will want students (especially later in their studies) to be able to integrate their knowledge across the subject. *Instant Notes Neuroscience* attempts to address each of these issues. Each topic is supported by a 'Key Notes' panel which gives a concise summary of the crucial points. Whenever a term appears for the first time it is in bold and immediately followed by a definition or explanation. Extensive cross-references are provided between topics so that students can forge the links that are important for integration.

This is a much slimmer volume than most neuroscience texts, which can be dauntingly large. A number of features contribute to this. First, I have tried to minimize the amount of detail without compromising the need for a database for further study. Second, while many of the methods used by neuroscientists are included, *individual* experiments or items of evidence are included only where I thought it essential to illustrate a point, or on matters that would need some justification to be convincing. Third, with a few exceptions, I have restricted examples to those most appropriate to the human condition. In so doing I have always qualified the species, since species differences matter. If not, then rats and cats would behave as humans do, which clearly they do not!

Section A introduces the cells of the nervous system, showing how they are specialized for the functions they serve. The next three sections are essentially cellular neuroscience. Section B is concerned mostly with action potentials, Section C with synapses, while Section D deals with how nerve cells act as information processors. These sections provide an introduction to the electrophysiological techniques used to study nerve cells, and say something about the molecular biology of the ion channels and receptors that govern their behavior. Section E takes a broad view of neuroanatomy and summarizes techniques, such as brain imaging, used to investigate nervous system structure. How information is encoded by the firing and connectivity of neurons is considered in Section F. All the material thus far might reasonably be found in first-year courses.

The next seven sections (G–M) form the core of systems neuroscience. Section G reviews the body senses, touch, pain and balance. Sections H and I deal with vision and hearing, respectively, while Section J looks at the chemical senses, smell and taste. The properties of skeletal muscle, motor reflexes, and the cortical control of voluntary movement are the subject of Section K, while the involvement of the cerebellum (including proprioception) and the basal ganglia in movement is covered in Section L. Neuroendocrinology, and both peripheral and central aspects of the autonomic nervous system appear in Section M, which also (and unusually for standard neuroscience texts) includes the functions of smooth and cardiac muscle, and the enteric nervous system. A short Section N describes the essential features of amine transmission, the basis for much neuropharmacology, and paves the way for understanding aspects of behavior, such as motivation and sleep that are included in Section O. Section P is



an overview of how the embryonic nervous system develops, ranging from how the basic plan is genetically specified, to how differences between male and female brains might arise. Section Q addresses how the nervous system continues to rewire itself on the basis of experience (i.e., learning and memory). Finally, although quite a number of nervous system disorders are considered at appropriate places throughout the book, section R takes the four most common neuropathologies, stroke, epilepsy, Parkinson's disease and Alzheimer's dementia and looks in some detail at what has gone amiss and what current and future treatments may do. Space precluded the inclusion of topics on two major psychiatric disorders (schizophrenia and depression) in the text; it is intended that these topics will be made available on the BIOS website free of charge. At the end of the book is a reading list for those who wish to take their studies further.

As a student, how should you use this book? Restrict your reading only to the sections and topics covered by your current course. That said, Sections A–F are likely to appear in, or be required knowledge for, just about any neuroscience program; you will probably need to work through these first. Later sections can be dipped into in any order. Read the main sections thoroughly first, making sure that you *understand* the ideas, and use the 'Related topics' to make links, just as you would if you were surfing the internet. Where appropriate, reference is made to areas that are covered in more detail in the companion volumes, *Instant Notes in Biochemistry*, 2nd edn, and *Instant Notes in Molecular Biology*, 2nd edn. At this stage you can incorporate additional material from lectures or other textbooks in the gaps at the end of topics, or highlight things which seem to be particularly important for your course. Studying *Instant Notes Neuroscience* 'little but often' is a good strategy. The information density in the text is high, so many short, concentrated, bursts are much more effective than a few eight-hour stints. The more times you work through a topic, the better your understanding, and the more likely you will be to remember it clearly. When it comes to revision, use the 'Key Notes' as a prompt. In addition, you should aim to be able to write, from memory, a few sentences about each of the terms that appears in bold in the main text. Being able to reproduce the simpler diagrams is also an effective way of getting your point across in an exam. Neuroscience is an extraordinary endeavor because it aims to reveal what, in essence, it is to be human; how we behave, think and feel as we do. At the moment we are a long way from being able to give a coherent account of any of these faculties; that there is so much still to be done is one reason that this science is so exciting. This book is an account of the remarkable progress made so far. I hope you find that it serves your needs well and that, like me, you enjoy discovering neuroscience.

## Acknowledgements

A number of colleagues – Barry Hunt, Vasanta Raman and John Wilkinson, all at the University of Hertfordshire – kindly read through some individual topics and made very helpful suggestions. David Hames (University of Leeds, UK), Kevin Alloway (Penn State University, USA), and Patricia Revest (Queen Mary and Westfield College, London University, UK), were each brave enough to read through the entire text and their thought-provoking comments have been important in shaping the final version. I am very grateful to all of these people for their time and expertise. Finally, I thank Jonathan Ray, Rachel Offord, Will Sansom and Fran Kingston at BIOS Scientific Publishers for their encouragement and patience.

Alan Longstaff

# A1 NEURON STRUCTURE

## Key Notes

### Cell body

The neuron cell body contains all the subcellular organelles found in a typical animal cell but it is specialized to maintain high rates of protein synthesis, as shown by the ribosome-packed Nissl bodies.

### Neurites

Neurites are long projections from the cell body. There are two types of neurite, dendrites and axons. Dendrites are large extensions of the cell body and receive most of the synaptic inputs impinging onto the cell. Neurons may have one or many dendrites. Neurons have a single axon arising from the axon hillock. Axon terminals form the presynaptic components of synapses.

### Axon or dendrite?

The two neurites can be distinguished on structural grounds. Dendrites contain many organelles and are capable of protein synthesis. By contrast, axons cannot synthesize protein, so axonal proteins are derived from the cell body. Axons and dendrites both have mitochondria. Organelles are transported into neurites via microtubules.

### Related topic

Morphology of chemical synapses (A3)

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Because there is a great variety of types of neurons, their cell bodies vary in size considerably. The smallest are some 5–8  $\mu\text{m}$  in diameter, the largest 120  $\mu\text{m}$  across.

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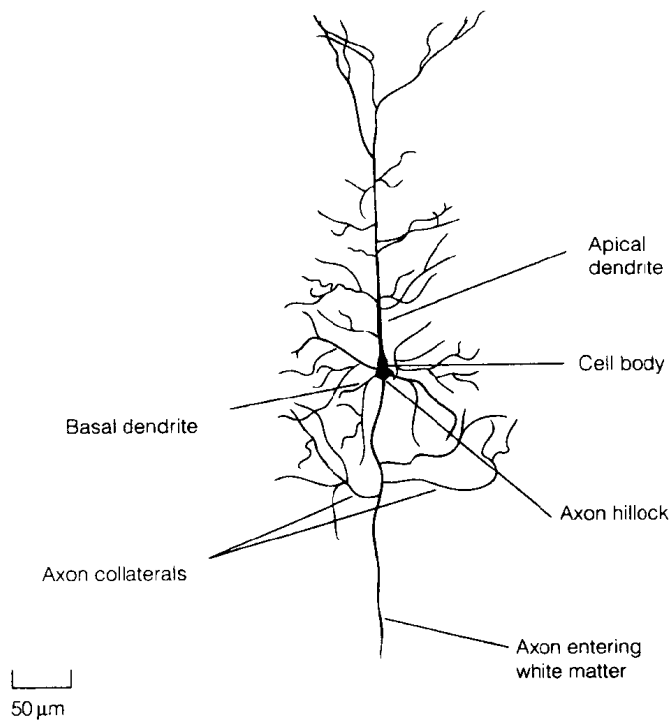


Fig. 1. Key features of a neuron. A drawing of a pyramidal cell showing the distribution of neurites (dendrites and axon).

Nerve cells usually have only one **axon** which arises typically from the cell body but may emerge from a proximal dendrite (the end of a dendrite closest to the soma). In either case, the site of origin is termed the **axon hillock**. Axons have diameters ranging from 0.2 to 20  $\mu\text{m}$  in humans (though axons of invertebrates can reach 1 mm) and vary in length from a few  $\mu\text{m}$  to over a meter. They may be encapsulated in a **myelin sheath**. Axons usually branch, particularly at their distal end (furthest from the soma). These branches are referred to as **axon collaterals**. The ends of an axon are swollen **terminals** (or **boutons**) and usually contain mitochondria and vesicles. Some axons have a tuft of branches (a **terminal arbor**) at their tip, each with its terminal bouton, some have boutons along their length where they are described as **varicosities**. Axon terminals form the presynaptic component of chemical synapses.

**Axon or dendrite?** Axons can be distinguished from dendrites on structural grounds. Axons tend to be long, untapered, less highly branched, never spiny and may have a myelin sheath, whereas dendrites are shorter, tapered, highly branched and may bear spines. Dendrites are extensions of the cell body in that they contain Golgi apparatus, rough endoplasmic reticulum and ribosomes – organelles not seen in axons. By contrast both axons and dendrites have mitochondria. Since axons do not possess protein synthetic machinery, proteins in axons must be made in the cell body and subsequently moved into and along the axon by a mechanism called axoplasmic transport. Axon terminals are often rich in mitochondria which indicates their high requirement for metabolic energy.

Differences in organelle composition are thought to result from the differing arrangements of **microtubules** in the two types of neurite. Microtubules are long protein polymers that are part of the internal scaffolding of cells called the **cytoskeleton**. Microtubules act as 'tramlines' along which organelles are moved within the cell. The two ends of a microtubule are different, designated + and - ; thus microtubules have a distinct polarity which means that organelles move along them in a specific direction. Mitochondria move in the - to + direction whereas other organelles move in the + to - direction. Both dendrites and axons have microtubules, but whereas dendrites have them orientated in either direction, those in axons are always arranged with their + ends away from the cell body. Thus axonal microtubules can transport mitochondria out of the cell body into the axon but cannot transport other organelles. Because microtubules are orientated in both directions in dendrites, all organelles are transported into these neurites.

When a neuron develops, it first grows a number of processes which are indistinguishable. It is not yet known how one of these is subsequently selected to differentiate into an axon. The first sign that a process will become an axon is that it grows at a much faster rate than those which are destined to be dendrites.



## A2 CLASSES AND NUMBERS OF NEURONS

### Key Notes

#### Neuron classification

Neurons may be classified by their morphology, function or by the neurotransmitter they secrete. Cells with one, two or three or more neurites are classed as unipolar, bipolar or multipolar respectively. The shape of the dendritic tree, or whether the dendrites have dendritic spines and the length of the axon have proved useful in categorizing neurons. Functional classification distinguishes between sensory neurons which respond directly to physiological stimuli and motor neurons which synapse with effectors.

#### Neuron numbers

The human nervous system may contain 300–500 billion neurons. Neuron density is quite constant across the cerebral cortex and between cerebral cortices of different mammals. Smaller brains have fewer neurons.

#### Related topics

Organization of the peripheral nervous system (E1)  
Organization of the central nervous system (E2)

### Neuron classification

There is no such thing as a 'typical' neuron. Nerve cells come in a wide variety of shapes and sizes with widely differing numbers and patterns of synaptic contacts using distinct neurotransmitters. Hence neurons are classified either according to morphology, function or by their neurotransmitters, and the assumption is that all neurons falling into a single class have similar functions.

Structural considerations to classifying a given cell include the size of the cell body, the number of neurites it has, the pattern of its dendritic tree, axon length and the nature of the connections it makes. A neuron with a single neurite is **unipolar**, one with two neurites is **bipolar** while a neuron with three or more neurites is said to be **multipolar** (Fig. 1). The majority of neurons in the vertebrate nervous system are multipolar but there are important exceptions. For example, a population of neurons in the retina which synapse with photoreceptors are bipolar and sensory neurons in the dorsal root ganglion are described as **pseudounipolar**; technically they are bipolar because they start life with two processes but these subsequently fuse. Invertebrate nervous systems are dominated by unipolar neurons.

Dendrites are used to classify neurons on the basis of whether or not they have dendritic spines and the overall pattern of their dendritic tree. The shape of any dendritic tree helps to determine the efficacy of its synaptic connections and so to the functioning of the cell. **Pyramidal** cells, so-called because of the shape of their cell bodies, comprise some 60% of neurons in the cerebral cortex and have dendrites which extend to fill a pyramidal space. A second population of cortical cells are termed stellate cells because of the star-like appearance of