

Introduction to the Anatomy & Physiology of The Nervous System

David Bowsher

Third edition

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ANATOMY & PHYSIOLOGY OF
THE NERVOUS SYSTEM

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THIRD EDITION

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PREFACE TO THE THIRD EDITION

Some changes have been made consistent with newer findings. These concern particularly the morphology of central neurones and their significance; the morphological basis of presynaptic inhibition; the function of non-specific sensory systems; and non-pyramidal motor systems. If the last-mentioned makes any contribution to getting rid of the word (and concept) 'extrapyramidal', much will have been achieved.

Some figures have been revised, and there are four new figures. For these my thanks are due to Hazel Blundell. The bibliography has been brought up to date.

Liverpool, 1974

David Bowsher

PREFACE TO FIRST EDITION

The forerunner of this small text first appeared in 1961, under the title of 'Introduction to Neuroanatomy'. In its original form, the book contained a fair amount of functional neuroanatomy, otherwise known as system neurophysiology. Many readers have, however, asked for fuller treatment of the physiological aspects of the nervous system. This is the result. It includes most of the material from 'Introduction to Neuroanatomy', revised, where necessary, in the light of more recent knowledge; and, in addition, completely new matter on the physiology of the nervous system, which I hope has been successfully integrated with the contents of my original book. Chapters IV and V form an entirely new departure; I should like most sincerely to thank my friend and colleague Professor Denise Albe-Fessard, who provided the information on which these chapters are based, and most helpfully criticized their text. Coupled with my gratitude, I hasten to exonerate Professor Albe-Fessard from any culpability for error in their content, which must rest entirely on myself. My thanks are also due to Mr D. J. Kidd, who drew the illustrations which have been specially designed for this text. The pictures are deliberately diagrammatic or semi-diagrammatic, rather than being pictorial representations of what can be seen during actual dissection of the brain, or in stained sections of the central nervous system, as these are illustrated in several excellent atlases and larger textbooks.

Indeed, this book is not intended in any way to supplant larger textbooks, but to serve as an introduction to them. The author wishes to impress upon students, particularly those studying the nervous system for the first time, that the subject cannot be learned from this book alone; the text is

meant to be used as an adjunct to lecture courses and brain dissection.

No references are given, because they clutter up the text, and students rarely want them; the author hereby apologizes to the many workers whose publications he has pirated without acknowledgment. A small select bibliography is given at the end; detailed references are to be found in all the larger textbooks, to which students should also refer for further data on any point requiring elaboration.

David Bowsher
Liverpool, 1967

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CHAPTER ONE

INTRODUCTION

It would be idle to pretend that the study of the structure and function of the central nervous system (CNS) is not difficult. Perhaps one reason for this is that, compared with most other parts of the body, relatively little is known about the CNS. But the main reason is that the human CNS is the most highly developed and complicated in the whole animal kingdom. Our livers and our larynxes, for example, differ only very slightly from those of much more lowly beasts; but our brains are our crowning glory, and set us apart from and above the rest of brute creation. In studying our own brains, therefore, we have to try and begin to understand what it is that makes us 'only a little lower than the angels'. This is a difficult task, and a great challenge; but the effort is well repaid if it brings some comprehension of that which makes Man what he is.

Structure and function are more intricately bound up with one another in the CNS than in any other part of the body, and cannot be meaningfully separated from one another. Thus any book or course of lectures on the 'anatomy' of the CNS must of necessity deal to a large extent with its 'physiology'; and vice versa. The difference is only one of emphasis, and it would be well for students to realize at the outset that research workers in basic neurology are tackling essentially similar problems; they are only designated 'neuroanatomists' or 'neurophysiologists' according to the experimental methods that they use.

Most students, especially when approaching the CNS for the first time, find its gross morphology difficult to comprehend. There seem to be two main reasons for this. The first is

that the nomenclature is confusing, containing many synonyms, and often meaningless; this latter because early observers were often unaware of the functional significance of what they observed, and so gave fanciful and functionally unhelpful names to what they saw. While many of the monstrous regiment of misnomers can now be discarded or replaced, many more of them are still left to plague the student of neurology in the second half of the twentieth century; the only thing he can do about this is to grin and bear it.

The second difficulty springs from the not unnatural attempt to visualize the morphology of the CNS in the same terms (or, as a neurologist might say, the same conceptual parameters) as the topographical anatomy of the rest of the body. Once the student realizes that he must take a completely different approach, the battle is already half won. For purposes of topographical anatomy, the vertical man is considered; then the directional signs superior, inferior, anterior and posterior are used. However, in the vertical man, the CNS is highly convoluted; so the first, and most important, thing to do is to dispense with these directional signs. Of course, the CNS has a true upper end, the forebrain, and a true lower end, the bottom of the spinal cord. When the CNS is considered along its length like this, it is called the **neuraxis**. By using the terms **rostral** (towards the beak) and **caudal** (towards the tail), direction up and down the neuraxis can be described irrespective of its bends and folds. It is important to realize that the directional signs are used only with reference to the neuraxis itself, and with no reference whatsoever to the rest of the body. The neuraxis has a front and a back, but the directions in which these face vary according to the bending and folding of the neuraxis; they are referred to, facultatively, as anterior or ventral, and posterior or dorsal; again, only with reference to the neuraxis itself, and not to the rest of the body. The neuraxis, like the rest of the body, has a midline,

so the terms medial and lateral are employed in the usual way.

Sections cut at right angles to the long axis of the neuraxis are **coronal**. This again is irrespective of its bends, so that, for example, a coronal section of forebrain is at 90° from a coronal section of spinal cord; but they are both at right angles to the neuraxis. Similarly, sections parallel to the front and back of the neuraxis are **horizontal**; while vertical sections in the long axis of the CNS are called **sagittal** if in the midline, and **parasagittal** if lateral to the midline but parallel with the sagittal plane.

The most important directional and spatial terms are given in the preceding paragraphs. Most other terms will be defined as the text proceeds, but a few more may usefully be given at this juncture:

Ascending—running in a rostral direction.

Descending—running in a caudal direction.

Orthodromic—in the direction of a nerve fibre **away** from the parent cell body.

Antidromic—in the direction of a nerve fibre **towards** the parent cell body.

Nucleus—A collection of nerve cells having common connections and functions.

Afferent	}	—coming towards
- petal		

Efferent	}	—going away from
- fugal		

Kinaesthesia—the conscious sensation of joint movement.

Proprioception—(unconscious) nervous impulses set up by the lengthening or shortening of muscles.

Exteroceptive—coming from outside the body.

Enteroceptive—coming from inside the body.

Modality—Quality of stimulus.

CHAPTER TWO

BASIC CELLULAR ELEMENTS AND DEVELOPMENT OF THE CENTRAL NERVOUS SYSTEM

The nerve cell is specialized for the conduction of impulses, and it sacrifices many other biological functions to this end. It cannot reproduce itself, and its metabolism is so simple and immediate that it cannot live for more than a few minutes without oxygen. It is probably the most delicate cell in the whole body, and requires a chemical environment even more constant than that of the plasma which bathes other cells.

As cells go, the nerve cell is fairly large (Fig. 1), though great

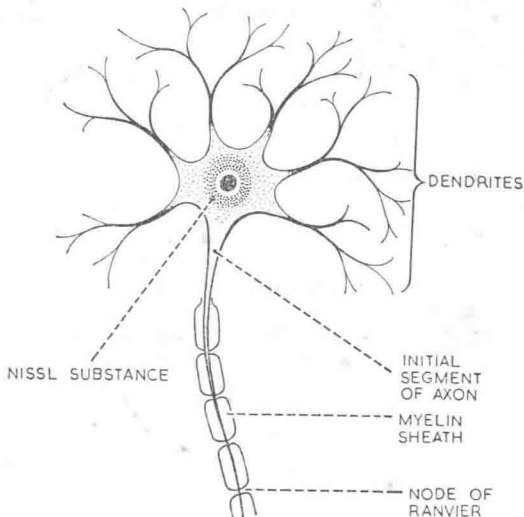


FIG. 1. Diagram of a nerve cell and its processes.

variation is to be found in different parts of the central nervous system (CNS). It contains a large nucleus, which has a nucleolus. The cytoplasm contains a granular substance which stains with basic (blue) dyes. Both the substance and the staining method are called after Nissl, who first described the phenomenon. The amount of **Nissl substance** in a cell diminishes after prolonged activity. Its regeneration appears to be dependent on the nucleolus. Attached to the cell body are a variable number of branching processes called **dendrites**. The area over which the dendrites of a single nerve cell extend is called the **dendritic field** of that cell.

In addition to the dendrites, each cell possesses a single process called the **axon** or nerve fibre. This may vary in length from less than a millimetre to over a yard. Any axon may or may not have one or more collateral branches whose destination may be quite different from that of the parent or stem axon (it may even turn back into the dendritic field of its own cell as a recurrent collateral).

The axon or collateral may remain with the CNS or pass out into a peripheral nerve. Those which end within the CNS do so by breaking up into a number of **terminal filaments** or **telodendria**. At the end of the telodendron is a small swelling called the **bouton terminal** or **synaptic knob**.

This bouton is classically in contact (contiguity not continuity) with the cell body or dendrite of another neurone, constituting an axosomatic or axodendritic **synapse** (Fig. 3).

The structure of the synaptic knob has also been elucidated by electron microscopy. The bouton is seen to contain a number of **synaptic vesicles** (Fig. 4). When a nervous impulse arrives at the bouton, it causes **transmitter substance** to be liberated from these vesicles; the details of its mode of action will be considered in Chapter 4.

The nerve cell and all its processes is called the **neurone**, and each neurone (of which the human nervous system contains

some 15–20 thousand million) is a self-contained and independent unit. Neurones whose cell bodies lie within the central nervous system are like that illustrated in Fig. 1, and have the cell body interposed between the dendrites and the axon.

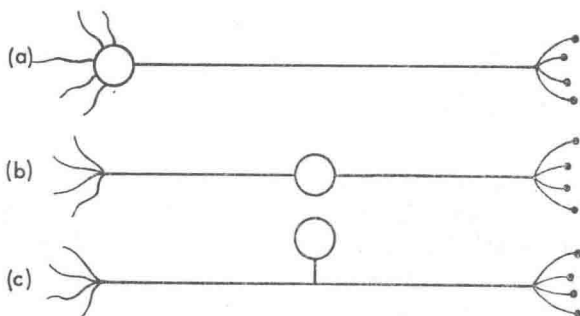


FIG. 2. Three common types of neurone (after Bodian and Hallowell Davis). In all cases, the dendritic ramifications, capable only of decremental electrotonic conduction, are at the left; the axonal portion is in the middle; and the telodendria and vesicle-containing synaptic knobs are at the right. Only the position of the cell body varies: (a) is the type most commonly found in the central nervous system; (b) is the bipolar type of neurone found in the retina and VIIIth cranial nerve; (c) is the pseudo-unipolar neurone characteristic of dorsal root and corresponding sensory cranial ganglia.

However, neurones whose cell bodies lie outside the CNS, and whose function is to conduct impulses from the periphery into the CNS, have the cell body as it were slid along the axon (Fig. 2), so that the dendrites run directly into the peripheral end of the axon; in nerves coming from the skin, the cell body (in the **dorsal root** or corresponding **sensory cranial nerve ganglion**) is on a side branch of the axon.

The neurone doctrine teaches that nervous conduction,

under normal conditions, starts at the dendritic end of the axon (whether this be the cell body or not) and travels towards the telodendria with their terminal buttons. Thus it will be seen that the function of the cell body, apart from providing a large area of membrane surface (see Chapter 4) is chiefly to ensure the maintenance of the various processes and their branches, which constitute the essential conducting mechanism of the neurone. The conditions under which the nervous impulse is generated and conducted, as well as the way in which impulses cross the synaptic junction between neurones, will be dealt with in chapter 4.

Two types of neurones within the CNS should be considered. First is the primitive **isodendritic** neurone (Fig. 3) with long straight dendrites. Its axon bears many collateral branches which go off in different directions to establish small numbers of synaptic contacts with large numbers of secondary neurones.

Since the number of synaptic knobs in contact with a neurone of any type is very large (up to 10,000 in some instances), it is usually the case that the more or less synchronous activation of a large number of synapses is necessary to fire the neurone; impulses arriving at one, or a very small number of synapses, will usually be ineffective.

Such neurones are generally found in the primitive reticular core of the neuraxis, forming the non-specific or extralemniscal system (see Chapter 11) and hypothalamus (Chapter 15). The pattern of their widely distributed efferents and heterogeneous afferents makes it evident that impulses arriving from a single afferent source are unlikely to fire a secondary neurone; but that each neurone is open to a very large number of afferent inputs, and able through its widely divergent output to influence the activity of large numbers of secondary neurones.

Second is the **tufted** neurone (Fig. 3) with a smaller but

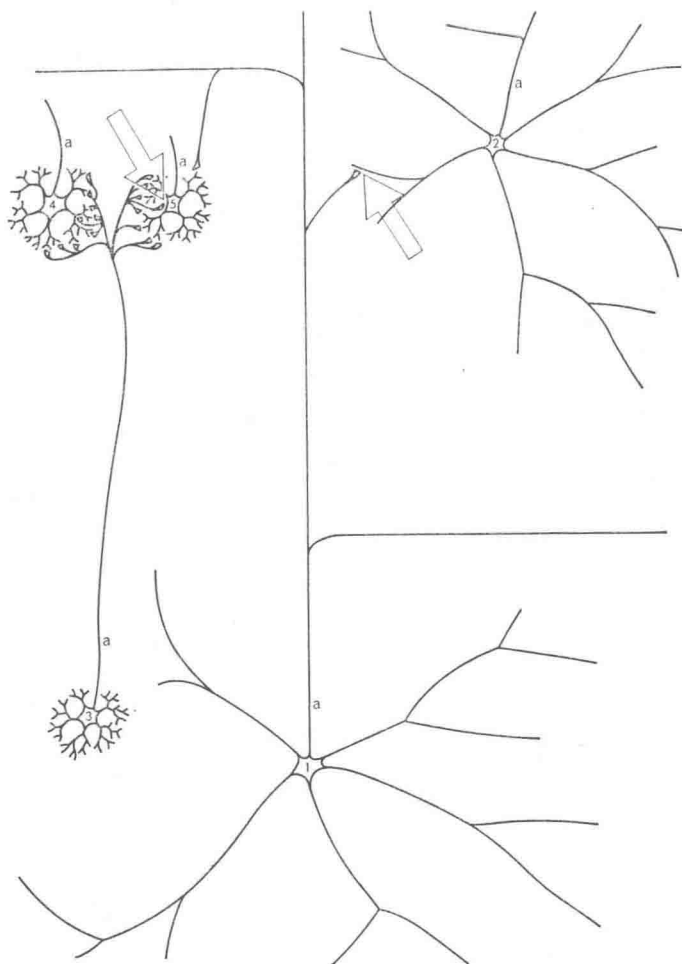


FIG. 3. 1 and 2 are isodendritic neurones, whose axons (a) have many collateral branches, giving a small number of contacts to a large number of secondary neurones, including those of the tufted type (3, 4 and 5). The axons (a) of the latter establish a large number of contacts with a small number of secondary neurones of their own type. The right-hand arrow indicates an axodendritic synapse, while the left-hand arrow is pointing to an axosomatic synapse.

denser bushy dendritic field. Its axon has a small number of collateral branches which tend to make multiple, concentrated, synaptic contacts with small numbers of secondary neurones. It is found in the recently evolved nuclei belonging to the specific or lemniscal systems (Chapter 10). The nature of the concentrated afferents and efferents means that such cells influence only a relatively small number of secondary neurones, but do so in a manner which is fairly certain to cause the latter to fire; this is the morphological basis of so-called **synaptic security**.

Within certain specific relay centres of the brain, such as the thalamus (Chapters 8 and 12) a type of **interneurone** is found which sometimes does not even possess an axon. Some of its processes, however, contain synaptic vesicles and enter into the composition of a **synaptic glomerulus** where they are post-synaptic to some structures and pre-synaptic to others (Fig. 4). All known interneurons of this type are inhibitory, and their vesicle-containing processes are probably responsible for the phenomenon known as **pre-synaptic inhibition** (see p. 35 below).

Every axon and its branches, as far as the terminal filament, is covered with a layer of white fatty substance known as **myelin**, except the first little bit, where it arises from the axon hillock; this is known as the **initial segment**. The larger the axon the thicker its myelin sheath—the largest nerve fibres in the human CNS are about $20\ \mu$ in diameter (including the axon sheath). Roughly speaking, large axons arise from large nerve cells and vice versa. The smallest axons (about $1\ \mu$ in diameter, including sheath) have only a very thin film of myelin, which could not be seen with the fat stains formerly used for myelin, and so these, to this day, are called 'unmyelinated axons'. The larger axons, both inside and outside the central nervous system, have their myelin arranged like a string of sausages, separated by the **nodes of**

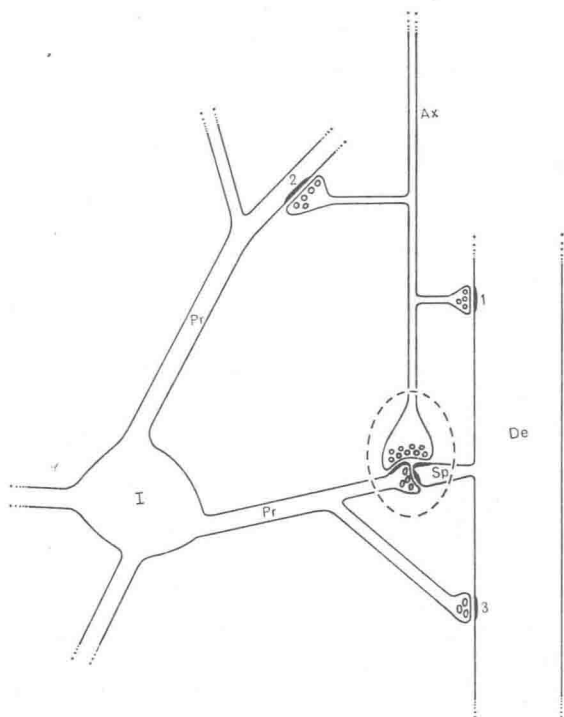


FIG. 4. Ax is an axon whose terminals, containing spherical vesicles, make excitatory synapses with the dendrite (De) of a relay neurone at 1 and with a process (Pr) of an inhibitory interneurone (I) at 2; this process in its turn has endings containing ovoid vesicles, one of which makes an inhibitory synapse with the dendrite at 3. The region within the dashed outline is a synaptic glomerulus, partly or wholly encapsulated by glial processes (not shown). In the glomerulus, an axon terminal is presynaptic to both a spine (Sp) of the relay neurone dendrite and to a terminal of an interneurone process, while the latter is also presynaptic to the dendritic spine.