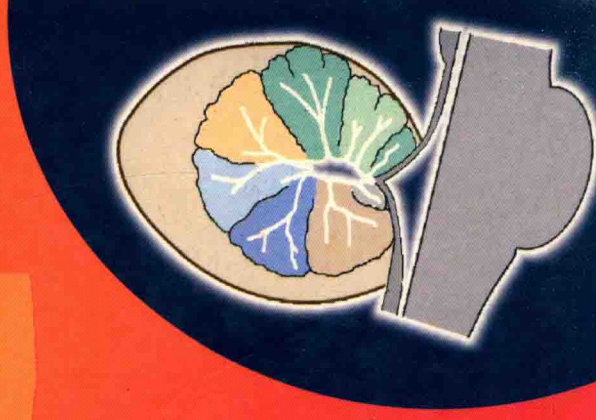

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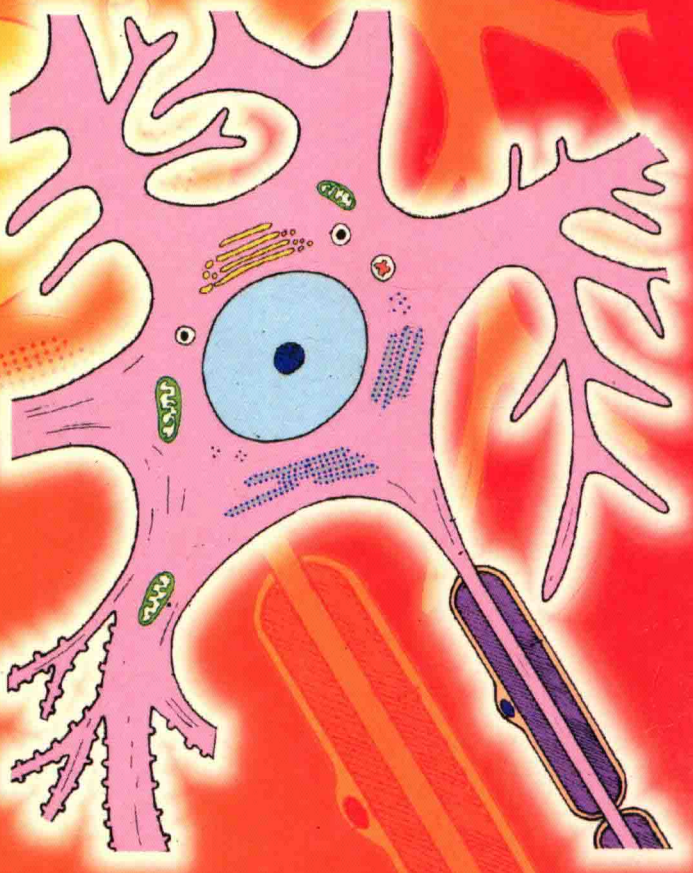

Seventh Edition

Inderbir Singh

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Textbook of

Human Neuroanatomy

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Inderbir Singh

MS., Ph.D., F. A. M. S

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Fax: +91-11-23276490, +91-11-23245683 e-mail: jaypee@jaypeebrothers.com
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  Tele Fax: +91-80-22281761 e-mail: jaypeemedpubbgl@eth.net
- 282 IIIrd Floor, Khaleel Shirazi Estate, Fountain Plaza
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  Fax: +91-44-28262331 e-mail: jpchen@eth.net
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  Fax: +91-40-24758499 e-mail: jpmedpub@rediffmail.com
- 1A Indian Mirror Street, Wellington Square, **Kolkata** 700 013,
  Phones: +91-33-22456075, +91-33-22451926 Fax: +91-33-22456075
  e-mail: jpbcal@cal.vsnl.net.in
- 106 Amit Industrial Estate, 61 Dr SS Rao Road, Near MGM Hospital
  Parel, **Mumbai** 400 012, Phones: +91-22-24124863, +91-22-24104532, +91-22-30926896
  Fax: +91-22-24160828 e-mail: jpmedpub@bom7.vsnl.net.in
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- "KAMALPUSHPA", 38 Reshimbag, Opp. Mohota Science College, Umred Road
  Nagpur 440 009, Phones: +91-712-3945220, +91-712-2704275
  e-mail: jpmednagpur@rediffmail.com

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Preface to Seventh Edition

I have great pleasure in presenting the **seventh edition** of NEUROANATOMY.

As in previous editions, the main effort has been to present a complicated subject in as simple a manner as possible. The major problem that faces the author of any student text book is to decide just how much to include out of the limitless volume of information available. Some facts are such that no student can afford to be without them. However, these essentials are often wrapped up in a huge mass of detail which often serves only to obscure the important principles relevant to future clinical studies. It is for this reason that, in this edition, essential matter is clearly demarcated from more advanced detail. Essential matter is given on white background, while more advanced matter is printed on a pink background.

In this edition a great deal of effort has gone into improving the get up of the book to make it more user friendly. The use of colour has been greatly increased. Many illustrations have been redrawn, and almost all others have been improved. The text has been revised and recomposed in a clear, easy to read, type-face.

I am much obliged to Mr. Jatinder P. Vij, CMD of Jaypee Brothers for being always extremely helpful and accommodating. His hard work and his pleasant nature make him a delight to work with.

I continue to be obliged to Prof. S.C. Srivastava, and to Dr. R.K.Yadav for very kindly providing a number of photographs.

As always. I am deeply indebted to readers who have sent words of encouragement and suggestions for improvement. I am grateful to all students who have read this book, because without them the book would have no reason to exist.

Rohtak

June 2006

INDERBIR SINGH

Contents

1

Introduction to Neuroanatomy

What is Neuroanatomy?

The human body consists of numerous tissues and organs that are diverse in structure and function. Yet they function together, and in harmony, for the well being of the body as a whole. It is obvious that there has to be some kind of influence that monitors and controls the working of different parts of the body. Although there are other mechanisms that help in such control (e.g. hormones) the overwhelming role in directing the activities of the body rests with the nervous system. Neuroanatomy is the study of the structural aspects of the nervous system. It cannot be emphasised too strongly that the study of structure is meaningless unless correlated with function. Division of a study of the nervous system into neuroanatomy and neurophysiology is only a matter of convenience.

Divisions of the Nervous System

The nervous system may be divided into (a) the ***central nervous system***, made up of the brain and spinal cord, and (b) the ***peripheral nervous system***, consisting of the peripheral nerves and the ganglia associated with them.

The brain consists of (a) the ***cerebrum***, made up of two large cerebral hemispheres, (b) the

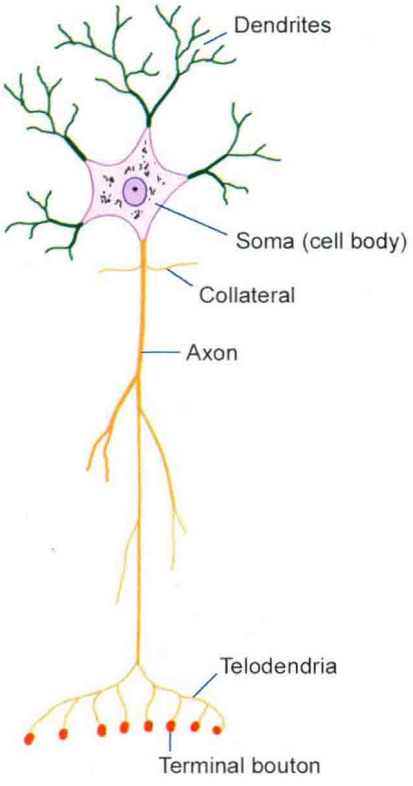

Fig. 1.1. Diagram showing the main parts of a typical neuron.

cerebellum, (c) the ***midbrain***, (d) the ***pons***, and (v) the ***medulla oblongata***. The midbrain, pons and medulla together form the ***brainstem***. The medulla is continuous, below, with the spinal cord. Peripheral nerves attached to the brain are called ***cranial nerves***; and those attached to the spinal cord are called ***spinal nerves***.

The peripheral nerves include those that supply skin, muscles and joints of the body wall and limbs, and those that supply visceral structures e.g., heart, lungs, stomach etc. Each of these sets of peripheral nerves is intimately associated with the brain and spinal cord. The nerves supplying the body wall and limbs are often called ***cerebrospinal nerves***. The nerves supplying the viscera, along with the parts of the brain and spinal cord related to them, constitute the ***autonomic nervous system***. The autonomic nervous system is subdivided into two major parts: the ***sympathetic*** and the ***parasympathetic*** nervous systems.

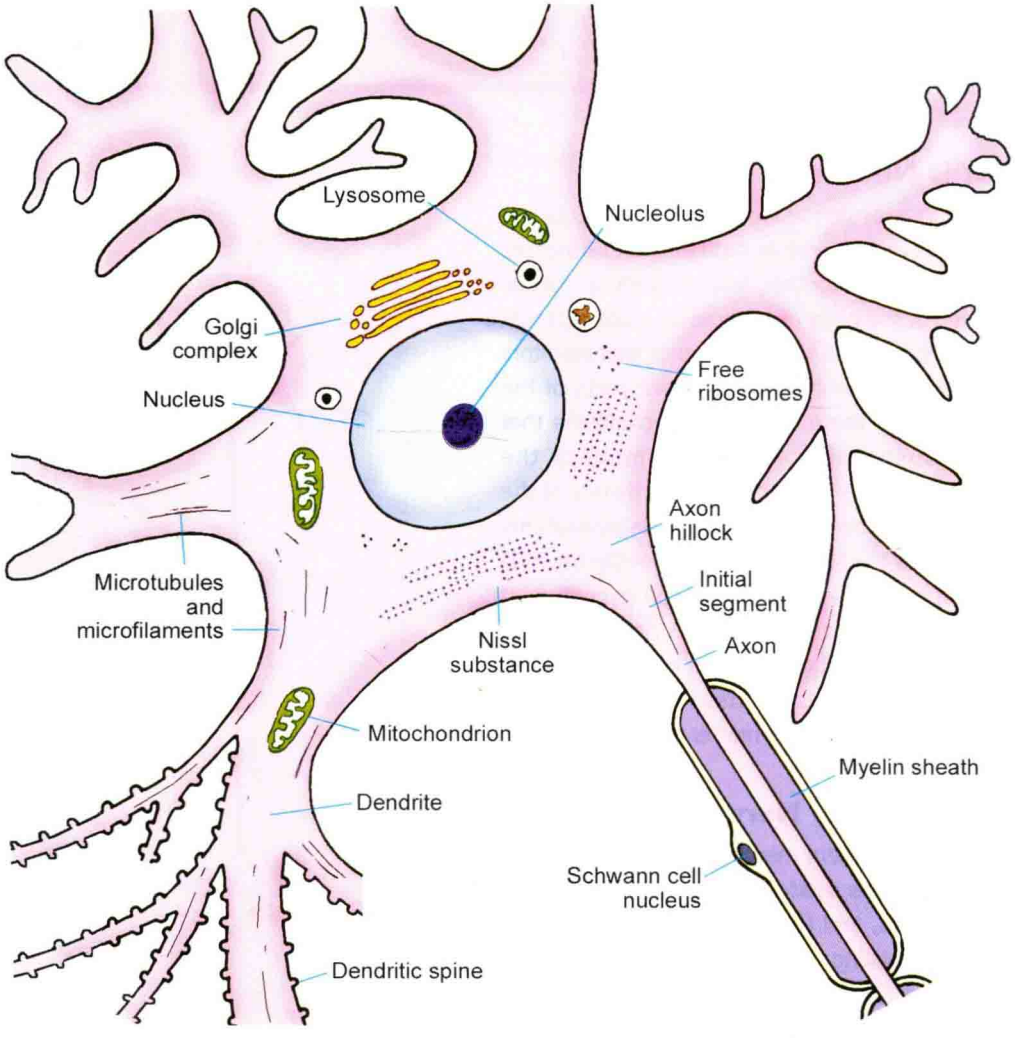

Fig. 1.2. Schematic presentation of some features of the structure of a neuron as seen by EM.

How neuroanatomy is studied

The study of neuroanatomy begins with the study of those features of the brain and spinal cord (and of the nerves attached to them) that can be seen with the naked eye. This is the study of gross anatomy. It includes the study of the surface features of the brain and spinal cord; and the courses, relations and distribution of peripheral nerves. Some details of the internal structure of the brain and spinal cord can be made out with the naked eye. However, the study of internal structure depends mainly on microscopic examination. Again some details of structure can be made out using ordinary histological methods, but the greater part of the information about the nervous system has been obtained using specialised methods. In recent years such studies have increasingly involved the use of histochemical methods and the study of tissues under the high magnifications possible only with an electron microscope (ultrastructure).

Tissues constituting the nervous system

The nervous system is made up, predominantly, of tissue that has the special property of being able to conduct impulses rapidly from one part of the body to another. The specialised cells that constitute the functional units of the nervous system are called ***neurons***. Within the brain and spinal cord neurons are supported by a special kind of connective tissue that is called ***neuroglia***. Nervous tissue, composed of neurons and neuroglia, is richly supplied with blood. It has been taught that lymph vessels are not present, but the view has recently been challenged.

The nervous system of man is made up of innumerable neurons. The total number of neurons in the human brain is estimated at more than 10^{12}. The neurons are linked together in a highly intricate manner. It is through these connections that the body is made aware of changes in the environment, or of those within itself; and appropriate responses to such changes are produced e.g., in the form of movement or in the modified working of some organ of the body. The mechanisms for some of these relatively simple functions have come to be known as a result of a vast amount of work done by numerous workers for over a century. There is no doubt that higher functions of the brain, like those of memory and intelligence, are also to be explained on the basis of connections between neurons, but as yet little is known about the mechanisms involved. Neurons are, therefore, to be regarded not merely as simple conductors, but as cells that are specialised for the reception, integration, interpretation and transmission of information.

Nerve cells can convert information obtained from the environment into codes that can be transmitted along their axons. By such coding the same neuron can transmit different kinds of information.

Neuron Structure

Elementary Structure of a Typical Neuron

Neurons vary considerably in size, shape and other features. However, most of them have some major features in common and these are described below (Figs. 1.1 to 1.4).

A neuron consists of a ***cell body*** which gives off a number of ***processes***. The cell body is also called the soma or ***perikaryon***. Like a typical cell it consists of a mass of cytoplasm surrounded by a cell membrane. The cytoplasm contains a large central nucleus (usually with a prominent nucleolus), numerous mitochondria, lysosomes and a Golgi complex (Fig. 1.2). In the past it has often been stated that centrioles are not present in neurons, but studies with the electron microscope (usually abbreviated to EM) have shown that centrioles are present. In addition to these features, the cytoplasm of a neuron has some distinctive characteristics not seen in other cells. The cytoplasm shows the presence of a granular material that stains intensely with basic dyes; this material is the ***Nissl substance*** (also called Nissl bodies or granules) (Fig. 1.3). When examined with the EM, these bodies are seen to be composed of rough surfaced endoplasmic reticulum (Fig 1.2). The presence of abundant granular endoplasmic reticulum is an indication of the high level of protein synthesis in neurons. The proteins are needed for maintenance and repair, and for production of neurotransmitters and enzymes.

Another distinctive feature of neurons is the presence of a network of fibrils permeating the cytoplasm (Fig. 1.4). These ***neurofibrils*** are seen, with the EM, to consist of microfilaments and microtubules. (The centrioles present in neurons may be concerned with the production and maintenance of microtubules).

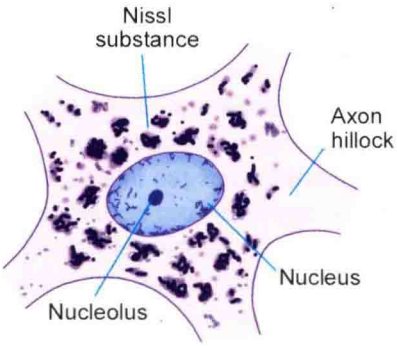

Fig. 1.3. Neuron stained to show Nissl substance. Note that the Nissl substance is not present in the axon and the region of the axon hillock.

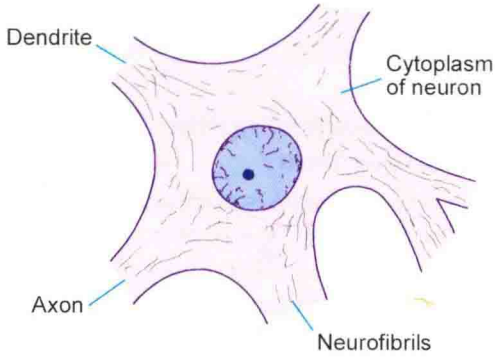

Fig. 1.4. Neuron stained to show neurofibrils. Note that the fibrils extend into both axons and dendrites.

Some neurons contain pigment granules (e.g., neuromelanin in neurons of the substantia nigra). Ageing neurons contain a pigment lipofuscin (made up of residual bodies derived from lysosomes).

The processes arising from the cell body of a neuron are called ***neurites***. These are of two kinds. Most neurons give off a number of short branching processes called ***dendrites*** and one longer process called an ***axon***.

The dendrites are characterised by the fact that they terminate near the cell body. They are irregular in thickness, and Nissl granules extend into them. They bear numerous small spines which are of variable shape.

The axon may extend for a considerable distance away from the cell body. The longest axons may be as much as a metre long. Each axon has a uniform diameter, and is devoid of Nissl substance.

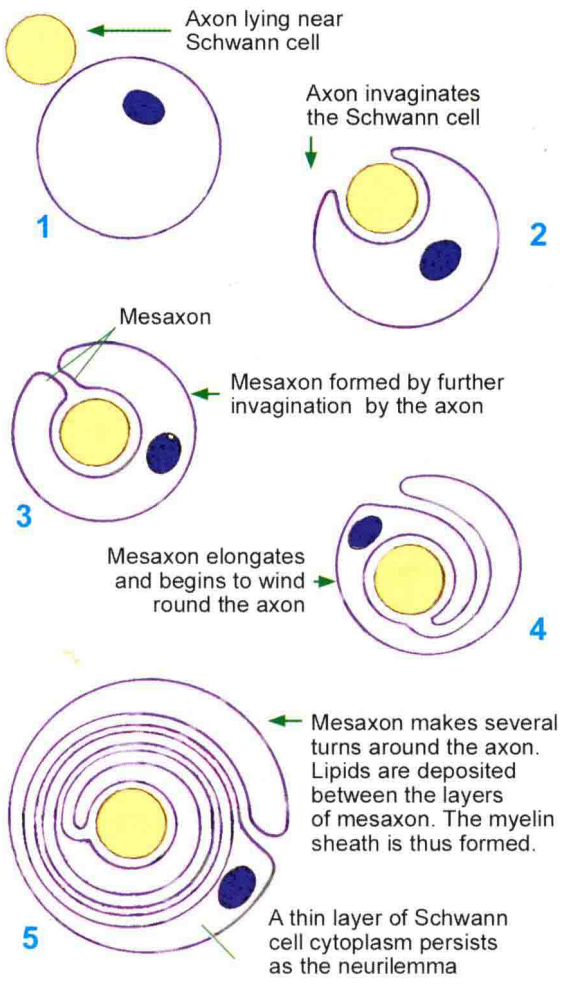

Fig. 1.5. Stages in the formation of the myelin sheath by a Schwann cell. The axon which first lies near the Schwann cell (1), invaginates into its cytoplasm (2,3), and comes to be suspended by a mesaxon. The mesaxon elongates and comes to be spirally wound around the axon (4,5). Lipids are deposited between the layers of the masaxon.

In addition to these differences in structure, there is a fundamental functional difference between dendrites and axons. In a dendrite, the nerve impulse ***travels towards the cell body*** whereas in an axon the impulse travels ***away from the cell body***.

We have seen above that the axon is free of Nissl granules. The Nissl-free zone extends for a short distance into the cell body: this part of the cell body is called the ***axon hillock***. The part of the axon just beyond the axon hillock is called the ***initial segment*** (Fig. 1.2).

During its formation each axon comes to be associated with certain cells that provide a sheath for it. The cells providing this sheath for axons lying outside the central nervous system are called ***Schwann cells***. Axons lying within the central nervous system are provided a similar covering by a kind of neuroglial cell called an ***oligodendrocyte***. The nature of this sheath is best understood by considering the mode of its formation (Fig. 1.5). An axon lying near a Schwann cell (1) invaginates into the cytoplasm of the Schwann cell (2,3). In this process the axon comes to be suspended by a fold of the cell membrane of the Schwann cell: this fold is called the ***mesaxon*** (3). In some situations the mesaxon becomes greatly elongated and comes to be spirally wound around the axon, which is thus surrounded by several layers of cell membrane (4,5). Lipids are deposited between adjacent layers of the membrane. These layers of the mesaxon, along with the lipids, form the ***myelin sheath***. Outside the myelin sheath a thin layer of Schwann cell cytoplasm persists to form an additional sheath which is called the ***neurilemma*** (also called the neurilemmal sheath or Schwann cell sheath). Axons having a myelin sheath are called ***myelinated axons***. The presence of a myelin sheath increases the velocity of conduction (for a nerve fibre of the same

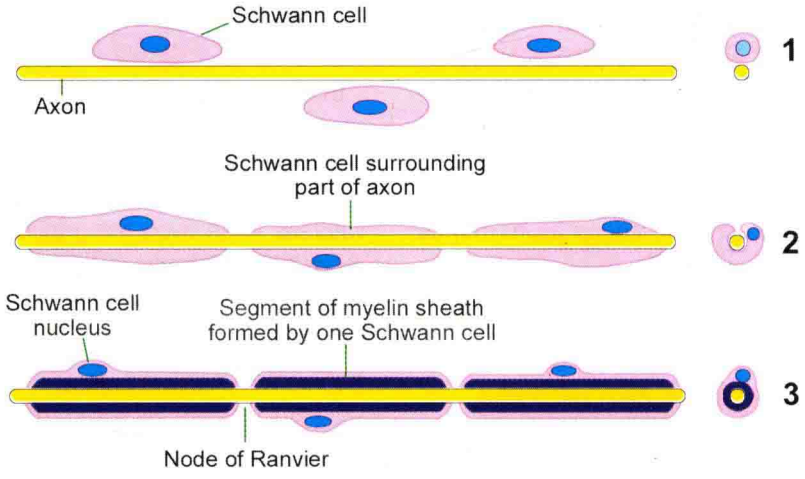

Fig. 1.6. Scheme to show that each Schwann cell forms a short segment of the myelin sheath. The small figures at the extreme right are transverse sections through the nerve fibre, at the corresponding stages.

diameter). It also reduces the energy expended in the process of conduction.

An axon is related to a large number of Schwann cells over its length (Fig. 1.6). Each Schwann cell provides the myelin sheath for a short segment of the axon. At the junction of any two such segments there is a short gap in the myelin sheath. These gaps are called the ***nodes of Ranvier***.

There are some axons that are devoid of myelin sheaths. These ***unmyelinated axons*** invaginate into the cytoplasm of Schwann cells, but the mesaxon does not spiral around them (Fig. 1.7). Another difference is that several such axons may invaginate into the cytoplasm of a single Schwann cell.

An axon may give off a variable number of branches (Fig. 1.1). Some branches, that arise near the cell body and lie at right angles to the axon are called ***collaterals***. At its termination the axon breaks up into a number of fine branches called ***telodendria*** which may end in small swellings (***terminal boutons*** or ***bouton terminaux***). An axon (or its branches) can terminate in two ways. Within the central nervous system, it always terminates by coming in intimate relationship with another neuron, the junction between the two neurons being called a synapse (page 9). Outside the central nervous system, the axon may end in relation to an effector organ (e.g., muscle or gland), or may end by synapsing with neurons in a peripheral ganglion.

Axons (and some dendrites that resemble axons in structure: see below) constitute what are commonly called ***nerve fibres***.

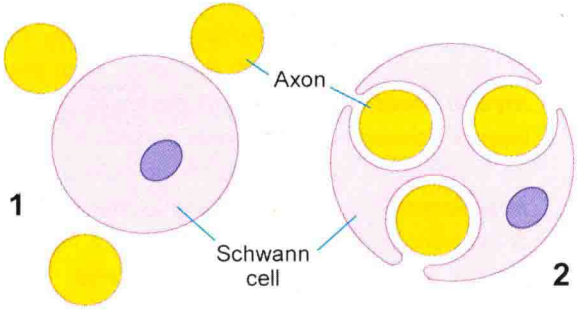

Fig. 1.7. Relationship of unmyelinated axons to a Schwann cell.

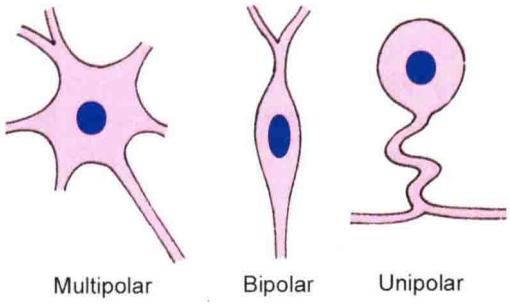

Fig. 1.8. Multipolar, bipolar and unipolar neurons.

Variability in Neuron Structure

Variation in the shape of neuronal cell bodies

Neurons vary considerably in the size and shape of their cell bodies (somata) and in the length and manner of branching of their processes. The cell body varies in diameter from about 5μm, in the smallest neurons, to as much as 120μm in the largest ones. The shape of the cell body is dependent on the number of processes arising from it. The most common type of neuron gives off several processes and the cell body is, therefore, ***multipolar*** (Fig. 1.8). Some neurons have only one axon and one dendrite and are ***bipolar***.

Another type of neuron has a single process (which is highly convoluted). After a very short course this process divides into two. One of the divisions represents the axon; the other is functionally a dendrite, but its structure is indistinguishable from that of an axon. This neuron is described as ***unipolar***, but from a functional point of view it is to be regarded as bipolar. (To avoid confusion on this account this kind of neuron has been referred to, in the past, as a ***pseudounipolar*** neuron but this term has now been discarded). Depending on the shapes of their cell bodies some neurons are referred to as ***stellate*** (star shaped) or ***pyramidal***.

In addition to the variations in size and shape, the cell bodies of neurons may show striking variations in the appearance of the Nissl substance. In some neurons, the Nissl substance is very prominent and is in the form of large clumps. In some others, the granules are fine and uniformly distributed in the cytoplasm, while yet other neurons show gradations between these extremes. These differences are correlated with function.

Variations in axons

The length of the axon arising from the cell body of a neuron is also subject to considerable variability. Some neurons have long axons, and connect remote regions. These are called ***Golgi type I*** neurons. In other neurons axons are short and end near the cell body. They are called ***Golgi type II*** neurons or ***microneurons***: these are often inhibitory in function. Very rarely, a neuron may not have a true axon.

As stated earlier, axons also differ in the nature of the sheaths covering them, some of them being myelinated and others unmyelinated. Axons also show considerable variation in the diameter of their cross sections.

Variations in dendrites

Dendrites arising from a neuronal cell body vary considerably in number, and in the extent and manner of branching. They also differ in the distribution of spines on them. These characteristics are of functional importance. The ***area*** occupied by the dendrites of a neuron is referred to as its ***dendritic field***. Different kinds of neurons have differing dendritic fields (See page 9).

Neurons also show considerable variation in the number and nature of synapses established by them.

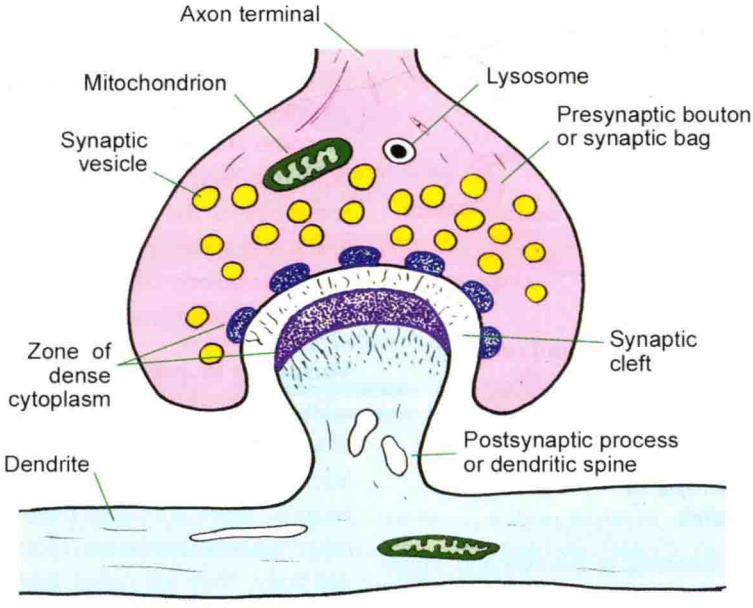

Fig. 1.9. Scheme showing the structure of a typical synapse as seen by EM.

FURTHER DETAILS ABOUT NEURONS

Axon hillock and initial segment:

The axon hillock and the initial segment of the axon are of special functional significance. This is the region where action potentials are generated (spike generation) resulting in conduction along the axon. The initial segment is unmyelinated. It often receives axo-axonal synapses that are inhibitory. The plasma membrane here is rich in voltage sensitive channels.

Axoplasmic flow:

The cytoplasm of neurons is in constant motion. Movements of various materials occurs through axons. This ***axoplasmic flow*** takes place both away from and towards the cell body. The flow away from the cell body is greater. Some materials travel slowly (0.1 to 2 mm a day) constituting a ***slow transport***. In contrast other materials (mainly in the form of vesicles) travel 100 to 400 mm a day constituting a ***rapid transport***.

Slow transport is unidirectional, away from the cell body. It is responsible for flow of axoplasm (containing various proteins) down the axon. Rapid transport is bi-directional and carries vesicular material and mitochondria. Microtubules play an important role in this form of transport. Retrograde axoplasmic flow may carry neurotropic viruses (e.g., polio) along the axon into the neuronal cell body.

Axoplasmic transport of tracer substances introduced experimentally can help to trace neuronal connections.

Some features of dendrites

(a) Dendrites can distinguished immuno-cytochemically from axons because of the presence in them of microtubule associated protein MAP-2 not present in axons.

(b) Dendritic spines vary in size and shape. Some spines contain aggregations of smooth

endoplasmic reticulum (in the form of flattened cisternae with associated dense material). The complex is referred to as the ***spine apparatus***.

(c) Actin filaments are present in dendritic spines.

(d) Some variations in the dendritic field are as follows. The field may be ***spherical*** (as in stellate cells), ***hemispherical***, ***disc-like***, ***conical*** or ***flat***. In some neurons (e.g., pyramidal), the neuron may have two separate dendritic fields. Apart from shape there is considerable variability in *extent* of the dendritic field. Some neurons (e.g., Golgi neurons of the cerebellum) have dendritic fields covering a very wide area. More than eighty per cent of the neuronal surface area (excluding the axon) may be situated on the dendritic tree. The frequency of branching of dendrites is correlated with the number of synapses on them. In some neurons the dendritic spines may number several thousand. Finally, it may be emphasised that the dendritic tree is not a 'fixed' entity, but may undergo continuous remodelling. This affords a basis for modification of neuronal behaviour.

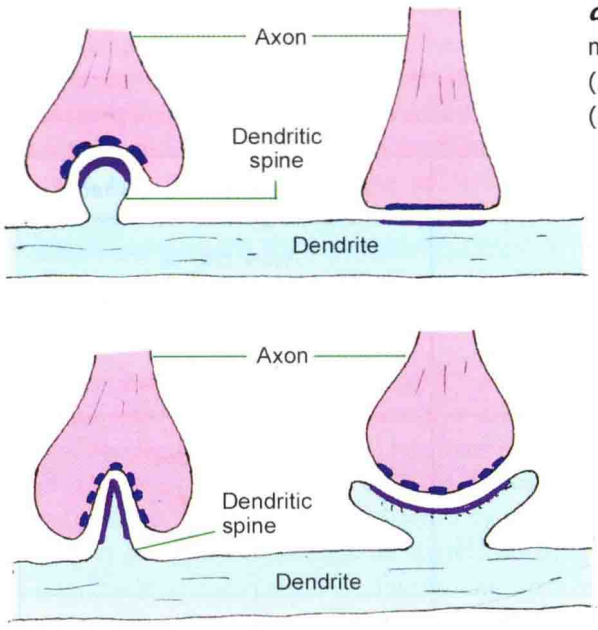

Fig. 1.10. Some variations in the orientation of axodendritic synapses

The Synapse

We have seen that synapses are sites of junction between neurons. Synapses may be of various types depending upon the parts of the neurons that come in contact. In the most common type of synapse, an axon terminal establishes contact with the dendrite of a receiving neuron to form an ***axodendritic synapse***. Synapses on dendrites may be located on spines or on the smooth areas between spines. The axon terminal may synapse with the cell body (***axosomatic synapse***) or, less commonly, with the axon of the receiving neuron (***axoaxonal synapse***). An axoaxonal synapse may be located either on the initial segment (of the receiving axon) or just proximal to an axon terminal.

In some parts of the brain (e.g., the thalamus) we see some synapses in which the presynaptic element is a dendrite instead of an axon. Such synapses may be ***dendro-axonic*** or ***dendro-dendritic***. In yet others the soma of a neuron may synapse with the soma of another neuron (***somato-somatic*** synapse), or with a dendrite (***somato-dendritic*** synapse).

The axon may terminate in a single bulb-like end called a ***bouton*** (or ***synaptic bag***). Alternatively, the terminal part of the axon may bear a number of such enlargements each of which synapses with the receiving neuron. We have seen that dendrites bear numerous spines. Axon terminals may synapse either with the spines or with smooth portions of the dendrite between the spines. Occasionally, an axon terminal may end by synapsing with the terminal bouton of another axon forming what is called a ***serial synapse***. In certain situations several neurons may take part in forming complex synapses. Such areas may be encapsulated by neuroglial cells to form

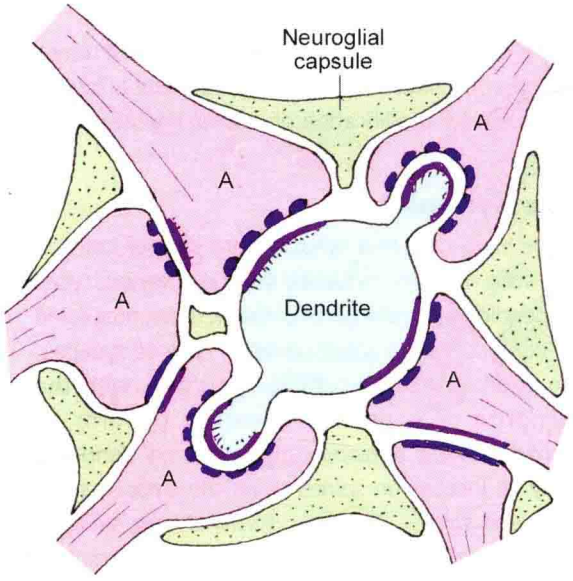

Fig. 1.11. Diagram to show a synaptic glomerulus.

synaptic glomeruli. Such glomeruli are found in the cerebellum, the olfactory bulb, the lateral geniculate body and in some other situations.

At some sites several synapses may be present around a short length of a dendrite and may be enclosed within a glial capsule. Such a complex is called a ***synaptic cartridge***.

A synapse transmits an impulse only in one direction. The two elements taking part in a synapse can, therefore, be spoken of as ***presynaptic*** and ***postsynaptic*** (Fig. 1.9). In an axo-dendritic synapse, the terminal enlargement of the axon may be referred to as the ***presynaptic bouton*** or ***synaptic bag***. The region of the dendrite receiving the axon terminal is the ***postsynaptic process***. The two are separated by a space called the ***synaptic cleft***. Delicate fibres or granular material may be seen within the cleft. On either side of the cleft there is a region of dense cytoplasm. On the presynaptic side this dense cytoplasm is broken up into several bits. On the postsynaptic side the dense cytoplasm is continuous and is associated with a meshwork of filaments called the ***synaptic web***.

The thickened areas of membrane on the presynaptic and postsynaptic sides constitute the ***active zone*** of a synapse. Neuro-transmission takes place through this region. Some variations in the structure of the active zone are described below.

Fig. 1.12. Classification of synapses on the basis of ultrastructure and neurotransmitters present

Asymmetric / symmetric	*Shape of vesicles*	*Neurotransmitter associated*
Asymmetric	Small spherical	Acetyl choline Glutamine Serotonin Some other amines
	Dense cored	Noradrenaline Adrenaline Dopamine
Symmetric	Pleomorphic	GABA Glycine