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.

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. Axons 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.

Related topics

Neuron diversity (A2)
Morphology of chemical synapses (C1)

Cell body

The **cell body** (**soma**, **perikaryon**) of a neuron (see *Fig. 1*) contains the nucleus, Golgi apparatus, ribosomes and other subcellular organelles, and is responsible for most of its routine metabolic 'housekeeping' functions. The neuron cell body resembles other cells, although it is specialized to maintain high levels of biosynthetic activity. The rough endoplasmic reticulum, for example, is so densely packed as to produce distinct structures called **Nissl bodies**, which are extremely rich in ribosomes. This reflects the high rates of protein synthesis of which neurons are capable.

Neurons come in a great variety of shapes and sizes. The smallest cell bodies are 5–8 μm in diameter, the largest 120 μm across.

Neurites

Neurons are distinguished from other cells by **neurites**. These are long cylindrical processes that come in two varieties: dendrites and axons. **Dendrites** are highly branched extensions of the cell body, may be up to 1 mm in length and can be 90% of the surface area of a neuron. Dendrites on some neurons are covered with hundreds of tiny projections termed **dendritic spines** on which synapses are made. Nerve cells with spines are called **spiny neurons**, those lacking them **aspiny neurons**. A neuron may have one or many dendrites, arranged in a pattern which is cell typical and collectively referred to as the **dendritic tree.** The majority of synaptic inputs from other neurons are made on dendrites.

Nerve cells generally have only one **axon.** It usually arises from the cell body but may emerge from a dendrite just where it leaves the cell body. In either case

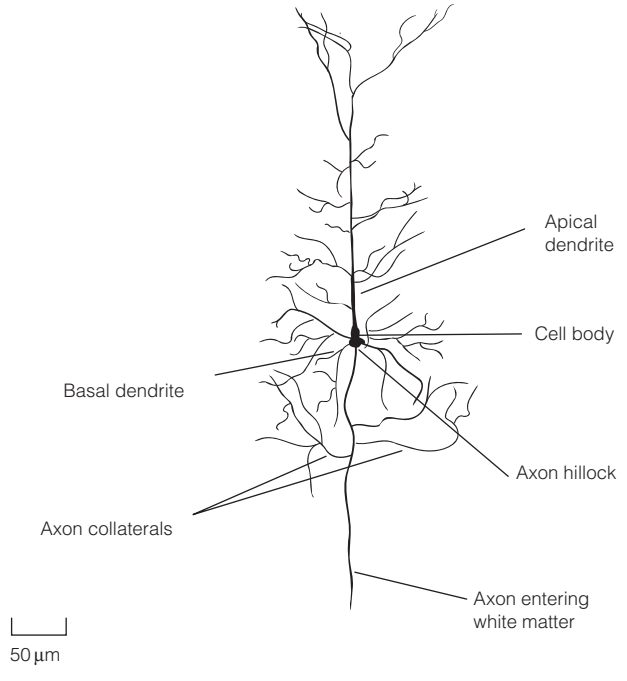

Fig. 1. Key features of a neuron. A drawing of a pyramidal cell showing the distribution of neurites (dendrites and axon).

the site of origin is termed the **axon hillock**. Axons have diameters 0.2–20 µm in humans (though axons of invertebrates can reach 1 mm) and vary in length from a few µm to over a meter. They may be encapsulated in a **myelin sheath**. Axons usually have branches, referred to as **axon collaterals.** The ends of an axon are swollen **terminals** (**boutons**) and usually contain mitochondria and vesicles. Some axons have swellings along their length called **varicosities**. Axon terminals and varicosities are the presynaptic components of chemical synapses.

Axon or dendrite? Axons can be distinguished from dendrites on structural grounds. Axons tend to be long, untapered, less highly branched, are 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). Since axons do not possess protein synthetic machinery, proteins in axons must be made in the cell body and moved along the axon by **axoplasmic transport**. Both axons and dendrites have mitochondria. Axon terminals are rich in mitochondria, indicating their high requirement for metabolic energy.

A2 Neuron diversity

Key Notes

Neuron classification

Neurons may be classified by their morphology, function or by the neurotransmitters 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, whether the dendrites have dendritic spines or not, and the length of the axon, have all proved useful in categorizing neurons. Functional classification distinguishes afferent neurons that provide input and efferent neurons that provide output to a region of the nervous system. Neuron shape is often a good guide to the neurotransmitters it secretes, and so to its function

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 (A4)
Organization of the central nervous system (A5)

Neuron classification

There is no such thing as a 'typical' neuron. Nerve cells come in diverse shapes and sizes, each with their own distinctive patterns of synaptic contacts and chemical transmitters. This allows neurons to be classified according to their morphology, neurotransmitters and function.

Structural ways to classify a nerve cell include the size of its 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 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, **bipolar** neurons in the retina synapse with photoreceptors, and sensory neurons in the dorsal root ganglion are described as **pseudounipolar**; so called because they start life as bipolar cells, having two processes, which 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 determine the efficacy of its synaptic connections and so 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 is termed **stellate cells** because of the star-like appearance of their dendritic trees. **Purkinje** cells of the cerebellar cortex have the unique feature that their extensive network of dendrites forms a two-dimensional array.

Neurons can also be classified on the basis of the lengths of their axons. **Projection** (**principal**, **relay** or **Golgi type I**) neurons have long axons, which

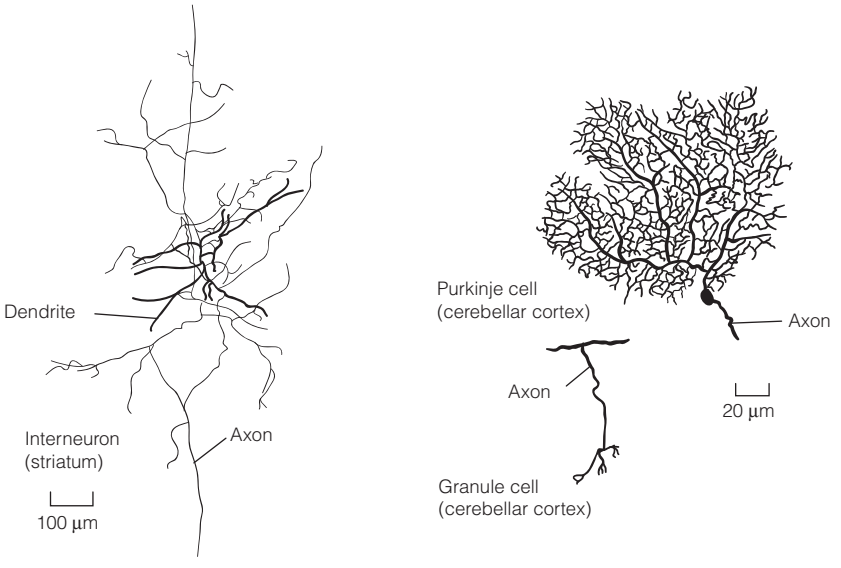

Fig. 1. The morphologies of three common types of neuron. The full length of the axons is not shown. The bifurcating axon of the granule cell extends for several millimeters in each direction. Note how the axon of the interneuron branches extensively.

extend way beyond the region of the nervous system in which their cell body resides. Pyramidal and Purkinje cells fall into this category. In contrast, **interneurons** (**intrinsic or Golgi type II** neurons) have short axons. These local circuit neurons, such as stellate cells, produce direct effects only in their immediate neighborhood.

By examining the connections that a neuron makes it is possible to classify neurons by function. Any given region of the nervous system receives inputs from **afferent** neurons and projects by **efferent** neurons to other regions of the nervous system or an effector organ (such as a muscle or gland). **Afferent neurons** that synapse with sensory receptors or which are themselves capable of responding directly to physiological stimuli are **sensory** neurons. Efferent neurons which synapse with skeletal muscles are termed **motor** neurons. Sometimes the term motor neuron is applied to projection neurons in motor pathways even if they do not directly synapse with a muscle.

Finally, neurons can be classed according to the neurotransmitters which they secrete. Moreover, there is often a clear correlation between neuron morphology and neurotransmitter. In other words, the shape of a neuron allows an intelligent guess to be made about which transmitter it secretes. For example, pyramidal cells release glutamate, whereas stellate and Purkinje cells secrete γ-aminobutyrate. This, in turn, provides very strong circumstantial evidence as to function, because usually glutamate excites, while γ-aminobutyrate inhibits, other neurons.

Neuron numbers

Estimates of the number of neurons in the nervous system can be made by statistical analysis of cell counts in thin-tissue sections viewed under light microscope. This shows that the number of neurons per unit area of the cerebral cortex is remarkably constant from one area of the cortex to another in humans,

and across mammalian species, at around 80 000 mm^{-2}. The exception is the primary visual cortex where the neuron density rises to 200 000 mm^{-2}. Assuming a total surface area for the human cerebral cortex of 2000 mm^2, these figures suggest that there are some 1.6×10^{11} neurons in the cerebral cortex alone. The most populous cells in the mammalian nervous system are small granule cells of the cerebellum; in humans they may number 10^{11}. Hence the human nervous system contains at least 2.5×10^{11} neurons; the total is likely to be between 300 and 500 billion! Smaller mammals have smaller brains because they have fewer neurons, not because their neurons are smaller.

A3 Glial cells and myelination

Key Notes

Classes of glial cells

Glial cells perform a number of functions that support neurons. There are many more glial cells than neurons. Glial cells can be assigned to one of three major populations: astrocytes, oligodendrocytes (including peripheral Schwann cells) and microglia.

Astrocytes

Astrocytes are large, numerous, star-shaped glia which have elongated processes tipped with endfeet. They cover synapses, form contacts with capillary endothelial cells and with the pia mater where they form a limiting glial membrane. The functions of astrocytes include homeostatic regulation of the extracellular K^+ concentration, the synthesis of transmitter glutamate and γ-aminobutyrate, removal of neurotransmitters from the synaptic cleft, storing glycogen, and supplying lactate to neurons.

Oligodendrocytes and Schwann cells

Oligodendrocytes in the central nervous system (CNS) and Schwann cells in the peripheral nervous system are responsible for forming the insulating myelin sheath that surrounds many axons. The sheath is produced by part of the glial cell spiraling around the axon a number of times. The sheath is interrupted at regular intervals by nodes of Ranvier, tiny gaps where the axon membrane is naked.

Microglia

Microglia are small immune cells derived from monocytes. In their macrophage guise they are key players in the inflammatory processes that accompany repair of nervous system injury.

Related topics

Blood–brain barrier (A8)
Neurotransmitter inactivation (C7)
Action potential conduction (B5)
Cell determination (N2)

Classes of glial cells

As well as neurons, the nervous system contains glial cells. These are thought not to be directly involved in information processing but instead perform a variety of supporting functions without which neurons could not operate. Estimates suggest that glial cells outnumber neurons perhaps by as much as ten-fold. It is hardly surprising then that the total cell density in nervous tissue is extremely high and the brain has the lowest extracellular space of any organ in the body. Glial cells are divided into **macroglia** and **microglia**. Several distinct populations of macroglia are recognized: astrocytes, oligodendrocytes and Schwann cells.

Astrocytes

Astrocytes are the largest and most numerous of glial cells. They are irregularly shaped cells and many have long processes, which superficially resemble the

dendrites of neurons. Astrocytes can readily be distinguished from neurons however; they do not have Nissl bodies and can be stained using immunocytochemistry for a specific astrocyte marker, **glial fibrillary acidic protein**. Astrocytes fill most of the space between neurons leaving gaps only about 20 nm across. Astrocyte processes surround synapses and some form **endfeet** which butt onto capillaries or onto the pia mater (the innermost layer of meninges) to produce a layer covering the surface of peripheral nerves and CNS called the **glial membrane.**

Astrocytes have a wide variety of functions:

1. Removing K^+ that accumulates in the extracellular space as a result of neural activity and dumping it, via their endfeet, into capillaries. This maintains appropriate potassium concentrations in the vicinity of neurons.
2. Uptake or synthesis of the precursors for the two major neurotransmitters, glutamate and γ-aminobutyrate.
3. Terminating the actions of small transmitter molecules by removing them from the synaptic cleft by way of specific transporters in their plasma membranes.
4. Providing energy substrates to neurons. Astrocytes take up glucose from blood and either store it as glycogen or convert it to lactate which is exported to neurons. This may be particularly important for highly active neurons that require more energy than can be supplied by glucose crossing the blood–brain barrier.
5. Ammonia detoxification via the ornithine–arginine cycle, and detoxification of free radicals.
6. As radial glial cells they guide neurons to their proper destinations in the developing brain.
7. Regulation of synapse formation in the developing brain and the production of new neurons in the adult brain.
8. Ensuring the integrity of the blood–brain barrier by influencing endothelial cells to form tight junctions.

Oligodendrocytes and Schwann cells

Oligodendrocytes in the CNS and **Schwann cells** in the peripheral nervous system have the common function of providing the **myelin sheath**, an electrically insulating covering around many axons. Those axons with a myelin sheath are said to be **myelinated**, those without are termed **unmyelinated**. The myelin sheath is formed in the peripheral nervous system in the following way. Schwann cells line up along the axon surrounding the axon with a pseudopodium-like structure, the **mesaxon**. For unmyelinated axons the process stops at this point. For myelinated axons the mesaxon spirals around the axon some 8–12 times. During this ensheathing most of the cytoplasm gets left behind (except in the innermost turn) so the majority of layers simply consists of a double thickness of plasma membrane (see *Fig. 1*). Each Schwann cell myelinates between 0.15 and 1.5 mm of axon. The thicker the axon the longer the region myelinated by a single glial cell. Between adjacent ensheathed regions is a tiny (0.5 μm) gap of naked axon called the **node of Ranvier**. Here the axon membrane is directly exposed to the extracellular space. Since a peripheral nerve may be quite long a few hundred Schwann cells might be required to generate the sheath. Myelinated axons vary in total nerve fiber diameter between 3–15 μm but across this range the proportion of the diameter contributed by the myelin sheath is roughly constant.

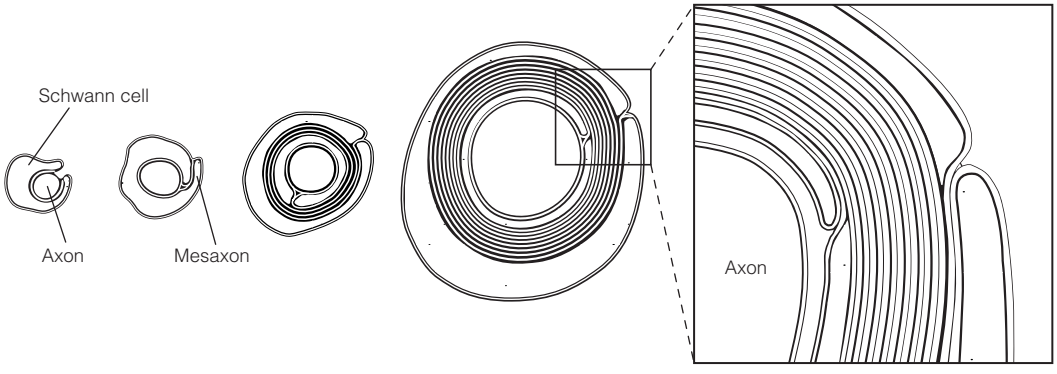

Fig. 1. Myelination of a peripheral axon. The myelin sheath is generated by the growth of the mesaxon which wraps itself around the axon. Redrawn from Gray's Anatomy, *37th edn, 1989, with permission from Harcourt Publishers Ltd.*

Myelination proceeds in a similar way in the CNS except that each oligodendrocyte extends several processes so that it can contribute to the myelination of several adjacent axons. This ensures that fewer glial cells are needed for CNS myelination, which saves space.

Multiple sclerosis is a progressive disorder in which multiple plaques (2–10 mm in size) of demyelination occur in the central nervous system, resulting in defects in the propagation of action potentials. The optic nerves, brainstem and cervical spinal cord are particularly vulnerable. It is thought to be an autoimmune disease in which the immune system mounts an attack on one or more of the proteins of which myelin is made. Immigrants from low- to high-prevalence zones (e.g. tropics to northern Europe) come to have the same risk of developing the disease as the high-prevalence zone natives if they arrive before the age of 10 years. The remissions seen in the disease presumably reflect attempts at repair and re-myelination.

Microglia

The smallest of the glial cells are the **microglia.** These are cells of the immune system. Derived from bone marrow monocytes, they migrate into the nervous system during development where they secrete growth factors, guide axons, and stimulate the differentiation of glial cells and the formation of blood vessels. Acting as macrophages they phagocytose debris generated by the programmed cell death that is normal during development. In the adult nervous system they cease being motile and may have some homeostatic function. Microglia are important in repair of nervous system damage. They proliferate and revert to their macrophage lifestyle, releasing cytokines, in a wide variety of conditions that produce inflammation of the nervous system such as infections, trauma and tumors. Cytokine release by activated microglia also contributes to pathological pain that can occur in a number of diseases, such as cancer. Scar tissue formation in the CNS as a result of the activities of microglia is called **gliosis**.

A5 Organization of the central nervous system

Key Notes

Spinal cord

The human spinal cord contains about one hundred million neurons. Peripheral white matter and central gray matter can be seen by the naked eye. The gray matter of the spinal cord contains neuron cell bodies. Sensory neuron fibers enter the dorsal horn of the gray matter in an ordered fashion, larger diameter fibers entering more medially and extending deeper than smaller ones. Motor neuron cell bodies lie in the ventral horn of the gray matter. The spinal gray is divided on morphological grounds into ten columns which, on transverse section, are called Rexed laminae. Each lamina has a distinctive set of inputs and outputs. The white matter contains tracts of axons ascending or descending the cord. Neural tracts or pathways are named for their origin and destination.

The brain

The brain has three structural components. White matter consists of fiber tracts or pathways. Embedded in this are nuclei which are clusters of neuron cell bodies. Two large brain structures, the cerebrum and cerebellum are covered by cortex, a thin rind of gray matter densely packed with neurons. Anatomically the brain has three principal divisions: hindbrain, midbrain and forebrain. The center of the brain is taken up with the cerebrospinal fluid (CSF)-filled ventricular system. The hindbrain consists of medulla, pons and cerebellum, while the midbrain is divided into a ventral tegmentum and a dorsal tectum. Together hindbrain and midbrain are the brainstem from which emerge most of the cranial nerves. With the exception of the cerebellum, which organizes high-level motor functions, the brainstem is mostly concerned with vital functions and functions requiring orchestrated activity of large parts of the brain (e.g. wakefulness). The forebrain consists of diencephalon and cerebrum. The diencephalon contains a dorsal thalamus, serving sensory functions among others, and a ventral hypothalamus, implicated in temperature and endocrine regulation, and appetitive behaviors. The cerebrum has two cerebral hemispheres heavily interconnected across the midline. Its surface is covered by cortex, which has been subdivided on the basis of structural differences into Brodmann areas. The cerebral cortex has motor, perceptual and cognitive functions. The core of the cerebrum is occupied by nuclei, which form two neural systems. The basal ganglia form the extrapyramidal motor system and the limbic system (which includes cortical areas) is concerned with emotion and learning.

Related topics

Early patterning of the nervous system (N1)

Spinal cord

The human spinal cord has about 10^8 neurons. It has 31 segments, each of which gives rise to a pair of spinal nerves. It ends at the level of the first lumbar vertebra. The lumbosacral nerve roots pass down the vertebral canal as the **cauda equina** so that they emerge from the vertebral column at their appropriate levels.

A transverse section through the spinal cord shows a butterfly-shaped central **gray matter** which contains neuron cell bodies, **neuropil** (dendrites and short lengths of axon) and glia. The **white matter** surrounding the gray is largely axons in ascending and descending tracts and gets its color from the high content of myelin. In the middle is the **central canal**, which contains **cerebrospinal fluid** (**CSF**), though in adult humans it is often closed.

Sensory fibers enter the spinal cord via the dorsal roots to synapse largely with cells in the **dorsal horns** of the spinal gray matter. Larger-diameter fibers enter more medially and extend more deeply into the dorsal horn than smaller ones. Motor neuron cell bodies lie in the **ventral horns** of the spinal gray and their axons exit via the ventral roots. The distribution of afferents to dorsal roots and efferents from ventral roots is referred to as the **Bell–Magendie law**. Some **visceral** afferents however enter the spinal cord via the ventral roots.

Ten distinct regions can be distinguished in the spinal gray matter on the basis of cell size. Each region occupies a long column that extends through the cord. On transverse section these columns appear as **Rexed laminae** (*Fig. 1*).

Each lamina has distinctive input–output relations, which reflect a measure of functional specialization. Small-diameter afferents carrying pain and temperature information terminate on **dorsal horn cells** (**DHCs**) in lamina II. Cutaneous mechanoreceptor afferents terminate in deeper layers of the dorsal horn. Lamina VI is present only in spinal segments associated with limbs and receives sensory input from joints and muscles that provides information about the position and movement of the limb in space. Lamina VII includes the cell bodies of the preganglionic autonomic axons. Lamina IX houses both α and γ motor neurons which go to skeletal muscles.

The white matter is organized into columns or **tracts** each specified by its origin and destination. For example, the tract which runs down the cord from the cerebral cortex is termed the corticospinal tract whereas the ascending pathway which terminates in the thalamus is the spinothalamic tract. *Fig. 2* shows the locations of the major tracts.

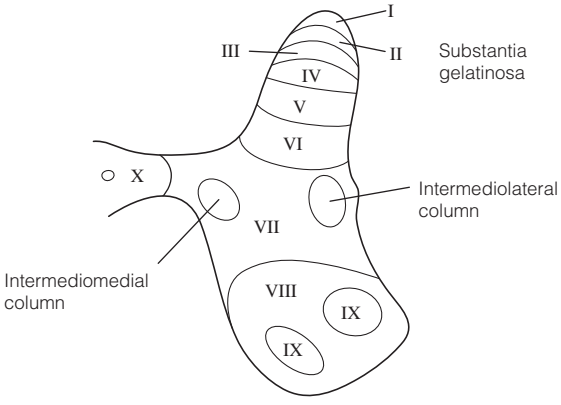

Fig. 1. Rexed laminae. Lamina VI is only present in spinal segments supplying the limbs.

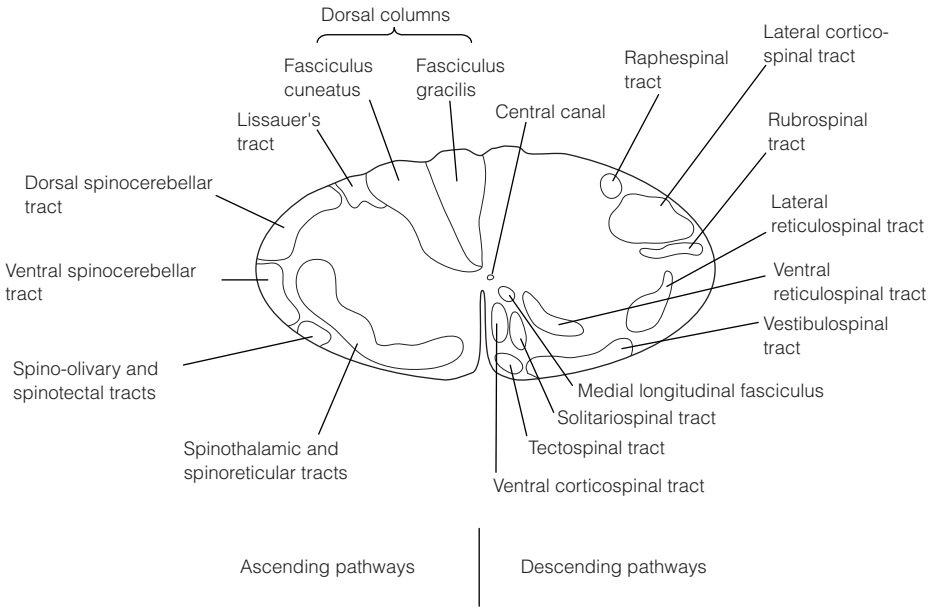

Fig. 2. Pathways in the spinal cord white matter.

The brain

There are three main structural components to the brain:

- **Tracts** or pathways enter the neuraxis at various levels, ascend or descend, and these, together with internal tracts which go from one part of the brain to another, constitute the white matter.
- **Nuclei** embedded in the white matter are clusters of neuron cell bodies and associated neuropil. Some neural structures are composed of groups of nuclei. The thalamus, for example, consists of some 30 nuclei. Interconnected nuclei in turn constitute neural systems.
- Two brain structures, the cerebrum and the cerebellum, are covered by **cortex**, a thin rind with a very high density of neuron cell bodies. In wiring terms cortex appears to be a simple circuit between just a few neuron types, repeated millions of times.

Together, the nuclei and cortex are the gray matter of the brain. **Neural systems** are comprised of interconnected nuclei and cortical regions, which have a common function. The visual system, for example, consists of the retinas, the lateral geniculate nuclei of the thalamus, the visual cortex and the pathways between them.

In the human embryo at the end of the 4th week the CNS is a hollow tube, the **neural tube**, the **caudal** (back) end of which becomes the spinal cord (*Fig. 3*). At its **rostral** (front) end are three swellings, **primary vesicles**, which are the most fundamental anatomical divisions of the brain. These are the **hindbrain**, **midbrain** and **forebrain**. As development unfolds the forebrain differentiates into a caudal **diencephalon** and a rostral **telencephalon** which in turn acquires two lateral swellings, the **cerebral hemispheres**. Down the center of the neural tube is the CSF-filled ventricular system.

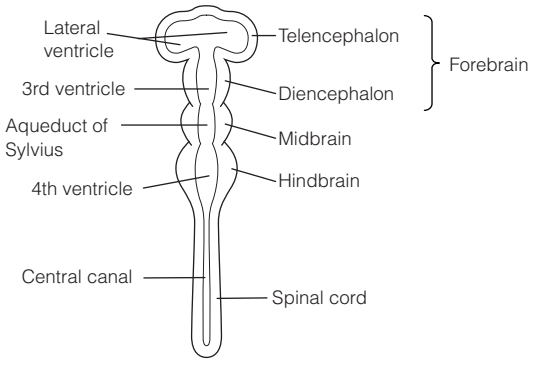

Fig. 3. The human embryo neural tube, at 28 days gestation.

Much of the neural tube is divided into a dorsal **alar plate** along the midline of which runs the **roofplate**, and a ventral **baseplate**, which has along its midline the **floorplate**. In the spinal cord and hindbrain these dorsal and ventral plates organize sensory and motor functions respectively. Such a clear distinction is not so obvious in the midbrain or forebrain.

The hindbrain subsequently develops into a caudal **medulla** and a rostral **pons** and (from about 12 weeks) a dorsal outgrowth, the **cerebellum**. The midbrain, which in the adult is the smallest part, acquires a ventral **tegmentum**, in which are found cell bodies of dopamine-using neurons that are part of a **motivation** system, and a dorsal **tectum**, which organizes visual and auditory reflexes. The hindbrain (minus the cerebellum) and midbrain together are often referred to as the **brainstem**. Much of the brainstem is occupied with vital (life-support) functions; for example, autonomic regulation of the cardiovascular system, and generation of the rhythmic neural output required for breathing. In addition, the brainstem contains the nuclei of most cranial nerves. A core of highly interconnected nuclei extending through the brainstem constitutes the **reticular system**. Many of its neurons (e.g. the midbrain dopamine cells mentioned above) use amine transmitters. The reticular system is involved in orchestrating global brain functions such as motivation, arousal, sleep and wakefulness and connects widely with the forebrain.

The diencephalon in the adult is differentiated into a dorsal thalamus and a ventral hypothalamus. The **thalamus** is a collection of over 30 distinct nuclei organized into five groups. All sensory input enters the cerebral cortex by way of the thalamus (ventral or posterior groups) with the exception of smell. Although clearly involved in sensory processes other nuclear groups are massively interconnected with cortical regions concerned with emotion (anterior group) and memory (medial group).

The **hypothalamus** is concerned with thermoregulation, triggering sleep, regulating endocrine systems, and goal-directed behaviors (eating, drinking and sexual behavior).

The smallest part of the diencephalon, the **pineal gland**, gets visual input and regulates circadian rhythms on the basis of the hours of light and dark.

The dominant part of the telencephalon is the **cerebrum**, two cerebral hemispheres linked across the midline by about 10^6 axons that constitute the **corpus callosum.** The cerebrum is massively developed in humans. Each hemisphere is

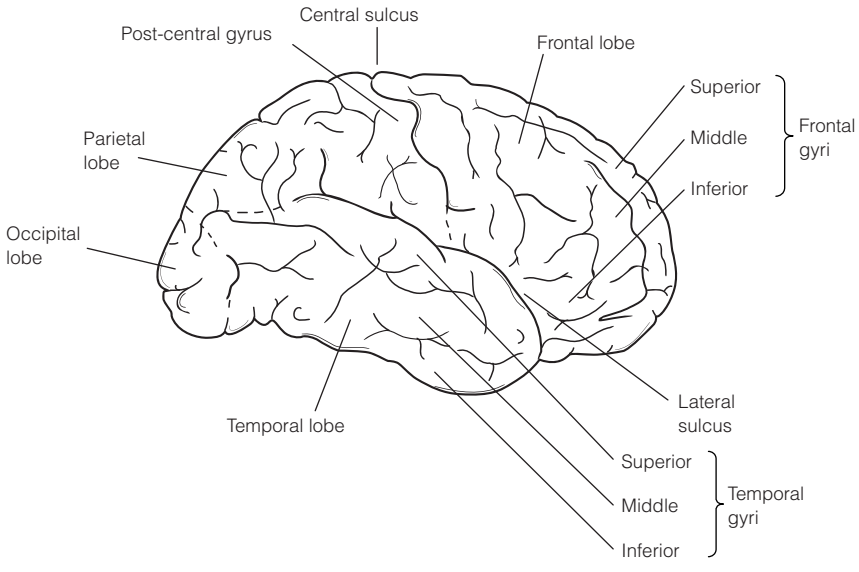

Fig. 4. Lateral surface of the human right cerebral hemisphere.

divided into four lobes named after the bones which overlie them (*Fig. 4*). The surface is covered by cortex and is highly convoluted giving it a high surface area in relation to its volume. The folds are called **gyri** (sing., **gyrus**), and the creases between them **sulci** (sing., **sulcus**). Most of the cerebral cortex is **neocortex** (new cortex), which has six layers. Cortical regions are mapped into **Brodmann** areas on the basis of differences in **cytoarchitecture**, that is, their cellular composition and relative thickness of the layers. The significance of this is that the Brodmann map corresponds quite well to how functions are localized in the cortex, though nowadays its main use is as a numerical guide.

The layers of the cerebral cortex are numbered from I, nearest to the pial surface through to VI which is the deepest (*Fig. 5*). The layers contain different proportions of two types of neurons, pyramidal cells which are output cells, and stellate cells that are interneurons. Layer I consists mostly of axons that run parallel to the cortical surface. Layers II and III have small pyramidal cells that project to other cortical areas. Layer IV is rich in interneurons and the site for the termination of most inputs to the cortex from the thalamus. Layer V has the largest pyramidal cells, which project to subcortical nuclei, brainstem and spinal cord. Layer VI pyramidal cells send their axons back to the same thalamic nucleus that supplied the inputs. The relative size of the layers differs with the function of the cortical region. For example, the sensory cortex has a thick layer IV because of its large number of thalamic inputs, whereas in motor cortex it is layer V which is particularly extensive because these neurons project to the brainstem and spinal cord to mediate motor activity.

The cerebral cortex is implicated in most brain activities, but is most often associated with the planning and execution of intentional movement, sensory perception and cognitive (problem-solving) functions. Those regions, which are not specifically devoted to sensory or motor activities, are called **association cortex**.

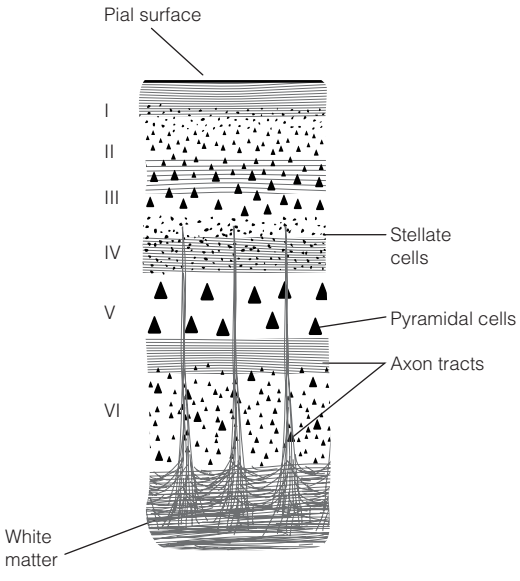

Fig. 5. Representative section through the neocortex (parietal lobe).

Within the core of each hemisphere lie clusters of nuclei that form major components of two neural systems, the basal ganglia and the limbic system (*Fig. 6*). The **basal ganglia**, responsible for organizing stereotyped patterns of movement, consists of the striatum, which lies in the forebrain, and two midbrain nuclei, the **subthalamus** and the **substantia nigra**. The **striatum** is subdivided into the **neostriatum**, itself composed of two nuclei, the **caudate** and **putamen**, and **paleostriatum** or **globus pallidus**. Anatomically the putamen and globus pallidus together form the **lentiform nucleus**.

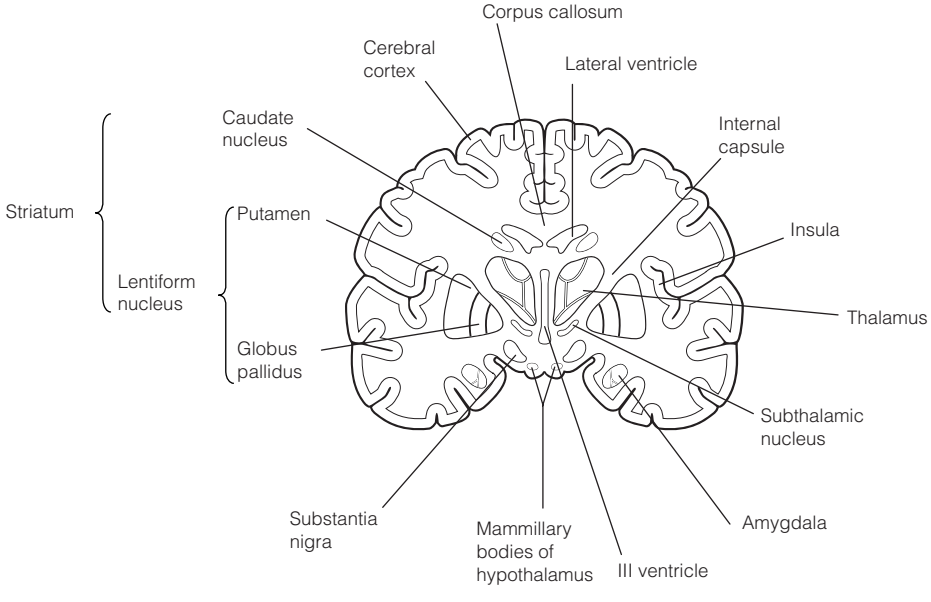

Fig. 6. Coronal section through the human cerebrum at the level of the posterior hypothalamus.

The **limbic system** is made from several heavily interconnected nuclei and several regions of cerebral cortex, which form a ring around the diencephalon (*Fig. 7*). The cortical regions are the **cingulate gyrus**, which lies above the corpus callosum and has contributions from medial, parietal and frontal lobes, and the **parahippocampal gyrus** and **uncus** which are part of the medial surface of the temporal lobe.

The medial and underside of the temporal lobe is occupied by the **hippocampal formation**, most of which is the **hippocampus** and **subiculum**. The hippocampus is **archaecortex** (ancient cortex) and has only three layers. Limbic system nuclei include the **amygdala**, **septal nucleus**, and the **mammillary bodies** (which are part of the hypothalamus). The hippocampus and amygdala are concerned with certain types of learning, and the limbic system in general is implicated in emotion.

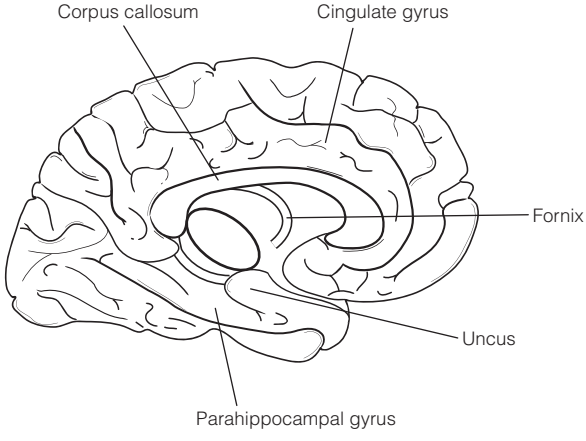

Fig. 7. Medial surface of the human left cerebral hemisphere.