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ANATOMY OF CENTRAL NERVOUS SYSTEM

Учебно-методическое пособие

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GENERAL ORGANIZATION OF THE NERVOUS SYSTEM: DIVISIONS AND FUNCTIONS

The **nervous system (NS)** is a complex of specialized structures of nervous tissue. It provides control and communication of all systems of the body, coordinates their activities and adjusts them to changing conditions of environment.

Functions of different parts of the NS can be described as follows:

– detecting changes occurring inside and outside the body (sensory input);

– conduction, processing, and interpretation of the sensory inputs in the nervous centers (integration);

– response to stimuli by activating effector organs (motor output).

Topographically, the NS is divided into the **central nervous system (CNS)** and the **peripheral nervous system (PNS)**. The CNS consists of the brain and the spinal cord. It contains the majority of nerve cell bodies and synaptic connections. The PNS is represented by 13 pairs of the cranial nerves and 31 pairs of the spinal nerves, with their ganglia, roots and ramifications within the body, and ganglia and plexuses of the autonomic nervous system (ANS).

The **CNS** provides:

– Regulation and coordination of the activity of all organs and systems;

– Functional integrity (unity) of the body;

– Higher mental activity — thinking, learning, memory, perception, etc. (involves self-generated stimulation).

The **PNS** constitutes the link between the CNS and structures in the periphery of the body, transmits sensory information and motor impulses.

Functionally, the NS can be divided into **somatic** and **visceral** parts, as well as **sensory (afferent)** and **motor (efferent)** divisions (Fig. 1).

The **somatic** (animal) nervous system provides conscious awareness of the external environment and controls the movements of the body, acting largely voluntary. It innervates skin, skeletal muscles and sense organs — the eye and ear.

The **visceral (vegetative)** part, also called the **autonomic nervous system (ANS)**, monitors conditions in the internal environment, controls functions of the heart, vessels, internal organs, and glands, regulates metabolic processes and homeostasis, acting largely involuntary.

The **sensory (afferent) division** of the nervous system transmits sensory information from receptors to the CNS and includes 2 parts:

1. The **somatic part**, which transmits impulses towards the CNS from **exteroceptors** — somatic receptors located in skin; **proprioceptors** — in skeletal muscles, tendons and joints; **special somatic receptors** — in the eye and ear.

2. The **visceral part**, which transmits information from **interoceptors** — visceral receptors in the internal organs and vessels, and from **special visceral receptors** — olfactory and gustatory.

The **motor (efferent) division** transmits impulses from the CNS to effectors. It also includes 2 parts:

1. The **somatic part** sends commands to the skeletal, striated muscles.

2. The **visceral part**, or **ANS**[1], regulates contraction of the myocardium, smooth muscles of the internal organs and vessels, glands secretion. The ANS, in turn, consists of the **sympathetic** and **parasympathetic divisions**.

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[1] In modern literature, the term ANS is applied specifically to the efferent part of the visceral nervous system.

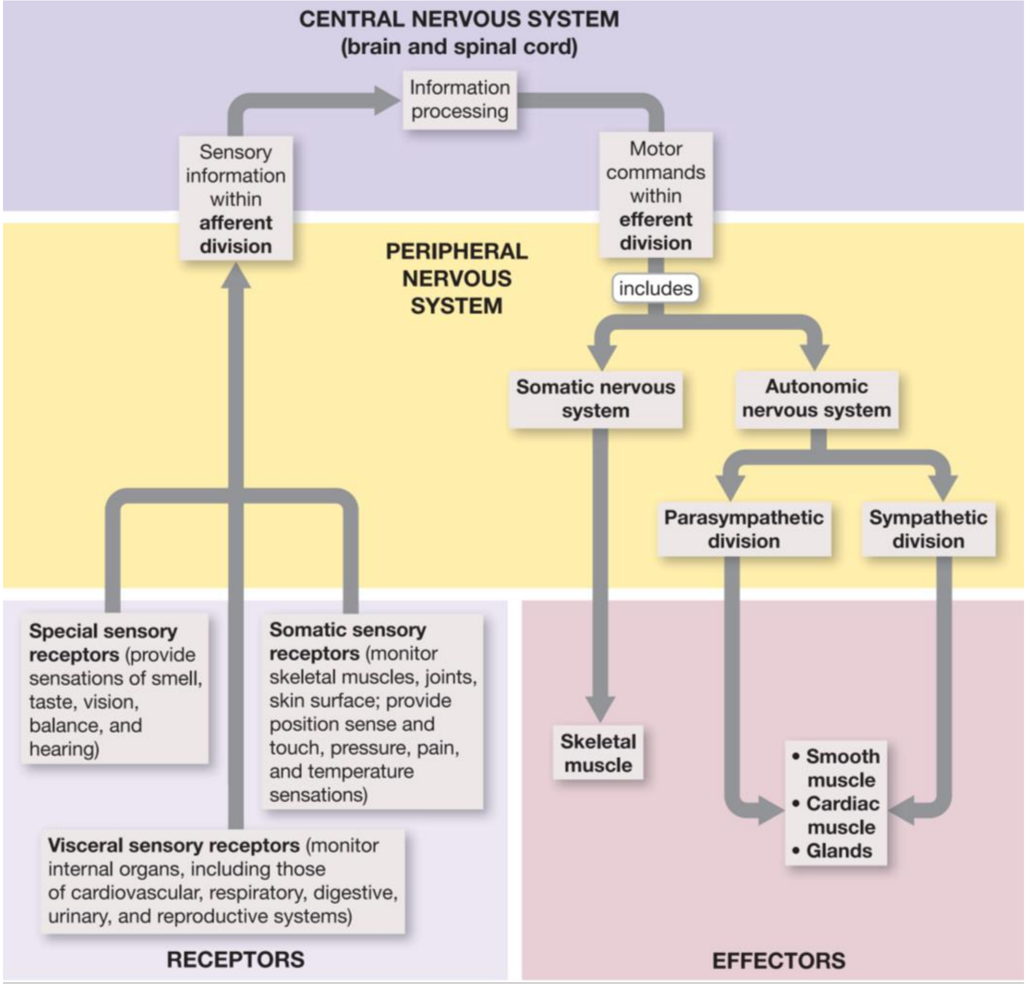

Fig. 1. Functional divisions and components of the central and peripheral nervous systems.

STRUCTURAL COMPONENTS OF THE NERVOUS SYSTEM

The nervous system is made up of nerve tissue, which comprises **nerve cells**, or **neurons**, and **neuroglia**. **Neurons**, are basic structural and functional units of the nervous system able to generate and transmit nerve impulses. Each **neuron** has a body and processes, commonly several dendrites and one axon (Fig. 2). The **body** receives information, generates the electrical impulse, or signal, and serves as a biosynthetic center of the cell. The **dendrites** collect and conduct stimuli to the neuron body; they have multiple branching processes that increase surface area for collecting stimuli from receptors. The **axon** transmits a signal away from the cell body and ends by **axon terminals** (terminal buttons) on another neuron or an effector organ (muscle or gland). Any long axon is called a **nerve fiber**. Typically, an axon forms side branches called **axon collaterals**, so that one neuron can send a signal to several neurons to modulate their activity.

Information is passed between neurons at **synapses**. In humans, most synapses transmit nerve impulses by means of chemicals[2] called *neurotransmitters*, which are released from the presynaptic neuron into the synaptic cleft, and then are bound by special receptors on the membrane of the postsynaptic neuron. This results in generating of a signal which modulates, excites or inhibits, the postsynaptic neuron activity.

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[2] Other than chemical synapses are electrical synapses. They are found in the retina and some parts of the CNS (e.g., the reticular nucleus of the thalamus, hippocampus, neocortex).

Neurons show a big variation in their structure such as size, shape, number of processes and vary in functions. By number of processes neurons can be multipolar, bipolar and unipolar (Fig. 2). Most neurons are *multipolar*, usually with numerous dendrites and a single axon. *Bipolar* neurons have two processes, an axon and a dendrite. *Pseudounipolar* neurons have one axon, which divides into the peripheral and central processes. The peripheral process conducts a signal from the receptor to the cell body, the central — transmits a signal to the CNS. True unipolar neurons are growing neurons, found during the prenatal period and only in limited regions of the CNS after birth.

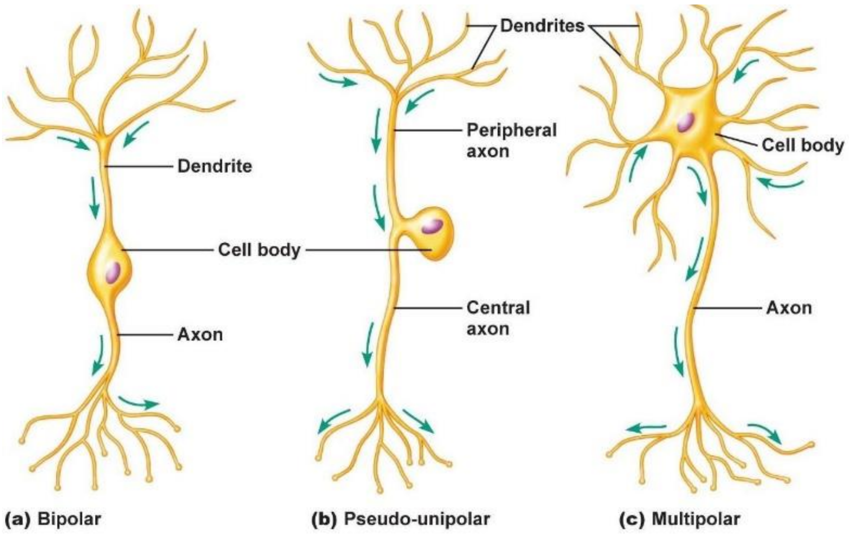

Fig. 2. Basic neuron types

Functionally neurons are classified as sensory neurons, motor neurons, and interneurons (Fig. 3).

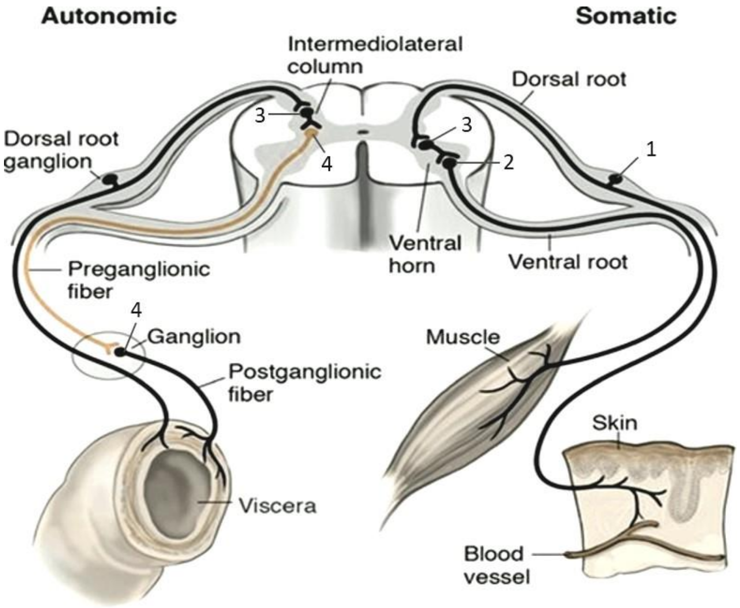

Fig. 3. Reflex arcs and location of functionally different type neurons:
1 — sensory neuron; *2* — motor neuron; *3* — interneuron; *4* — autonomic neurons

Sensory (afferent) neurons transmit impulses from sensory receptors to the CNS. Depending on the location of the receptors, *somatic sensory* and *visceral sensory neurons* are distinguished. The cell bodies of the sensory neurons form **sensory ganglia** in the PNS.

Majority of these neurons are pseudounipolar. Bipolar neurons (olfactory, gustatory, optic, acoustic, vestibular neurons) concern with the special senses.

Motor (efferent) neurons, multipolar, transmit impulses away from the CNS to effector organs. The *somatic motor neurons* have their cell bodies in the CNS and terminate in the skeletal muscles. In the ANS, the cell body of the *1st visceral motor neuron* is located in the CNS, while the cell body of the *2nd visceral motor neuron* lies in the PNS **autonomic ganglion** and its axon terminates on a smooth muscle or glandular cell.

Interneurons, or **association neurons**, lie between the sensory and the motor neurons. They are multipolar, rare bipolar, neurons. The majority (up to 99.8 %) of interneurons form **sensory** and **relay nuclei** of the CNS.

In the PNS, cell bodies of neurons form **sensory ganglia** of cranial and spinal nerves and **autonomic (efferent) ganglia**. The neurons' processes form *nerve fibers, nerve roots, nerves and their branches, plexuses, nerve endings.*

In the CNS, the cell bodies of neurons, together with unmyelinated processes (dendrites and nearby unmyelinated parts of axons) and neuroglia, make up the **gray matter**. Clusters of nerve cell bodies form **nuclei** in the brain and spinal cord. Aggregations of neurons organized by layers form the **cortex** of the cerebrum and cerebellum, **laminae** of the gray matter in the spinal cord. Nuclei and certain regions of the cerebral cortex serve as *integration nerve centers*, which process and integrate information: *sensory centers* receive signals, *motor centers* send signals out, *relay centers* transmit signals between regions of the CNS. Neurons' processes, or fibers, form the **white matter**. The bundles of fibers compose tracts, fasciculi, lemnisci, commissures.

The essential component of the nerve tissue are **neuroglial cells**. These cells are more numerous than neurons and are necessary for their normal functioning. They provide structural and metabolic support to neurons, nourish, protect, separate, repair neurons, secrete CSF, etc. In the CNS, the neuroglial cells are represented by astrocytes, oligodendrocytes, microglia, and ependymal cells; in the PNS, by Schwann and satellite cells (Fig. 4, 5).

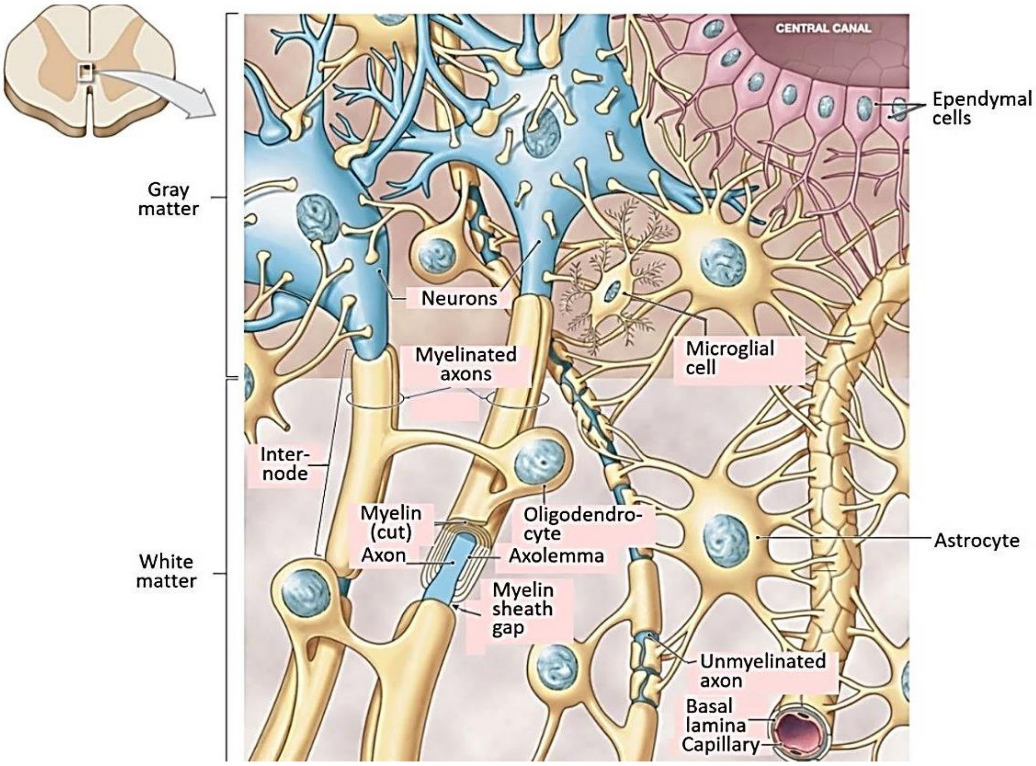

Fig. 4. Neuroglial cells of the CNS (spinal cord)

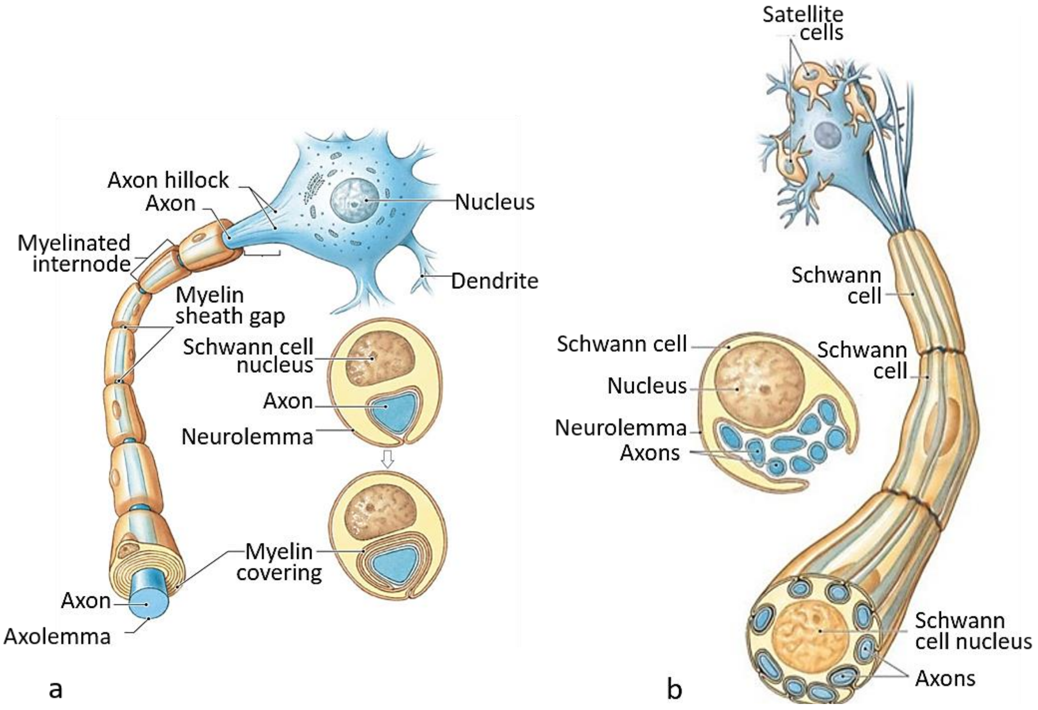

Fig. 5. Neuroglial cells of the PNS:
a — myelinated; *b* — unmyelinated fibers

ADVANCED: **Astrocytes** (“astra” in Latin means “star”) are the most abundant brain cells that got their name because of the numerous processes. They carry out many important functions: provide structural and metabolic support for neurons; take part in formation and function of synapses and regulate the transmission of electrical impulses within the brain; interact with blood vessels and regulate the local blood flow, form the blood-brain barrier, etc.

Oligodendrocytes are spherical shape cells with a few long processes that form a myelin sheath that supports and insulates neuron axons. Myelinated axons form white matter of the CNS (myelin is a lipoprotein, that gives the white color to myelinated fibers).

Microglia are small macrophages-like cells arising from monocytes. They protect CNS from bacteria and viruses, remove apoptotic cell and cell debris, involved in synaptic organization, brain protection and repair.

Ependymal cells form ciliated simple columnar epithelium that lines cavities of the brain and spinal cord filled with cerebrospinal fluid (CSF). They create the blood-CSF barrier and participate in CSF production. The major sites of CSF production are choroid plexuses of the cerebral ventricles.

Schwann cells, similar to oligodendrocytes in the CNS, surround axons of neurons to insulate them and prevent interference from nearby neurons. In unmyelinated fibers, bundles of axons are enveloped by the cytoplasm of a single Schwann cell. In myelinated fibers plasma membrane of the Schwann cell wraps multiple times around one axon to form a myelin sheath. The gaps between adjacent Schwann cells, nodes of Ranvier, allow electrical impulses to jump from one node to another for fast conduction of a nerve impulse. Myelinated fibers are axons of sensory and somatic motor neurons, preganglionic autonomic neurons (lightly myelinated). Unmyelinated fibers are axons of postganglionic autonomic neurons.

Satellite cells surround neurons cell bodies within ganglia of the PNS. They protect neurons and control their microenvironment by regulating transport of substances through the neuron cell membrane. By function they are compared with the astrocytes in the CNS.

To transmit nerve impulses through the nervous system, neurons are connected in chains. The chain of neurons involved in a **reflex**[3] is called the **reflex arc** (Fig. 6). Depending on the number of neurons involved, reflex arcs can be of two types:

– The simplest, *monosynaptic reflex arc* consists of only *2 neurons (1 synapse)*: 1) an **afferent (sensory) neuron** that receives a signal from a **receptor**, detecting a change

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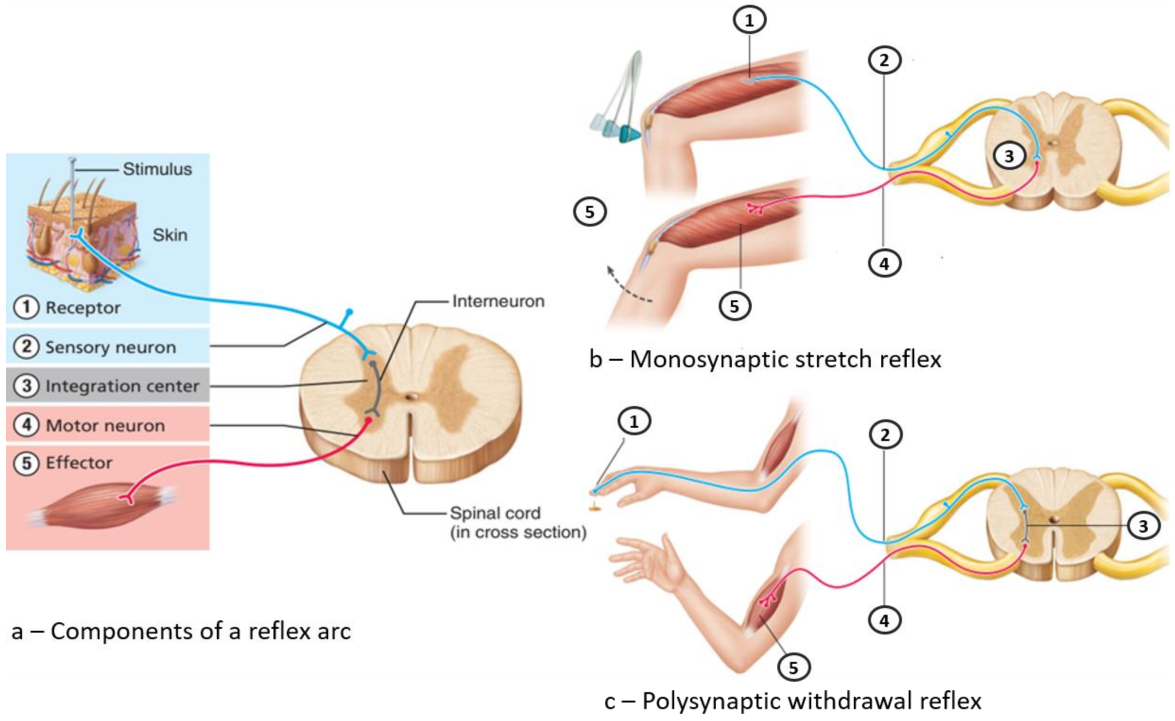
[3] A reflex is an immediate stereotyped response of the body to a specific sensory stimulus.

in the external or internal environment, and 2) an **efferent (motor) neuron** that sends a command to the **effector** — the muscle or gland reacting by contraction or secretion. Synapses between sensory and motor neurons occurs in the CNS at the **integration nerve center**. Monosynaptic reflex arcs are involved in tendon (stretch) reflexes, such as the patellar reflex.

– More common *polysynaptic reflex arcs* include one or more interneurons interposed between the sensory and motor neurons; hence, they involve 2 or more synapses.



a – Components of a reflex arc

b – Monosynaptic stretch reflex

c – Polysynaptic withdrawal reflex

Fig. 6. Components and types of reflex arcs

Reflex arcs with integration centers in the spinal cord serve **spinal reflexes**, for example, contraction of a muscle in respond to its stretching or withdrawal of the hand when touching a hot object (Fig. 6). Reflex arcs with integration centers in the brain stem serve **brain stem reflexes**, such as blinking when the cornea is touched.

Somatic reflex arcs conduct impulses resulting in contraction of skeletal muscles, while **visceral (autonomic) reflex arcs** provide contraction of smooth muscles, myocardium, or secretion of glands. The efferent part of the autonomic reflex arcs consists of 2 motor neurons — the first is located in the CNS, the second — in the PNS autonomic ganglion (Fig. 3).

DEVELOPMENT OF THE NERVOUS SYSTEM

The development of the nervous system of the human embryo starts at the beginning of the 3rd week (≈ day 17) during the stage of gastrulation. By this time, 3 primary germ layers are distinguished in the embryonic disc — the ectoderm, mesoderm, and endoderm. The notochord develops along the midline of the body (it remains as the nucleus pulposus of the intervertebral discs). It induces the transformation of the overlying ectoderm into *neuroectoderm*, giving rise to the neural tube, then the spinal cord and brain, and the neural crest — a source of the PNS neurons and some other cells of the body.

Four main stages can be distinguished in the development of the nervous system — the successive formation of the neural plate, neural groove, and neural tube, and the cell differentiation (Fig. 7):

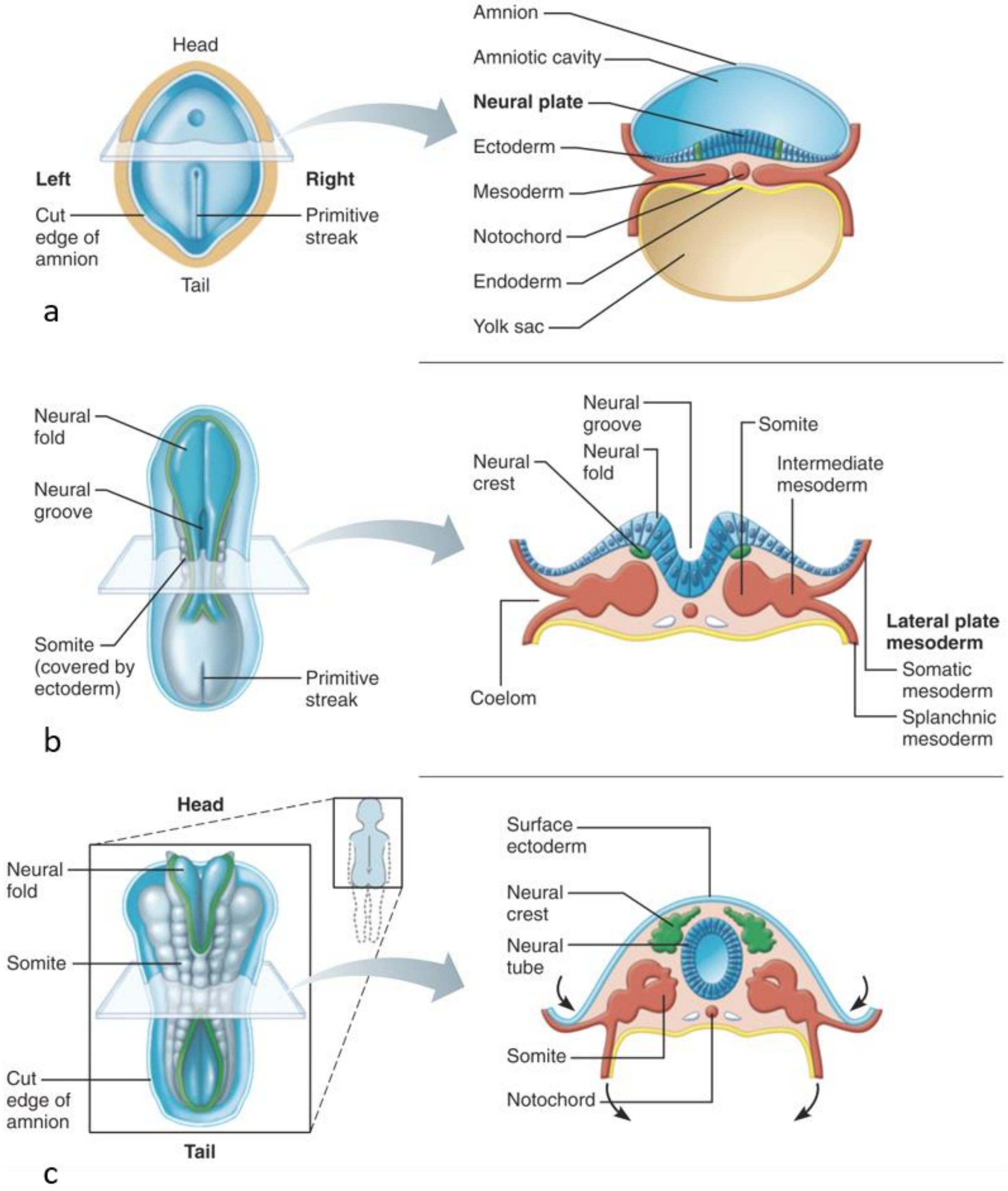


Fig. 7. Early stages of the nervous system development: embryos of 17 (*a*), 20 (*b*), and 22 (*c*) days

1. The midline neuroectoderm forms a longitudinal thickening, called the **neural plate**.

2. The lateral edges of the neural plate elevate and form the **neural folds**; the **neural groove** develops between them. At the ridges of the neural folds, the **neural crests** are formed by cells that do not participate in the neural tube formation.

3. The neural groove deepens; the neural folds and crests of both sides merge together above the groove, making it the **neural tube**. The neural tube separates from the surface ectoderm, and the neural crest delaminates from the neural tube.

The neural tube closure begins at the end of the 3rd week in the region that will become the neck. Then it proceeds both cranially and caudally. By the end of the 4th week, the cranial and caudal neuropores close as well, and cells of the neural tube begin a period of rapid division. The wider cranial part of the neural tube forms the cerebral vesicle, while the rest of it becomes the spinal cord.

4. The cell differentiation results in formation of cavities, gray and white matter of the CNS, ganglia and fibers of the PNS (Fig. 8).

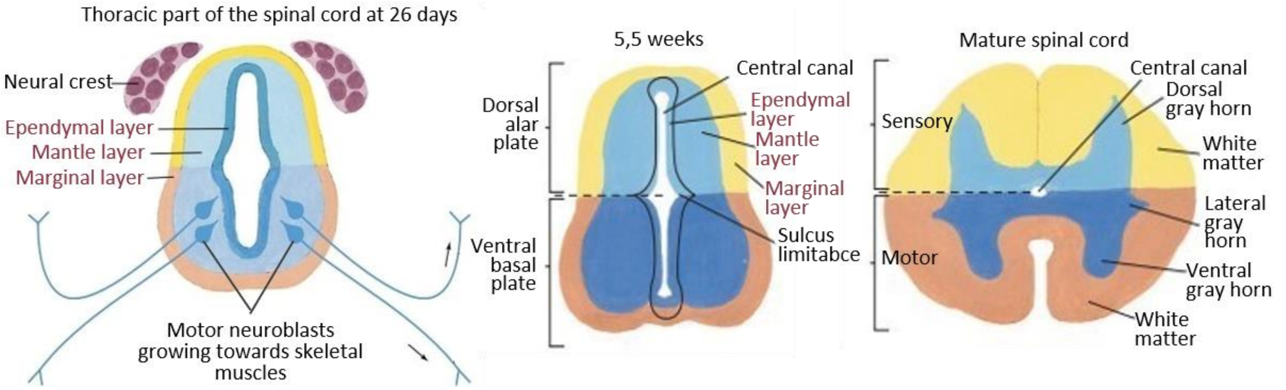


Fig. 8. Cell differentiation in the developing spinal cord

Cells facing the cavity of the neural tube become ependymal cells. They form the inner **ependymal layer**, which forms a lining for the walls of the spinal cord central canal and cerebral ventricles. Other cells of the neural tube move externally and become neuroblasts and glial cells (astrocytes and oligodendrocytes). They form the **mantle layer** — *future gray matter* of the CNS. Axons of developing here neurons form externally the **marginal layer** — *future white matter* of the CNS. Some axons extend outside the neural tube and together with cells of the neural crest form the PNS.

Transformations in the developing spinal cord

On both sides of the developing spinal cord, the mantle layer is divided by the sulcus limitans into 2 clusters of neuroblasts: the dorsal — alar plate, and the ventral — basal plate (Fig. 8). The alar plate becomes the posterior horn. Developing here interneurons send axons to the marginal layer and form the white matter of the spinal cord. The basal plate becomes the anterior and lateral horns, containing motor and autonomic neurons, axons of which emerge in the anterior roots. The neural crest cells on either side of the spinal cord form segmentally arranged groups of sensory neurons, the spinal ganglia, Other cells migrate to become autonomic neurons of the PNS[4].

Until the 3rd antenatal month, the spinal cord grows at the same rate as the spine and it occupies the entire vertebral canal. Then the growth of the spinal cord slows down and on the 6th month the spinal cord ends at the sacrum. At birth, the spinal cord is about 14 cm long and ends at the level of the L3 vertebra. During childhood, the spinal cord attains its adult position, terminating at the level of the intervertebral disc between the L1and L2 vertebrae.

Transformations in the developing brain

After the closure of the neural tube (by the 4th week), an expansion develops at its rostral end — the cerebral vesicle, which then transforms into 3, then into 5 cerebral vesicles, giving rise to the respective parts of the brain (Fig. 9). The three brain vesicles are: 1) **prosencephalon**, or **forebrain**; 2) **mesencephalon**, or **midbrain**; 3) **rhombencephalon**, or **hindbrain**. During the 4th week, the 1st and the 3rd vesicles divide each into two. The prosencephalon forms the **telencephalon** and **diencephalon**. The rhombencephalon forms the **metencephalon**, giving rise to the pons and cerebellum, and the **myelencephalon**, which becomes the medulla oblongata.

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[4] In addition to sensory and autonomic neurons, neural crest cells are the source of the cells of the pia mater and arachnoid, adrenal medulla cells, Schwann and satellite cells, melanocytes, head mesenchyme involved in the formation of the pharyngeal arches, bones of the skull, and the cardiac septa.

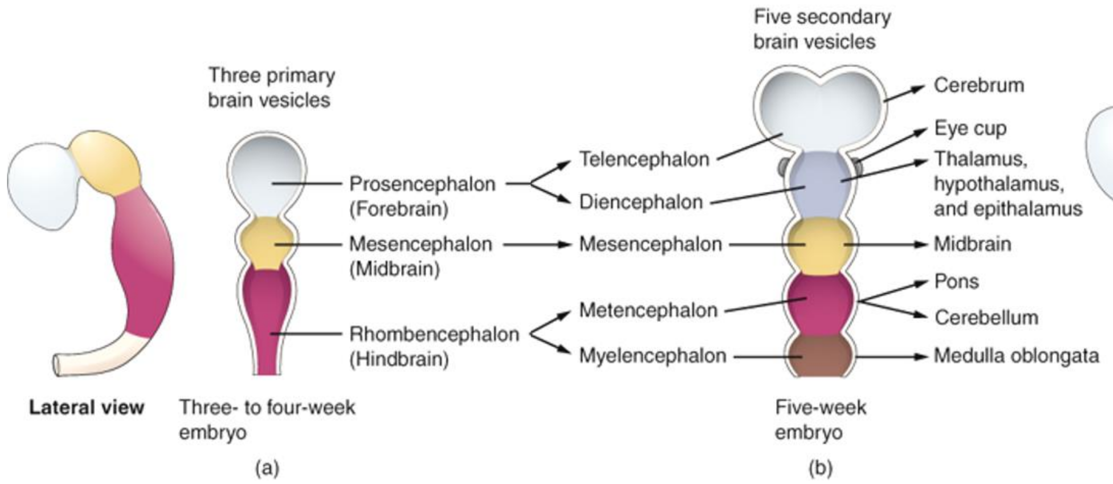

Fig. 9. Transformations of the brain vesicles in embryos of 3 to 5 weeks

The telencephalon forms a pair of swellings, the **hemispheres**, which expand over the diencephalon. The rapid growth of the cortex of the hemispheres results in the formation of gyri and sulci. The formation of sulci starts during the 6th month, continues until birth, and some new sulci develop even after birth.

During formation of brain vesicles, a series of flexures successively develop: the *cervical flexure*, at the junction of the hindbrain and spinal cord; the *mesencephalic flexure*, in the midbrain region; the *pontine flexure*, dividing the metencephalon and myelencephalon; and the last formed, the *telencephalic flexure* at the border between the telencephalon and diencephalon. These flexures lead to the orientation of the various parts of the brain as in the adult.

Outgrows of the ventral surface of the telencephalon gives rise to the **olfactory bulbs** and **tracts**, connected with the olfactory nerves (CN I).

Bulges on the lateral walls of the embryonic diencephalon, the optic vesicles, give rise to the retina of the eyes and the optic nerves (CN II).

Congenital malformations due to improper closure of the neural tube

Failure of the neural tube closure (more common at the caudal neuropore) or close position of the neural tube to the body surface prevents full development of the vertebral arch, which remains open. This anomaly is called *spina bifida* (cleft spine) and most often occurs in the L5 or S1 vertebrae. The spina bifida may cause protrusion of the meninges, cauda equina, or spinal cord: in *meningocele*, only the meninges herniate through a bony defect; in *meningomyelocele*, the meninges and neural tissue (or cauda equina) herniate. *Spina bifida occulta* is associated with a tuft of hair or skin dimple at the level of a bony defect with no herniation of the spinal cord or spinal meninges.

Anencephaly is the failure of the rostral neuropore to close. The calvaria of the skull remains open and the forebrain does not develop. Smaller neural tube defects in this region can lead to the formation of cranial clefts and herniations of parts of the brain or meninges.

SPINAL CORD

The spinal cord (*Lat.* medulla spinalis) is a part of the CNS, which performs the following functions:

– Sensory and motor segmental innervation of the body;

– Two-ways communication through pathways between the body and the brain;

– Coordination of somatic and autonomic spinal reflexes (such as regulation of muscle tone and reflex movements of the muscles of the trunk and limbs, regulation of the work of internal organs, blood pressure, body temperature).

External structure of spinal cord

The **spinal cord**, about 41–42 cm long, is located in the vertebral canal (Fig. 10). It extends from the level of the foramen magnum of the occipital bone, or attachment of the first pair of the spinal nerves, to the level of the upper border of the L2 vertebra. Superiorly, the spinal cord continues with the medulla oblongata. At the lower end, it narrows into the **conus medullaris (medullary cone)** connecting with a thin filament of connective tissue, the **filum terminale**. Most of the filum passes inside the dural sac (up to the S2 vertebra), the remaining part fuses with the investing dura mater and attaches to the coccyx.

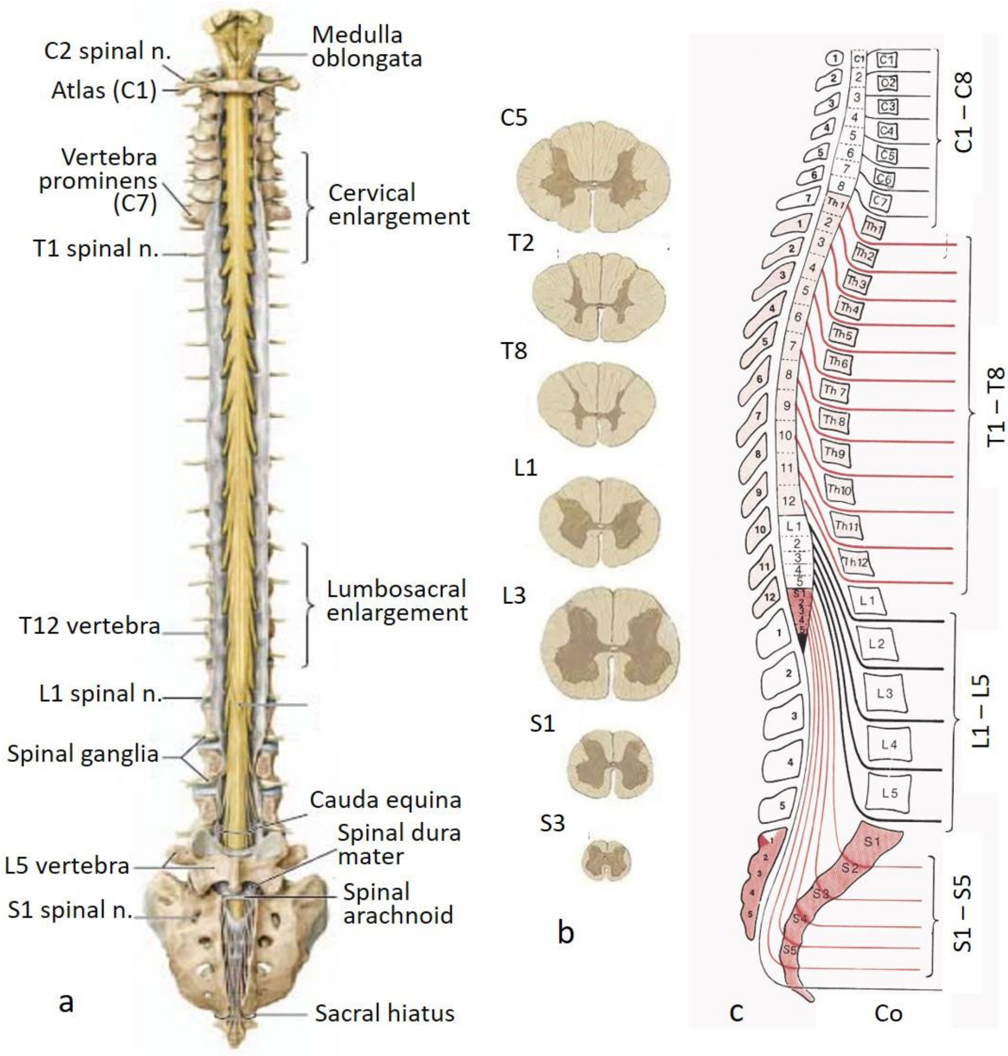

Fig. 10. Spinal cord:
a — position in the vertebral canal; *b* — transverse sections through spinal segments; *c* — spinal segments and nerves and their relationship to the vertebrae

Two grooves, the **posterior (dorsal) median sulcus** and the wider **anterior (ventral) median fissure**, run the length of the spinal cord and partially divide it into right and left halves (Fig. 11). Each half has two furrows, the **anterolateral (ventrolateral) sulcus** and the **posterolateral (dorsolateral) sulcus**. They divide the white matter of the spinal cord into 3 funiculi (*syn.* white columns) on each side — the **anterior**, **posterior**, and **lateral** (between the antero- and posterolateral sulci) **funiculus**. The posterior funiculus, in turn, is divided by the **posterior intermediate sulcus** into the **gracile fasciculus** medially and the **cuneate fasciculus** laterally.

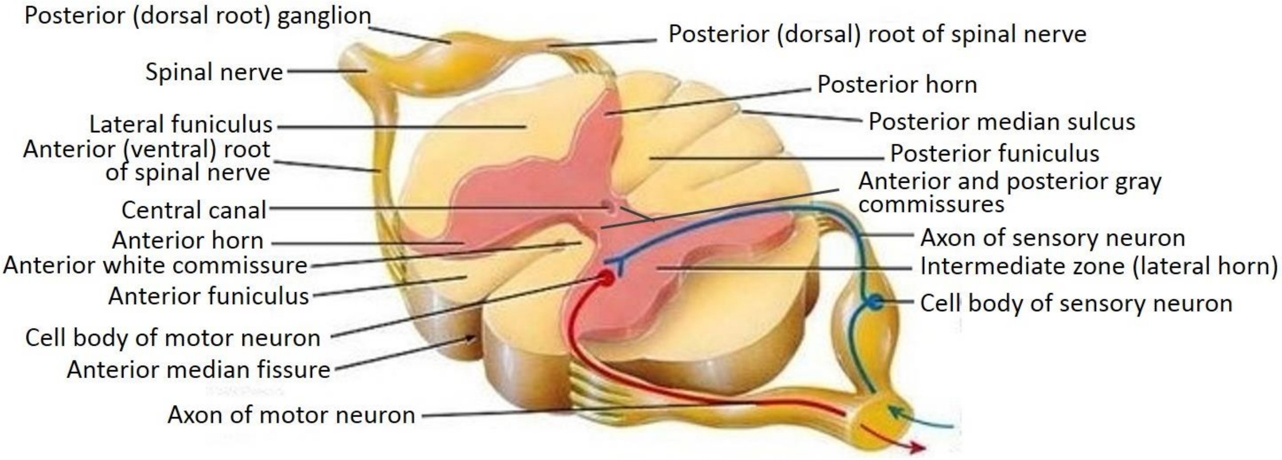

Fig. 11. Structure of the spinal cord (a spinal segment)

Thirty-one pairs of spinal nerves (PNS structures) attach to the spinal cord by anterior and posterior roots. The **posterior (dorsal) root** is sensory. It carries the **spinal ganglion** (*syn.* **dorsal root ganglion**) containing the pseudounipolar sensory neurons. The central processes of these neurons compose the posterior root, which enters the spinal cord at the posterolateral sulcus. The motor **anterior (ventral) root** consists of axons of the motor neurons, which lie in the spinal gray matter (predominantly in the anterior horn), and exits the spinal cord at the anterolateral sulcus. The anterior and posterior roots pass within the vertebral canal and fuse in the intervertebral foramina to form the spinal nerves that send their branches throughout the body.

A section of the spinal cord from which a pair of spinal nerves (or two pairs of spinal roots) emerges is called the **spinal segment** (Fig. 10, 11). The number of spinal segments mainly corresponds to the number of vertebrae and coincides with the number of spinal nerves. There are 31 spinal segments/nerves, which are divided into 8 cervical (C1–C8), 12 thoracic (T1–T12), 5 lumbar (L1–L5), 5 sacral (S1–S5) and 1 coccygeal (Co). Each spinal segment connects by the spinal nerve with a specific area of the skin — the **dermatome**, and muscle/s — the **myotome** (Fig. 12).

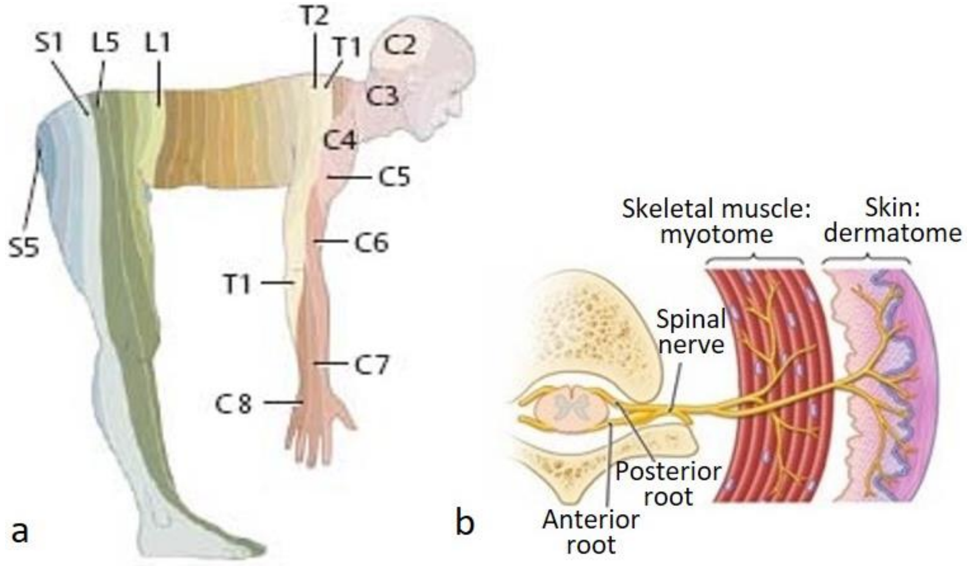

Fig. 12. Segmental innervation of the body:
a — dermatomes; *b* — scheme of segmental innervation of skin and skeletal muscles

In the cervical and lumbar regions, where the nerves to the upper and lower limbs arise, the spinal cord forms thickenings — the **cervical** and **lumbosacral enlargements** (*Lat.* intumescentia cervicalis and intumescentia lumbosacralis).

Since the spinal cord is shorter than the vertebral column, the spinal segments are located above the corresponding vertebrae. The roots of most spinal nerves must descend some distance before reaching their corresponding intervertebral foramina (Fig. 10). The collection of lumbar and sacral spinal nerve roots that run vertically at the lower end of the vertebral canal forms the **cauda equina** ("horse's tail").

Only in the upper neck, the position of the spinal segments corresponds to the appropriate vertebrae. The discrepancy between their positions increases towards the caudal end of the spinal cord. The lower cervical and upper thoracic spinal segments (C5–T4) are located 1 vertebra above the vertebra of the same number; the middle thoracic segments (T5–T8) — 2 vertebrae above; the lower thoracic segments (T9–T12) — 3 vertebrae above. All lumbar segments are located at the level of the T10–T12 vertebrae, and the remaining segments, from S1 to Co1, — at the level of the L1 vertebra.

Internal structure of spinal cord

The ***gray matter*** (*Lat.* substantia grisea) of the spinal cord is located inside the white matter and is organized in **columns** (anterior, posterior, and intermediate gray columns) extending the entire length of the spinal cord. In the cross-section the gray matter by its shape reminds a butterfly or the letter "H" (Fig. 11). In each half of the spinal cord it consists of the **anterior (ventral) horn**, the **posterior (dorsal) horn**, and the **intermediate zone** between the anterior and posterior horns. At the thoracic and upper lumbar levels of the spinal cord (T1–L2 segments), the intermediate zone projects laterally to form the **lateral horn**. The right and left gray masses are connected by the **anterior** and **posterior gray commissures**, which surrounds a narrow tubular cavity, the **central canal** containing cerebrospinal fluid (CSF). At the upper end the central canal connects with the 4th ventricle of the brain.

In the gray matter, neurons of different structure and functions form longitudinally oriented collections. In the cross-sections, they are distinguished as nuclei or laminae (Rexed's laminae). Relationships between them are shown in the Fig. 13.

The ***posterior horn*** (laminae I–VI) is concerned with exteroceptive and proprioceptive sensations. The interneurons of this horn receive sensory signals from the sensory neurons of the spinal ganglia and relay the information: 1) to the brain, through the ascending tracts, and 2) to motor neurons of the anterior horns to serve spinal reflexes. The prominent nuclear groups of the posterior horn, from dorsal to ventral, are as follows:

– **Marginal zone** (**marginal nucleus**, lamina I), a thin layer of cells that caps the apex of the posterior horn;

– **Gelatinous substance** (**substantia gelatinosa**, lamina II), a thicker more ventral cell layer in the head of the posterior horn;

– **Nucleus proprius** (laminae III–IV), a poorly defined cell group in the center of the dorsal horn.

The ***intermediate zone*** (lamina VII), with exception of the Clarke's nucleus, is concerned with the visceral innervation. Autonomic motor neurons form: the *sympathetic center* located in the **lateral horn** (T1–L2 segments); the *parasympathetic center* located at the level of S2–S4 segments.

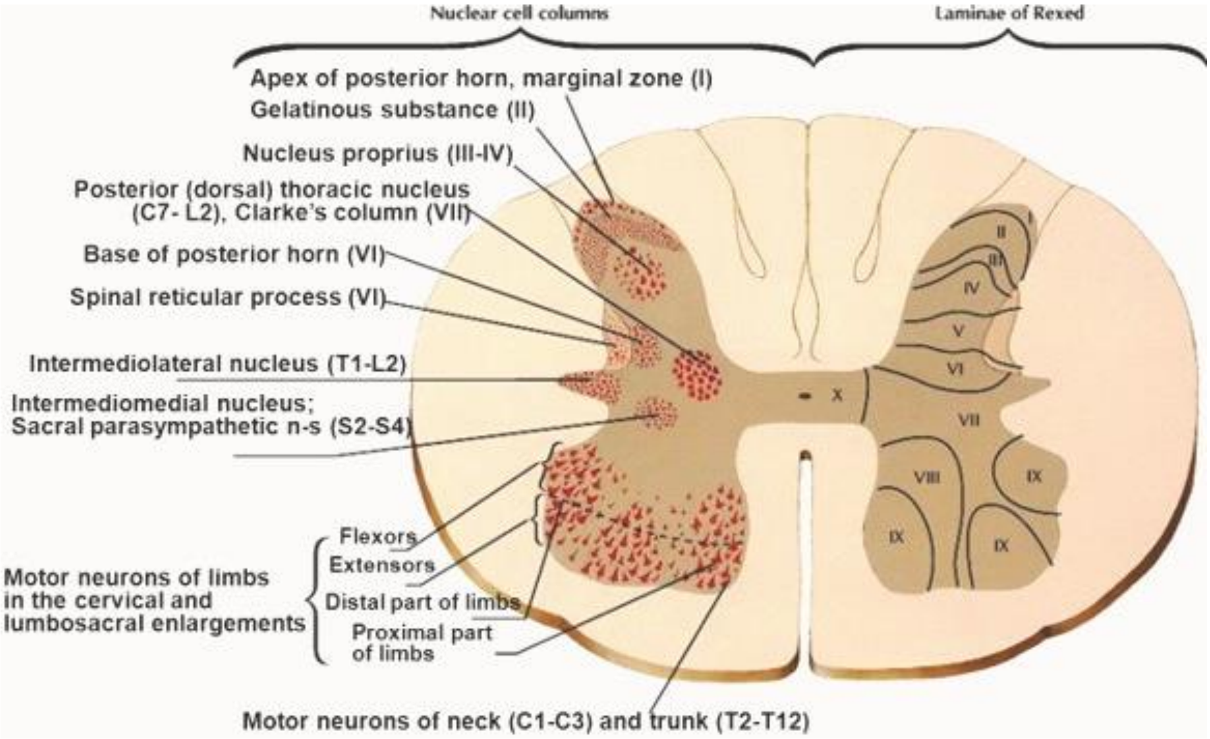

Fig. 13. Subdivisions of the gray matter of the spinal cord

The intermediate zone consists of the *central (medial)* and *lateral parts*:

1. The **central (medial) intermediate substance** surrounds the central canal and contains:

– **Posterior (dorsal) thoracic nucleus (Clarke's nucleus)** lying at the base of the posterior horn along the C8–L2 spinal segments. Similar to the posterior horn nuclei, it receives sensory information and relays it to the brain (to the cerebellum);

– **Intermediomedial nucleus**, a small group of scattered neurons ventral to the Clarke's nucleus. It receives primary visceral afferent information and may be involved in visceral reflexes.

2. The **lateral intermediate substance** contains autonomic centers:

– **Intermediolateral nucleus (columna intermediolateralis)** in the lateral horn at the T1–L2 segments — the sympathetic center;

– **Sacral parasympathetic nucleus** at the S2–S4 segments.

The ***anterior horn*** (laminae VIII and IX) contains **motor nuclei** of the spinal nerves that control the skeletal muscles contraction. The descending tracts, originating in the brain, end on the motor neurons of the anterior horn. The **lateral motor nuclei** are located in the cervical (C5–T1) and lumbosacral (L2–S3) enlargements of the spinal cord and innervate the muscles of the limbs. The **medial motor nuclei** innervate muscles of the trunk and neck. (The *central motor nuclei* contain the nuclei of accessory and phrenic nerves in the cervical segments; the nucleus of pudendal nerve in the sacral segments.)

The ***white matter*** (*Lat.* substantia alba) of the spinal cord surrounds the gray matter and forms 3 funiculi (white columns) — the **anterior**, **posterior**, and **lateral funiculi**. Each funiculus consists of short and long bundles of fibers, mainly myelinated axons, running in ascending and descending directions (Fig. 14):

– Short bundles of fibers, the **fasciculi proprii**, are composed of fibers connecting groups of neurons within the spinal cord — in one segment (horizontally directed fibers) and between distant segments. Proper spinal fibers lie next to the gray matter in each funiculus.

– Long bundles of fibers, called **tracts** (**pathways**) or **fasciculi**, occupy most of the white matter. They connect the spinal cord with the brain in both directions:

1. **Ascending (afferent, sensory) tracts** carry sensory information from the periphery of the body through the spinal cord to the brain.

2. **Descending (efferent, motor) tracts** carry motor commands from the brain to the spinal cord to cause the muscle contraction.

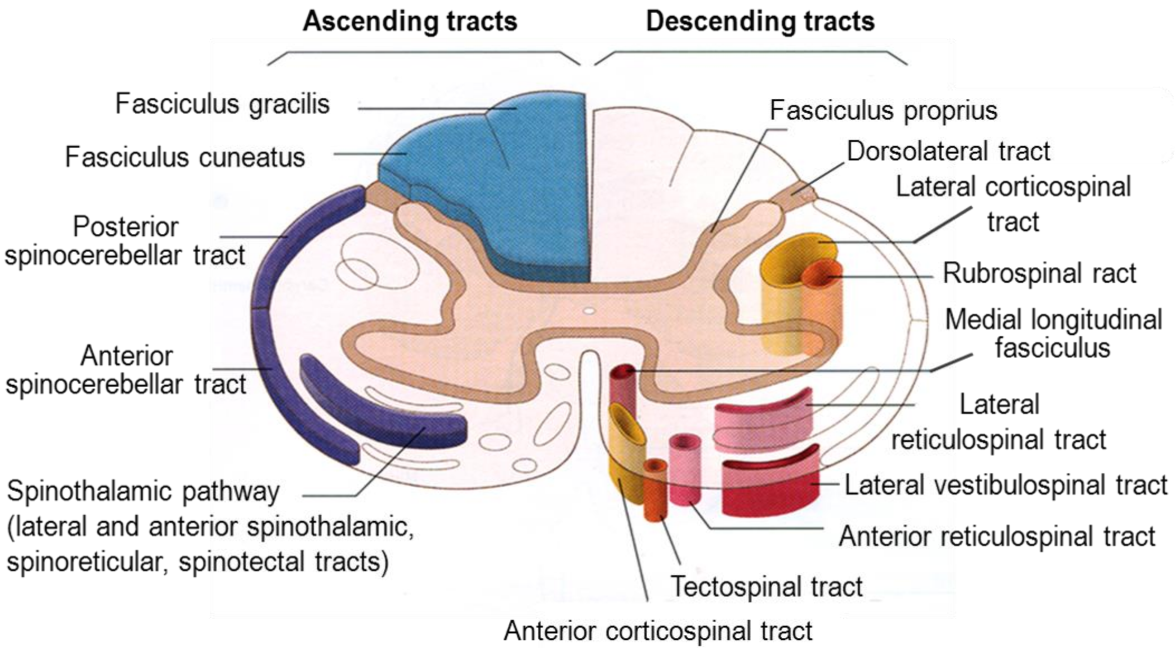

Fig. 14. Long and short (propriospinal) tracts in the transverse section through the cervical part of the spinal cord

The **anterior white commissure** lies anterior to the gray commissure of the same name (Fig. 10). It is formed by transverse fibers crossing the midline, both proper and long tracts fibers (mainly the spinothalamic and anterior spinocerebellar tracts).

The ***posterior (dorsal) funiculus*** contains ascending tracts that transmit conscious proprioceptive and tactile sense to the cerebral cortex:

– **Gracile fasciculus** (Tract of Goll, *Lat.* fasciculus gracilis), lies medially;

– **Cuneate fasciculus** (Tract of Burdach, *Lat.* fasciculus cuneatus) lies laterally.

Most of the fibers of these tracts terminate in their respective nuclei in the medulla oblongata.

The ***lateral funiculus*** contains tracts of both directions.

The main *descending* tracts are:

– **Lateral corticospinal tract (tractus pyramidalis lateralis)**, conveys conscious motor commands from the cerebral cortex to the anterior horn motor neurons, and then to the muscles of limbs.

– **Rubrospinal tract** (Tract of von Monakow), the extrapyramidal tract, conveys motor commands from the nucleus ruber of the midbrain to the anterior horn motor neurons for subconscious control over the skeletal muscles.

– **Lateral reticulospinal tract** (*syn.* Medullary reticulospinal tract), the extrapyramidal tract, transmits motor impulses from the reticular formation of the medulla oblongata to the anterior horn motor neurons for subconscious control over the skeletal muscles.

– **Hypothalamospinal fibers**, transmit impulses from the hypothalamus to the autonomic centers of the spinal cord.

The main *ascending* tracts are:

– **Posterior** and **anterior spinocerebellar tracts** (Tract of Flechsig and Tract of Gowers, respectively), transmit proprioceptive sensation to the cerebellum, which is subconsciously processed.

– **Lateral spinothalamic tracts**, conveys conscious pain and temperature sensation to the thalamus of the diencephalon that reaches the cerebral cortex.[5]

The ***anterior funiculus*** contains one ascending and the remaining descending tracts:

– **Anterior spinothalamic tracts** conveys tactile (touch) sensation through the thalamus of the diencephalon to the cerebral cortex.

– **Anterior corticospinal tract (tractus pyramidalis anterior)** conveys conscious motor commands from the cerebral cortex, through the anterior horn motor neurons, to the muscles of the trunk.

– *Extrapyramidal tracts*, such as the vestibulospinal and tectospinal tracts, reticulospinal fibers, transmit motor impulses from the brain stem to the motoneurons of the anterior horn to innervate skeletal muscles.

MENINGES OF SPINAL CORD

In the vertebral canal, the spinal cord is surrounded and isolated by three connective tissue membranes, the spinal meninges: the **dura** (**dura mater**), or *pachymeninx*, and two delicate layers — the **arachnoid** and the **pia mater**, collectively called the *leptomeninx* (Fig. 15). The meninges cover, protect, and stabilize the spinal cord and the brain, as well as their blood vessels. Cerebrospinal fluid (CSF), which fills the subarachnoid space, acts as a cushion for the CNS structures and protects them from injury.

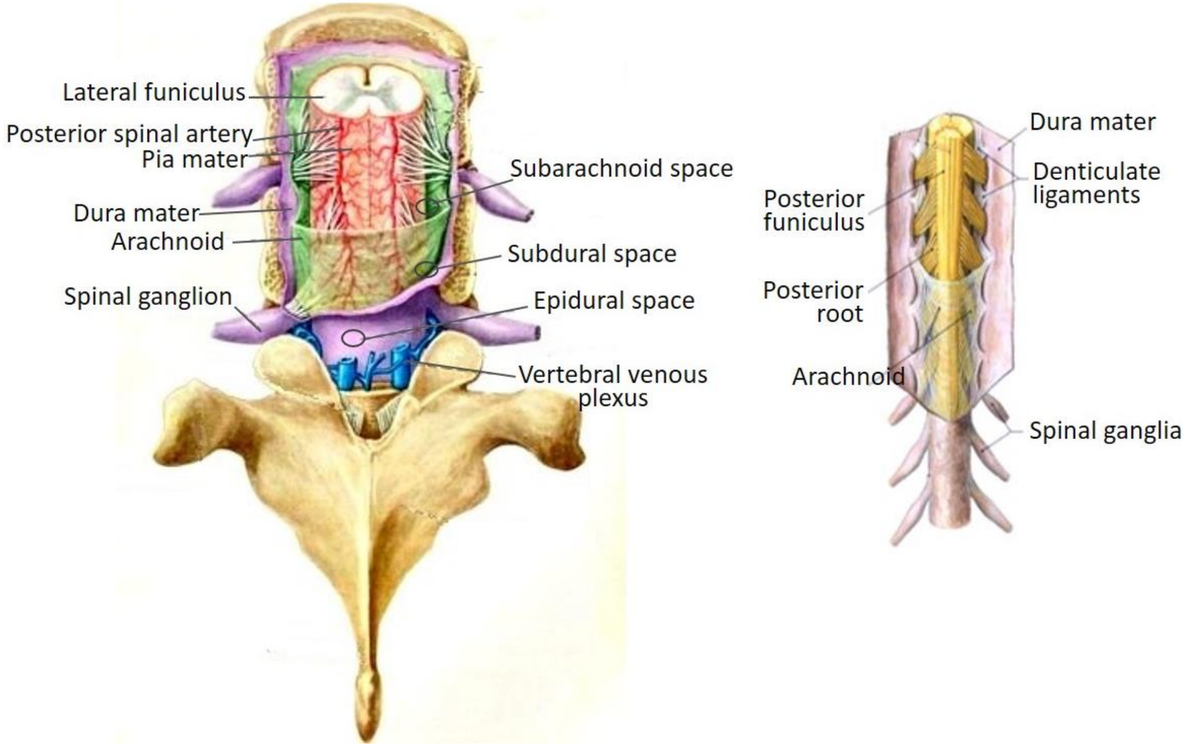

Fig. 15. Meninges of the spinal cord

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[5] This tract is a major component of the **anterolateral system**, which includes tracts occupying the adjacent parts of the lateral and anterior funiculi, such as the anterior and lateral spinothalamic tracts, spinoreticular, spinomesencephalic, and spinotectal tracts that ascend as a bundle through the spinal cord and the brain stem.

The **dura mater** is the outermost thick fibrous membrane, which forms a tubular sheath around the spinal cord extending from the foramen magnum to the sacrum (S2 vertebra), were the dura mater together with the arachnoid covers the filum terminale externum. Lateral extensions of the dura mater enclose the roots of the spinal nerves and attach to the borders of the intervertebral foramina.

The **epidural space**, filled with fat tissue and venous plexus, separates the dura mater from the periosteum of the vertebral canal.

The **subdural space** is a capillary gap between the dura mater and arachnoid, lined from both sides by the endothelial layer and containing a thin film of fluid.

The **arachnoid** is a thin and transparent avascular membrane. It resembles a spider web because of arachnoid trabeculae. They project through the subarachnoid space to the pia mater and fix the blood vessels of the spinal cord.

The **pia mater** is the innermost thin fibrous vascular membrane. It follows sulci of the spinal cord, closely adherent to the neural tissue and contains blood vessels that supply it. Lateral extensions of the pia mater, the **denticulate ligaments**, oriented in the coronal plane, pass between the anterior and posterior roots along the length of the spinal cord. They attach at their apices to the arachnoid and dura mater and help to suspend the spinal cord. The inferior extension of the pia mater is the **filum terminale** attaching to the coccyx.

The **subarachnoid space** is between the arachnoid and pia mater. It is rather wide and filled with **cerebrospinal fluid** (CSF). Widened parts of the subarachnoid space are called cisterns. The **lumbar cistern** extends from L1 to S2 vertebrae surrounding the cauda equina.

The lumbar cistern is the site of the lumbar puncture (spinal tap), that is a procedure to obtain CSF for analysis, or inject a certain medicine to the subarachnoid space. Lumbar puncture is performed by inserting a needle between the spinous processes of the vertebrae L3-L4 or L4-L5. Similar levels are used for epidural anesthesia, made by injecting an anesthetic into the epidural space.

BRAIN

The brain lies within the cranial cavity and consists of the cerebrum, cerebellum, and brain stem (Fig. 16, 17). The **cerebrum** is the largest part, comprising the right and left cerebral hemispheres, which are partially separated by the falx cerebri of the dura mater. The **diencephalon** is a part of the cerebrum almost entirely hidden under the hemispheres.

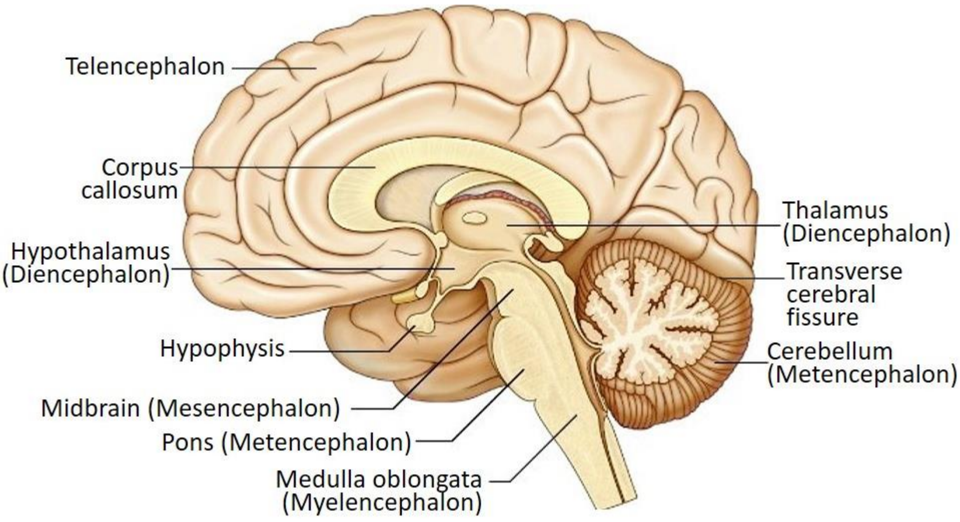

Fig. 16. Parts of the brain (sagittal section)

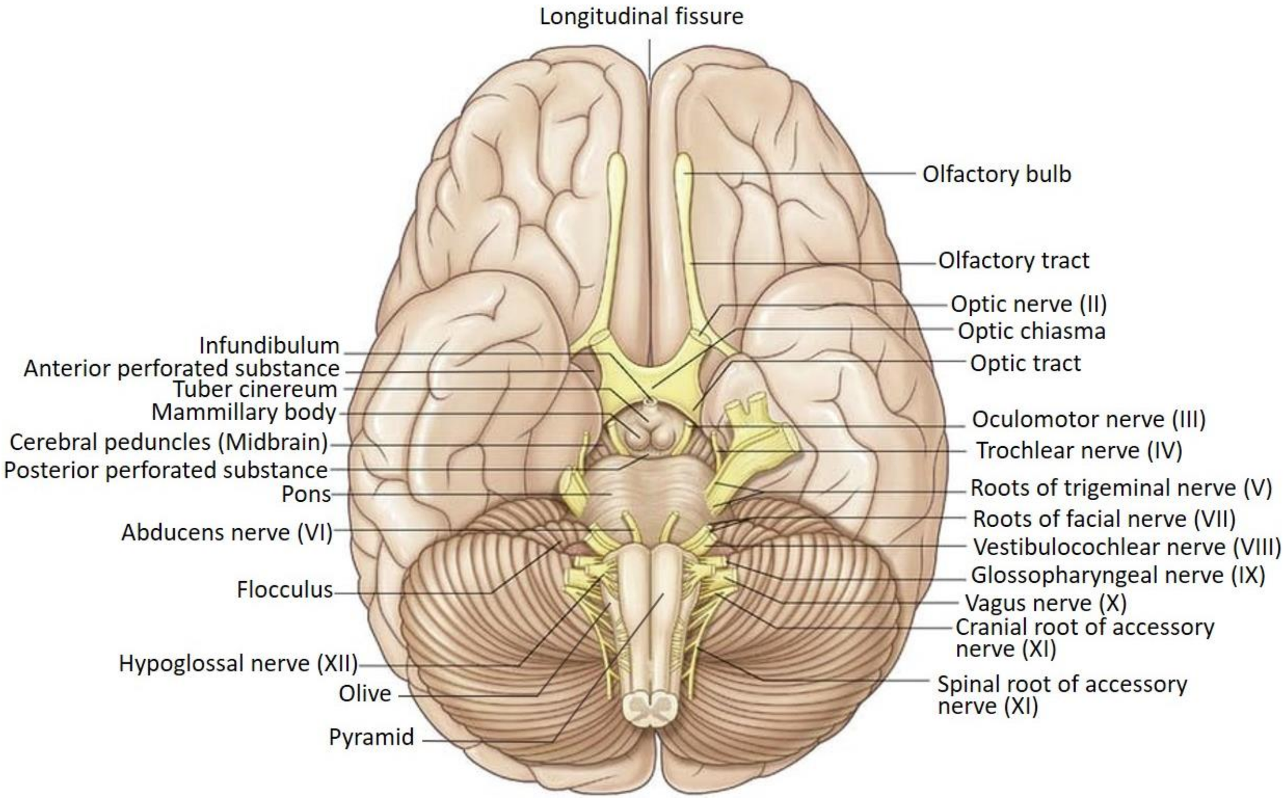

Fig. 17. Base of the brain

The **cerebellum** is the second largest part of the brain. It lies in the posterior cranial fossa below the posterior part of the cerebrum, separated from it by the **transverse cerebral fissure** and by the tentorium cerebelli, a projection of the dura mater into the fissure.

The **brain stem** is an elongated region of the brain between the diencephalon and the spinal cord. It connects the cerebrum with the cerebellum, and both with the spinal cord. The brain stem consists of 3 parts: the **medulla oblongata**, **pons**, and **midbrain** that have similar structural and functional features. The majority of the cranial nerves arise from the brain stem at the base of the brain.

According to the embryonic development, the brain is subdivided into the **prosencephalon** (forebrain), which consists of the **telencephalon** and **diencephalon**; the **mesencephalon** (midbrain); and the **rhombencephalon** (hindbrain), comprising the **metencephalon**, which consists of the pons and cerebellum, and the **myelencephalon**, or medulla oblongata.

Superiorly, the cerebral hemispheres, comprising the *telencephalon*, are separated by the **longitudinal cerebral fissure**, at the bottom of which lies the **corpus callosum** connecting the hemispheres. The most pronounced structures visible on the base of the hemispheres, from front to back, are the olfactory bulbs, tracts, and trigons, and the anterior perforated substances — areas pierced by many small vessels. The *diencephalon* structures are the optic chiasm in the middle, formed by the optic nerves, the tuber cinereum with the infundibulum, and two round elevations, the mammillary bodies. The pituitary gland (syn. hypophysis), attached to the infundibulum, remains in the sella turcica when the brain is removed from the skull. The structures of the *mesencephalon* (midbrain) facing the base of the brain are the cerebral peduncles, which are two broad bundles of nerve fibers, extending between each cerebral hemisphere and the anterior border of the pons. The *rhombencephalon* structures are the cerebellar hemispheres, a bulging bridge between them — the pons, the middle cerebellar peduncles connecting both sides of the pons to the cerebellar hemispheres (belong to the *metencephalon*), and the medulla oblongata (*myelencephalon*) posteriorly adjacent to the pons. It narrows caudally and continues with the spinal cord at the foramen magnum.

MEDULLA OBLONGATA (MYELENCEPHALON)

The **medulla oblongata**, or **myelencephalon,** is a continuation of the spinal cord above the foramen magnum. The inferior (caudal) part of the medulla oblongata has a similar structure with the spinal cord. The superior (rostral) part connects to the pons. On the anterior surface, the medulla and the pons are separated by a distinct transverse groove. On the posterior surface, they together form a depression, the **rhomboid fossa** — the floor of the 4th ventricle.

External structure of medulla oblongata

On the ***anterior surface*** of the medulla, the **anterior funiculi** of the spinal cord expand and form elevations, the **pyramids**, on both sides of the **anterior median fissure** (Fig. 18). At the lower ends of the pyramids, their fibers, which cross the midline, form the **decussation of pyramids**. The **lateral funiculus** continues rostrally with an oval swelling, the **olive**. The olive lies lateral to the pyramid, between the **anterolateral sulcus** and an extension of the **posterolateral sulcus**. The **inferior cerebellar peduncle** begins from the lateral surface of the medulla above the olive. Posterior to the olive, the rootlets of three cranial nerves (CN) arise one below the other: the **glossopharyngeal nerve (CN IX),** the **vagus nerve (CN X),** and the cranial part of the **accessory nerve (CN XI).** The **hypoglossal nerve (CN XII)** emerges from the anterolateral sulcus between the pyramid and olive.

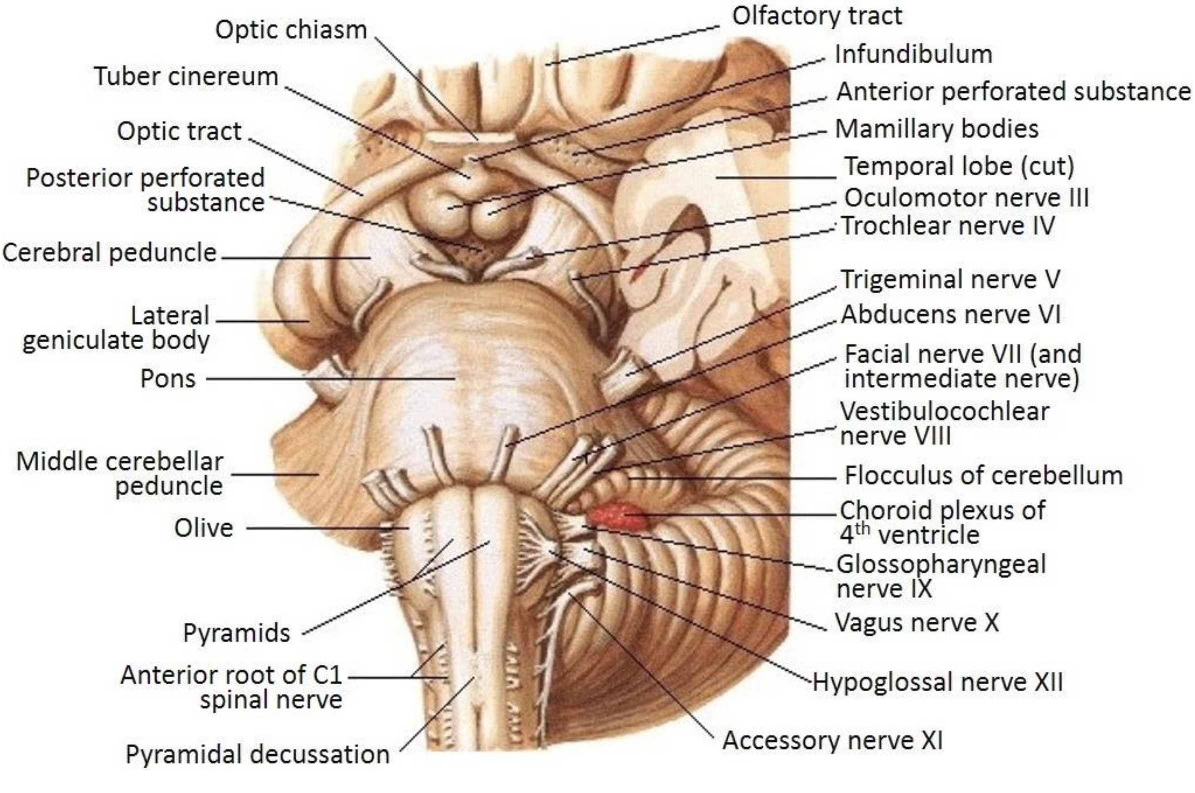

Fig. 18. Brain stem (medulla oblongata, pons, midbrain) with the cranial nerves attached to it, cerebellum, and diencephalon (anterior view)

On the ***posterior surface*** of the inferior part of the medulla, the **posterior funiculi** pass alongside the **posterior median sulcus**. Each funiculus contains two fasciculi, the **gracile fasciculus** medially and the **cuneate fasciculus** laterally, with the **gracile** and **cuneate tubercles** at their upper ends (Fig. 19). The superior medulla forms the lower half of the **rhomboid fossa**, which is bounded by the **inferior cerebellar peduncles**. The peduncles run apart from each other upward and laterally to connect to the cerebellum.

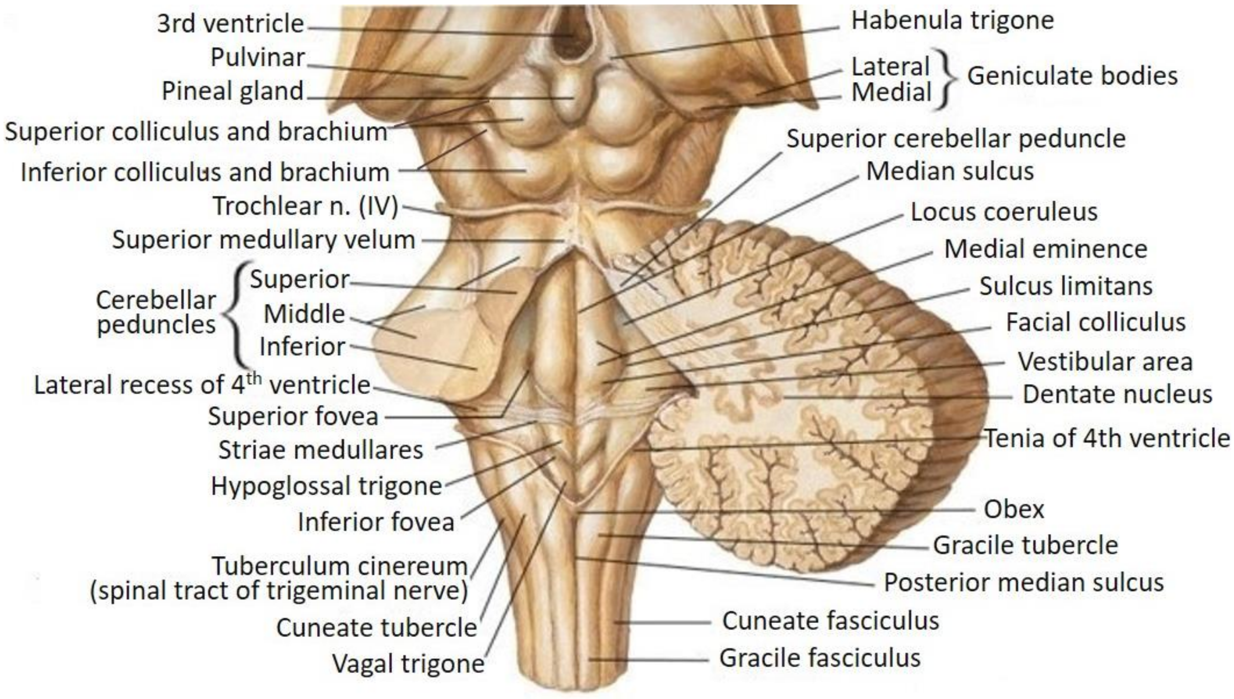

Fig. 19. Brain stem (medulla oblongata, pons, midbrain), cerebellum, and diencephalon (posterior view)

Internal structure of medulla oblongata

The ***gray matter*** of the medulla oblongata contains nuclei associated with autonomic control, motor and sensory relay, and nuclei of the cranial nerves (Fig. 20):

1. **Cranial nerves nuclei** of the last 4 cranial nerves — glossopharyngeal (CN IX), vagus (CN X), accessory (CN XI), and hypoglossal (CN XII); the spinal nucleus of the trigeminal nerve (CN V); and the nuclei of the vestibulocochlear nerve (CN VIII) lying at the pontomedullary junction — two cochlear nuclei, medial and inferior vestibular nuclei.
2. **Reticular nuclei** — nuclei of the **reticular formation (RF)**:

– visceral centers, including the vital cardiovascular and respiratory centers, centers of swallowing, coughing, sweating, gastric secretion, etc.;

– subconscious (extrapyramidal) motor centers.

3. **Gracile** and **cuneate nuclei**, lying in the same-named tubercles, which relay sensory information from the gracile and cuneate fasciculi to the thalamus (via the medial lemniscus).
4. **Olivary nuclei (inferior olivary complex)**, which relay information from the spinal cord and brain regions to the cerebellum.

The ***white matter*** contains long and short tracts and fibers (Fig. 20). *Long afferent (sensory)* fibers include tracts, transmitting information from the spinal cord to the thalamus, and tracts terminating in the cerebellum. *Long efferent (motor)* fibers include tracts from the brain to the spinal cord: originating in the cerebral cortex — pyramidal tracts, and in the brain stem nuclei — extrapyramidal tracts.

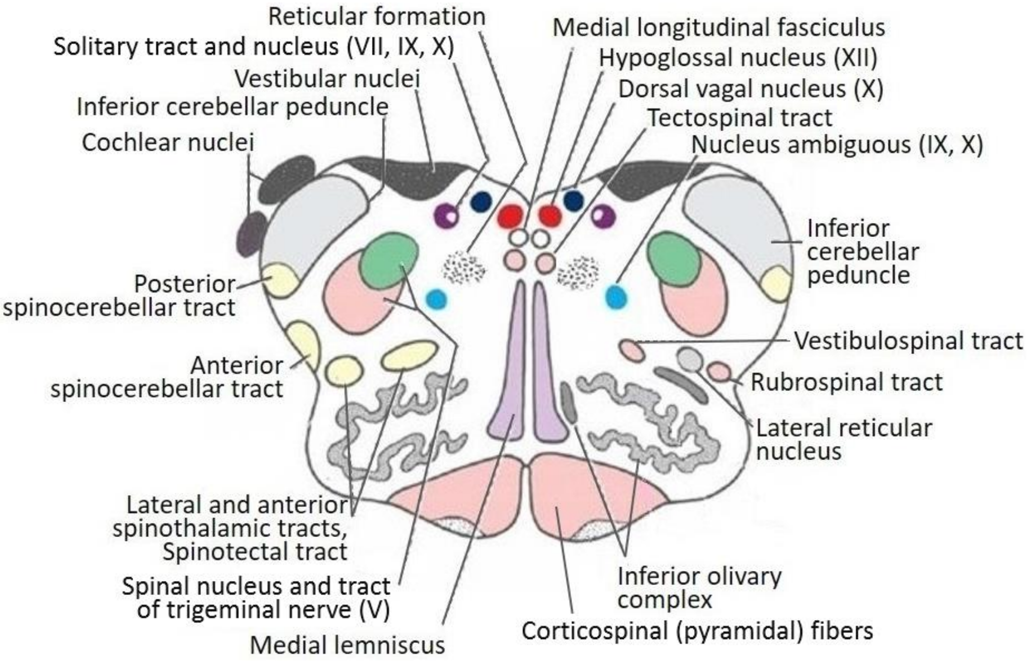

Fig. 20. Internal structure of the medulla oblongata at the level of the rhomboid fossa

1. Most **afferent (sensory)** fibers run *dorsally*, in the **gracile** and **cuneate fasciculi**. They transmit proprioceptive and fine touch information and terminate in the corresponding nuclei of the medulla. Axons arising from the **gracile** and **cuneate nuclei** cross the midline and form the **decussation of medial lemniscus** (*syn.* sensory decussation) beneath the rhomboid fossa. Rostral to the decussation, the axons continue in a bundle, called the **medial lemniscus**, to the thalamus.

2. Most **efferent (motor)** fibers run *ventrally* through the pyramids and are called **pyramidal tracts**. These fibers originate in the cerebral cortex and transmit conscious motor commands to skeletal muscles:

– The **corticonuclear fibers** end in the motor nuclei of the cranial nerves;

– The **corticospinal fibers** run through the pyramids to the spinal cord. At the lower end of the pyramids, around 80 % of them cross the midline, forming the **decussation of pyramids** (*syn.* motor decussation), and continue as the **lateral corticospinal tract**. Uncrossed fibers form the **anterior corticospinal tract**.

3. Other ascending and descending fibers pass in the *dorsolateral* parts of the medulla:

– The ascending fibers form 2 main groups: 1) the **spinal lemniscus**, in which the **spinothalamic tract (fibers)** is the main contributor; and 2) the **spinocerebellar tracts**: the posterior spinocerebellar tract passes from the lower part of the medulla to the cerebellum through the inferior cerebellar peduncle; the **anterior spinocerebellar tract** ascends further to the pons;

– The descending fibers are the **extrapyramidal tracts** (such as the rubrospinal, reticulospinal tracts, etc.).

4. **Short tracts** connect the medulla with the cerebellum (e.g., olivocerebellar and vestibulocerebellar fibers).

5. **Medial longitudinal fasciculus** is located dorsally along the midline and consists of ascending, descending, and crossing fibers. It connects the vestibular nuclei with the nuclei controlling the eye movements (CN III, CN IV, and CN VI) and motor nuclei of the upper cervical spinal segments. The fasciculus is responsible for coordination of eyes and head movements.

ADVANCED:

– **Posterior (dorsal) longitudinal fasciculus** (Schutz's bundle) lies under the surface of the rhomboid fossa and in the dorsal part of the tegmentum of the pons and midbrain. It contains descending fibers from the hypothalamus to autonomic nuclei of the brain stem and the spinal cord, known there as the **hypothalamic tract**. Ascending fibers (mainly gustatory) pass from the RF and the solitary nucleus of the vagus nerve (CN X) to the hypothalamus.

– **Spinal tract of trigeminal nerve** passes dorsolaterally. It contains the sensory fibers originated in the sensory ganglia of the cranial nerves — trigeminal (CN V), glossopharyngeal (CN IX), vagus (CN X), and facial (VII) nerves, which end in the spinal nucleus of the trigeminal nerve. Axons arising from the spinal nucleus cross the midline to form the bundle on the opposite side — the **trigeminal lemniscus**.

PONS

The **pons** (bridge) is a part of the brainstem located ventral to the cerebellum between the medulla oblongata (caudally) and the midbrain (rostrally). The pons and the cerebellum belong to the **metencephalon**.

External structure of pons

The bulging ***ventral surface*** of the pons has distinct rostral and caudal borders, with the cerebral peduncles of the midbrain and the medulla, respectively (Fig. 18). The lateral borders of the pons, from which the **middle cerebellar peduncles** originate, correspond to imaginary lines between the insertions of the **trigeminal** (CN V) and **facial** (CN VII) **nerves**. Numerous transverse ridges on the ventral surface of the pons are formed by the nerve fibers passing from the pons to the cerebellum. A shallow groove along the midline of the anterior surface, the **basilar sulcus**, lodges the basilar artery.

Three cranial nerves emerge along the posterior border of the pons: the **abducens nerve** (CN VI) above the pyramid of the medulla; the **facial** (CN VII) and **vestibulocochlear** (CN VIII) **nerves** above the olive, in the *cerebellopontine angle*, which is a region limited by the pons, cerebellum and middle cerebellar peduncle.

The ***dorsal surface*** of the pons is the upper (rostral) part of the rhomboid fossa hidden under the cerebellum (Fig. 19). Together with the medulla oblongata it forms the floor of the 4th ventricle. Rostrally, the dorsal surface of the pons continues with the quadrigeminal plate of the midbrain.

Internal structure of pons

The pons is divided into the ventral **basilar part**, and the dorsal part, the **tegmentum** (Fig. 21).

The ***basilar part of pons*** is composed of the ***white matter***, containing transverse and vertical nerve fibers, and scattered areas of ***gray matter* —** the **pontine nuclei**.

Vertical fibers originate in the cerebral cortex:

– **Corticospinal fibers** descend through the pons into the pyramids of the medulla oblongata and further into the spinal cord;

– **Corticonuclear fibers** terminate in the motor nuclei of the cranial nerves located in the pons and the medulla;

– **Corticopontine fibers** originate in different lobes of the cerebral hemispheres and terminate in the pontine nuclei.

Transverse fibers are the **pontocerebellar fibers** arising from the **pontine nuclei**. They form the **middle cerebellar peduncles** of the contralateral side and end in the cortex of the cerebellum. Thus, the pontine nuclei serve as relay centers that connect the cerebral cortex with the cerebellum.

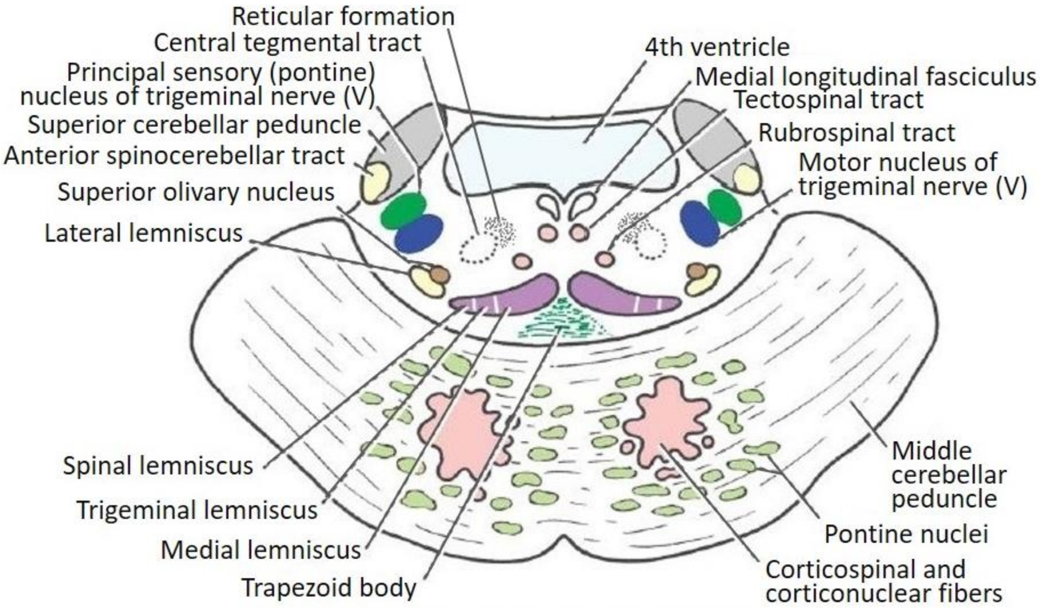

Fig. 21. Internal structure of the pons (transverse section through the rostral part of the pons)

The ***tegmentum of pons*** (dorsal part) is a continuation of the dorsal part of the medulla and rostrally continues with the tegmentum of the midbrain. The arrangement of the white and gray matter in the tegmentum of the pons and midbrain is principally similar.

The ***gray matter*** of the tegmentum includes the nuclei of four **cranial nerves**, from **CN V** to **CN VIII**, the nuclei of the **pontine reticular formation (RF)**, the **nuclei of trapezoid body**, the **superior olivary nucleus** (and some others):

1. The nuclei of the cranial nerves lie beneath the floor of the rhomboid fossa: medially, the nucleus of the **abducens nerve** (CN VI) and nuclei of the **facial nerve** (CN VII) ventral to it; laterally, nuclei of the **trigeminal nerve** (CN V) and nuclei of the **vestibulocochlear nerve** (CN VIII) (in particular, the lateral and superior vestibular nuclei, and the cochlear nuclei at the border with the medulla).
2. The **pontine RF** is a continuation of the medullary RF, composed of multiple nuclei and fibers. It occupies the region on the sides of the midline.
3. The **superior olivary nucleus** and the **nuclei of trapezoid body** are groups of nuclei on both sides of the caudal pons, topographically and functionally related to the trapezoid body. Some fibers of the trapezoid body synapse in these nuclei.

The ***white matter*** of the tegmentum contains fibers of different directions: ascending, descending, and transverse.

1. The **trapezoid body** is a part of the auditory (acoustic) pathway. It consists of *transverse fibers* that arise in the cochlear nuclei (CN VIII) and cross the midline at the caudal pons, right above the basilar part. In the rostral pons crossed and uncrossed acoustic fibers join in a bundle, the **lateral lemniscus**, which ascends to the midbrain.
2. Most *ascending fibers* pass in the **medial, spinal,** and **trigeminal lemnisci**, which transmit sensory information to the thalamus, from which it is relayed to the cerebral cortex:

– The **medial lemniscus** is formed by the decussated axons of the gracile and cuneate nuclei of the medulla. In the pons the medial lemniscus changes orientation from vertical to horizontal and passes medially above the trapezoid body. It transmits sensation from the muscles and skin of the body as well as the sense of taste.

– The **spinal lemniscus** (syn. **anterolateral tract**) consists of the **spinothalamic fibers** and some other tracts originating in the spinal cord (see “medulla”). It passes through the medulla and pons lateral to the medial lemniscus and transmits sensation from the skin of the body and internal organs.

– The **trigeminal lemniscus (trigeminothalamic tract)** contains fibers arising from the sensory nuclei of the trigeminal nerve at the levels of the upper spinal cord, medulla, and pons[6]. It transmits sensation from the face and part of the head.

The **anterior spinocerebellar tract** passes from the spinal cord through the medulla and pons, up to the midbrain, where it enters the superior cerebellar peduncles to reach the cerebellum.

3. *Descending fibers* in the tegmentum belong to the motor extrapyramidal tracts originating in the brainstem, such as the **rubrospinal, tectospinal, reticulospinal tracts**. Most of their fibers pass into the spinal cord, some end in the brainstem — in the motor nuclei of the cranial nerves, reticular formation, etc.

ADVANCED: The **central tegmental tract** is the important efferent pathway of the extrapyramidal motor system. It runs through the central part of the tegmentum of the midbrain and pons lateral to the medial longitudinal fasciculus. It contains descending fibers that course from the basal nuclei (striatum and pallidum) to the midbrain red nucleus, and further from the red nucleus (mainly) and RF to the inferior olivary nucleus of the medulla. Some fibers run to the spinal cord. The olivary nucleus, in turn, is connected with the contralateral cerebellum. The central tegmental tract also contains ascending fibers from the RF of the brainstem to the thalamus and subthalamic region, as well as taste fibers from the solitary nucleus.

CEREBELLUM

The **cerebellum** (small brain) lies in the posterior cranial fossa dorsal to the medulla and pons, separated from the occipital lobes of the cerebrum by the transverse cerebral fissure. The cerebellum is the integrative center for the maintenance of equilibrium, control of muscle tone and posture, coordination of muscle action in both stereotyped (e.g., walking) and nonstereotyped (skilled) movements.

External structure of cerebellum

The cerebellum consists of two **hemispheres** and a narrow unpaired central part, the **vermis** (worm). On the superior surface these parts are continuous with each other with no borders. Inferiorly the vermis lies in the depression between the hemispheres, the *vallecula,* and is separated from them by deep grooves (Fig. 22).

A superficial layer of grey matter, the **cerebellar cortex**, covers the white matter. The cortex forms numerous narrow folds — *folia* (leaves), separated by deep grooves — *fissures*, running mainly in transverse direction. In sectional view this pattern gives the cerebellum a characteristic tree-like appearance, called the **arbor-vitae** (tree of life) (Fig. 23).

The deepest **horizontal fissure** passes along the posterior border of the cerebellar hemispheres and divides them into the superior and inferior parts. The shallower **primary fissure** runs across the superior surface of the hemispheres and vermis closer to the anterior border.

The cerebellum is divided into 3 lobes: the **anterior, posterior** and **flocculonodular lobes** (Fig. 22, 23). The primary fissure is the boundary between the anterior and posterior lobes. These lobes consist of many smaller lobules and together form the main part of the cerebellum — the *cerebellar body*.

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[6] In the caudal pons the trigeminal lemniscus passes dorsal to the medial and lateral lemnisci, in the rostral part of the pons between them.

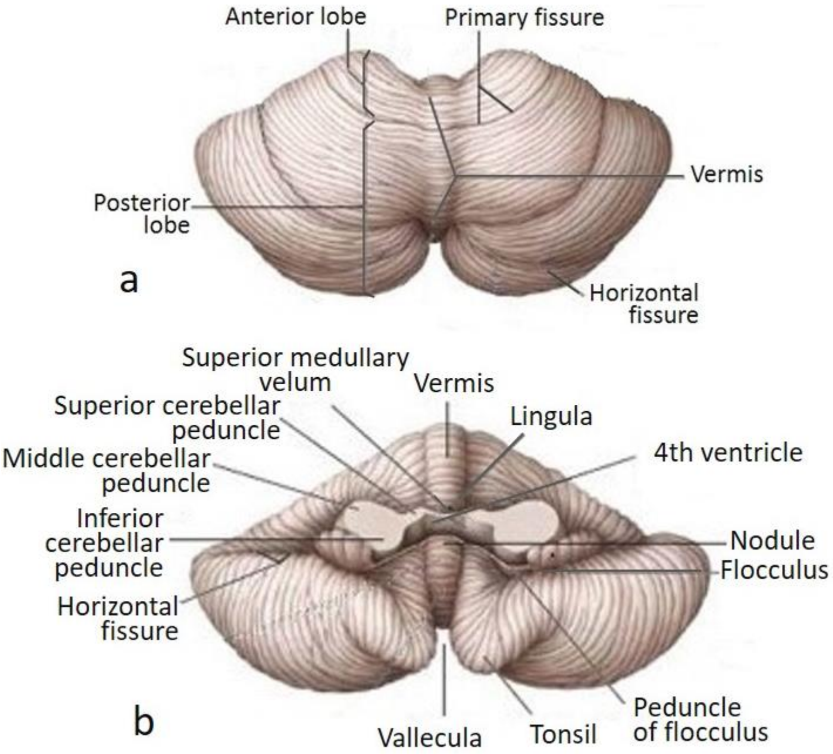

Fig. 22. External structure of the cerebellum:
a — superior view; *b* — anterior view

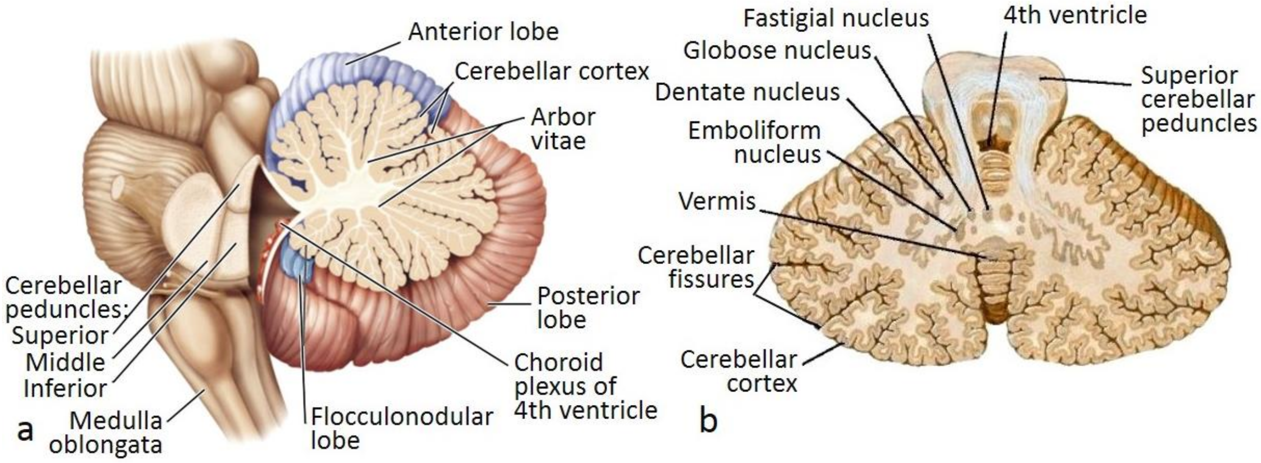

Fig. 23. Cerebellum:
a — paramedian section through the vermis; *b* — nuclei of the cerebellum in the coronal section

The **flocculonodular lobe** is located on the inferior surface of the cerebellum, separated from the posterior lobe by a distinct fissure (posterolateral fissure). It comprises the **nodule**, paired **flocculus**, and **peduncles of floccule**. The **nodule** is the most ventral lobule of the posterior end of the vermis, lying above the medulla. The **flocculi** are small sections of the cerebellum lying right behind the middle cerebellar peduncles. Each flocculus is connected with the nodule by a thin lamina of white matter, called the **peduncle of flocculus**. The **inferior medullary velum** is stretched between the latter.

Three pairs of thick bundles of fibers, the **cerebellar peduncles**, connect the cerebellum to nearby brain regions (Fig. 23):

– The **inferior cerebellar peduncles** pass along the lower margins of the rhomboid fossa and connect the cerebellum with the medulla oblongata;

– The **superior cerebellar peduncles** pass along the superior margins of the rhomboid fossa from the cerebellum to the midbrain;

– The **middle cerebellar peduncles** connect the cerebellum with the pons on the base of the brain.

Internal structure of cerebellum

The ***grey matter of the cerebellum*** consists of the **cerebellar cortex** — a thin layer covering the central core of white matter (described above), and the **cerebellar nuclei** — small masses of grey matter within the white matter (Fig. 23, *b*).

The cerebellar cortex receives inputs from different parts of the CNS: the vestibular nuclei; the spinal cord — directly or through the inferior olivary nucleus and RF; the cerebral cortex through the pontine nuclei. Most efferent fibers, leaving the cerebellar cortex (axons of Purkinje cells), end in the cerebellar nuclei, which, as well, receive afferents from extracerebellar sources.

The paired nuclei are located symmetrically on both sides of the midline:

– The **fastigial nucleus** — close to the midline in the anterior part of the vermis;

– The **globose nucleus** — in the medial part of the cerebellar hemisphere, consists of 2–3 small masses;

– The **emboliform nucleus** — lateral to the globose nucleus;

– The **dentate nucleus** — a thin folded lamina of grey matter in the center of the cerebellar hemisphere, resembles by shape the inferior olivary nucleus of the medulla oblongata.

White matter of the cerebellum is represented:

– by the **white matter of the cerebellar hemispheres**, which is mainly formed by axons of Purkinje cells connecting the cerebellar cortex to the cerebellar nuclei;

– by the paired **cerebellar peduncles**, which contain fibers entering or leaving the cerebellum (Fig. 24):

1) The **inferior cerebellar peduncle** contains mainly ascending fibers arising in the *spinal cord* or *medulla*, such as the **posterior spinocerebellar tract**, **vestibulocerebellar** and **olivocerebellar fibers**. Efferent fibers pass to the vestibular nuclei and the RF.

2) The **middle cerebellar peduncle** contains the **pontocerebellar fibers**, arising in the *pontine nuclei* and crossing to the opposite side. They transfer signals coming from the cerebral cortex (by the corticopontine tract) to the cerebellar cortex.

3) The **superior cerebellar peduncle** contains the afferent pathway from the spinal cord, the **anterior spinocerebellar tract**. Short efferent fibers course 1) to the *midbrain* — to the contralateral **red nucleus** and the **RF** of the brainstem (to modulate motor activity); 2) to the **thalamus** of the *diencephalon*, for projection to the cerebral cortex.

ADVANCED: One of the functions of the cerebellum is motor adaptation. The cerebellum modifies routine motor programs in response to changes in the environment, such as walking uphill versus walking on flat surface. It compares the movements planned and voluntary initiated by the cerebrum with the current body position. Feedback from the cerebellum to the cerebral cortex adjusts the motor commands sent to the spinal cord, resulting in fine-tuning and coordination of movements.

This process involves the **olivary nucleus**, which relays to the cerebellum inputs from the premotor and sensorimotor cortex, from the spinal cord, and from the **red nucleus**. On the other hand, the red nucleus relays output signals from the cerebellum to the thalamus and further to the cerebral cortex. The red nucleus, receiving collaterals of cortical fibers descending to the olive, detects a mismatch between a movement intended and a movement organized, and influences the appropriate cell groups in the olive until the two are harmonized (“movement correction”).

The cerebellum and the inferior olivary nucleus are also involved in cognition (motor memory). When learning a new motor skill, the cerebellum refines movements, corrects them for errors. After practice, the skill can be performed automatically, like riding a bike or playing piano. The cerebellum as well plays some role in language, problem solving, and task planning.

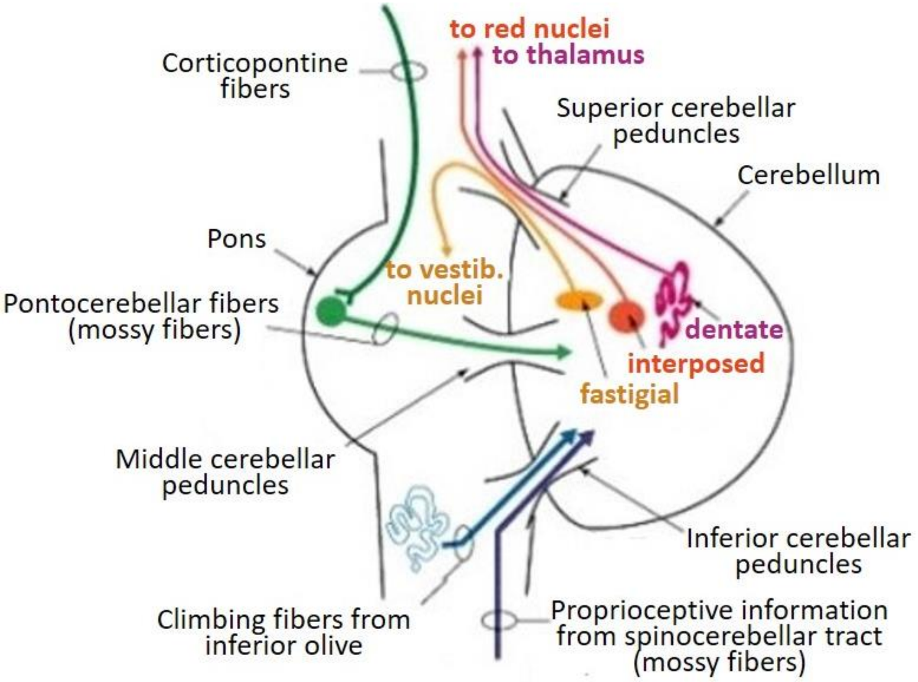

Fig. 24. Principle pathways of the cerebellar peduncles (“interposed” — globose and emboliform nuclei)

From developmental, phylogenetic and functional points of view the cerebellum is often divided into 3 parts: the oldest — archicerebellum (present in all vertebrates), old — paleocerebellum, and new — neocerebellum (Fig. 25). The last two parts are present only in mammals.

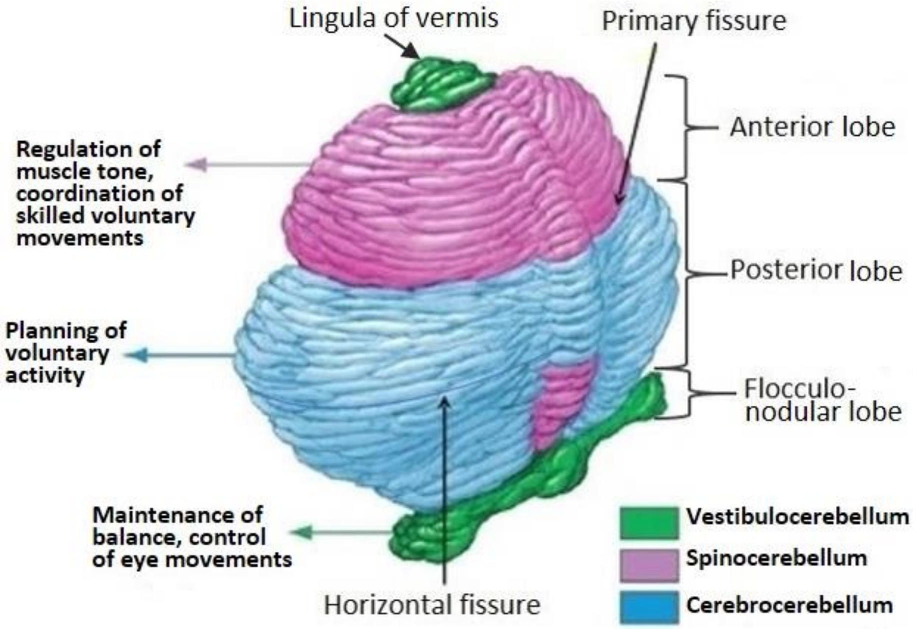

Fig. 25. Subdivisions of the cerebellum and their main functions: the cerebellum is represented as if it has been ‘opened out’ so that the superior and inferior aspects can both be seen

The **archicerebellum** (vestibulocerebellum) corresponds to the flocculonodular lobe (and lingula of the vermis) and contains the *fastigial nuclei*. It is connected with the vestibular nuclei, influences the eyes position and the maintenance of body equilibrium.

The **paleocerebellum** (spinocerebellum) mainly corresponds to the anterior lobe with the *globose* and *emboliform nuclei* (includes, as well, the posterior end of the vermis, paravermian area, and cerebellar tonsil). It has connections predominantly with the spinal cord (afferent — via the spinocerebellar tracts and efferent — via the red nucleus and rubrospinal tract). It controls muscle tone, coordinates work of antagonistic muscle groups, maintains posture and gait.

The **neocerebellum** corresponds to the posterior lobe, enlarged in primates, and the *dentate nucleus*. It has reciprocal connections with the cerebral cortex (afferent — through the pontine nuclei, efferent — through the red nucleus and thalamus). It is involved in voluntary motor function, fine coordination of skilled movements initiated by the cerebral cortex (including phonation and articulation), motor adaptation and cognition.

FOURTH VENTRICLE

The **fourth (IV) ventricle** is a cavity of the rhombencephalon (hindbrain). It connects caudally to the central canal of the spinal cord, rostrally to the midbrain aqueduct (Fig. 26, 27). In the IV ventricle, a roof and a floor are distinguished. The **floor** is the **rhomboid fossa** formed by the dorsal surfaces of the pons and medulla oblongata and surrounded by the superior and inferior cerebellar peduncles.

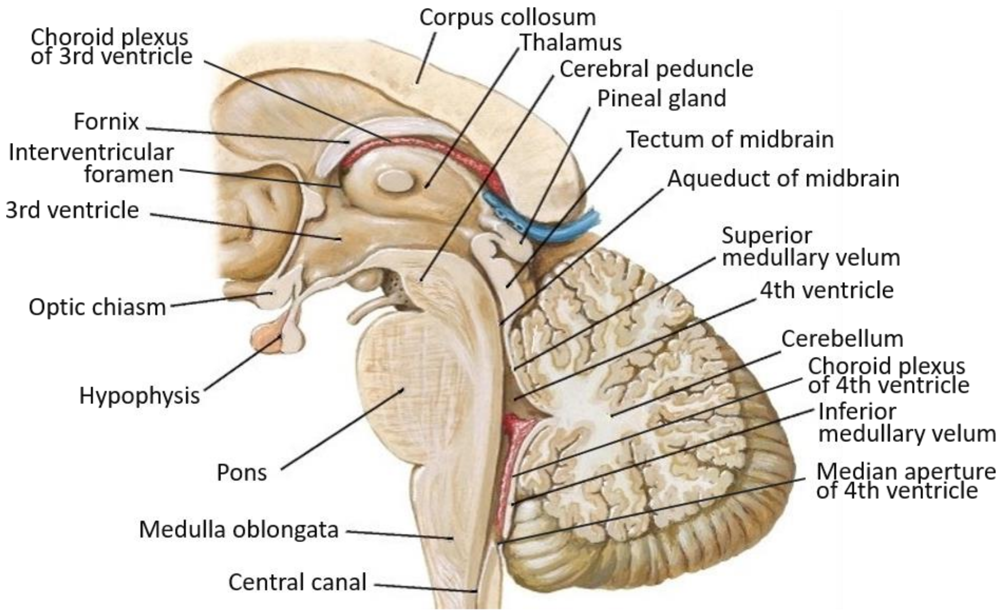

Fig. 26. Sagittal section through the cavities of the 3rd and 4th ventricles and aqueduct of midbrain

The tent-like **roof** is formed by the superior medullary velum, the inferior medullary velum, and the cerebellum between them. The **superior medullary velum** is a thin sheet of white matter, which stretches between the superior cerebellar peduncles, and narrows as it approaches the tectum of the midbrain. The **inferior medullary velum** is a thin non-nervous membrane — the tela choroidea[7], which stretches between the inferior cerebellar peduncles and reaches the nodule of the vermis. The **choroid plexus of the IV ventricle** is attached to the inferior medullary velum from the midline to the lateral recesses.

The **lateral recesses** are extensions of the lateral corners of the IV ventricle. They curve ventrally around the inferior cerebellar peduncles and end by the **lateral apertures of 4th ventricle** (**foramina of Luschka**) (Fig. 27). The unpaired **median aperture of 4th ventricle**

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[7] The tela choroidea is a double-layered structure consisting of pia mater fused with ependyma of the cerebral ventricles. Fringes of the tela choroidea, which surround blood capillaries and project into the ventricles of the brain, form the choroid plexuses.

(**foramen of Magendie**), is located in the center of the lower part of the inferior medullary velum, above the opening of the central canal. Through these three apertures the 4th ventricle and the entire ventricular system of the brain communicates with the subarachnoid space.

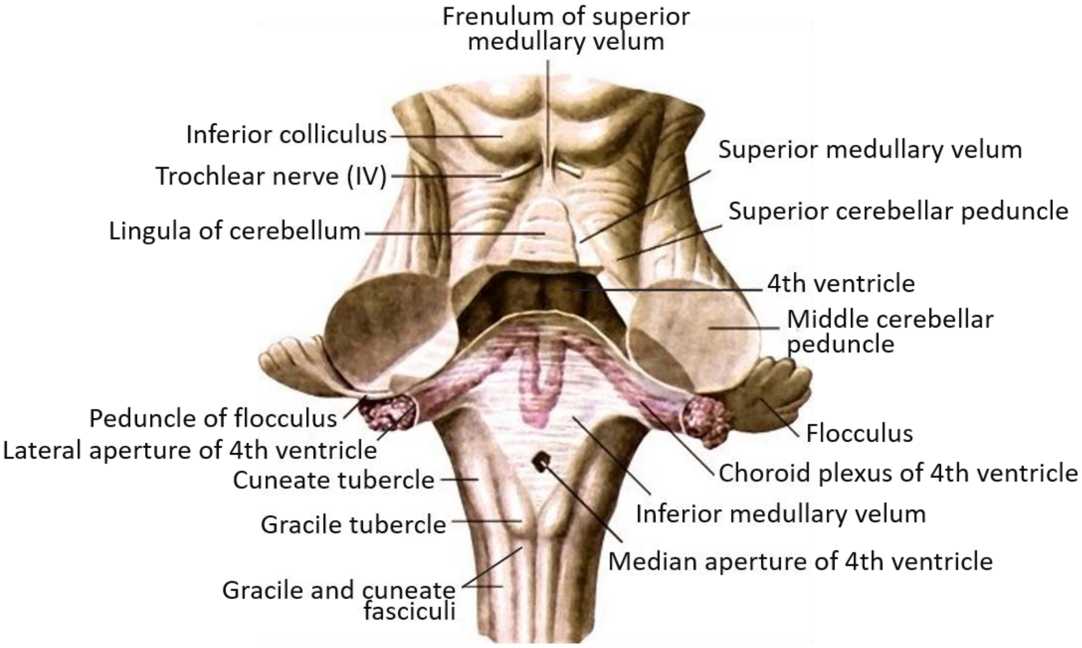

Fig. 27. Fourth ventricle: superior view (cerebellum is removed)

RHOMBOID FOSSA

The rhomboid fossa is the floor of the IV ventricle (Fig. 28). It is a diamond-shaped area formed by the posterior surfaces of the pons ($^{2}/_{3}$) and medulla oblongata ($^{1}/_{3}$). It extends from the beginning of the central canal inferiorly to the opening of the aqueduct of midbrain superiorly. The lateral boundaries of the rhomboid fossa are the inferior cerebellar peduncles below, and the superior cerebellar peduncles above.

The rhomboid fossa is divided into right and left halves by the **median groove**, and into anterior and posterior parts by the *medullary striae of fourth ventricle*. A ridge on each side of the median groove is called the **median eminence**. A slight groove, the **sulcus limitans**, passes on its lateral side. The **locus coeruleus**[8] is an area of bluish color located lateral to the sulcus limitans in the rostral part of the pons.

At the caudal part of the pons, the median eminence contains a swelling, the **facial colliculus**, which is formed by a loop of the facial nerve (CN VII) fibers around the nucleus of the abducens nerve (CN VI). In the region of the medulla oblongata, the median eminence contains the **hypoglossal trigone**, which lies next to the median sulcus above the hypoglossal nucleus (CN XII), and the **vagal trigone**, which lies laterally and inferiorly, above the dorsal nucleus of vagus nerve (CN X). Lateral triangles of the rhomboid fossa, the **vestibular areas**, correspond to the location of the vestibular nuclei (CN VIII).

The ***gray matter of the rhomboid fossa*** breaks up to numerous nuclei, among which are the relay nuclei of sensory and motor pathways, nuclei of the reticular formation, and nuclei of the cranial nerves. The latter are organized in a certain order: the motor nuclei — medially, the sensory nuclei — laterally, and the autonomic (parasympathetic) nuclei — between them (Fig. 29). Out of 10 pairs of cranial nerves, attached to the brainstem,

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[8] The locus coeruleus is a noradrenergic nucleus of the RF, a part of the ascending reticular activating system.

the **oculomotor (CN III)** and **trochlear (CN IV) nerves**, have their nuclei rostral to the rhomboid fossa in the midbrain. Nuclei of the next 4 nerves, CN V–VIII, are mainly located in the pons, and nuclei of the last 4 nerves, CN IX-XII, — in the medulla with few of them extending to the spinal cord.

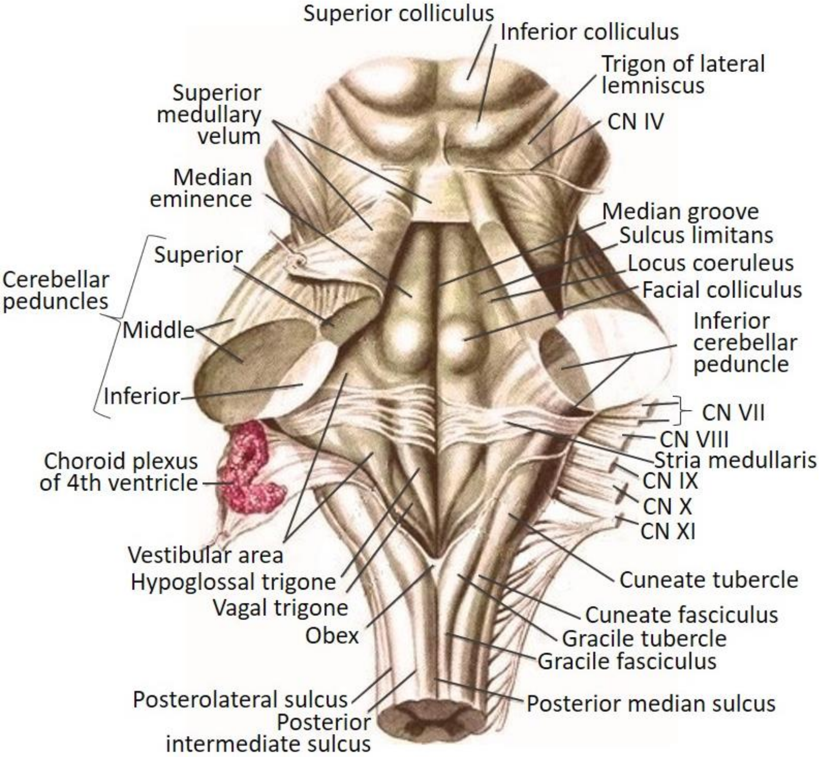

Fig. 28. Rhomboid fossa (superior view of the brainstem, the cerebellum is removed)

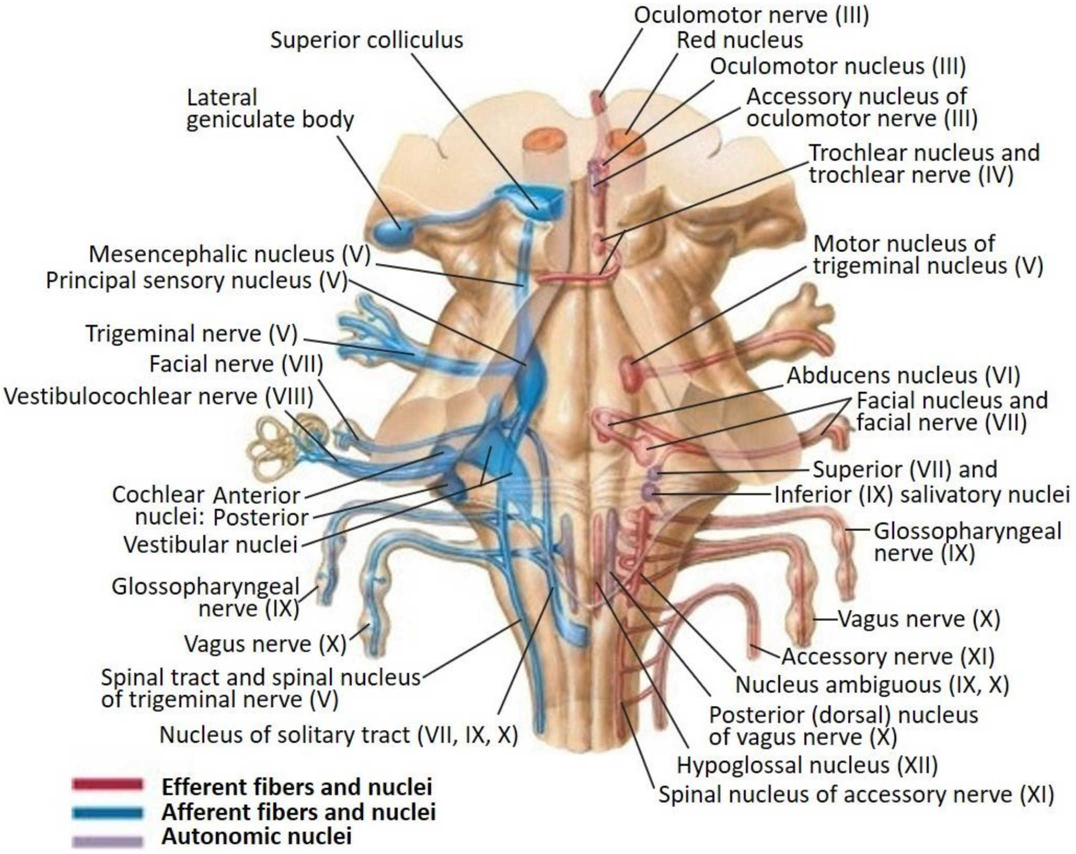

Fig. 29. Projection of cranial nerves nuclei on the dorsal surface of the brainstem

Depending on the nature of the nuclei, the cranial nerves can be classified as **motor**, having only motor nuclei (somatic, or both somatic and autonomic parasympathetic nuclei); **sensory**, having only sensory nuclei; and mixed, having both motor and sensory nuclei.

The **trigeminal nerve** (**CN V**), mixed, has 4 nuclei — one *motor* and 3 *sensory*:

– The **motor nucleus** in the tegmentum of the pons;

– The **principle sensory nucleus** (*syn.* **pontine nucleus**) in the tegmentum of the pons;

– The **spinal nucleus**, extending from the pontine nucleus through the medulla oblongata to the spinal cord substantia gelatinosa;

– The **mesencephalic nucleus**, extending from the pons to the tegmentum of the midbrain.

The **abducens nerve** (**CN VI**) has one *motor* **nucleus of abducens nerve** (*syn.* abducens nucleus) in the tegmentum of the pons beneath the facial colliculus.

The **facial nerve** (**CN VII**), mixed, has 4 nuclei located in the tegmentum of the caudal pons:

– The **motor nucleus of facial nerve**;

– The *parasympathetic* **superior salivatory nucleus**;

– The *parasympathetic* **lacrimal nucleus**;

– The *sensory* **nucleus of solitary tract** (*syn.* solitary nucleus). The rostral part of this nucleus belongs to the CN VII, the caudal part — to the CN IX and CN X.

The **vestibulocochlear nerve** (**CN VIII**) has 2 groups of *sensory* nuclei, 2 cochlear and 4 vestibular nuclei, located in the vestibular area of the rhomboid fossa, at the border between the pons and the medulla oblongata; the cochlear nuclei are lateral to the vestibular nuclei:

– The **anterior (ventral)** and **posterior (dorsal) cochlear nuclei**;

– The **medial**, **superior**, **lateral,** and **inferior vestibular nuclei**.

The **glossopharyngeal nerve** (**CN IX**), mixed, has 3 nuclei located under the surface of the rhomboid fossa in the medulla:

– The *motor* **nucleus ambiguous**, common for the CN IX, X and XI;

– The *parasympathetic* **inferior salivatory nucleus**;

– The *sensory* **nucleus of solitary tract** (*syn.* solitary nucleus), common for the CN VII, IX, and X.

The **vagus nerve** (**CN X**) is mixed and has 3 nuclei:

– The *motor* **nucleus ambiguous**, common for the CN IX, X and XI;

– The *parasympathetic* **posterior (dorsal) nucleus of vagus nerve**, located in the area of the vagal trigone;

– The *sensory* **nucleus of solitary tract** (*syn.* solitary nucleus), common for the CN VII, IX and X.

The **accessory nerve** (**CN XI**) has the *motor* **nucleus of accessory nerve** (*syn.* **accessory nucleus**), located in the spinal cord, and a small part of the **nucleus ambiguous**.

The **hypoglossal nerve** (**CN XII**) has the *motor* **nucleus of hypoglossal nerve** (*syn.* hypoglossal nucleus) located in the medulla oblongata in the area of the hypoglossal trigone.

MIDBRAIN (MESENCEPHALON)

The area of the brain at the border between the rhombencephalon and midbrain (called the isthmus of the rhombencephalon) includes the superior cerebellar peduncles with the superior medullary velum and an area on the lateral side of the brainstem, called the **trigon of lateral lemniscus** (Fig. 28, 30). The trigone contains fibers of the auditory pathway and is bounded superiorly by the superior cerebellar peduncle, inferiorly by the cerebral peduncle, and anteriorly by the brachium of superior colliculus.

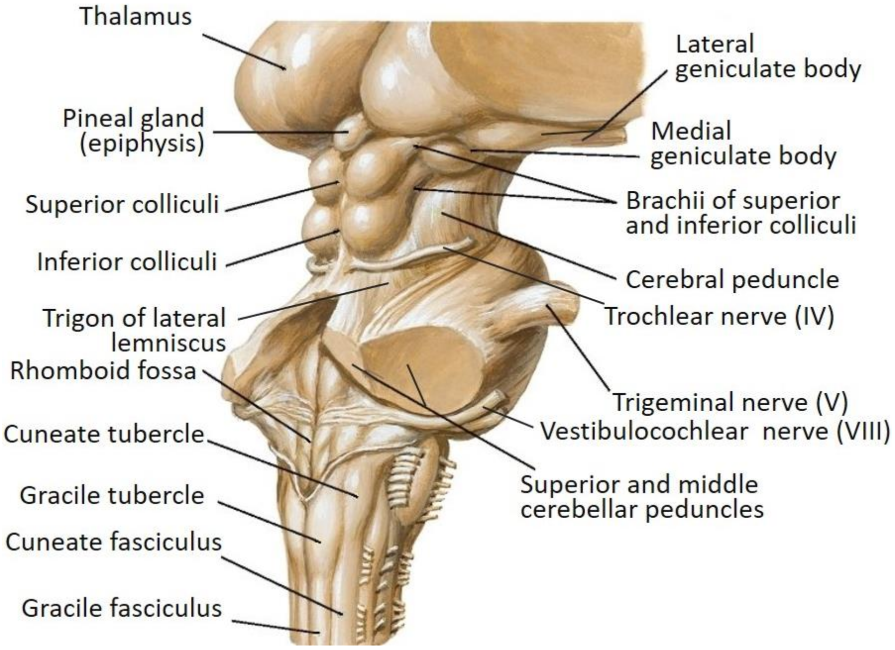

Fig. 30. Midbrain (mesencephalon): posterolateral view of the brainstem

The **midbrain** is a part of the brain stem, about 2 cm long, that connects the pons and cerebellum with the forebrain (Fig. 26, 30, 31). A narrow tubular cavity, the **aqueduct of midbrain** (*syn.* **cerebral aqueduct**), traverses the midbrain, connecting the 3rd and 4th ventricles. The cerebral aqueduct serves as a landmark that divides the midbrain into 2 parts: the smaller dorsal part, the **tectum of midbrain**, which is overlapped from the top by the cerebellum and corpus callosum, and the larger ventral part formed by two big rollers, the **cerebral peduncles**.

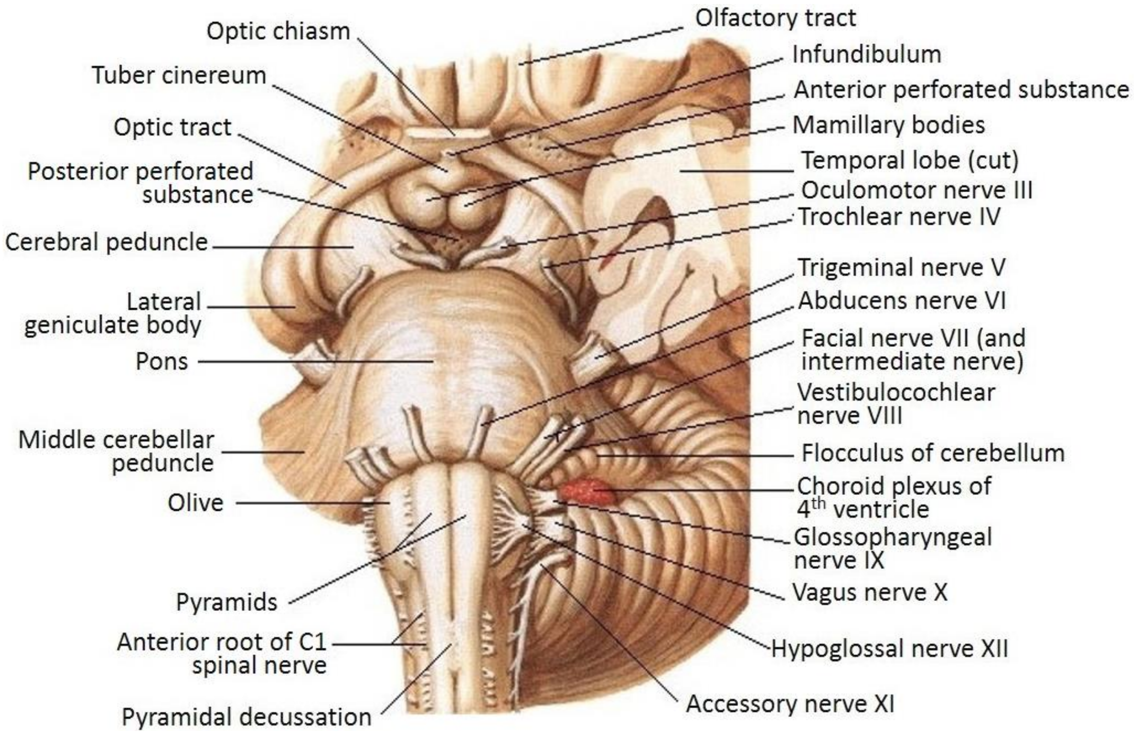

Fig. 31. Parts of the brainstem and the cranial nerves at the base of the brain

External structure of midbrain

The **tectum of midbrain** (*syn.* **quadrigeminal plate**) consists of 4 colliculi, two **superior** and two **inferior colliculi** (Fig. 30). The pineal body of the diencephalon lies between the superior colliculi. On either side of the tectum, small ridges, called brachii, run anterolaterally from the colliculi to the diencephalon structures. The **brachium of superior colliculus** connects to the *lateral geniculate body*. The longer and thinner **brachium of inferior colliculus** connects to the *medial geniculate body*. The thin **trochlear nerve (CN IV)** exits immediately below the inferior colliculus; before exiting its fibers cross the midline. The trochlear nerve winds around the cerebral peduncle and appears lateral to it on the base of the brain.

The **cerebral peduncles** are visible at the base of the brain (Fig. 31). They connect the pons with the hemispheres and form boundaries of a deep depression, the **interpeduncular fossa**. The floor of the fossa is the **posterior perforated substance**, pierced by many small blood vessels. The **oculomotor nerve (CN III)** emerges from the medial side of the cerebral peduncle.

Internal structure of midbrain

In the cross-section, the midbrain can be divided into 2 main parts — the **tectum of midbrain** above the level of the cerebral aqueduct and the **cerebral peduncles** below it (Fig. 26, 32).

1. The **tectum of midbrain** (*lat.* **tectum mesencephali**, *syn.* **lamina tecti**) has two pairs of colliculi containing gray matter:

– The **superior colliculi** are visual reflex centers (receive fibers from the *optic tracts*) and participate in other mesencephalic reflexes (respond to auditory and tactile stimuli).

– The **inferior colliculi** are the subcortical auditory centers. They transmit signals from the *lateral lemniscus* to the medial geniculate bodies (to be sent to the cerebral cortex) and initiate auditory reflexes (by communicating with the superior colliculi).

2. The **cerebral peduncles** are subdivided into:

– the dorsal part — **tegmentum**;

– the ventral part — **base of peduncle**, which, in turn, consists of the **substantia nigra**, the upper part adjacent to the tegmentum; and the **crus cerebri** facing the base of the brain.

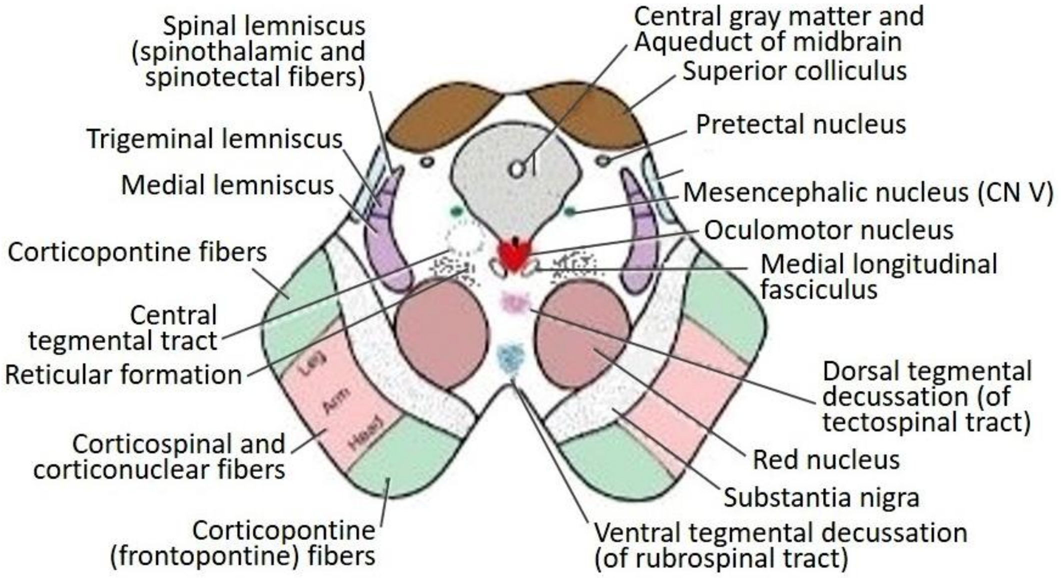

Fig. 32. Internal structure of the midbrain: transverse section through the superior colliculi

The **central structures of midbrain** are the **cerebral aqueduct** and the surrounding **periaqueductal gray substance** (syn. **central gray substance of midbrain**).

The gray matter of the cerebral peduncles comprises the substantia nigra and nuclei located in the ***tegmentum**:* nuclei of the cranial nerves, RF nuclei, red nucleus, and some others (tegmental, interpeduncular, etc.).

The **substantia nigra** has a dark color due to the melanin it contains. It is a part of the extrapyramidal (motor) system, providing dopamine to the basal nuclei of the telencephalon.

The **nucleus ruber** (**red nucleus**) gives rise to the extrapyramidal **rubrospinal tract**. The red nucleus integrates information from the cerebrum and cerebellum and sends subconscious motor commands to the skeletal muscles.

The **nuclei of the cranial nerves (III, IV, and V)** are the following:

– Nuclei of the oculomotor nerve (**CN III**), located at the level of the superior colliculi: motor **nucleus of oculomotor nerve** (*syn.* oculomotor nucleus) and parasympathetic **accessory nucleus (Edinger-Westphal nucleus)**;

– Motor **nucleus of trochlear nerve** (*syn.* trochlear nucleus) (**CN IV**), located at the level of the inferior colliculus;

– Sensory **mesencephalic nucleus of trigeminal nerve** (**CN V**), located in the caudal part of the midbrain near the periaqueductal gray substance, as the nuclei of the CN III and CN IV lie within the substance.

The white matter of the tegmentum of midbrain contains:

– Anterior (ventral) tegmental decussation (Meynert’s decussation), formed by the **rubrospinal fibers** crossing the midline;

– Posterior (dorsal) tegmental decussation (decussation of Forel), formed by the **tectospinal fibers** crossing the midline;

– Decussation of superior cerebellar peduncles formed by the **anterior spinocerebellar tracts** at the caudal part of the tegmentum;

– Other bundles of fibers that pass through the length of the brainstem (*described above with the medulla oblongata and pons*):

- **spinal lemniscus (**spinothalamic fibers), **medial lemniscus**, **trigeminal lemniscus** (tracts of the trigeminal nerve), all ascend to the thalamus;
- **lateral lemniscus** (acoustic), terminates at the inferior colliculi;
- **medial** and **dorsal longitudinal fasciculi**.

The white matter of the crus cerebri contains descending fibers that originate in the cerebral cortex and continue into the pons, medulla oblongata and spinal cord:

– **Corticospinal fibers**;

– **Corticonuclear fibers**;

– **Corticopontine fibers**.

ADVANCED: The **pretectum** (*Syn.* pretectal region), according to the last Anatomical Terminology, is a caudal part of the diencephalon but it is often classified as a part of the midbrain. The pretectum contains a bilateral group of interconnected nuclei located anterolateral to the superior colliculi of the midbrain and posterior to the thalamus. The pretectal nuclei relay information from the retina of the eye to the Edinger-Westphal nucleus and mediate the pupillary light reflex (narrowing the pupils in response to the intensity of light). They are also involved in accommodation reflex, antinociception (reducing the perception of pain) and regulation of sleep.

RETICULAR FORMATION OF BRAINSTEM

The reticular formation (RF) is a phylogenetically older part of the brainstem, represented by a network of neurons interconnected by thin bundles of myelinated fibers. It contains nuclei of different sizes, as well as centers formed by scattered neurons. The RF is located deep in the dorsal part of the brainstem, filling the spaces between the cranial nerve nuclei, ascending and descending tracts (Fig. 33). Caudally it projects to the spinal cord, rostrally to the hypothalamus and thalamus. Through the thalamus the RF communicates with the cerebral cortex.

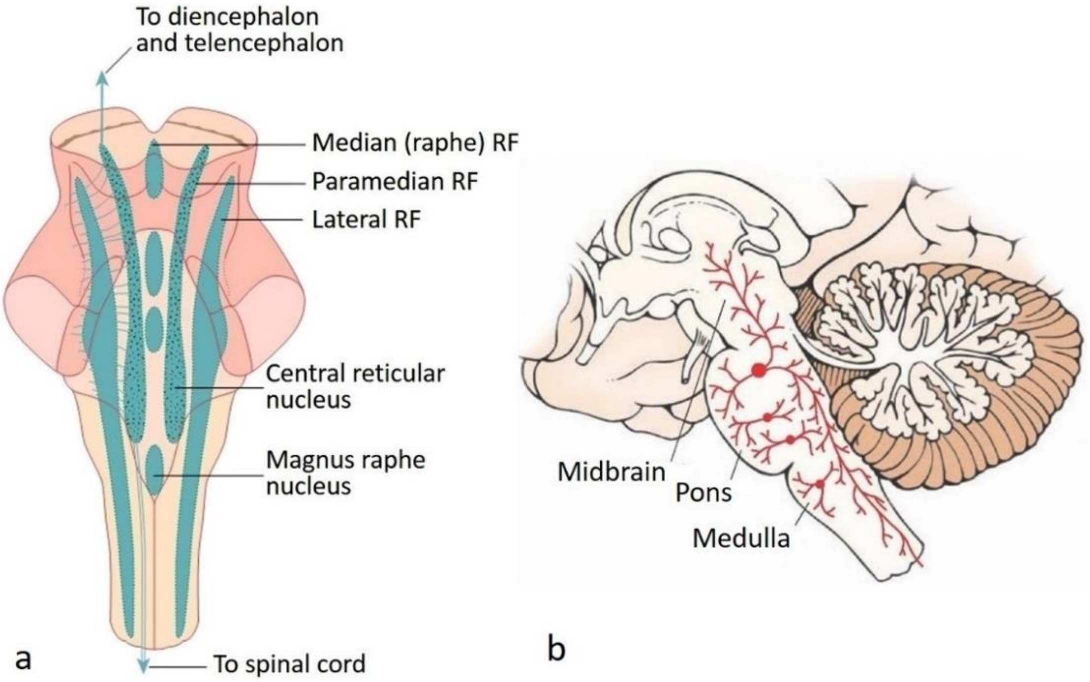

Fig. 33. Reticular formation of the brain stem:
a — general organization, *b* — large cells in the magnocellular region of the reticular formation, giving off ascending and descending axons and collaterals to adjacent structures

The RF has multiple reciprocal, afferent and efferent, connections with all parts of the CNS: the spinal cord, cerebellum, brain stem centers, all parts of the cerebrum (diencephalon, striatum, cerebral cortex, limbic system, etc.), projects to autonomic and motor nuclei of the brain and spinal cord, receives collaterals from sensory pathways.

The RF is an important integrative system of the CNS, which takes part in the ***regulation of motor, visceral, sensory functions, and the cerebral cortex activity***:

1. The RF controls complex motor and visceral activities by influencing motor and autonomic neurons of the spinal cord and cranial nerves:

– regulates *motor activity of the body, i.e. muscle tone for automatic control of posture and locomotion,* by inhibiting (medullary RF) or activating (pontine RF) motor neurons of the spinal cord, acting through the reticulospinal tracts;

– integrates activity of motor and autonomic neurons of the spinal cord and cranial nerves for *complex reflex responses to stimuli*, such as swallowing, vomiting, coughing, sneezing, etc.;

– *regulates visceral functions*, such as respiration and circulation, salivation, micturition (bladder function).

The *cardiovascular center* in the medulla controls cardiac output, heart rate, and blood pressure through the sympathetic and parasympathetic centers of the brain and spinal cord.

The *respiratory centers* activate “breathing” muscles through projections to the spinal motor neurons: 1) the center in the medulla initiate inspiration and expiration in response to O_2 or CO_2 blood levels; 2) the center in the pons adjusts the rhythm of breathing under the influence of cerebral cortex, limbic system, or hypothalamus.

2. The RF is a part of the *ascending reticular activating system (ARAS)*, which regulates the level of activity of the cerebral cortex. The ARAS includes collaterals of all sensory tracts (spinothalamic, trigeminal, visual, auditory, olfactory, etc.) to the neurons of the RF, which via the thalamic nuclei project to the cerebral cortex. Stimulation of the RF causes the state of wakefulness, alertness, and attention, its inhibition decreases the level of conciseness. Together with the hypothalamus, the RF plays role in *regulating sleep-wake cycle.*

3. Some RF nuclei *modulate pain and other sensory impulses*, suppressing their transmission in neurons giving rise to the spinothalamic and trigeminothalamic pathways.

4. Sensory stimulation of the RF, due to its connection with the limbic system, plays a role in the *regulation of mood, emotional behavior and visceral reactions*.

ADVANCED: The RF contains aminergic neurons, producing neurotransmitters — serotonin, dopamine, noradrenalin and adrenalin, which influence different areas and functions of the CNS. The neurons of the RF are mainly organized in three longitudinal cell columns on each side.

The *lateral,* parvocellular RF contains mainly small neurons. It receives collaterals from all sensory pathways, including somatic pathways from the spinal cord and trigeminal nerve nuclei and all special sense pathways. The lateral RF predominantly projects into the paramedian RF.

The *paramedian,* magnocellular, RF contains large neurons that send long axons to the brain and spinal cord and are involved in the regulation of motor functions (Fig. 33, *b*). The magnocellular nuclei give rise to efferent pontine and medullary reticulospinal tracts and mediate activity of motor nuclei of the cranial nerves.

The *median* RF forms raphe nuclei, located along the midline, which contain mainly serotonergic neurons. The raphe nuclei have reciprocal relationships with different parts of the CNS, including the limbic system and multiple cortical areas. They are involved in the regulation of mood, aggression, cognitive functions, sleep-wake cycle, and modulation of pain impulses at the level of the spinal cord.

DIENCEPHALON

The diencephalon is a part of the *prosencephalon (forebrain)* that extends from the midbrain to the telencephalon and almost completely surrounded by the cerebral hemispheres. The main subdivisions of the diencephalon are the following: the paired thalami, the epithalamus, the hypothalamus, the subthalamus, and the diencephalon cavity, the 3^{rd} ventricle (Fig. 34, 35).

THALAMUS

The thalamus is the main subcortical sensory center, which relays information from sensory pathways to the cortex, a relay center connecting many subcortical structures of the brain with the cortex, as well as a relay between different cortical regions.

External structure of thalamus

The **thalamus** is an oval egg-shaped body of grey matter, covered by a thin layer of white matter. The narrow anterior pole of the thalamus, the **anterior thalamic tubercle**, ends at the interventricular foramen, the wide posterior pole, the **pulvinar**, reaches the midbrain (Fig. 34). The *dorsal surface* of the thalamus forms the floor of the lateral ventricle and is adjacent laterally to the telencephalon — the stria terminalis and caudate nucleus. In the depth of the brain, the *lateral aspect* of the thalamus is adjacent to the internal capsule composed of white matter. A fascicle of nerve fibers, the **stria medullaris of thalami,** courses above the *medial surface* of the thalamus, which forms the lateral wall of the 3rd ventricle. Here, both thalami are frequently connected by the **interthalamic adhesion (massa intermedia)**. *Inferiorly*, the thalamus continues with the hypothalamus and the subthalamus (Fig. 35).

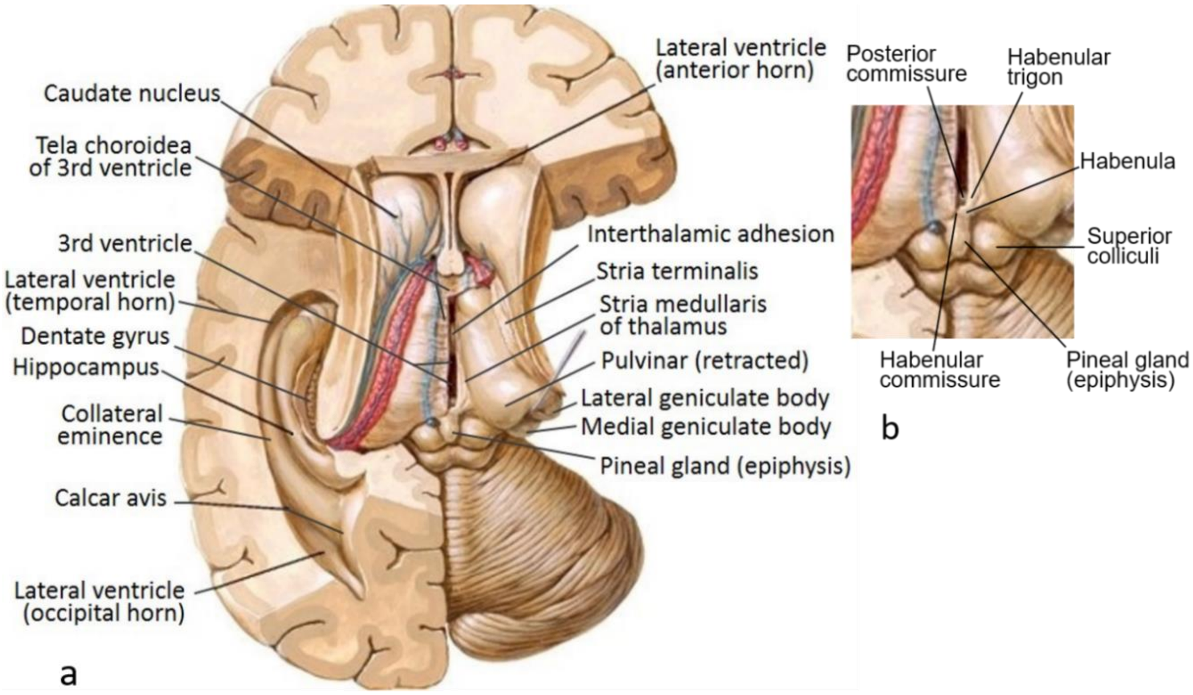

Fig. 34. Diencephalon: thalamus, epithalamus (b — enlarged), and third ventricle (superior view); lateral ventricle of telencephalon

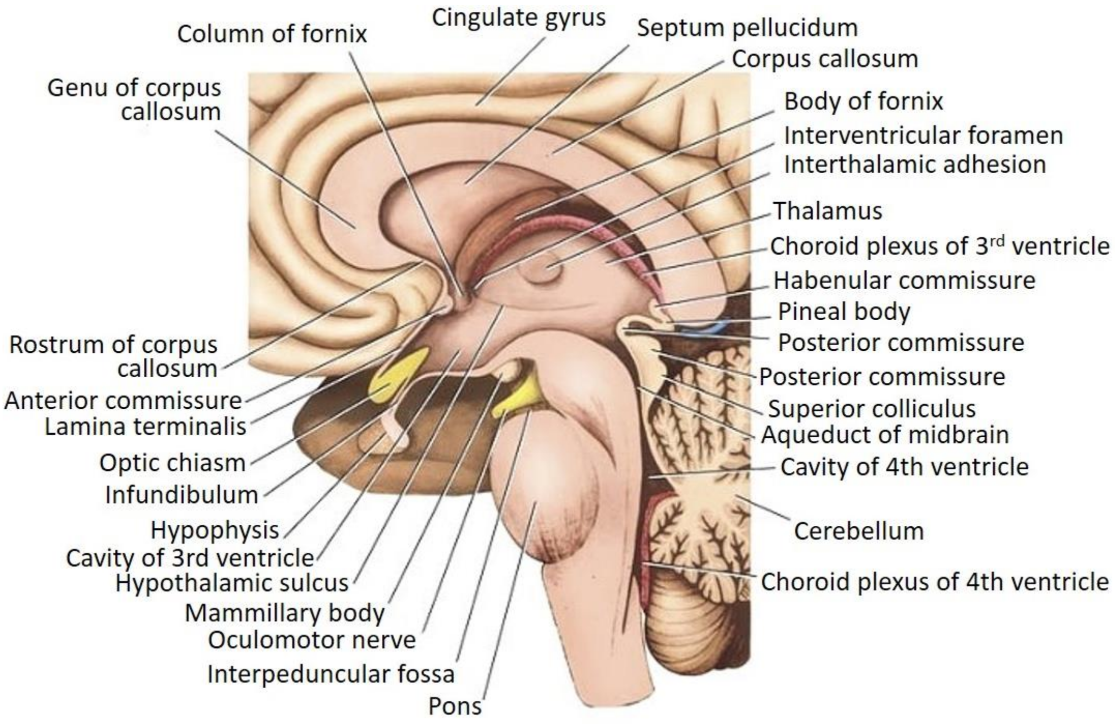

Fig. 35. Diencephalon and third ventricle (median sagittal section of the brain)

Two geniculate bodies, also called the **metathalamus**, lie ventrolateral to the pulvinar of thalamus (Fig. 30, 34). The **lateral geniculate body** is an elongated structure, the posterior extension of the optic tract. It is a subcortical visual center projecting to the cerebral cortex. Via the brachium of superior colliculus, it is connected with the superior colliculus of the midbrain. The **medial geniculate body** is a well-defined oval body, the auditory center. It receives the acoustic fibers from the inferior colliculus via the brachium of inferior colliculus.

Internal structure of thalamus

Within the thalamus, the grey matter is divided by the Y-shaped **internal medullary lamina** of white matter into three main groups of nuclei: **lateral** (the largest), **medial**, and **anterior nuclei**. Each group is subdivided into smaller groups and nuclei with different connections and functions (Fig. 36, Table 1). Several groups of cells, the **intralaminar nuclei**, are embedded within the internal medullary lamina. The narrow **reticular nucleus** is separated from the lateral surface of the thalamus by the external medullary lamina.

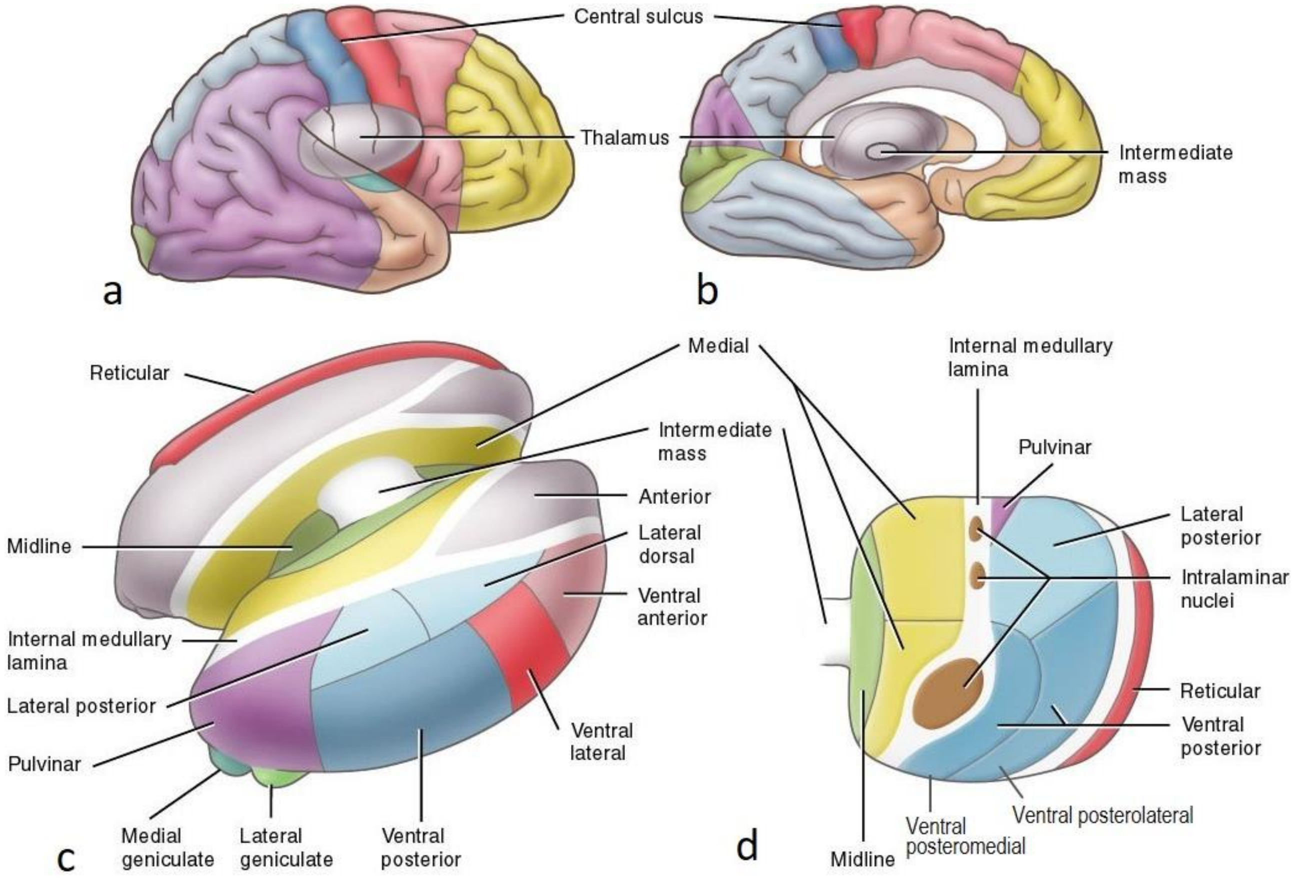

Fig. 36. Nuclei of the thalamus and thalamocortical relationships:
a — lateral view of right cerebral hemisphere; *b* — medial view of left cerebral hemisphere; *c* — superolateral view of thalamus showing locations of thalamic nuclei; *d* — transverse section of right thalamus

The thalamic nuclei are of 3 main types:

1. The *specific relay nuclei*, which receive impulses from the somatic and special sensory pathways, motor centers, and relay them to specific functional cortical areas, such as the primary sensory areas, or motor areas (e.g., ventral posterior nuclei — VPL and VPM, lateral and medial geniculate nuclei, ventral anterior and lateral nuclei of the lateral group).
2. *Nonspecific nuclei*, which receive afferent impulses usually after passage through the RF, they project to numerous cortical regions and are involved in consciousness and attention (e.g., intralaminar and reticular nuclei).

3. *Association nuclei*, which receive a majority of their input from the cerebral cortex and project to other cortical association regions (e.g., anterior and pulvinar nuclei, medial nuclei).

Table 1

Major nuclei of the thalamus

Nuclei	Function and connection
Anterior nuclei	Part of limbic system, project mainly to cingulate and parahippocampal gyri; role in emotional states, attention, memory
Lateral nuclei	
Ventral anterior and lateral nuclei	Relay information from cerebellum and basal nuclei to motor areas of cerebral cortex
Ventral posterior nuclei: Ventral posterolateral nucleus (VPL) Ventral posteromedial nucleus (VPM)	Relays sensory information from the body and limbs to somatosensory cortex of parietal lobe Relays sensory information, including taste sense, from head to somatosensory cortex of parietal lobe
Pulvinar nuclei	Have reciprocal connections with many cortical regions; integrate somatosensory, visual and auditory input from the cortex for projection to association areas of cerebral cortex for spatial orientation; Relay visual information from retina and superior colliculi for directing visual attention
Lateral dorsal nuclei Lateral posterior nuclei	Relay visual information from pretectum and superior colliculi to limbic system and parietal association cortex Relay information between superior colliculi and superior parietal lobe, projects to limbic cortex
Nuclei of geniculate body (metathalamus):	
Lateral geniculate nucleus Medial geniculate nucleus	Projects visual information to visual cortex Projects auditory information to auditory cortex
Medial nuclei Mediodorsoal nuclei (*syn.* dorsomedial nuclei)	Integrate sensory and other information, arriving from primary olfactory cortex, amygdala, other cortical regions, and relay it mainly to the prefrontal association cortex and limbic cortex; influence emotional state, attention, crucial role in memory and cognition, planning, organization, abstract thinking
Intralaminar nuclei	Receive visceral and pain information from RF and send it to multiple cortical and subcortical regions; involved in arousal
Reticular nucleus (not a part of the RF)	Receives inputs from other thalamic nuclei and the cerebral cortex and projects back to thalamus. Modulates activity of thalamus nuclei and filters signals to associated areas of cortex; amplifies important, or suppress unnecessary signals

ADVANCED: FUNCTIONS: The thalamus is the main subcortical sensory and integrating center, which serves as the “gateway” of the cerebral cortex:

– *Relays all sensory information to the cerebral cortex* (special sensory, proprio- and exteroceptive, except olfaction) — filters, sorts sensory signals, and sends them to appropriate regions of the cortex. The thalamus itself provides crude awareness of sensation, and, if damaged, can be a source of pain;

– *Transmits signals between subcortical (cerebellum and basal nuclei) and cortical motor centers* — takes part in motor control;

– *Relays information from the reticular formation to the cerebral cortex* — activates the cerebral cortex and regulates states of consciousness and alertness;

– *Transmits signals between the limbic subcortical structures and limbic cortex* — is involved in emotions, instinctive drives, memory formation;

– *Transmits information between regions of the cerebral cortex, including the prefrontal cortex* — is involved in higher mental activity (attention, planning, abstract thinking etc.).

EPITHALAMUS

The **epithalamus** is a small region immediately rostral to the midbrain tectum (Fig. 34, 35). It consists of the habenular structures, adjacent to the pineal gland lying between the superior colliculi. The **pineal gland** (*syn.* **epiphysis cerebri**, **pineal body**) is an endocrine gland that secretes the hormone melatonin involved in the regulation of the sleep-waking (circadian) cycle. A thing cord, the **habenula**, connects each side of the pineal gland with the **habenular trigon**. The **habenular commissure** connects the right and left habenulae. The habenular trigon contains the **habenular nuclei**[9], which through the stria medullaris of thalami, have connections with the limbic system.

SUBTHALAMUS

The **subthalamus** (*syn.* ventral thalamus) corresponds to an area of the lateral wall of the 3rd ventricle, located below the posterior segment of the hypothalamic sulcus (Fig. 35). It contains nerve fibers of various pathways that terminate in the thalamus and the **subthalamic nucleus** (*syn.* corpus of Luys). The subthalamic nucleus connects with the substantia nigra and globus pallidus and is involved in motor functions associated with the basal ganglia.

HYPOTHALAMUS

The **hypothalamus** is the most ventral part of the diencephalon that forms the floor and lateral walls of the 3rd ventricle below the anterior parts of the hypothalamic sulci. The hypothalamus contains a **number of nuclei** and **bundles of fibers** within the walls of the 3rd ventricle. It also includes structures visible at the base of the brain that are listed below (front to back) (Fig. 35, 37):

– **optic chiasm**, the decussation of the optic nerves fibers that continue as the **optic tracts** to the lateral geniculate bodies;

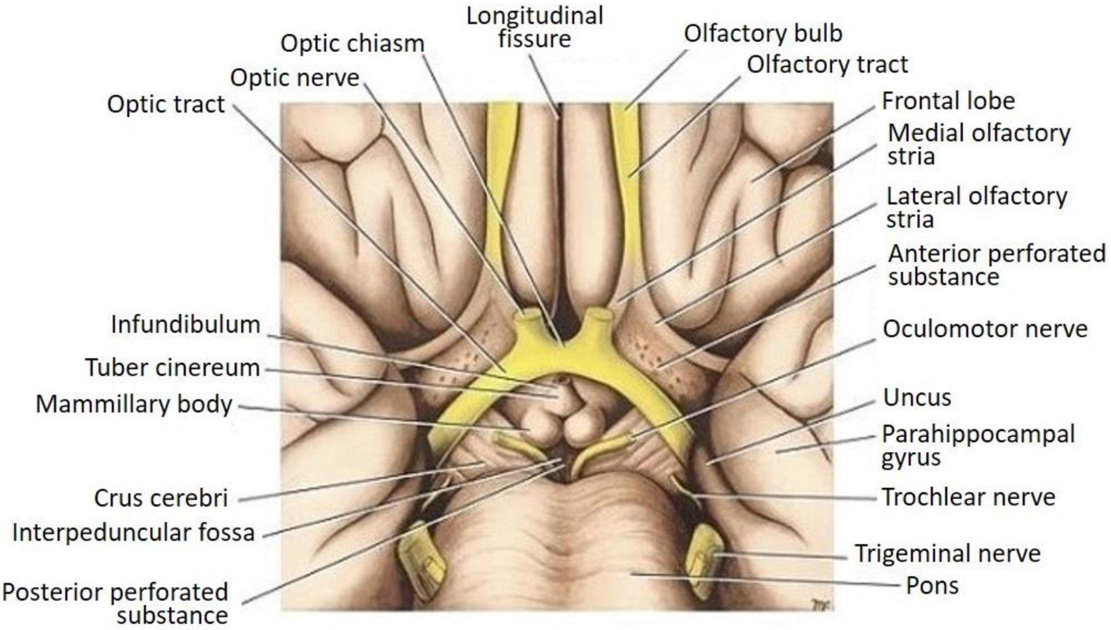

Fig. 37. Inferior surface of the brain in the region of diencephalon (hypothalamus) and midbrain

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[9] The habenular nuclei relay impulses from the limbic system and hypothalamus to the brainstem centers playing a role in motor activity; they are involved in emotional and cognitive behavior, as well as regulation of the sleep-wake cycle.

– **tuber cinereum**, a small elevated area, with a thin hollow structure, the **infundibulum** [**pituitary stalk**], attached below to the **pituitary gland,** or **hypophysis**[10];

– **mammillary bodies** (containing *mammillary nuclei*), two rounded elevations, which are part of the limbic system, connected by the fornix with the hippocampus;

– **posterior perforated substance**, an area of grey matter between the cerebral peduncles, transmitting small branches of the posterior cerebral arteries.

The hypothalamus has extensive connections with most parts of the CNS — the spinal cord, brainstem, cerebral cortex and limbic system of the forebrain, as well as with the central organ of the endocrine system — the hypophysis.

FUNCTIONS: Through numerous connections, the hypothalamus integrates sensory stimuli from the internal and external environment and responds by regulating and integrating functions of the endocrine system, autonomic nervous systems, and somatic motor behavior. This allows maintaining the body homeostasis and makes the hypothalamus the principal part of the autonomic nervous system.

The nuclei of the hypothalamus perform the following functions:

– Control of the autonomic (sympathetic and parasympathetic) nervous system and regulation of visceral functions, such as heart rate and blood pressure, digestion, respiratory tracts, glands secretions, and other visceral activities;

– Control of endocrine system: regulation of hormone production in the adenohypophysis by secreting releasing or inhibiting hormones (the hypophysis, in turn, controls function of other endocrine glands);

– Production of hormones oxytocin and antidiuretic hormone (ADH, vasopressin), which through the neuron axons reach the neurohypophysis, where enter the blood circulation;

– Regulation of the body temperature; food intake: hunger and satiety; thirst sensations and water balance (release of ADH);

– Control of emotional reactions, motivational behavior (e.g., sexual and feeding behaviors), stress-response (hypothalamus is executive center of the limbic system);

– Regulation of sleep-awake cycle;

– Formation of memory (mammillary bodies).

ADVANCED: The hypothalamus receives afferents stimuli via receptors for circulating hormones and through neural connections with the limbic system, olfactory lobe, retina, cerebral cortex, thalamus, brain stem and spinal cord. The main efferent connections include the pituitary gland, autonomic centers of the brainstem and spinal cord, thalamus, cerebral cortex, and limbic system, through which the hypothalamus regulates the endocrine, autonomic, and somatic motor systems.

The nuclei of the hypothalamus are subdivided in the mediolateral direction into the *periventricular zone* — a thin layer of neurons, mainly involved in regulation of the endocrine system; *medial zone* containing most of the nuclei; and the *lateral zone,* which mainly contains one large nucleus (Fig. 38). The medial and lateral zones are separated by the columns of fornix.

In the anteroposterior direction, **3 regions** are distinguished: 1) **anterior** (supraoptic) — above the optic chiasm; 2) **intermediate** (middle, or tuberal) — includes the infundibulum, tuber cinereum and the area above it; 3) **posterior** (mammillary) — the mammillary body and the area above it. The **preoptic area** (nuclei) is a region adjoining the lamina terminalis anterior to the hypothalamus, located at the junction of the diencephalon and telencephalon (Fig. 38, Table 2).

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[10] The pituitary gland remains in the sella turcica under the plate of dura mater — the diaphragma sellae, which has aperture for the infundibulum to passes through.

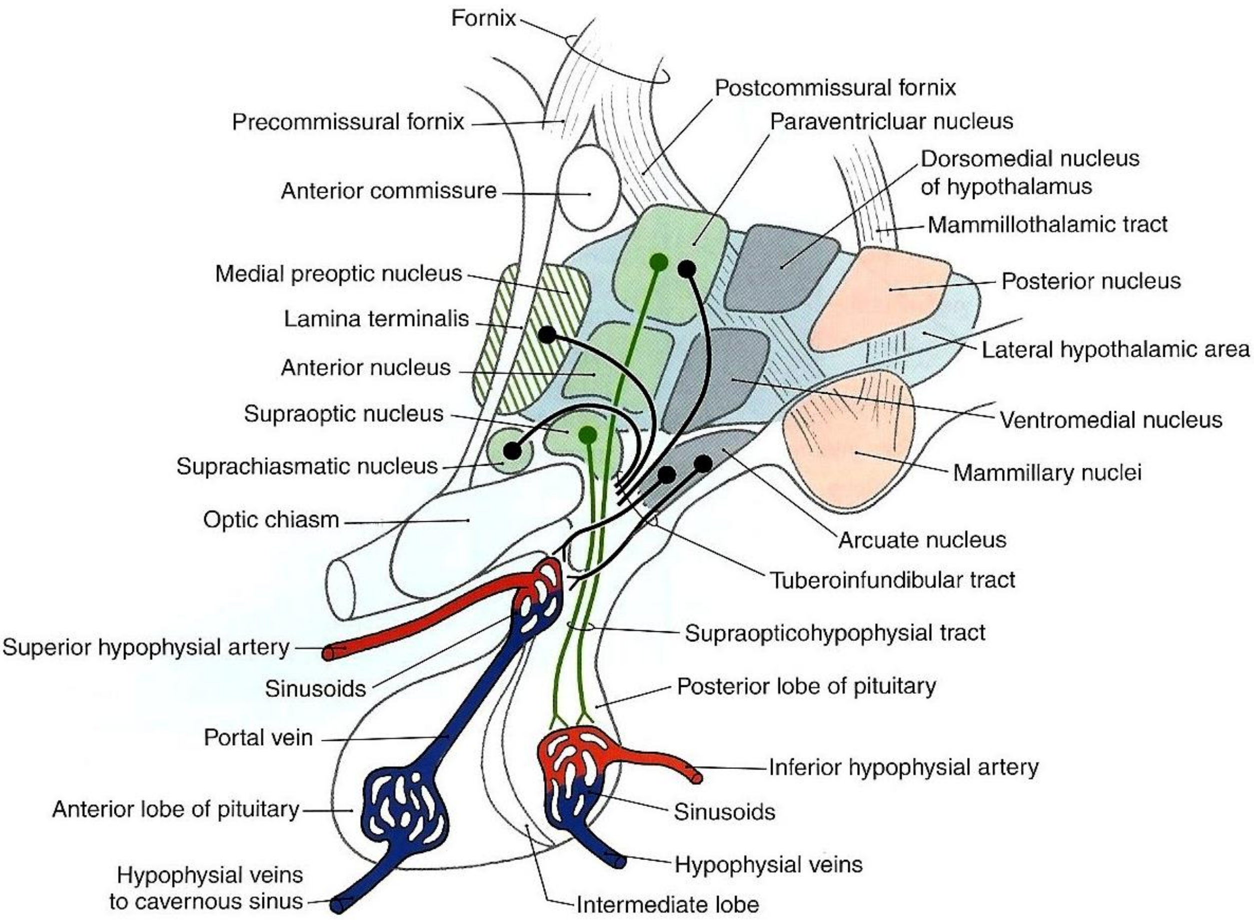

Fig. 38. Major hypothalamic regions and their nuclei (view from the cavity of the third ventricle): anterior (green), intermediate (gray), and posterior (pink) regions

Table 2

Hypothalamic nuclei and their main functions

Region/nucleus	**Main function**
	Anterior region
Preoptic nuclei: anterior, posterior	Thermoregulation — reduce temperature of the body by sweating, dilating skin capillaries, quick breaths; Regulate secretion of GnRH*, which controls sexual development and functions; Have receptors to testosterone: regulate sexual and stress behavior; Stimulate parasympathetic nervous system
Nuclei: 1) Supraoptic 2) Paraventricular	Secrete hormones that are accumulated in the neurohypophysis: 1) antidiuretic hormone (AD), regulates water balance reducing water loss at the kidneys; 2) oxytocin, stimulates contraction of the uterus and mammary gland ducts
Suprachiasmatic nucleus	Regulates circadian (daily) rhythms, i.e. hormone secretion and behavior according to the light input from the retina, and regulates sleep-wake cycle together with the pineal gland
Anterior hypothalamus	Stimulates parasympathetic nervous system projecting axons to autonomic nuclei in the brain stem and spinal cord
	Middle region
Arcuate nucleus (Tuberal area)	Produces releasing and inhibitory hormones that control release of adenohypophysis hormones
Dorsomedial nucleus	Stimulates gastrointestinal tract (plays role in obesity); Controls mood, fear and rage behavior, sexual activity
Ventromedial nucleus	Regulates feeding behavior: satiety center, which decreases eating

End of the Table 2

Region/nucleus	Main function
Lateral hypothalamus/zone	
Lateral nucleus	Hunger center, which increases eating (lesion may cause anorexia)
Zona incerta**	Thirst center — controls the intake of water
Posterior region	
Mammillary body	Part of the limbic Papez circuit involved in memory
Posterior nucleus	Stimulates sympathetic nervous system projecting axons to autonomic nuclei in the brain stem and spinal cord; Thermoregulation — conserves heat
Tuberomammillary nucleus	Maintains awake state

* GnRH — gonadotropin releasing hormone; ** Zona incerta is located alongside the lateral nucleus.

THIRD VENTRICLE

A cavity of the diencephalon, the **3rd ventricle**, is a narrow cleft between the two thalami. It has superior, inferior, anterior, posterior and two lateral walls (Fig. 35, 39).

The *lateral wall* is formed by the medial surface of the thalamus and below it by the hypothalamus.

The *superior wall (roof)* is a thing membrane covering the cleft between the thalami, the **tela choroidea**. Its fringe-like projections form the **choroid plexus of third ventricle**. On both sides, through the gap between the fornix lying above the roof and the thalamus, the choroid plexus extends into the lateral ventricle (Fig. 39).

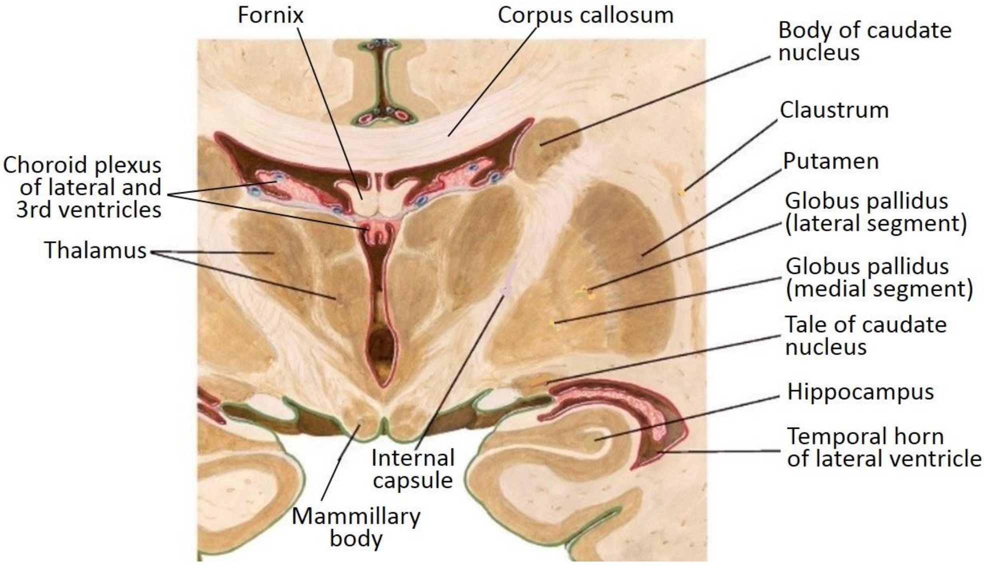

Fig. 39. Cavities of the 3rd ventricle and lateral ventricles in the frontal section of the hemispheres at the level of the mammillary bodies

The *anterior wall* comprises the paired **column of fornix**, the **anterior commissure** (a bundle of transverse fibers), and the **lamina terminalis** — a thin layer of brain tissue descending to the optic chiasm.

The *inferior wall (floor)* extends from the lamina terminalis to the aqueduct of midbrain (Fig. 35, 37). It is formed by the hypothalamic structures (front to back): the optic chiasm, tuber cinereum with the infundibulum and hypophysis, mammillary bodies, posterior perforated substance, and the cerebral peduncles of the midbrain. The inferior wall has two extensions: the **supraoptic recess** above the optic chiasm and the **infundibular recesses**.

The narrow *posterior wall* is formed by the epiphysis with the ***pineal recess,*** limited by two commissures: the **habenular commissure** above, and the **posterior** (**epithalamic) commissure** below.

The opening of the **cerebral aqueduct** lies under the posterior commissure and connects the 3rd and the 4th ventricles. The 3rd ventricle communicates as well with the lateral ventricles through the **interventricular foramina** (foramina of Monroe), located on both sides between the column of fornix and the thalamus.

TELENCEPHALON

The telencephalon is the largest part of the forebrain (prosencephalon). It consists of two **cerebral hemispheres** united by the thick sheet of transverse nerve fibers, the **corpus callosum**, which lies in the depth of the **longitudinal cerebral fissure**. The cerebral hemispheres are covered by a thin layer of grey matter, the **cerebral cortex**, or **pallium**. The ridges, **cerebral gyri**, and furrows, **cerebral sulci**, increase the area of the cortex. Nerve fibers beneath the cortex form the **white matter**. In the white matter of the hemispheres there are clusters of neurons — the **basal nuclei** (*syn.* **basal ganglia**) and cavities of the telencephalon, the **lateral ventricles**.

Structures of gray and white matter located superficially or deeply in the basal portions of the hemispheres, such as the **olfactory structures**, **amygdaloid body**, etc., are collectively referred to as the **basal forebrain** (*Lat.* Pars basalis telencephali)[11].

CEREBRAL HEMISPHERES AND LOBES. CEREBRAL CORTEX

Each cerebral hemisphere has three **margins**: superior, inferomedial, and inferolateral; three **surfaces:** superolateral, medial, and inferior; and three **poles**: **frontal**, **temporal**, and **occipital**, which are the blunt tips of the respective lobes of the hemispheres. Each hemisphere is formed by four big **cerebral lobes** — the **frontal**, **parietal**, **occipital**, and **temporal lobes**, and a small fifth lobe, the **insula**, which is not visible on the surface. Besides, certain cortical areas of the frontal, parietal and temporal lobes on the medial surface of the hemisphere compose the **limbic lobe** (Fig. 40, 41, 42).

The patterns of the cortical gyri and sulci vary from brain to brain, but some are sufficiently constant to serve as descriptive landmarks. Deep primary sulci divide the hemispheres into the lobes. The **lateral sulcus** (Sylvian fissure) separates the temporal lobe from the frontal and parietal lobes. It begins from the **lateral fossa** on the inferior surface of the hemisphere and runs backward along the superolateral surface. The **insula** lies in the depth of the lateral sulcus, covered with the **opercula** (lips), which are parts of the frontal, parietal and temporal gyri. The **central sulcus** (sulcus Rolandi) is a border between the frontal and parietal lobes. It runs vertically on the superolateral surface, between the **precentral sulcus** anteriorly and the **postcentral sulcus** posteriorly. The **parietooccipital sulcus** is a vertical groove on the medial surface of the hemisphere, located posterior to the corpus callosum. This sulcus and an imaginary line extending from it along the superolateral surface of the hemisphere are the boundaries of the occipital lobe.

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[11] The basal forebrain includes olfactory structures, anterior perforate substance and groups of nuclei: cholinergic magnocellular and septal nuclei, amygdaloid body, ventral pallidum, ventral striatum (nucleus accumbens) and some others.

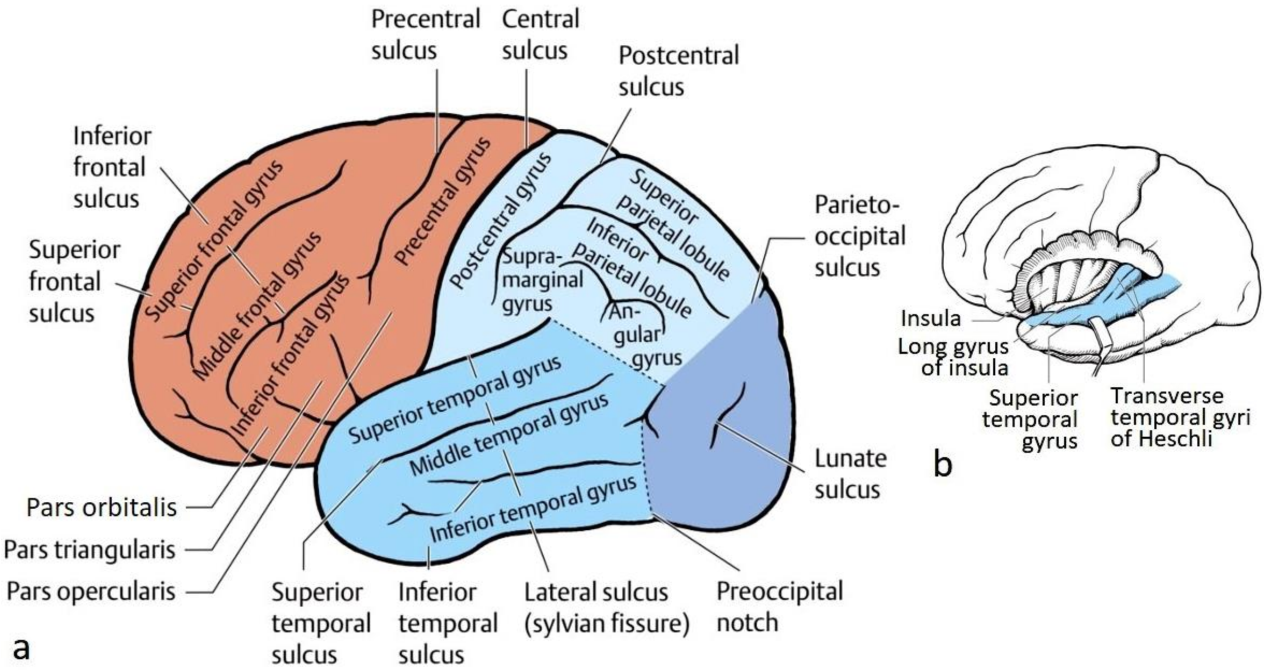

Fig. 40. Superolateral surface of the hemisphere:
a — gyri and sulci (red — frontal lobe; light blue — parietal lobe; blue — temporal lobe; violet blue — occipital lobe); *b* — insula and superior aspect of the superior temporal gyrus (revealed by dissection)

Superolateral surface of the hemisphere

The lateral surface of the ***frontal lobe*** contains the **precentral gyrus** bounded by the precentral sulcus in front and central sulcus behind (Fig. 40). Further forward, the longitudinally oriented the **superior** and **inferior frontal sulci** divide the **superior, middle,** and **inferior frontal gyri**. (The anterior and ascending rami of the lateral sulcus divide the inferior frontal gyrus into the orbital, triangular, and opercular parts.)

The ***parietal lobe*** contains the **postcentral gyrus**, lying between the central and postcentral sulci. Posterior to the postcentral gyrus, the parietal lobe is divided by the longitudinally oriented **intraparietal sulcus** into the **superior** and **inferior parietal lobules**. The part of the inferior parietal lobule surrounding the posterior end of the lateral sulcus is the **supramarginal gyrus**, the part capping the superior temporal sulcus is the **angular gyrus**.

The lateral surface of the **t*emporal lobe*** consists of the **superior, middle,** and **inferior temporal gyri** separated by the **superior** and **inferior temporal sulci**. The surface of the superior temporal gyrus facing the lateral sulcus forms the **transverse temporal gyri** (Heschl’s convolutions).

The lateral surface of the ***occipital lobe*** contains several inconstant occipital gyri.

Medial surface of the hemisphere

On the medial surface of the hemisphere below the cortex lies a massive band of white matter, the **corpus callosum** (Fig. 41). Its central part is the **body**, the posterior end is the **splenium**, and the anterior end is the **genu**, which narrows to form the **rostrum of corpus callosum**, reaching below the **anterior commissure**. The rostrum connects to a thin plate — the **lamina terminalis**, which limits the third ventricle in front and is attached to the optic chiasm below. The **septum pellucidum**, formed by two laminae with a cavity between them, is stretched between the rostrum and body of corpus callosum and the **body** and **column of fornix** lying below.

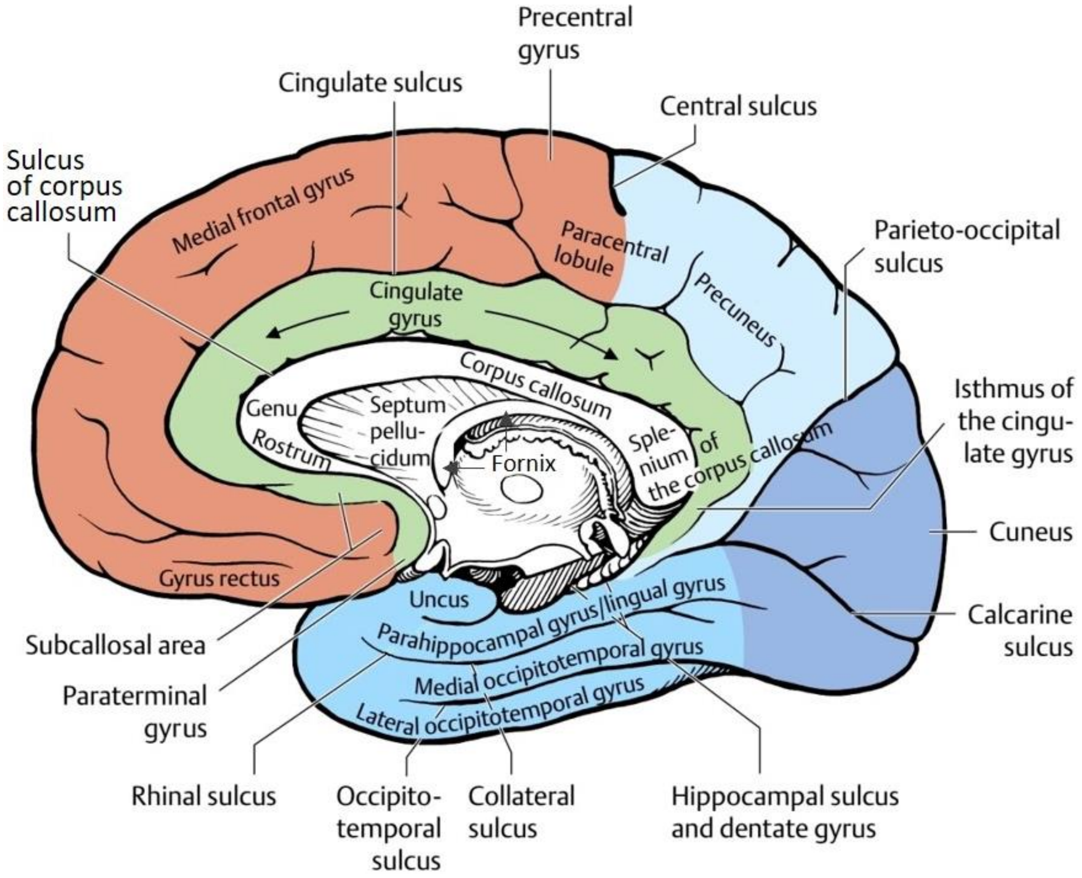

Fig. 41. Gyri and sulci on the medial surface of the hemisphere (red — frontal lobe; light blue — parietal lobe; blue — temporal lobe; violet blue — occipital lobe; green — limbic lobe)

The cerebral cortex is separated from the corpus callosum by the **sulcus of corpus callosum**. The **cingulate sulcus** runs parallel to the previous one. It starts anteriorly under the genu of corpus callosum, adjoining here the **subcallosal area** (lying below the rostrum of corpus callosum), and ends posteriorly on the superior margin of hemisphere. The **cingulate gyrus** lies between the sulcus of corpus callosum and the cingulate sulcus. Above the anterior segment of the cingulate sulcus is the **medial frontal gyrus**, which merges superiorly with the superior frontal gyrus. The small **paracentral lobule** lies behind the medial frontal gyrus, bounded posteroinferiorly by the end of the cingulate sulcus. The paracentral lobule surrounds the upper end of the central sulcus connecting the precentral and postcentral gyri.

An area, called the **precuneus**, lies between the cingulate and parietooccipital sulci, above the subparietal sulcus. The **cuneus** (“wedge”) is the triangular shape region of the occipital lobe between the parietooccipital sulcus and **calcarine sulcus**. The calcarine sulcus extends from the medial surface of hemisphere on the inferior surface.

Inferior surface of hemisphere

The inferior surface of the frontal lobe lies on the upper wall of the orbit (Fig. 42). It consists of irregular **orbital gyri**. The **olfactory sulcus**, containing the **olfactory bulb** and the **olfactory tract**, runs parallel to the inferomedial margin of hemisphere. The **gyrus rectus** extends medial to the olfactory sulcus.

The inferior surface of the temporal lobe is continuous with the occipital lobe (Fig. 41, 42). Along these lobes, three sulci run parallel to each other: 1) the **hippocampal sulcus**, the closest to the brain stem, continues posteriorly into the **calcarine sulcus**; 2) the **collateral**

sulcus lies more lateral, its anterior end is called the **rhinal sulcus**[12]; 3) the **occipitotemporal sulcus** lies closer to the lateral border of hemisphere. The hippocampal and collateral sulci are borders of the **parahippocampal gyrus.** The anterior end of the parahippocampal gyrus curves backward and forms the hook-shaped **uncus**. The posterior end continues with the **lingual gyrus** lying between the collateral and calcarine sulci. The occipitotemporal sulcus separates the **medial** and **lateral occipitotemporal gyri**.

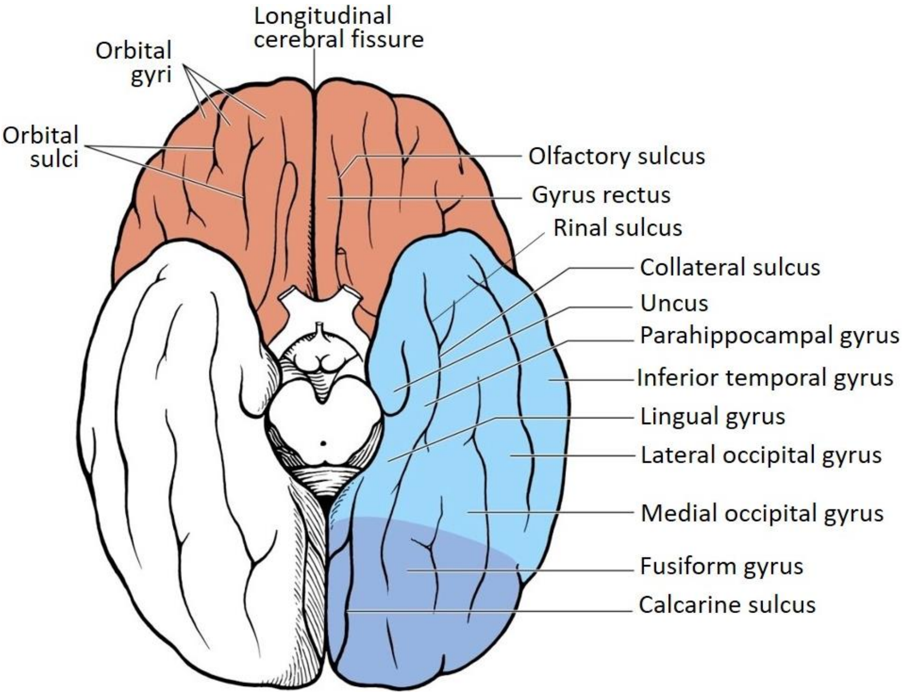

Fig. 42. Gyri and sulci on the inferior surface of the hemisphere (red — frontal lobe; blue — temporal lobe; violet blue — occipital lobe)

A narrow region behind the splenium of corpus callosum, the **isthmus**, connects the parahippocampal gyrus with the cingulate gyrus; together they are known as **fornicate gyrus**.

Limbic lobe

The limbic lobe is a C-shaped region of the cortex on the medial surface of the hemisphere functionally related to the limbic system. It includes areas of the frontal, parietal, and temporal lobes. The main structures of the limbic lobe are the **cingulate** and **parahippocampal gyri, uncus, hippocampus, dentate gyrus**, and **subcallosal area** (Fig. 41, 43).

The **hippocampus** (*syn.* **hippocampal formation**) is formed by the temporal cortex, which folds along the hippocampal sulcus into the temporal (inferior) horn of the lateral ventricle (Fig. 34, 43). The hippocampus, which means "seahorse", was named because of the curved shape, which its body has in the coronal section. The hippocampus consists of the **cornu ammonis**, or **hippocampus proper**, an elevation along the inferomedial wall of the temporal horn, the **dentate gyrus**, a notched band in the depth of the hippocampal sulcus, and the wall of this sulcus (subiculum). The fibers emerging from the hippocampus form a band along its medial edge — the **fimbria of hippocampus**, which is posteriorly continues with the crus of fornix.

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[12] The rhinal sulcus separates the *entorhinal cortex,* which is an anterior part of the parahippocampal gyrus, and the located laterally *perirhinal cortex*.

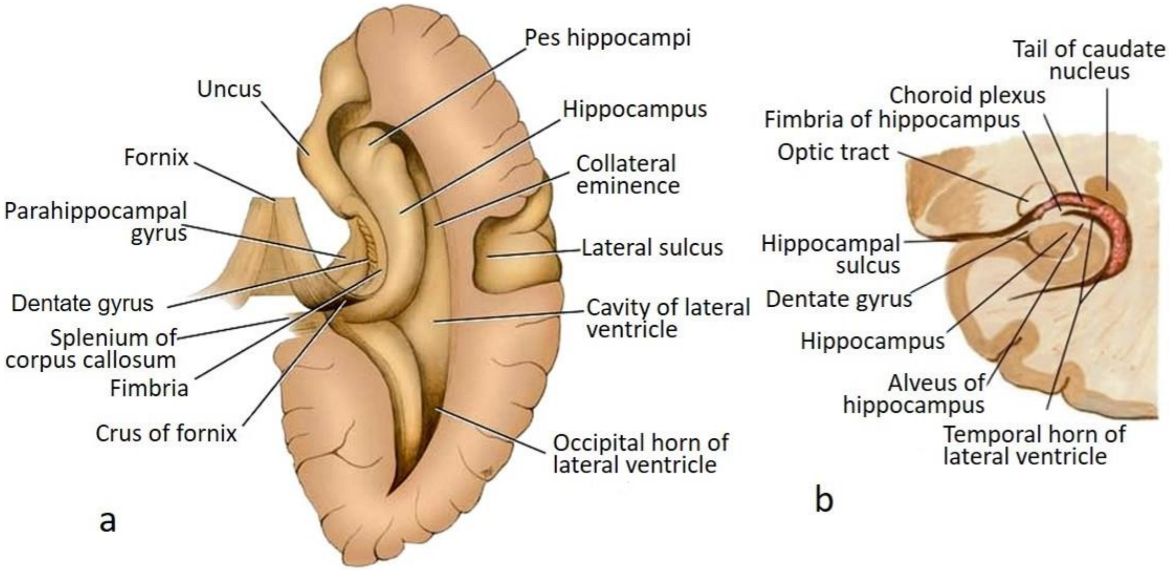


Fig. 43. Hippocampus (of the right hemisphere):
a — in the cavity of the lateral ventricle; *b* — in the coronal section through the temporal horn

Structure of cerebral cortex

The **cerebral cortex**, or **pallium,** is a thin layer of gray matter (2–4 mm) covering the surface of the cerebral hemispheres. A small subcortical area of the pallium, the **claustrum**, lies in the white matter deep to the insular cortex. Most of the cortex, approximately 90 %, is the *neocortex*, which generally consists of 6 layers of different shape neurons (Fig. 44). The phylogenetically older and simpler organized *allocortex* includes the olfactory and limbic cortices (3–5-layered *paleocortex*), and the hippocampus (3-layered *archicortex*).

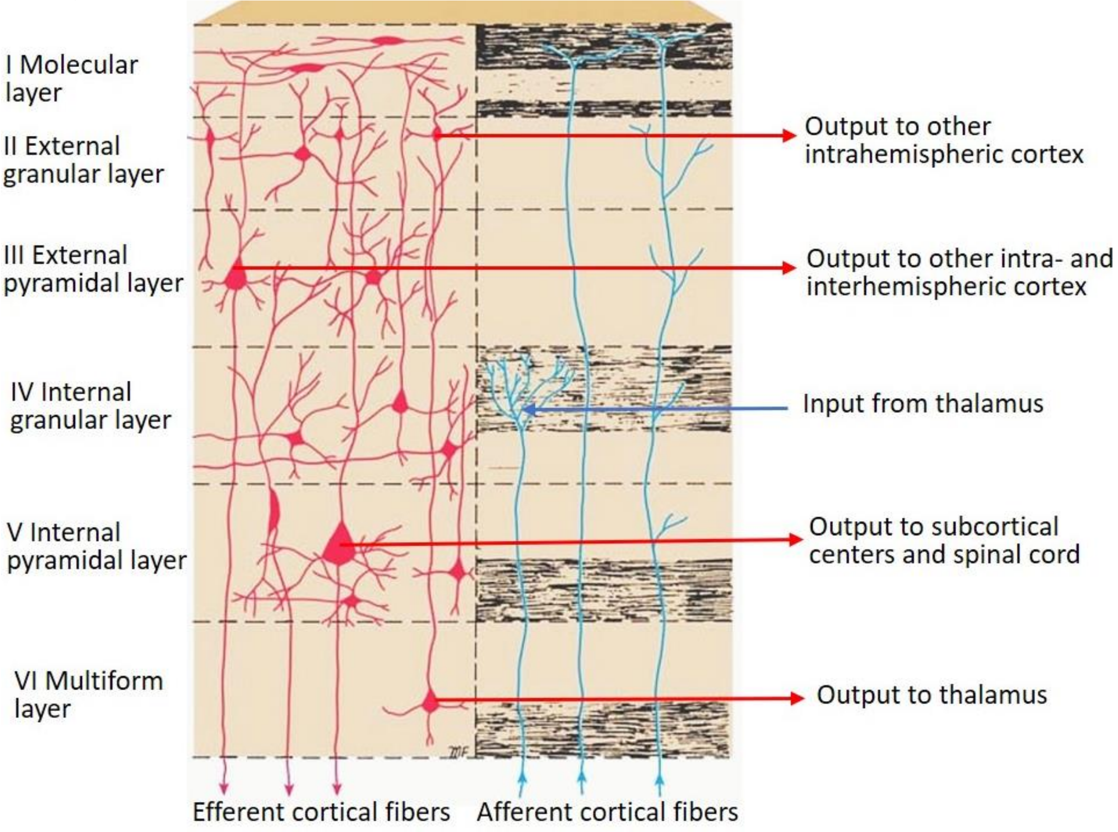


Fig. 44. The layers of the neocortex showing the neurons and the nerve fibers (on the right)

ADVANCED: The following layers are commonly distinguished in the neocortex of the adult brain:

1. **Molecular layer:** contains few cells, but many fibers, connects with apical dendrites of the pyramidal cells and non-specific nuclei of the thalamus.
2. **External granular layer:** contains small granular cells, receives information from other cortical regions.
3. **External pyramidal layer:** contains larger pyramidal cells; their axons direct to the white matter to connect with other cortical regions.
4. **Internal granular layer:** contains mainly small, granular cells, numerous in the primary sensory cortex, which receive input from the thalamus.
5. **Internal pyramidal layer:** contains medium or large pyramidal cells (in the precentral gyrus, 3–4 % are the giant pyramidal cells of Betz) that project out of the cortex to the striatum, brainstem and to the spinal cord through the pyramidal tracts.
6. **Multiform layer:** contains cells of many shapes (triangular and fusiform) that project to the thalamus and connect with other cortical regions.

The arrangement of cells and fibers, the thickness of the layers vary in different locations of the cerebral cortex. Based on the structural differences, about 52 areas (Brodmann's areas) of the cerebral cortex were defined, which are presented in the form of the cytoarchitectonic (Brodmann's) map (Fig. 45). The map is used to designate the functional areas of the cortex. In particular, in the case of primary cortical areas, there is a good correspondence between the Brodmann's areas and the localization of cortical functions.

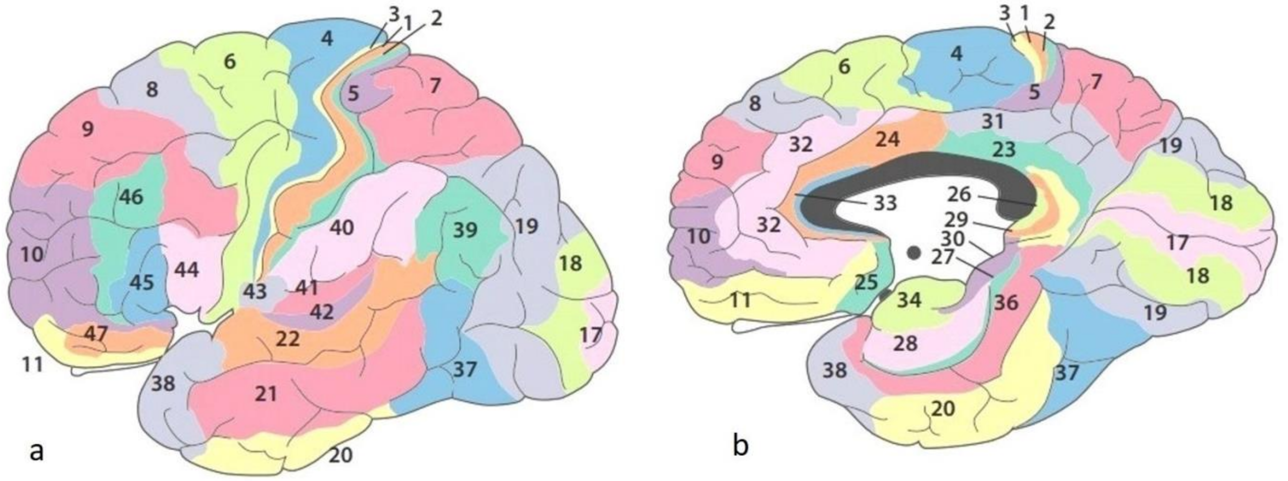


Fig. 45. Cytoarchitectonic map of the cerebral cortex:
a — lateral view; *b* — medial view

Functional areas of cerebral cortex

The cerebral cortex is the highest information processing center that allows people to be aware of themselves and their sensations, provides the highest level of motor control by initiating voluntary movements, and is the site of conscious thought processes, memory and all intellectual functions. In accordance with these functions, the following functional areas of the cerebral cortex can be distinguished (Fig. 45, 46):

1. **Primary sensory areas** receive and process sensory information and make us aware about sensations without their interpretation.
2. **Primary motor areas** initiate impulses that cause voluntary contraction of skeletal muscles.
3. **Association areas** (**unimodal association areas**) are adjacent to primary ones and process information derived from, or travelled to, the primary areas:

– **Sensory association areas** (secondary sensory areas) compare a new sensory input with memories of the previous experience to interpret and identify an object or signal;

– **Motor association areas** integrate information from extrapyramidal centers, cortical sensory areas and primary motor areas to plan and coordinate complex motor actions.

4. **Integrative areas** (**multimodal association areas**) process and analyze information from multiple primary and association areas of the cortex, perform abstract intellectual and higher psychic functions (e.g., speech, calculation, judgment), plan complex patterns of movements, control social behavior.

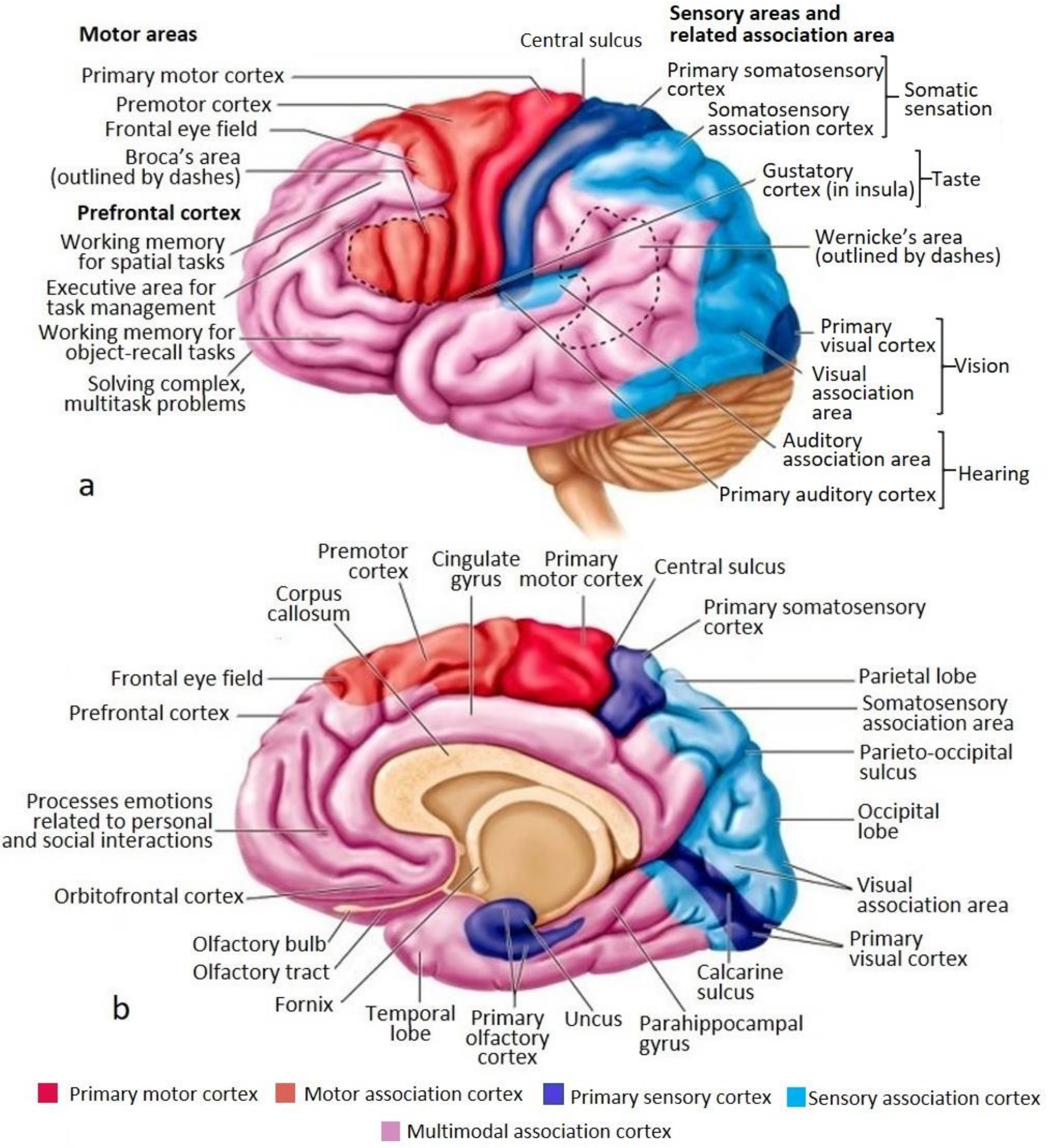


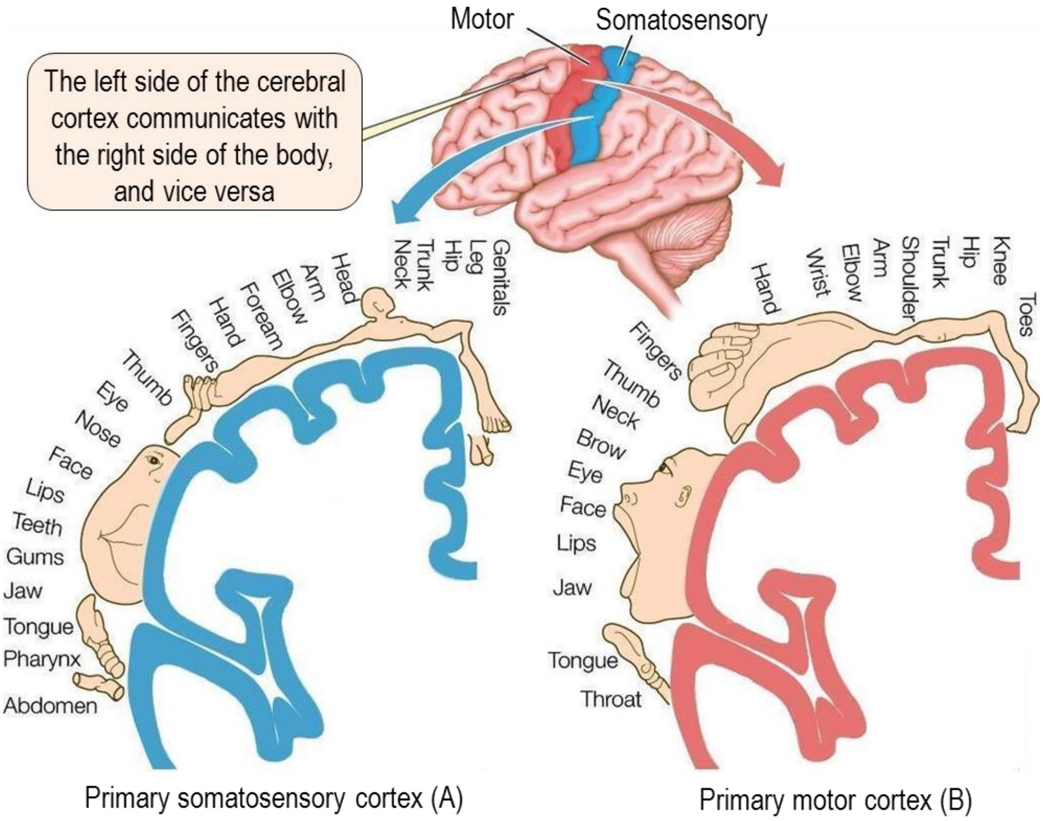
Fig. 46. Functional areas of the cerebral cortex:
a — lateral; *b* — medial view of the hemisphere

Primary sensory and motor areas of the cortex

Primary sensory areas are regions of the sensory systems that receive sensory inputs from the thalamus — general somatic senses (skin sensations and proprioception), vision, hearing, balance, and taste. Only olfactory information bypasses the thalamus.

The **primary somatosensory cortex** corresponds to the postcentral gyrus and the posterior part of the paracenrtral lobule (areas 3, 1, 2). It is concerned with conscious awareness of general sensation coming from skin receptors (pain, temperature, touch, and pressure) and proprioceptors (sense of vibration and position of the body parts), involved in spatial discrimination, i.e. two-point tactile sense.

The postcentral gyrus receives sensory input from the contralateral side of the body in a precise somatotopic (point-to-point) pattern. The projection of body parts onto the postcentral gyrus is inverted: the head is projected onto its lower part, the hand — onto the middle part, the torso — onto the upper part, and the lower limb is projected onto the paracentral lobule (Fig. 47).



The left side of the cerebral cortex communicates with the right side of the body, and vice versa

Fig. 47. Representation of the body parts in the precentral and postcentral gyri:
A — primary somatosensory cortex; *B* — primary motor cortex

Lesion: affects sensation on the opposite side of the body, in particular, perception of pain, temperature, and touch, two-point tactile discrimination, and proprioception.

The **primary visual cortex** is an area on the medial surface of the occipital lobe surrounding the calcarine sulcus (area 17) and responsible for visual perception of shape, color, intensity and movements of visual stimuli. It receives afferent fibers from the lateral geniculate body of the same side, carrying impulses from the homonymous halves of the retina of both eyes, that is, from the contralateral visual fields of both eyes. Thus, the left visual fields of both eyes are represented in the right hemisphere, and the right visual fields — in the left hemisphere.

Unilateral lesion: causes blindness in the contralateral visual fields (contralateral hemianopsia).

The **primary auditory cortex** is located in the superior temporal gyrus, in the transverse gyri of Heschl (area 41), most of which are hidden in the lateral fissure (Fig. 40, *b*). It receives afferents from the medial geniculate body and is concerned with the conscious perception of sounds.

Unilateral lesion: causes only partial deafness in both ears and a decrease in the perception of sound direction, due to a partial (not complete) decussation of acoustic fibers in the brainstem and, hence, their bilateral projections.

The **primary gustatory** (taste) area is located near the face area of the somatosensory cortex — above the lateral sulcus in the frontoparietal operculum (area 43) and in the anterior insula. Association areas give subjective awareness of flavor (in the insula) and are involved in identifying different tastes and feeling of their reward value (in the orbitofrontal cortex).

The **olfactory areas**, related to the sense of smells, include the uncus and the adjacent cortical region posterior to it (areas 34 and 27). The highest association olfactory area, responsible for identifying a variety of odors, is located in the posterior part of the orbitofrontal cortex.

Lesions: cause hyposmia, anosmia, olfactory agnosia.

The **vestibular areas** are bilateral and more diffuse than other sensory areas. They are mainly located in the parietal lobe at the beginning of the intraparietal sulcus and other regions within the somatosensory cortices, as well as in the temporo-parietal cortex, and in the posterior insula. These regions receive vestibular, exteroceptive, proprioceptive, and visual motion stimuli.

Lesions of the parietal areas can lead to confusions in spatial orientation.

The **primary motor area** occupies the precentral gyrus and the anterior part of the paracentral lobule (area 4). It controls voluntary movements, sending direct motor commands to the skeletal muscles of the opposite side of the body (and to some ipsilateral muscles of the trunk and face). Similar to the postcentral gyrus, the body parts in the precentral gyrus are represented in the inverted fashion (Fig. 47).

Lesion: results in muscle weakness or paralysis in the opposite side of the body.

Association areas of the cortex

The **somatosensory association area** is located in the superior parietal lobule posterior to the primary somatosensory cortex (area 5). It is responsible for interpretation of the general somatic sensory information (e.g., object size, texture, and shape), which is necessary for recognition of an object by touch.

Lesion: affects the ability to understand the somatic stimuli and recognize objects by touch (astereognosis, or tactile agnosia), usually affecting the opposite side of the body.

The **visual association area** occupies the occipital lobe (areas 18 and 19) adjacent to the primary visual cortex. It is concerned with the interpretation of visual images and their recognition.

Lesion: visual agnosia, i.e. deficit in recognition of visual objects, written or printed words (alexia), colors, faces, etc.

The **auditory association area** surrounds the primary auditory cortex in the superior temporal gyrus (areas 42, 22). It is responsible for the interpretation and recognition of auditory stimuli.

Lesion: auditory agnosia, i.e. the inability to recognize the significance of sounds.

The **sensory speech area** (**Wernicke's area**), responsible for language comprehension, is located in the dominant hemisphere in the posterior part of the superior temporal gyrus (area 22), and usually includes adjacent parts of the inferior parietal lobule (areas 39 and 40).

Lesion: inability of understanding spoken words (sensory aphasia), which also affects control over one's own speech[13]. Involvement of the inferior parietal lobule additionally causes difficulty in reading and writing.

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[13] Association areas related to the language function, according to the theory of I. P. Pavlov's (1932), belong to the 2nd signal system, in contrast to the 1st signal system dealing with the nonverbal stimuli.

The **posterior parietal association cortex** (area 5, 7) is located in the superior parietal lobule posterior and inferior to the somatosensory cortex. It is responsible for the orientation of a person in space, understanding the position of body parts ("body image"), feeling one's own body and awareness of the contralateral half of the body. This area (mainly in the left hemisphere) contributes, together with motor areas, in planning and execution of purposeful actions with objects and tools, learned motor skills.

Lesions: cause apraxia — inability to perform learned complex purposeful movements, which is due to loss of sensory input to the premotor cortex, where movements are organized; lesions in the right hemisphere reduce the ability to perceive one's own body and may cause somatosensory and visual neglect (denial) of the contralateral side of the body.

The **parietal association cortex**, which occupies the inferior parietal lobule — the supramarginal (area 40) and angular (area 39) gyri, is a multimodal association area in which visual, auditory, and somatosensory information converge. In the dominant hemisphere, it is involved in language functions such as reading and writing, calculation and spatial orientation.

The **angular gyrus**, in particular, is responsible for understanding the meaning of written words.

Lesions: in dominant hemisphere, leads to impaired writing (sensory agraphia or dysgraphia), lack of understanding of arithmetic rules (dyscalculia), inability to identify fingers and distinguish between right and left; often associated with sensory aphasia — difficulties in reading and understanding speech, speaking meaningfully.

The **motor association areas** (areas 6, 8) are located within the frontal lobe, anterior to the primary motor area. The **premotor area** (PA) includes the posterior portions of all three frontal gyri. The **supplementary motor area** (SMA) is located on the medial surface of the hemisphere in front of the paracentral lobule. Both areas are interconnected with the extrapyramidal system (basal nuclei and cerebellum) and the primary motor cortex. Motor association areas elaborate and select motor programs[14], i.e. a sequence of contractions of synergic muscle groups, to perform complex skilled movements, which are then executed by the primary motor cortex of both sides. In addition, these areas act directly via the pyramidal tracts, contributing about 30 % of their fibers.

A region associated with **complex hand movements**, such as **writing** is located in the middle frontal gyrus (area 6), in front of the territory of hand of the primary motor area.

Lesions of the premotor area lead to apraxia — an impairment of the performance of learned movements (in the correct sequence), in the absence of muscle weakness. Damage to middle frontal gyrus adjacent to the primary motor area (area 6) causes agraphia, i.e. a loss of a previous ability to write.

The **eye motor field** is a part of the premotor area, located in the middle frontal gyrus closer to the prefrontal cortex (lower part of area 8). It controls voluntary conjugate eyes movements, as occur when scanning the visual field. Unilateral electric stimulation of this area causes movement of both eyes to the opposite side.

Lesions: result in impaired eye movements with deviation of gaze towards the side of the lesion.

The **motor speech area** (**Broca's area**) is located in the inferior frontal gyrus (areas 44 — pars opercularis, 45 — pars triangularis), usually in the left hemisphere (in ≈95 % of right-handed and in more than half of left-handed people). It controls speech production and interconnected with other areas involved in language function.

Lesion: causes motor aphasia, i.e. inability to produce fluent speech, while a person is able to understand spoken or writing words.

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[14] The PA selects motor programs based on visual stimuli or on abstract associations, as the SPA — based on remembered sequences of movements.

The **prefrontal cortex** (**frontal association area)** occupies the frontal lobe anterior to the premotor and supplementary motor areas, accounting for approximately 20 % of the entire cerebral cortex. The prefrontal cortex receives input from other association areas and limbic lobe, via the thalamus receives information from the hypothalamus and brain stem centers. It contains the highest-level integration centers responsible for behavior control (planning appropriate actions and evaluating their consequences), higher mental and psychic functions, and personality. The lateral aspect of the prefrontal cortex is related to intellectual and cognitive functions — analysis, problem solving, judgement, planning, decision making, etc., as well as initiative in motor activity. The medial and inferior surfaces are involved in control of the emotional and goal-directed behaviors (related to the limbic system).

Lesions: cause different cognitive, emotional, and personality disorders, impulsive behavior, aggressive tendencies, change in social behavior.

The **insula** is a multimodal association area that integrates information from association areas of the cortex. It is involved in gustatory, olfactory, auditory, vestibular sensations, processing of nociceptive signals. The insula receives visceral sensation and regulates autonomic functions, such as heart rate and blood pressure, respiration, and body homeostasis. It is involved in the processing of various emotions (happiness, sadness, and anger) and is essential for self-awareness, cognition, decision-making, and the ability to speak.

OLFACTORY STRUCTURES (RHINENCEPHALON)

Structures concerned with the conduction and processing smell are the phylogenetically oldest parts of the telencephalon. They include the olfactory structures of the basal forebrain and the cortical olfactory areas (Fig. 48).

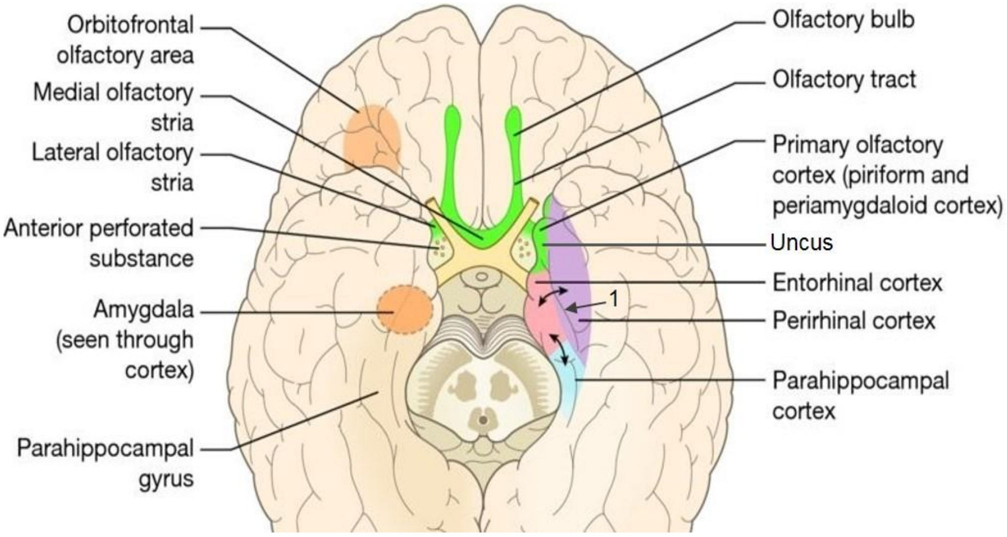

Fig. 48. Olfactory structures and olfactory cortex: 1 — rhinal sulcus

The **olfactory structures** (*syn.* **Rhinencephalon**[15], **olfactory lobe**) lie on the inferior surface of the frontal lobe, separated from its cortex. They include the **olfactory bulb**, **olfactory tract**, **olfactory trigone**, **medial** and **lateral olfactory striae**[16]. These structures

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[15] Anatomical terminology (2003 and 2018) says: “The term rhinencephalon has been omitted because it is no longer in common use and the areas/structures, listed under this designation in previous terminologies, subserve considerably more than just olfactory functions”.

[16] The listed structures were previously referred to as the *peripheral part* of the rhinencephalon; the limbic lobe, not entirely olfactory in function, was previously referred to as the *central part* of the rhinencephalon.

receive olfactory signals from the nasal cavity through the olfactory nerve. The olfactory bulb and tract lie in the olfactory sulcus. The olfactory tract widens and forms the olfactory trigone, which divides into two striae: the lateral olfactory stria terminates in the olfactory cortex and the amygdala, the medial — in the olfactory bulb of the opposite side.

The **cortical olfactory areas** receive signals from the olfactory structures, process them and make us aware about smells. These include the *piriform cortex* of the temporal lobe — the **uncus** together with a narrow area immediately behind it adjacent to the hippocampal sulcus (Fig. 46, *b*). The **olfactory orbitofrontal cortex**, located anterior to the temporal pole, is the highest association center for smell discrimination, responsible for identifying a variety of odors.

ADVANCED: Currently in neuroanatomy, the term **primary olfactory cortex** is used to designate structures that receive direct axonal projections from the olfactory bulb. Most of them do not play a role in smell, such as the *anterior perforate substance* posterior to olfactory trigone, the *periamygdaloid cortex* (cortical amygdala), which occupies the anterior portion of the parahippocampal gyrus, the *entorhinal cortex*, located medial to the rhinal sulcus posterior to the amygdala (Fig. 48). Neurons of these regions form connections with association cortical areas, limbic lobe, thalamus, and hypothalamus, and act as integration centers involved in working memory, navigation, perception of time and other functions.

Odors are analyzed only in a small fraction of spatially dispersed neurons of the *piriform cortex*. These neurons project directly or via the thalamus (the anterior nucleus) to the olfactory orbitofrontal cortex.

BASAL NUCLEI (CORPUS STRIATUM)

The **basal nuclei** (*syn.* basal ganglia), or **corpus striatum,** are compact masses of gray matter embedded deep in the white matter of the cerebral hemisphere, which play a key role in the regulation of motor functions. The corpus striatum is the central component of the so-called *extrapyramidal system*, which includes as well the motor centers of the brain stem, involved in control of muscle tone, posture and movements, in addition to the motor cortex.

The general function of the basal nuclei is to facilitate movements and behavior that are required and appropriate in any particular context and to inhibit unwanted movements or inappropriate behavior (“program selection”).

The **corpus striatum** consists of the **caudate nucleus** and the **lentiform nucleus**, composed of 2 parts, the **putamen** and **globus pallidus** (Fig. 49, 50).

The **caudate nucleus** has 3 parts — the head, body and tail (Fig. 51, 52). It curves around the thalamus contributing to the wall of the lateral ventricle. The larger **head** (*Lat.* caput) forms the lateral wall of the frontal horn. The **body** (*Lat.* corpus), separated by the stria terminalis from the thalamus, forms the floor of the body (central part). The **tail** (*Lat. cauda*) descends in the roof of the temporal horn and anteriorly reaches the amygdaloid body.

The **lentiform nucleus** in the horizontal section of the hemisphere has the shape of a lens. Its medial narrower part faces the **internal capsule**, which separates it from the head of the caudate nucleus anteriorly and from the thalamus posteriorly. The lateral wider part faces the layer of white matter, the **external capsule** (Fig. 51, 52). The lentiform nucleus is divided by laminae of white matter into 3 sections: the lateral darker one is the **putamen** (means shell); the other two — the **medial** and **lateral segments of globus pallidus** (means pale globe).

The globus pallidus or **pallidum** is the phylogenetically older part of the basal nuclei. The putamen and caudate nucleus are phylogenetically newer structurally and functionally related parts, which together are called the **striatum** (Fig. 49). Beneath the anterior limb of the internal capsule the putamen and caudate nucleus are connected by stripes of gray matter (hence the name).

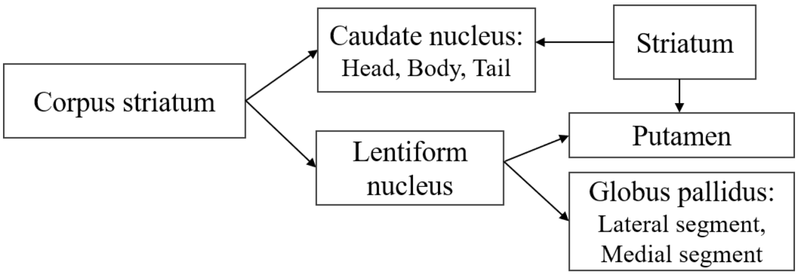

Fig. 49. Organization of the basal nuclei

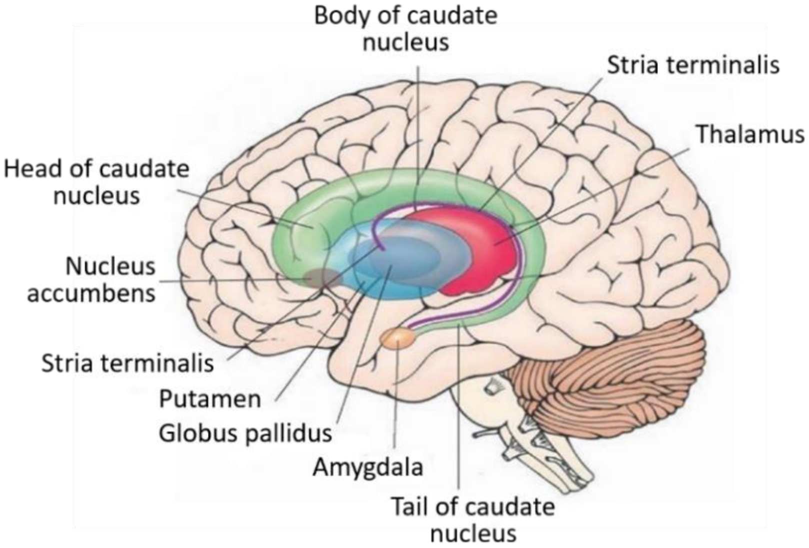

Fig. 50. Projection of the basal nuclei and thalamus on the superolateral surface of the hemisphere

The claustrum and amygdaloid body are masses of gray matter, sometimes mentioned as components of the basal nuclei[17] (Fig. 51, 52).

The **claustrum** is a thin layer of the pallium inside the white matter. The **external capsule** separates the claustrum from the putamen. The **extreme capsule** separates it from the insular cortex.

The **amygdaloid body** (*syn.* **amygdaloid complex**, or **amygdala**) belongs to the limbic system. It consists of groups of nuclei, located within the temporal pole immediately rostral to the tail of the caudate nucleus, anterior and superior to the tip of the temporal horn of the lateral ventricle.

ADVANCED: The main functions carried out by the basal nuclei/ganglia are:

– motor control, i.e. participation in planning and correction of motions: choosing an appropriate movement, facilitating the onset and ending of voluntary movement, modulation of its intensity;

– choosing an appropriate behavior in a given situation, important in social interactions;

– learning, i.e. the formation of new habits and motor memory by memorizing the sequence of movements;

– integration of motor activity of the cortex with emotions, motivations and goals, resulting in certain motor actions — goal-directed and reward-directed behaviors.

From the functional point of view the basal ganglia include: the striatum (caudate nucleus and putamen), globus pallidus, GP (external and internal segments), substantia nigra (SN) of the midbrain, and subthalamic nucleus of the diencephalon. These structures control movements of the skeletal muscles in cooperation with the cerebral cortex and the thalamus (ventrolateral nucleus).

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[17] The amygdaloid body and claustrum have been referred to as basal nuclei in previous editions of Anatomical Terminology (2003, 2018).

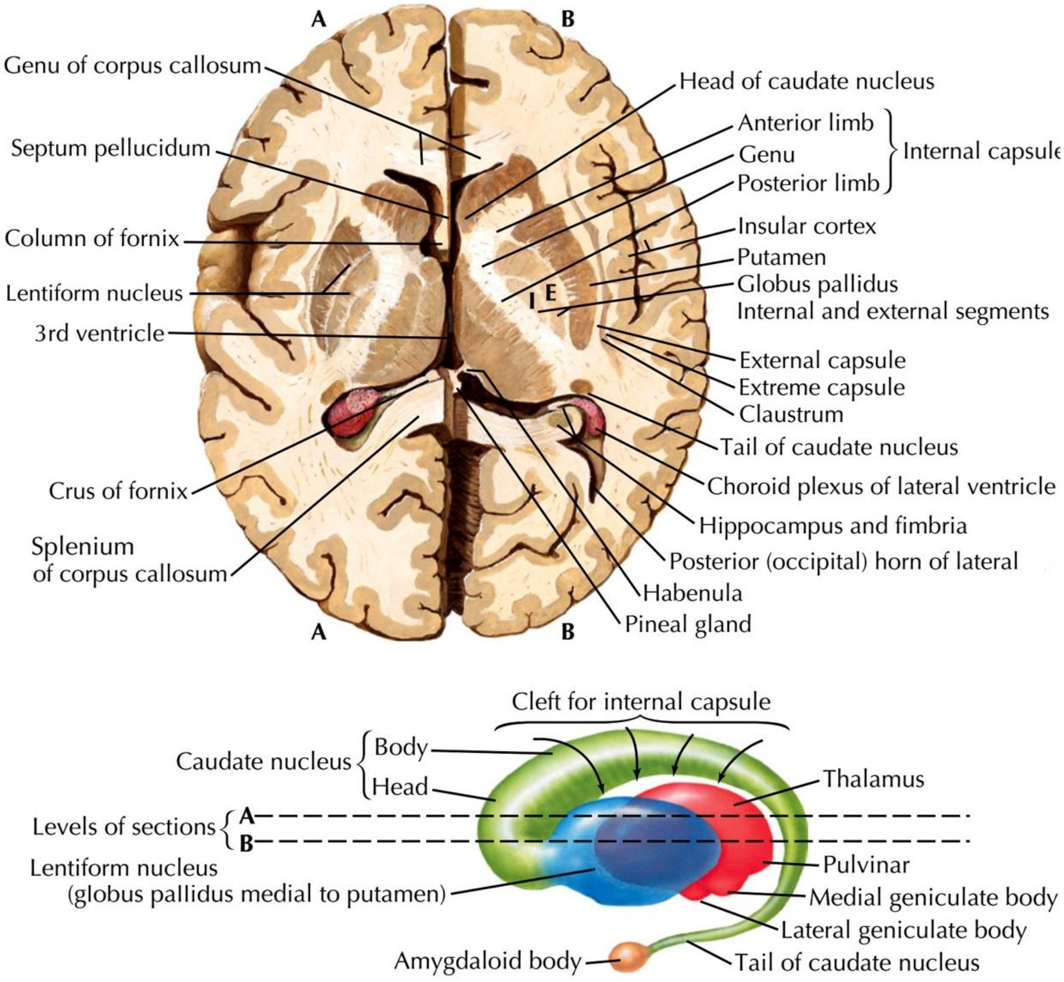

Fig. 51. Horizontal brain section through the basal nuclei

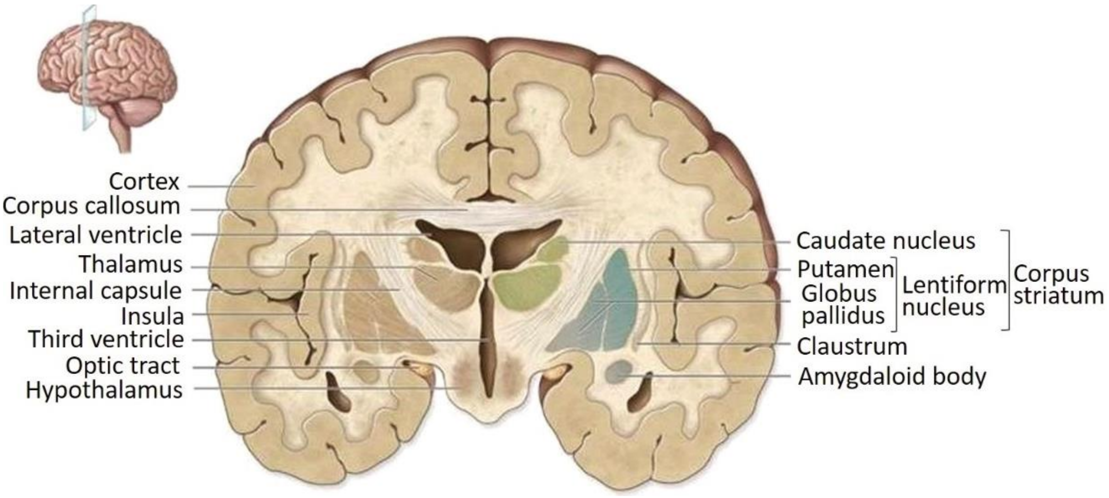

Fig. 52. Frontal brain section through the basal nuclei at the level of amygdala

The basal nuclei receive input ("motor plan") from large areas of cerebral cortex, from the premotor cortex, afferent and association cortical areas, subcortical structures), integrate and process this information, select an appropriate plan of movements, and return it back through the thalamus to the cortical motor areas to execute the proper movement through the pyramidal tracts (Fig. 53).

According to the classical concept, the basal nuclei control movements in two ways: the ***direct pathway***, which increases motor activity and necessary movements, and the ***indirect pathway***, which inhibits motor activity and suppresses unwanted competing movements (Fig. 54).

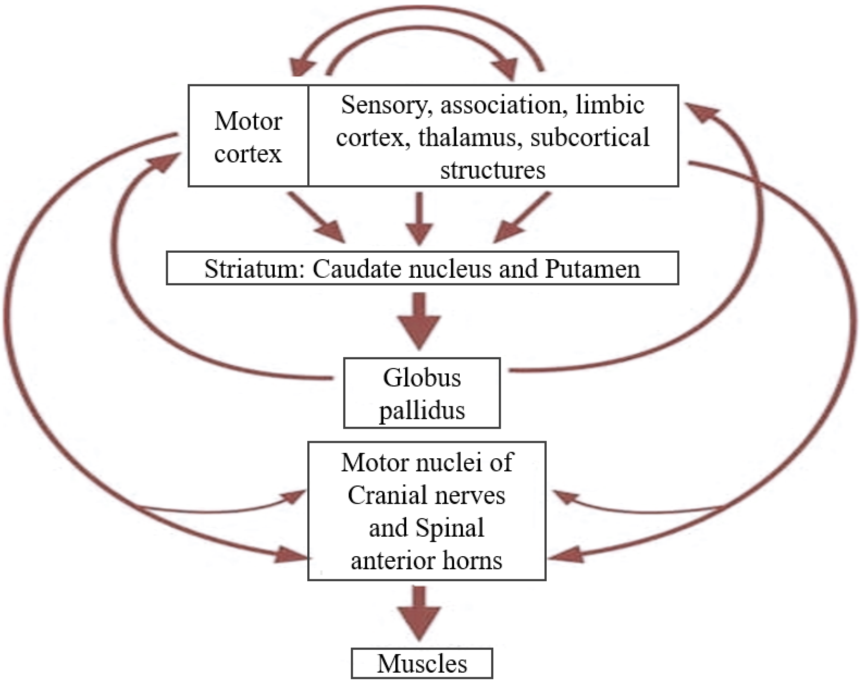

Fig. 53. Diagram showing the main functional connections of the basal nuclei

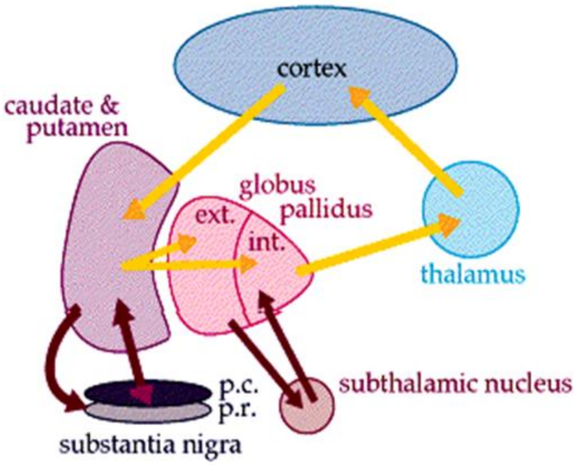

Fig. 54. Direct and indirect pathways of the basal nuclei:
p.c. — pars compacta; p.r. — pars reticulata

The ***direct pathway*** involves the *striatum* (input) and the *internal segment of GP* (output). It decreases the inhibitory effect of the thalamus on the cortex and causes its activation.

The ***indirect pathway*** involves the *striatum* (input); the *external segment of GP* and *subthalamic nucleus* (intermediate nuclei); and the *internal segment of GP* (output). It enhances inhibition of the cortex by the thalamus and suppresses motor activity.

These pathways depend on the activation or suppression of SN dopaminergic neurons that supply dopamine to the striatum. The cortical input to the striatum activates two different groups of neurons. One group projects to the SN pars reticulata, which in turn activates the release of dopamine by neurons in the SN pars compacta. The other group projects to the pars compacta and reduces the release of dopamine. The impact of dopamine on the striatum initiates the direct pathway, increasing cortical excitation. The lack of dopamine and the effect of cholinergic neurons found in the striatum and producing acetylcholine initiate the indirect pathway, reducing cortical excitation.

Other functions of the basal ganglia, in addition to motor control, are based on their connection with the limbic and prefrontal association cortices. The limbic pathway involves the *nucleus accumbens* of the ventral striatum, which is a part of the basal forebrain ventrally adjacent to the rostral parts of the caudate and lentiform nuclei (Fig. 50).

Abnormal function of the basal ganglia leads to movement disorders (dyskinesias), known as extrapyramidal syndrome.

Degeneration of dopaminergic neurons in the substantia nigra leads to dopamine deficiency and the development of Parkinson's disease, characterized by a hypokinetic state: slowed movements, difficulty initiating them, resting tremor and cogwheel rigidity, difficulty in speech, a mask-like face, and postural instability. This can be accompanied by cognitive disorders, depression, lack of motivation.

On the other hand, in Huntington's disease, the loss of neurons in the striatum reduces the inhibitory effect on the cortex and leads to a hyperkinetic state characterized by involuntary, continuous movement (chorea), especially of the limbs and face.

LATERAL VENTRICLES

The cavities of the telencephalon are two **lateral ventricles**. Each ventricle occupies a considerable part of the cerebral hemisphere and consists of the **body** and **3 horns**: 1) the **frontal (anterior) horn**; 2) the **occipital (posterior) horn**; 3) the **temporal (inferior) horn**. Each horn projects into the corresponding lobe. The **body**, or **central part**, is located in the parietal lobe and connects the frontal horn with the occipital and temporal horns (Fig. 34, 55).

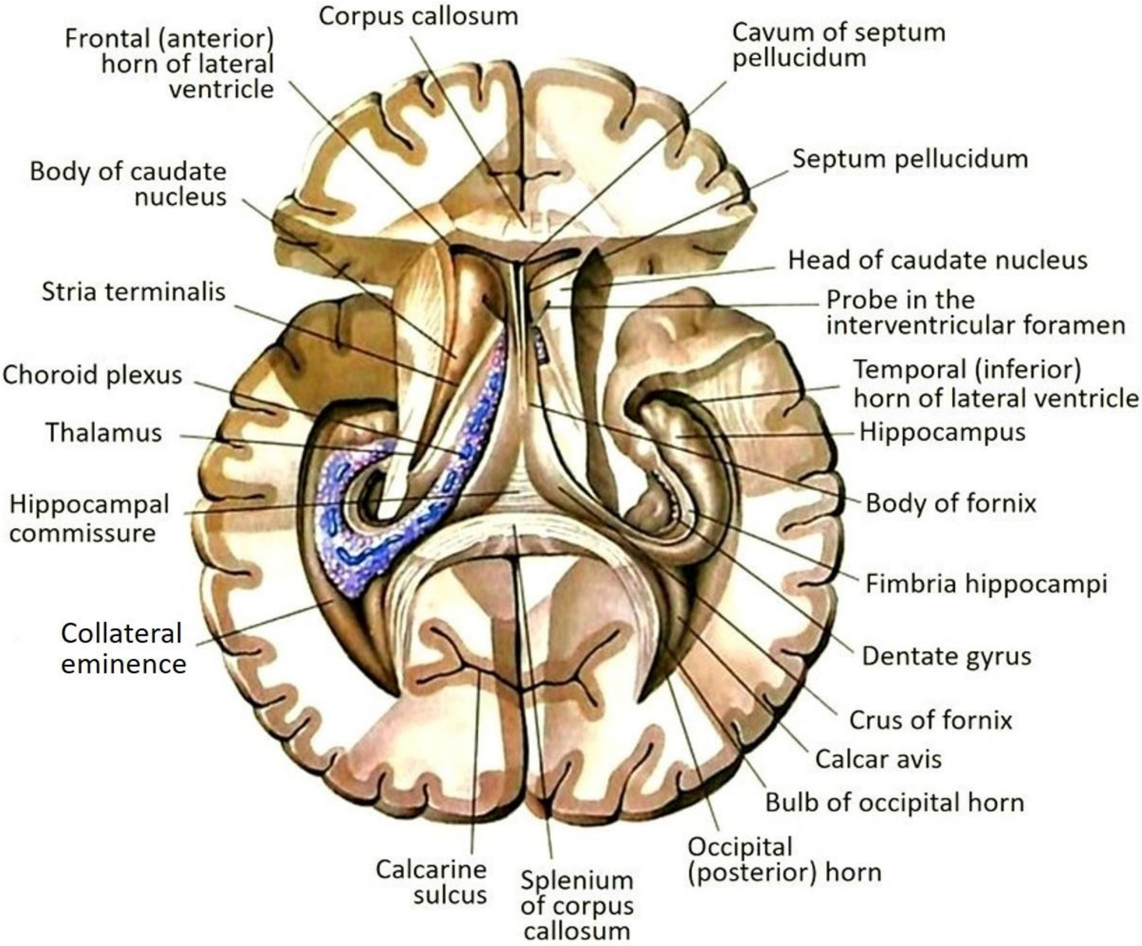

Fig. 55. Lateral ventricles

The *superior wall* of the anterior horn and body of the lateral ventricle is formed by the **corpus callosum**. Its extension in the posterolateral direction, called the **tapetum**, forms the *roof* and *lateral wall* for the posterior and inferior horns.

The remaining walls of the lateral ventricles and their associated structures are as follows:

1) In the ***frontal horn***, the *anterior wall* is formed by the **genu** and **rostrum of corpus collosum**. The *lateral wall* is formed by the **head of caudate nucleus**. The *medial wall* is the **septum pellucidum** stretched between the genu of corpus callosum and the column of fornix. It separates the anterior horns from each other. The **interventricular foramen (foramen of Monro)** is located between the column of fornix and the thalamus. It connects each anterior horn with the 3rd ventricle.

2) The ***body (central part)*** extends from the interventricular foramen to the splenium of corpus callosum. The *floor (inferior wall)* of the body is formed by the upper surface of the **thalamus**, and lateral to it, by the **stria terminalis** and **body of caudate nucleus**. The *medial wall* is formed by the septum pellucidum, and in the posterior part, by the fornix. The **choroid plexus** lies along the medial wall, covers the thalamus and continues to the inferior horn. Through the space between the thalamus and the fornix, it connects with the choroid plexus of the 3rd ventricle (Fig. 39).

3) The ***occipital horn*** is the smallest. On the *medial wall*, it has an elevation, the **calcarine spur** (*Lat.* **calcar avis**), formed by the calcarine sulcus protruding from the medial surface of the occipital lobe.

4) The ***temporal horn*** is the largest. It curves from the body downward and then forward to the uncus. The *lateral wall* and most of the *roof* are formed by the **tapetum**. The *medial part of the roof* is formed by the **tail of caudate nucleus**, **stria terminalis**, and **crus of fornix**, lying one under the other. The crus of fornix continues with the **fimbria hippocampi**, attached to the medial surface of the hippocampus. The *medial wall* is formed by the **hippocampus**, which is an elongated elevation of the temporal cortex protruding from the hippocampal sulcus. The **choroid plexus** lies along the medial wall. The *floor* of the temporal horn is formed by the **collateral eminence —** an elevation above the collateral sulcus of the cerebral cortex.

WHITE MATTER OF TELENCEPHALON

The white matter of the telencephalon consists of bundles of nerve fibers, which, depending on the direction, are divided into three types: association, commissural, and projection fibers (Fig. 56).

Association fibers of telencephalon include fibers that connect cortical areas of the same hemispheres (Fig. 56, 57). *Short association fibers*, the **arcuate fibers**, connect the adjacent gyri within a lobe. *Long association fibers*, longitudinally oriented, link one lobe with another and lie deeper in the white matter. Bundles of long association fibers include the following:

– The **superior longitudinal fasciculus** links the frontal, parietal, occipital lobes, and superior part of the temporal lobe; its lower part, called the **arcuate fasciculus**, connects the occipitotemporal region with the frontal lobe, uniting the speech centers located there;

– The **inferior longitudinal fasciculus** links the occipital and temporal lobes;

– The **uncinate fasciculus** links the frontal lobe with the anterior part of the temporal lobe;

– The **cingulum** underlies the cortex of the cingulate gyrus and connects it with the parahippocampal gyrus and uncus.

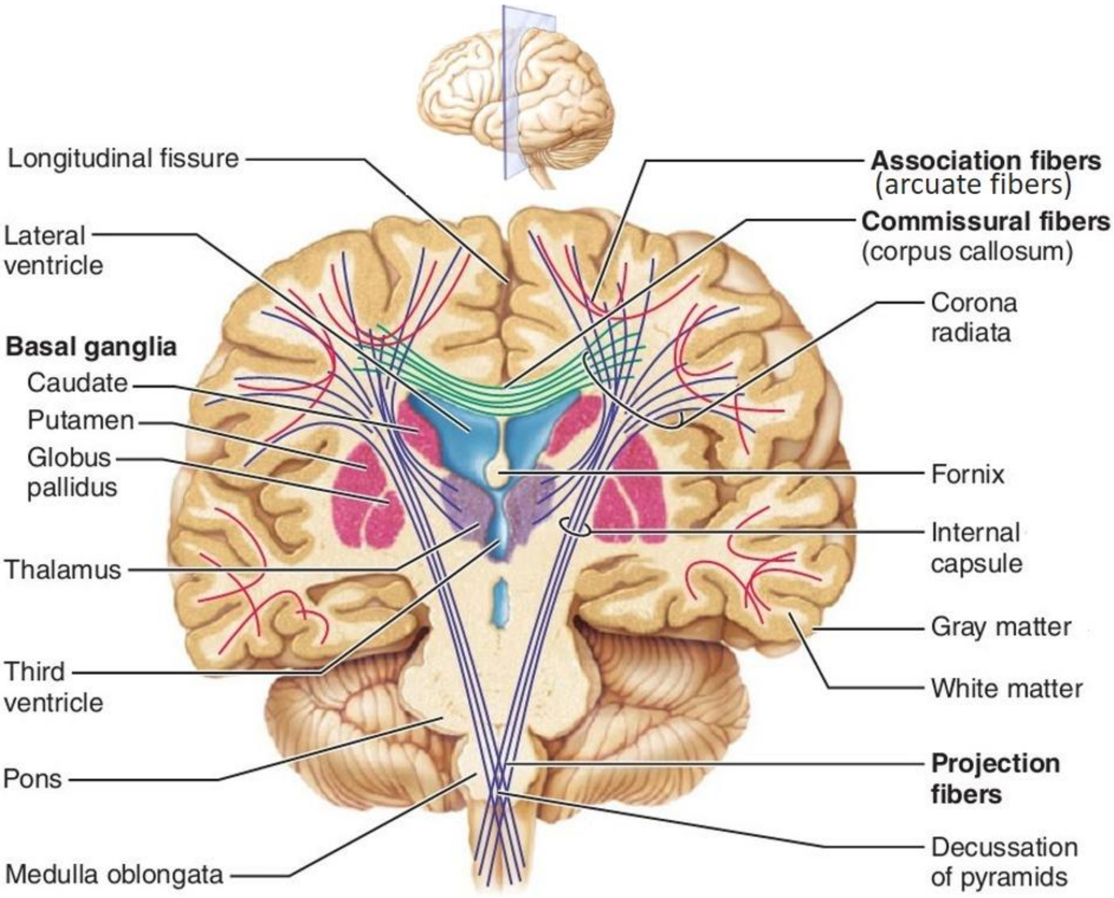

Fig. 56. White matter of the telencephalon: association (short), commissural, and projection fibers

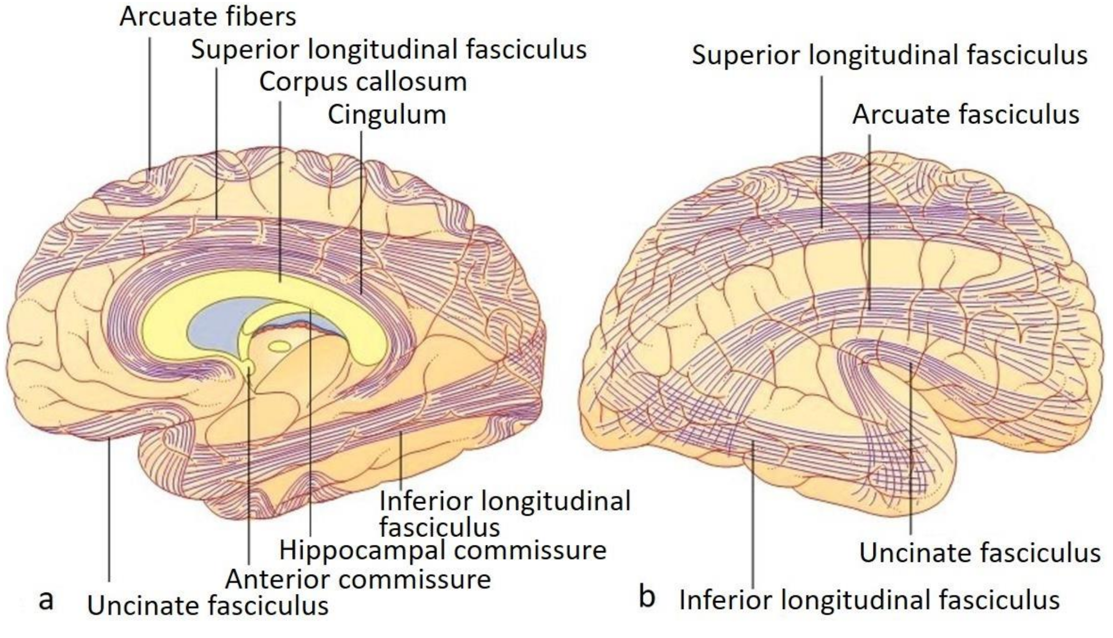

Fig. 57. Association fibers of the telencephalon: projection on the medial (*a*) and superolateral (*b*) surfaces of the right hemisphere. Commissural fibers (*a*)

Commissural fibers of the telencephalon are composed of transversally oriented fibers that connect the symmetrical strictures of the right and left hemispheres (Fig. 57):

1. The **corpus callosum** is the largest commissural tract linking the cortical areas of the opposite hemispheres (Fig. 41). It transfers information between the hemispheres and

integrates their work. The major middle part of the corpus callosum is the **body** (*syn.* **trunk**). The anterior curved end is the **genu**. It narrows to form the **rostrum**, which continues with the lamina terminalis. The posterior thickening is the **splenium**. The genu and body of corpus callosum form walls of the frontal horns and central parts of the lateral ventricles. The fibers of the corpus callosum, passing laterally and downward over the occipital and temporal horns, are called the **tapetum**.

2. The **anterior commissure** is a small transverse bundle of fibers in front of the column of fornix. It connects the right and left olfactory lobes and the limbic structures of the anterior parts of the temporal lobes.

3. The **hippocampal commissure** (*syn.* **commissure of fornix**) is a plate of transverse fibers under the splenium of corpus callosum stretching between the beginning of the right and left crura of fornix. It interconnects the contralateral hippocampal formations.

Projection fibers of the telencephalon run vertically in both directions: rostrally — afferent, caudally — efferent. They connect the cerebral cortex with the thalamus, brain stem, and the spinal cord. Towards the cortex, the projection fibers become a fan-shaped mass, the **corona radiata** (Fig. 56). Closer to the thalamus, they converge into a compact structure of white matter — the **internal capsule** (Fig. 58).

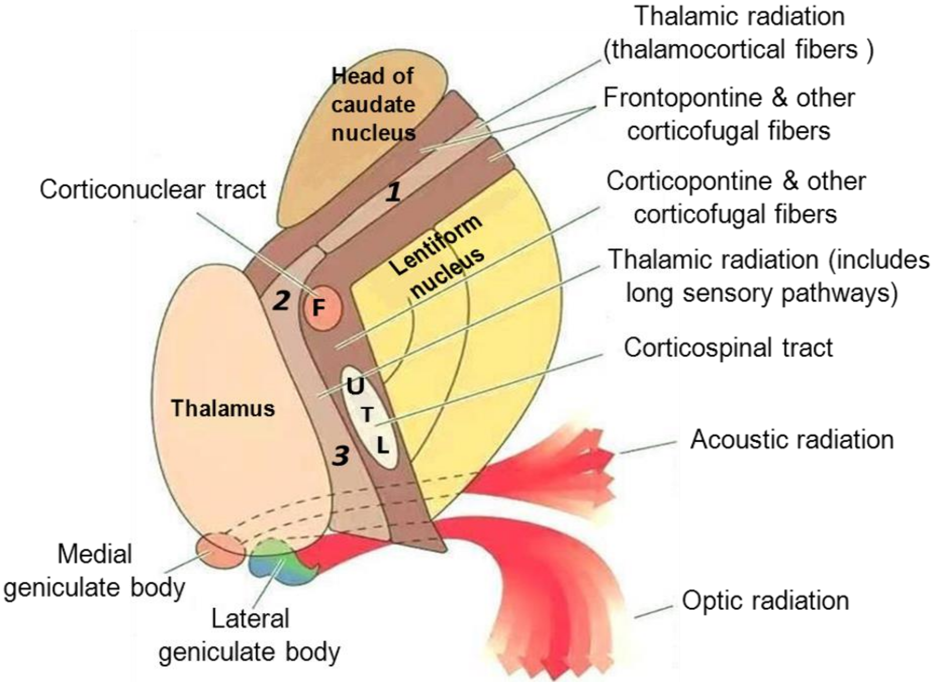

Fig. 58. Internal capsule:
1 — anterior limb; 2 — genu; 3 — posterior limb. Corticospinal fibers to the upper limb — U, trunk — T, lower limb — L. Descending fibers are shown in dark brown, ascending fibers in light brown

On the horizontal section of the hemispheres, the **internal capsule** is V-shaped and has 3 parts: 1) the **anterior limb** — between the lentiform nucleus and the head of caudate nucleus, 2) the **posterior limb** — between the lentiform nucleus and the thalamus, and 3) the **genu** — a bend at the connection of two limbs.

Descending fibers of the internal capsule originate in the cerebral cortex of all lobes of the hemisphere (Fig. 58). The **pyramidal tracts** arise primarily in the frontal lobe and pass through:

– the ***genu***, containing the **corticonuclear fibers** to the motor nuclei of the cranial nerves;

– the ***posterior limb***, containing the **corticospinal fibers**: to the **upper limb** (anteriorly), **trunk** (in the middle), **lower limb** (posteriorly). After the decussation of pyramids in the medulla these fibers form the **lateral** and **anterior corticospinal tracts**.

The remaining descending (corticofugal) fibers pass through both *anterior* and *posterior limbs*: most run to the pons (corticopontine fibers), the rest to the thalamus and brainstem.

Ascending fibers — **thalamocortical fibers (thalamic radiation)**, run from numerous nuclei of the thalamus to widespread areas of the cerebral cortex through all parts of the internal capsule.

The ***posterior limb*** includes final sections of sensory pathways:

1. **Thalamocortical fibers to the parietal lobe** (from ventroposterior nuclei), which carry somatosensory information from the body and head (continuation of the **dorsal column-medial lemniscal**, **spinothalamic**, and **trigeminothalamic pathways**).
2. **Acoustic radiation,** posterior to the thalamic radiation, which projects from the lateral geniculate body to the temporal lobe.
3. **Optic radiation**, posterior to the acoustic radiation, which projects from the medial geniculate body to the occipital lobe.

The **fornix** is a paired C-shaped bundle of fibers, which connects the structures of the limbic system of the telencephalon and hypothalamus. The fornix consists of the crus, body, and column (Fig. 59, 60). The **crus of fornix**, a posterior continuation of the **fimbria of hippocampus**, originates in the temporal horn of the lateral ventricle. It curves anteriorly and becomes the **body of fornix**, which lies below the trunk of corpus callosum. The **column of fornix** descends anterior to the thalamus forming the anterior wall of the III ventricles, then deepens into its lateral wall to terminate in the mammillary body and the septal area.

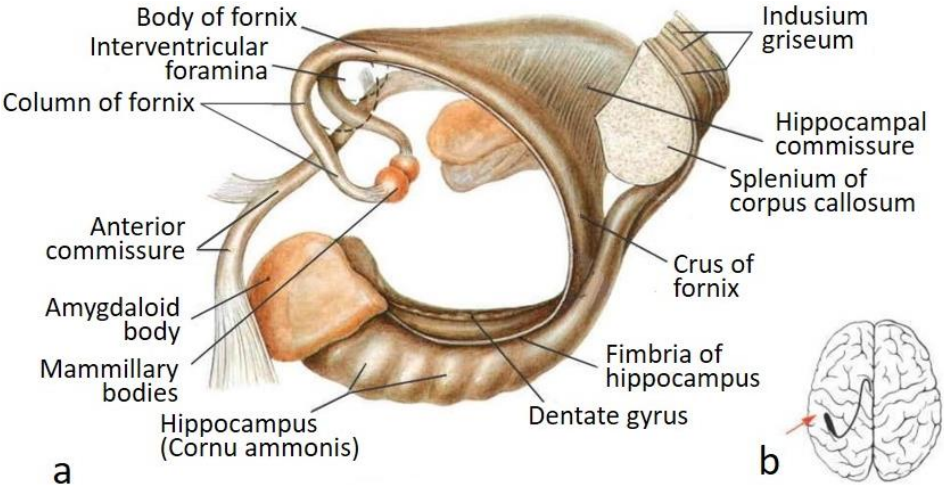

Fig. 59. Fornices and anterior commissure:
a — left view; *b* — projection of the fornix onto the surface of the hemisphere (arrow points to the hippocampus)

LIMBIC SYSTEM

The limbic system (“limbus” in Latin means “border”) is a complex of interconnected structures of the medial aspect of the cerebral hemisphere around the corpus callosum and midbrain. It consists of the *limbic cortex*, which includes the phylogenetically old parts of the cortex associated with the sense of smell in primitive mammals, and some subcortical structures, such as the *amygdala*, *septal nuclei*, *mammillary bodies* and others (Fig. 60).

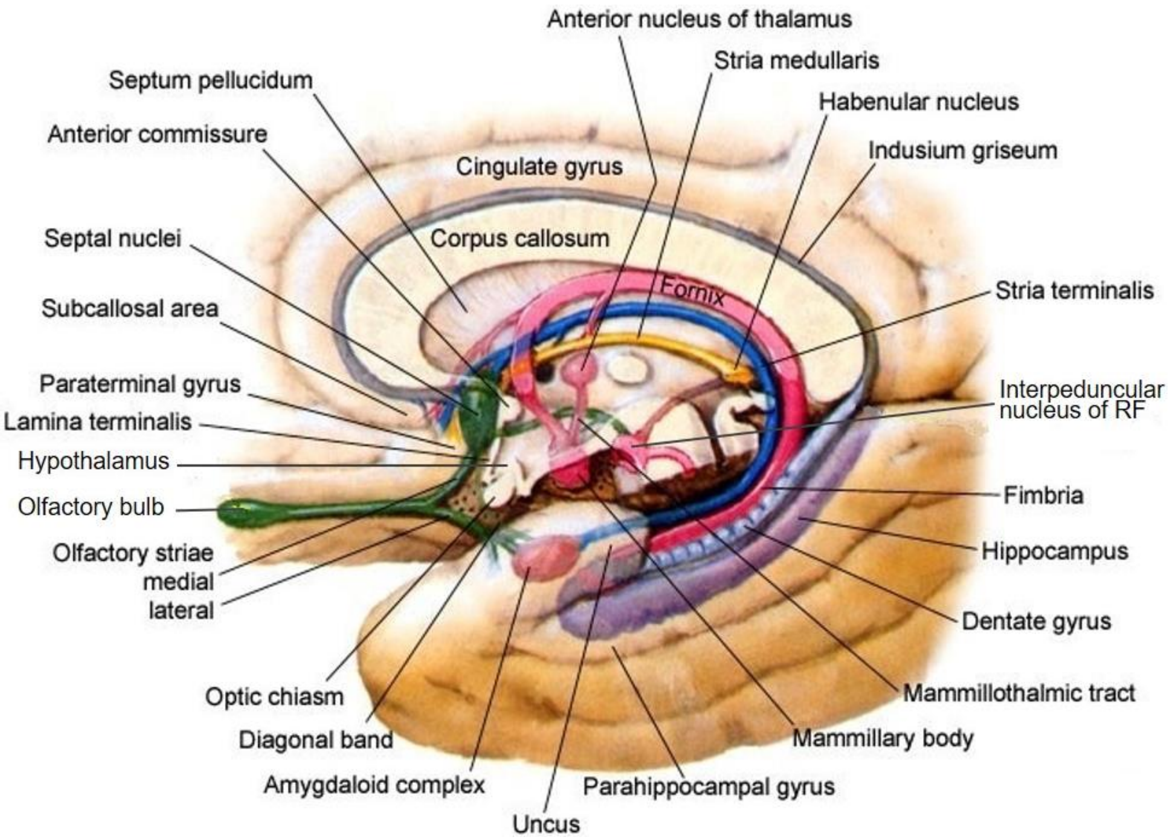

Fig. 60. Major structures of the limbic system

In primitive mammals, the limbic system is concerned with mechanisms of attack and defense, feeding and reproduction, which are necessary for survival and species preservation. In human, the limbic system is an important integrating system of the brain. It is involved in the regulation of emotions (fear, anger, rage, pleasure) and emotional responses: autonomic (changes in visceral functions, for example, heart and breathing rates, sweating) and somatic (such as emotional motor behaviors, facial expressions, gestures); regulation of sexual, feeding and motivational behaviors, learning and memory formation. The limbic system is also an important element in the body’s response to stress, as it is closely connected to the endocrine and autonomic nervous systems.

The major components of the limbic system are:

1. *Cortical and subcortical structures of the telencephalon*:

– **limbic lobe**, which includes the **cingulate** and **parahippocampal gyri**, the **uncus**, and the **hippocampus** (cornu ammonis, dentate gyrus and adjacent wall of the hippocampal sulcus);

– **amygdaloid body** (*syn.* **amygdala**), located in the depth of the temporal pole;

– **septal nuclei (area)**, located in the subcallosal area of the frontal cortex, below the rostrum of corpus callosum and anterior to the lamina terminalis.

2. *Structures of the diencephalon*:

– **mammillary bodies** of the hypothalamus;

– **anterior** and **medial nuclei of thalamus**.

Centers *functionally related* and often attributed to the limbic system are:

– **olfactory structures** (olfactory bulb, olfactory tract, olfactory trigone, medial and lateral olfactory striae) of the telencephalon;

– **hypothalamic nuclei**;

– **nucleus accumbens** of the ventral striatum;

– **medial orbitofrontal cortex** (an area of the prefrontal cortex occupying the inferomedial surface of the frontal lobe);

– **habenular nuclei** of the epithalamus;

– **reticular formation**, and some others.

The limbic system components are interconnected (mainly reciprocally) by fiber bundles, such as the **fornix**, **stria terminalis**, **stria medullaris of thalami**, etc., forming complex pathways or circuits associated with various functions in which the limbic system is involved. An example of such a pathway is the memory circuit, or Papez circuit (Fig. 61).

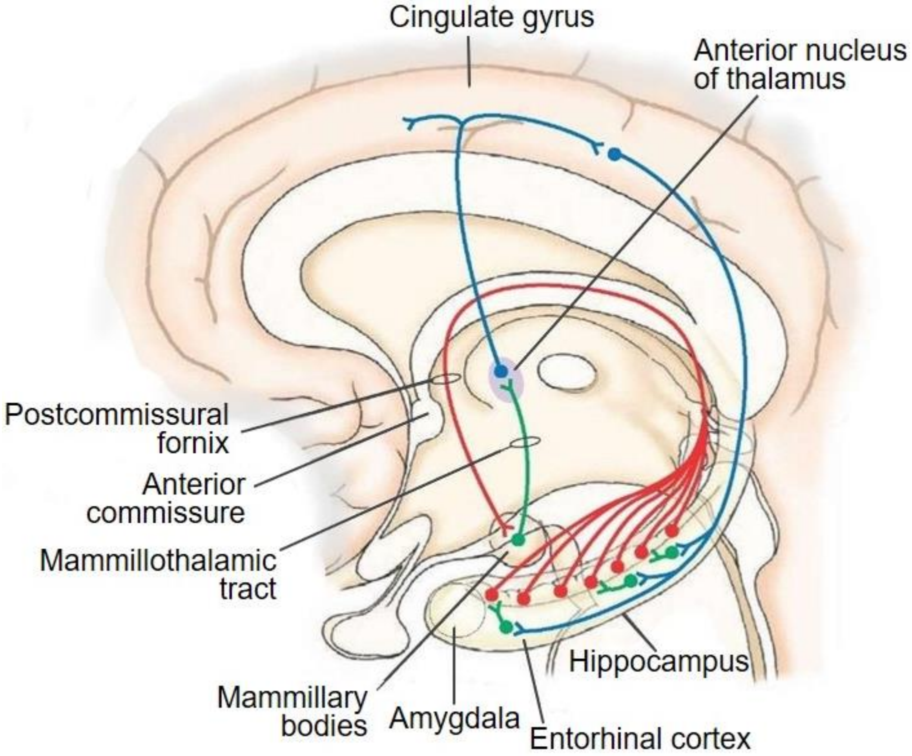

Fig. 61. The interconnection of limbic structures that constitute the Papez circuit

ADVANCED: The main fiber tracts of the limbic system are:

– The **fornix** connects the hippocampus with the mammillary bodies, anterior hypothalamus, and septal nuclei;

– The **mammillothalamic tract** connects the mammillary body with the thalamus (anterior nucleus);

– The **stria terminalis** connects the amygdala with the septal nuclei and the anterior hypothalamus (preoptic areas);

– The **ventral amygdalo-fugal pathway** is a short way for the amygdala to connect with the septal nuclei and the hypothalamic nuclei;

– The **stria medullaris of thalami** connects the limbic system, via the septal nuclei, with the habenular nuclei, which through the interpeduncular nuclei project to the midbrain reticular formation;

– The **medial forebrain bundle** connects the prefrontal cortex, the septal nuclei and the hypothalamus.

The hippocampus and the amygdala, located within the temporal lobe, are the main entry of sensory (olfactory, visual, auditory, somatosensory, and visceral) and cognitive information into the limbic system.

The **hippocampus** receives input from the *entorhinal cortex* (area 28), located in the anterior part of the parahippocampal gyrus (Fig. 48). The entorhinal cortex, in turn, receives information from the primary olfactory cortex and many association areas of the cortex. The **amygdala** receives direct input from the olfactory bulb, and the rest of the information from the cerebral cortex through the thalamus.

In the memory pathway (Papez circuit) information, integrated in the entorhinal cortex, is transmitted along the following path (Fig. 61): hippocampus (subiculum → dentate gyrus → hippocampus proper) → fornix → mammillary body → mammillothalamic tract → anterior thalamic nuclei → thalamocortical fiber passing through the internal capsule → cingulate gyrus → cingulum. The cingulum, returns impulses to the entorhinal cortex, thus completing the circuit. The entorhinal cortex provides both input and output of the limbic system: information consolidated (cataloged) as memories in the hippocampus and cingulate gyrus is sent through the entorhinal cortex to the prefrontal and association cortex for long-term storage.

The **hippocampus** is associated with the transformation of short-term memory into long-term memory, including the formation of visuospatial memory, and is also responsible for spatial orientation and navigation.

Bilateral damage to the hippocampus leads to an inability to remember new events (anterograde amnesia), loss of orientation and sense of direction. Damage to other components of the Papez circuit can also affect memory. Degeneration in the hippocampus occurs in Alzheimer's disease. Atrophy of the mammillary bodies (e.g., in chronic alcoholics) can cause amnesia, as well.

The **mammillary bodies** are involved in the formation of memory, transmitting information through the mammillothalamic tract between the amygdala and hippocampus and the thalamus and cingulate gyrus.

The **amygdala**, which has direct projections from the hippocampus and a variety of reciprocal connections with many regions of the brain, is involved in several circuits of the limbic system. The amygdala plays a major role in generating emotions, such as fear, anxiety (worry), anger, or pleasure, by giving emotional meaning to incoming information. Together with the hippocampus and cingulate gyrus, the amygdala is involved in the formation of emotional memories, especially those associated with the fearful experience and smell. The output of the amygdala to the hypothalamus and brain stem plays an important role in the regulation of visceral functions, "fight-or-flight" response, sexual and feeding behavior. The amygdala is also involved in circuits associated with formation of motivations, goal-directed and reward-seeking behavior.

Bilateral damage to the amygdala reduces fear, aggression, and emotional responses, may cause increased sexuality and food intake, and a tendency to explore surrounding objects by mouth or sniffing. In Alzheimer's disease, atrophy of the amygdala correlates with atrophy of the hippocampus.

The **cingulate gyrus** is interconnected with other structures of the limbic system, such as the amygdala, nucleus accumbens, hypothalamus, hippocampus, as well as with the prefrontal and parietal cortex. The *anterior* cingulate gyrus (areas 24, 32, and 33) is involved in emotions and motivations, emotional reactions to pain, smell and other stimuli by modulating visceral functions and somatic activities. It also plays a role in problem-solving, decision-making, social communication and adaptation. The *posterior* part of the cingulate gyrus (areas 23 and 31), together with the hippocampus and mammillary body, plays a role in the control of attention and the arousal state, learning, and the formation of long-term memory.

Lesions of the anterior part of the cingulate gyrus produce emotional disturbances, alterations in autonomic regulation, decrease motivation, affect social behavior; this part is reduced in schizophrenia more than posterior part. *Lesions of the posterior part* are associated with antegrade memory loss and visuospatial dysfunction (loss of orientation). In Alzheimer disease, atrophy of the cingulate gyrus is more pronounced in the posterior part.

The **septal nuclei** are connected with most of the limbic structures and project to several hypothalamic nuclei and the habenular nuclei of the epithalamus. They contribute to the regulation of emotional behavior, autonomic functions, and the formation of memory. Through projections of the habenular nuclei, the septal nuclei influence the nucleus accumbens. Together they are involved in the circuit associated with motivations and goal-directed behavior, play a role in a sense of reward, and are associated with drug addiction.

The **nucleus accumbens** is a key structure in the brain reward system that links emotions to motivations, goal-directed behavior, and learning. It is activated during anticipation and experience of pleasure and reward, and is involved in addictive aspects of behavior.

The **hypothalamic nuclei** (preoptic, dorsomedial, lateral, ventromedial nuclei) are the main output of the limbic system and are often considered a part of it. The hypothalamus acts through both hormones release and through neural pathways to the autonomic centers of the brainstem and spinal cord. It regulates visceral responses to emotions and stress, generates motivations, and controls motivational behavior, such as sexual, feeding, and other behaviors.

The **medial orbitofrontal cortex** is a part of the prefrontal cortex related to the limbic system via projections from the medial dorsal nucleus of the thalamus. It modulates emotional and goal directed behavior, controls and suppresses sexual and antisocial behavior.

MENINGES OF THE BRAIN

The brain is enclosed in the same tree membranes as the spinal cord: the **dura mater**, **arachnoid**, and **pia mater**, although the cranial meninges have some structural features. The cranial dura mater consists of two layers, folds inside the skull, separating parts of the brain, and forms channels that carry venous blood. The cranial arachnoid forms granulations that ensure the outflow of CSF into the venous system. The pia mater is involved in the formation of the choroid plexuses of the brain ventricles that produce CSF.

The **cranial dura mater** (*syn*. dura mater encephali) consists of the **periosteal** and **meningeal** layers. They are closely connected to each other and separate only to form the dural venous sinuses and the trigeminal cave.

The **periosteal layer** (*syn*. endocranium) lines the inner surface of the skull. It serves as the periosteum for the skull bones and contains blood vessels to supply them with blood. The periosteal layer is most firmly attached to the sutures and the base of the skull. At the margin of the foramen magnum, it continuous with the periosteum of the vertebral canal.

The **meningeal layer** lies deeper and continuous with the spinal dura. It forms reflections or processes, that project into the cranial cavity to form partitions between parts of the brain (Fig. 62).

The four largest processes are:

1. The **falx cerebri** is a crescent-shaped septum that lies in the sagittal plane between the right and left cerebral hemispheres. It attaches along the groove for superior sagittal sinus extending from the crista galli anteriorly to the tentorium cerebelli posteriorly.
2. The **falx cerebelli** attaches along the internal occipital crest and slightly projects between the cerebellar hemispheres.
3. The **tentorium cerebelli** is a large tent-shaped septum, dividing the cranial cavity into the supratentorial compartment, which contains the cerebral hemispheres, and the infratentorial compartment, which contains the cerebellum. At the midline, the tentorium cerebelli connects with the falx cerebri. Posteriorly, it attaches to the occipital bone along the groove for transverse sinus. Then its margin turns medially, attaching on both sides to the superior border of the petrous part of the temporal bone.
4. The **diaphragma sellae** forms a roof over the hypophysial fossa of the sphenoid bone. It has a small opening for passage of the infundibulum of the neurohypophysis.

At the apex of the petrosal part of the temporal bone, on its anterior surface, the dura mater splits to form the **trigeminal cave** containing the trigeminal ganglion of the CN V.

Dural venous sinuses

The **dural venous sinuses** are canals enclosed by layers of the dura mater and lined inside with the endothelium. The dural sinuses do not collapse and provide a constant outflow of the venous blood from the skull. They drain the brain, meninges, skull bones, orbit, and internal ear, mainly to the internal jugular vein, and communicate with the extracranial veins, through the emissary veins, and the internal vertebral plexus.

Based on the location and direction of blood flow, the dural sinuses can be divided into two groups. One group includes sinuses located along the calvaria and in the posterior cranial fossa: the unpaired **superior** and **inferior sagittal sinuses, straight sinus, confluence of sinuses, occipital sinus,** and the paired **transverse** and **sigmoid sinuses** (Fig. 62). Another group includes sinuses of the cranial base anterior to the foramen magnum: the **sphenoparietal**, **cavernous, intercavernous**, **superior** and **inferior petrosal sinuses** (Fig. 63).

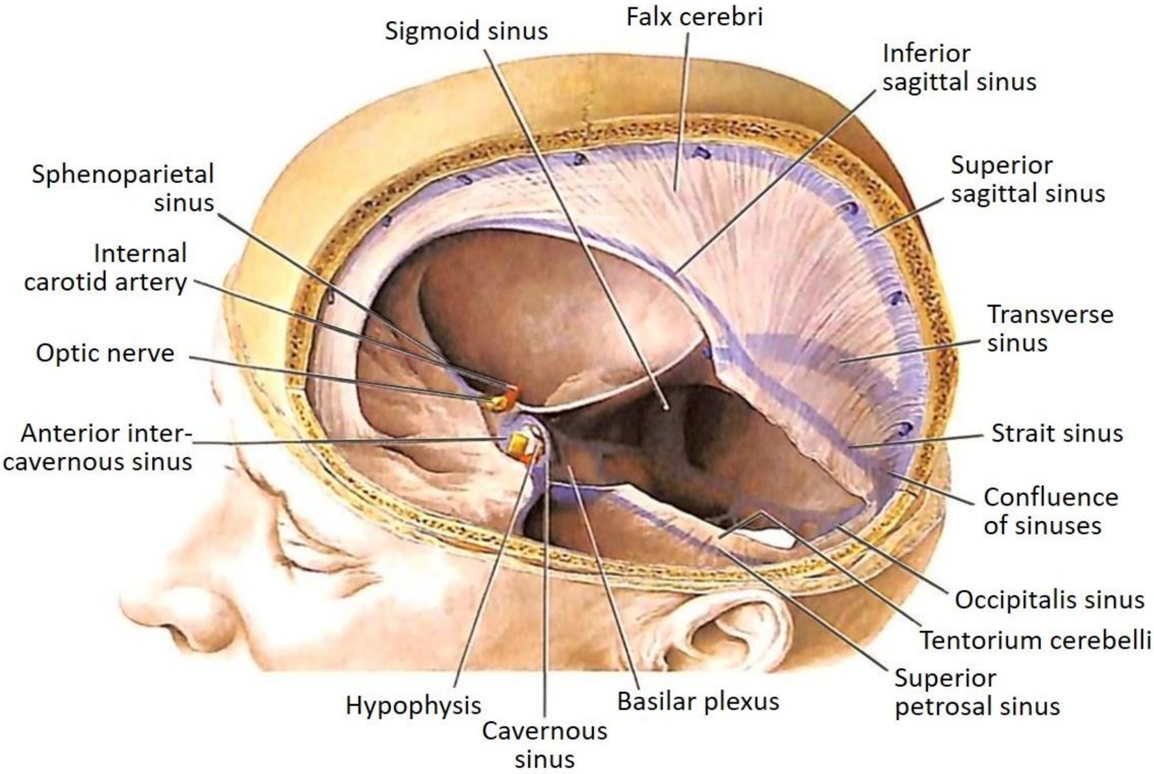

Fig. 62. Cranial dura mater

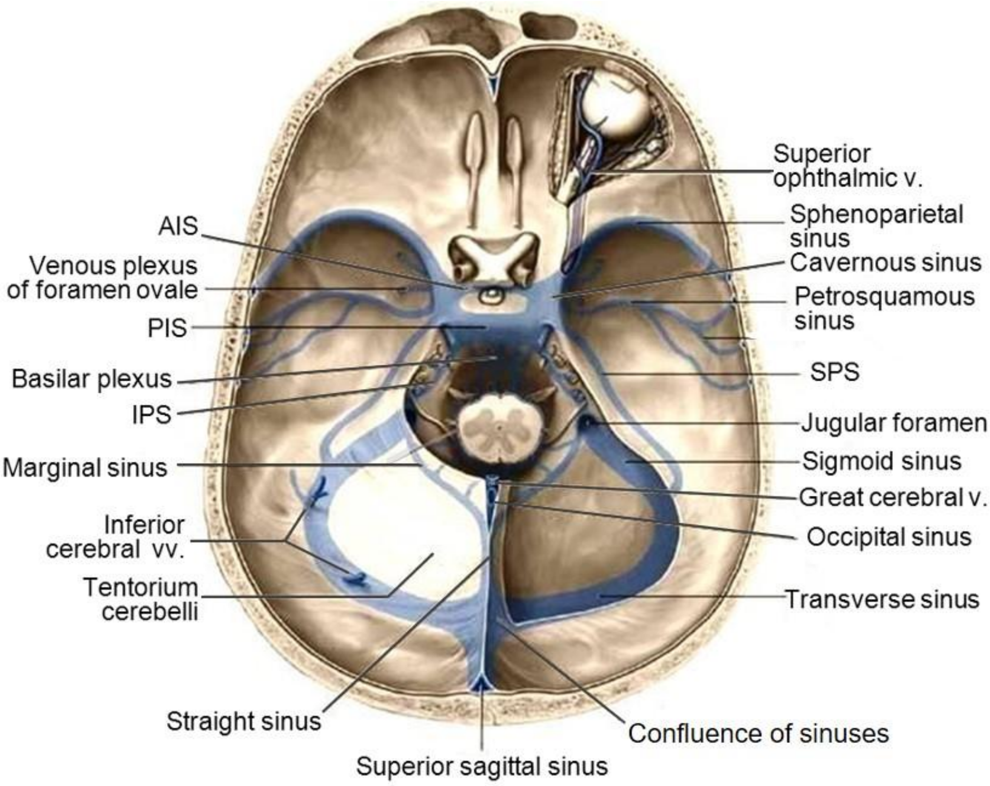

Fig. 63. Dural venous sinuses with tributaries in the cranial base (superior view of the opened cranial cavity: tentorium cerebelli is removed on the right side): AIS and PIS — anterior and posterior intercavernous sinuses; SPS and IPS — superior and inferior petrosal sinuses

– The **superior sagittal sinus** lies in the midline of the calvaria along the attachment of the falx cerebri and, on both sides, has 2–3 extensions, the **lateral lacunae** (Fig. 64). It ends at the **confluence of sinuses** (commonly it continues as the right transverse sinus).

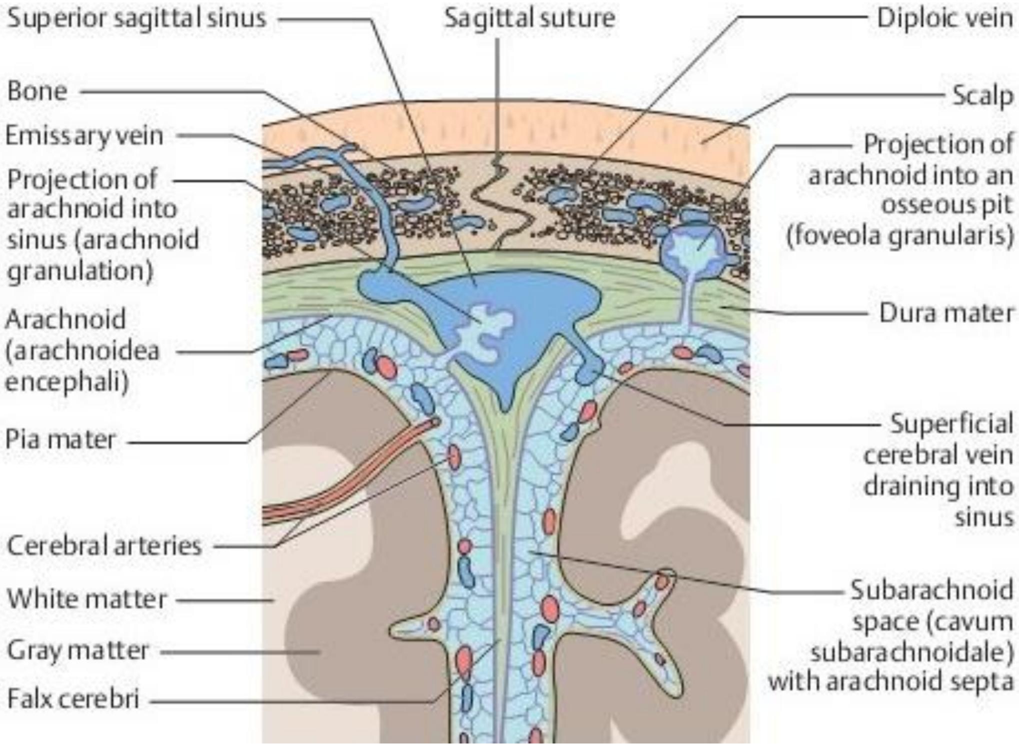

Fig. 64. Coronal section of the skull and brain through the superior sagittal sinus

– The smaller **inferior sagittal sinus** passes along the inferior margin of the falx cerebri and posteriorly empties into the straight sinus.

– The **straight sinus** (*Lat.* Sinus rectus) passes through the junction of the falx cerebri and tentorium cerebelli. Anteriorly it connects with the inferior sagittal sinus and the **great cerebral vein**, draining the deep structures of the brain. Posteriorly it joins with the confluence of sinuses.

– The **confluence of sinuses** is a dilation of sinuses at the internal occipital protuberance where several sinuses are connected: the superior sagittal sinus, straight sinus, right and left transverse sinuses, and occipital sinus.

– The **transverse sinuses** pass along the attachment of the tentorium cerebelli to the occipital bone, from the confluence of sinuses to the mastoid angles of the parietal bone. Here, they continue as the sigmoid sinuses.

– The S-shaped **sigmoid sinus** (right and left) passes inferomedially in the respective groove of the posterior cranial fossa and, at the jugular foramen, connects with the ***internal jugular vein***.

– The smallest **occipital sinus** passes along the attachment of the falx cerebelli to the internal occipital crest. It continues with the paired **marginal sinus**, which surrounds the foramen magnum and communicates with the internal vertebral plexuses, sigmoid sinus, and sinuses of the middle cranial fossa.

– The **cavernous sinuses** are located in the middle cranial fossa on both sides of the sella turcica. Each sinus is presented by a venous plexus enclosed in the dural cavity. The internal carotid artery and the abducens nerve (CN VI) run through the cavernous sinus, and several cranial nerves pass in its lateral wall (CN III, IV, V). The cavernous sinus drains the superior ophthalmic vein and the **sphenoparietal sinus**, which lies along the lesser wings of the sphenoid bone. Through the openings in the cranial base it connects with the extracranial pterygoid venous plexus. The right and left cavernous sinuses are connected by canals along the anterior and posterior borders of the diaphragma sellae — the **anterior** and **posterior intercavernous sinuses**. The drainage of the cavernous sinuses occurs into the petrosal sinuses and the basilar venous plexus.

– The **superior** and **inferior petrosal sinuses** pass along the respective borders of the petrous parts of the temporal bones. The **superior petrosal sinuses** run along the attachment of the tentorium cerebelli; posteriorly they join the lateral ends of the transverse sinuses. Each **inferior petrosal sinus** passes in the petro-occipital fissure, receives the labyrinthine vein, and drains into the internal jugular vein. The inferior petrosal sinuses of both sides are connected on the clivus by the **basilar venous plexus,** which communicates through the foramen magnum with the internal vertebral plexus.

The **cranial arachnoid** is avascular membrane, similar to that of the spinal cord. It lies directly beneath the dura mater (Fig. 64). Only a capillary **subdural space** is between the two meninges. The arachnoid forms finger-like villi — the **arachnoid granulations** (granulationes Pacchioni), the number of which increases with age. The largest and numerous granulations are located along the superior borders of the cerebral hemispheres. The granulations protrude through the walls of the superior sagittal sinus and the lateral lacunae (and some other dural sinuses as well) to transfer the cerebrospinal fluid (CSF) from the subarachnoid space to the venous system.

The **pia mater**, a vascular connective tissue lamina, is separated from the arachnoid by the **subarachnoid space** containing **cerebrospinal fluid** (Fig. 64).

The cranial subarachnoid space communicates with the same space of the spinal cord at the foramen magnum, and with the brain cavity through the openings of the 4th ventricle. While the pia mater adheres to the surface of the brain, following its contours, sulci and depressions, the arachnoid bridges across them. Due to this, in certain areas, especially at the base of the brain and hemispheres, the arachnoid and pia mater are more separated from each other and form wider regions of the subarachnoid space, called **cranial subarachnoid cisterns**. The major cisterns are as follows (Fig. 65):

– The **cerebellomedullary cisterns — lateral** and **posterior** (cisterna magna), between the posterior surface of the medulla and the cerebellum, communicate with the IV ventricle by the median aperture;

– The **pontocerebellar cistern**, covers the cerebellopontine angle, communicates with the IV ventricle by the lateral aperture;

– The **cistern of lateral cerebral fossa** (Sylvian cistern), in front of the temporal pole, at the beginning of the lateral sulcus;

– The **chiasmatic cistern**, anterior to the optic chiasm;

– The **interpeduncular cistern**, covers the interpeduncular fossa, and contains the arterial circle of Willis;

– The **quadrigeminal cistern**, on the dorsal surface of the brainstem, between the splenium of corpus callosum and the cerebellum; contains the great cerebral vein.

The pia mater, rich in capillaries, together with the epithelial lamina — a layer of modified ependymal cells, forms the **tela chorioidea** in part of the wall of the brain ventricles and the **choroid plexuses** inside the ventricles.

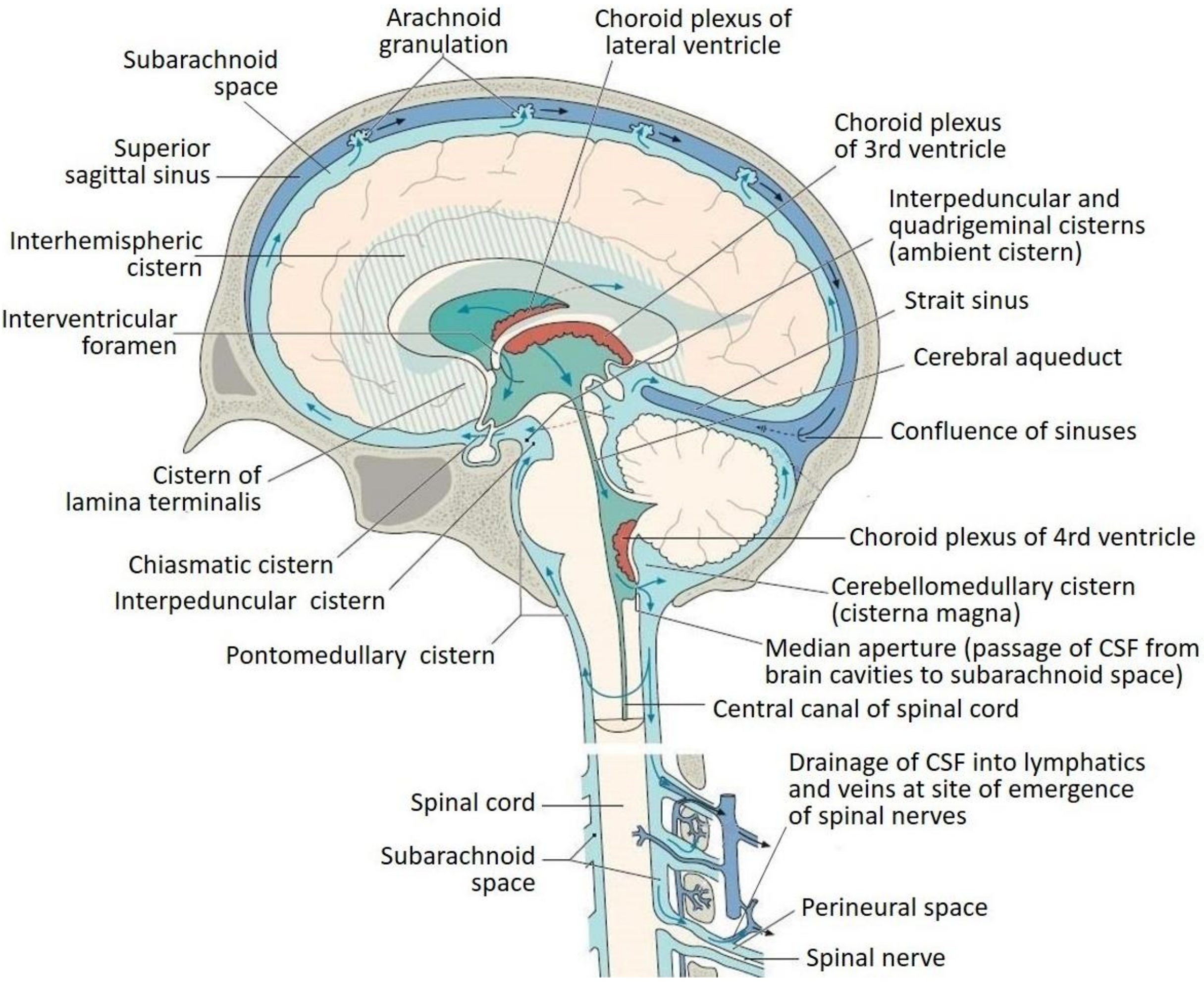

Fig. 65. Circulation and outflow of the cerebrospinal fluid

Circulation of cerebrospinal fluid

Most CSF is produced in the choroid plexuses by filtration of blood plasma from the capillaries through the layer of ependymal cells (which form the blood-CSF barrier) into the ventricles (Fig. 65). The choroid plexuses are found in all ventricles, but in the lateral ventricles they are the largest and produce the greater amount of CSF. From the lateral ventricles CSF flows through the interventricular foramina (foramina of Monro) into the 3rd ventricle and then by the aqueduct of midbrain (aquaeductus Sylvii) into the 4th ventricle. Here, some CSF mixes with that of the blind central canal of the spinal cord. From the 4th ventricle the CSF enters the subarachnoid spaces through three openings: the median aperture (foramen of Magendie) and the two lateral apertures (foramina of Luschka).

In the subarachnoid space, CSF bathes the brain and the spinal cord and then passes through the arachnoid granulations into the venous blood of the dural sinuses (Fig. 65). CSF reabsorption occurs as well into the lymphatic vessels, through perineural spaces along the roots of the cranial and spinal nerves at their exit from the skull and vertebral canal.

ADVANCED: CSF is a clear fluid reminding plasma but with slightly different electrolyte levels and a very low protein concentration. It is more similar in composition to perilymph, due to the communication between the subarachnoid space and the perilymphatic space of the internal ear.

CSF plays an important role in the normal functioning of the CNS:

– provides a liquid cushion around the CNS structures to protects them from being crushed under their own weight or mechanical trauma;

– supplies nutrients to the brain and spinal cord and removes waste products;

– regulates homeostasis in the CNS: chemical stability, pH, regulates the distribution of neuroendocrine factors, temperature and pressure;

– carries hormonal and chemical signals between parts of the CNS.

CSF is constantly produced and reabsorbed, with around 100–160 ml being present at any time. The choroid plexuses produce up to 70 % of CSF. The rest is fluid formed by the ependymal lining of the ventricles and the epithelium surrounding the subarachnoid space, and a small amount arises in the perivascular channels, that is, the spaces surrounding small vessels in the nerve tissue itself. CSF reabsorption, in addition to filtration into the dural venous sinuses, occurs through the ependyma of the brain ventricles, as well as into the lymphatic system.

SENSORY AND MOTOR PATHWAYS OF THE NERVOUS SYSTEM

Communication between the brain and the periphery of the body involves the CNS tracts passing in the white matter of the spinal cord and brainstem, and the spinal and cranial nerves of the PNS. These structures form **sensory (ascending, afferent)** and **motor (descending, efferent) pathways or tracts,** consisting of chains of neurons and associated nuclei that transmit similar information.

CNS tracts or **pathways** are bundles of nerve fibers (usually axons) that convey similar information, have a common origins, direction, and destination, and usually have a specific position in the white matter of the brain and spinal cord (Fig. 14). The axons of specific tracts are characterized by relatively uniform diameter, myelination, and conduction velocity.

Sensory pathways carry sensory information from outside and inside the body to the brain. They include receptors, sensory nerve fibers, sensory ganglia and sensory roots of the cranial and spinal nerves, located in the PNS, and the sensory tracts of the CNS in the spinal cord and/or brainstem. Sensory information reaching the nerve centers of the brain is processed there and an appropriate response is created.

Motor pathways transmit motor commands initiated in the brain. They include motor tracts of the CNS and motor fibers of the PNS that form motor roots, cranial and spinal nerves, and motor endings in skeletal muscle or viscera.

ASCENDING PATHWAYS

Ascending, sensory or afferent, tracts/pathways transmit sensory information from the receptors towards the brain. They inform the brain about changes in the external environment or internal conditions in the body.

The ascending pathways can be classified depending on the location of receptors and the nature (modality) of the signals they transmit, as follows:

1. The **exteroceptive** and **proprioceptive pathways**, commonly referred to as **somatosensory pathways**, conduct sensations from “soma” (in Latin *soma* means body), i.e. from skin and musculoskeletal receptors:

– ***Exteroceptors*** are located in the skin (and mucosal membranes of ectodermal origin); they provide the general sensations — pain, temperature, and touch (tactile sensation): pressure and vibration caused by stretching of skin and hair displacement;

– ***Proprioreceptors*** are located in muscles, muscle tendons, and joints; they provide proprioception — information about changes in muscle length and tension, joint angle, which is integrated into the muscle and joint sense, i.e. the sense of body parts position and movement, as well as sensation of deep pressure and vibration.

2. The **visceral sensory pathways** conduct information from ***interoceptors*** — receptors located in the internal organs and vessels.

3. **Pathways of special senses** (optic, acoustic, vestibular, olfactory, and gustatory) carry signals from the different kinds of special receptors in the sense organs.

Although an individual tract occupies a certain area of the white matter, it may considerably overlap with other tracts, as well as transmit information of different modalities (e.g., proprio- and exteroceptive, somatic and visceral).

Part of the ascending pathways ends in the cerebral cortex, and the sensory signals transmitted along them reach our consciousness. Other tracts terminate in the cerebellum where sensory signals are processed subconsciously.

Pathways of the cortical direction consist of chains of at least **3 neurons**:

– The **first-order neuron**, or primary afferent neuron (commonly pseudounipolar), is located in the PNS — in the spinal ganglion (dorsal root ganglion) or the sensory ganglion of the cranial nerve. The axon of the sensory neuron splits into two processes. The peripheral process serves as a "dendrite" and connects to the receptor via a spinal or cranial nerve. The central process enters the spinal cord through the dorsal root of the spinal nerve or enters the brain through the sensory root of the cranial nerve.

– The **second-order neuron** is located in the gray matter of the spinal cord (commonly in the posterior horn nuclei), or gracile and cuneate nuclei in the medulla oblongata, or sensory nuclei of the cranial nerves.

– The **third-order neuron**, projecting to the cerebral cortex is located in the thalamus.

The *pathways to the cerebellum* consist of **2 neurons** since the axon of a second-order neuron terminates in the cerebellum.

Somatosensory pathways that carry sensory signals ***from the body*** through the spinal cord, according to their morphophysiological properties, functions and topography are divided into 3 main groups (Fig. 14):

– **dorsal column-medial lemniscal system** (**pathways**), which comprises gracile and cuneate fasciculi of the spinal posterior funiculus and the medial lemniscus of the brain stem;

– **anterolateral system** (**pathways**), which unites all sensory tracts of the anterior and lateral funiculi intermingling with each other (except those transmitting signals to the cerebellum). Among them the largest is the **spinothalamic** pathway;

– **spinocerebellar pathways**.

The pathways conducting somatosensory information ***from the head*** and ***face*** form homological pathways in the brain stem.

DORSAL COLUMN-MEDIAL LEMNISCAL (DCML) PATHWAY

Dorsal column-medial lemniscal pathway (*syn.* dorsal column pathway, fasciculi gracilis and cuneatus, fasciculi of Goll and Burdach) is concerned with conscious proprioception (muscle and joint sense, sense of body parts position), sense of vibration and pressure, and the tactile sense — fine or discriminative touch[18].

The pathway conducts impulses from the skin (exteroceptors), muscles and joints (proprioceptors) of the limbs, body, and neck. The fibers comprising the pathway are heavily myelinated, thick and somatotopically organized. These allow for a fast and accurate assessment of the sensory stimuli — their localization, nature and intensity.

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[18] Fine touch is a conscious ability to localize precisely the area of the body touched and identify 2 simultaneously applied stimuli — two-point discrimination; spatial discrimination makes possible stereognosis, i.e. recognizing objects by touch.

The DCML pathway consists of the **gracile** and **cuneate fasciculi** of the posterior funiculus (*syn.* dorsal column) of the spinal cord and the **medial lemniscus** in the brain stem (Fig. 14, 66).

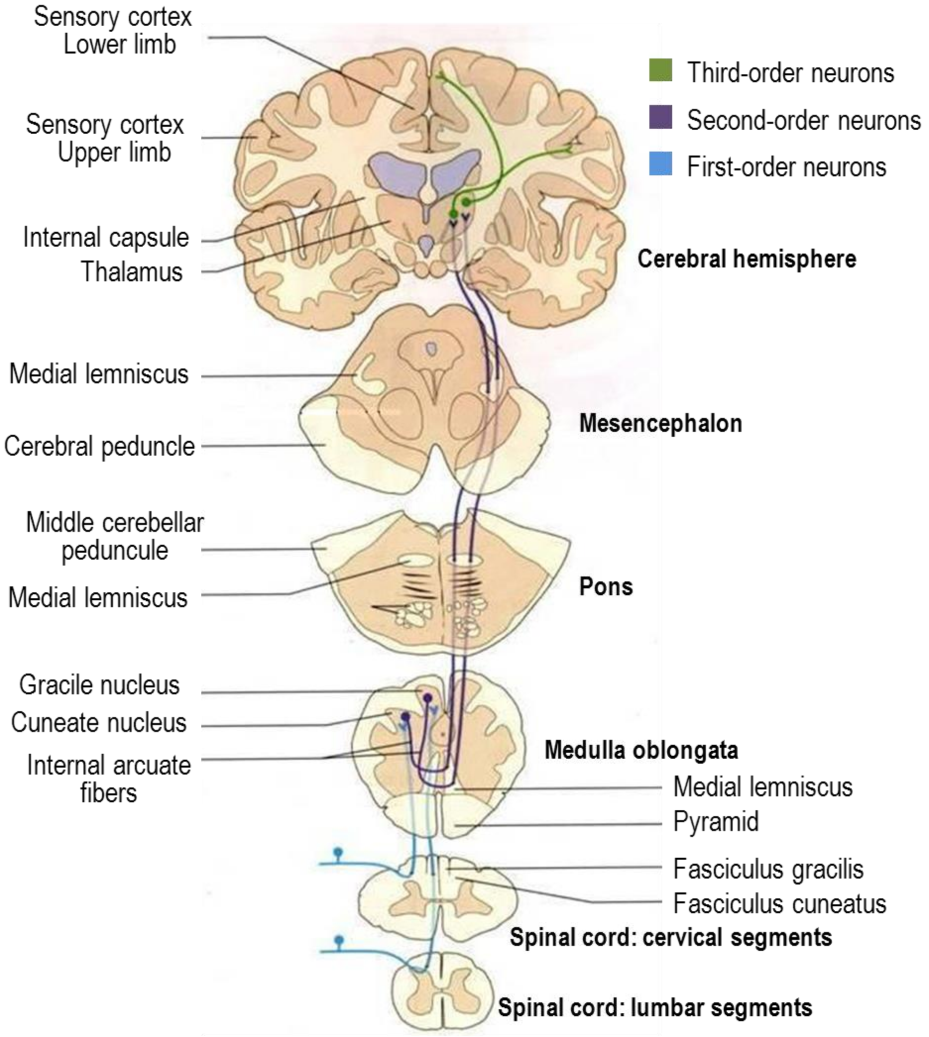

Fig. 66. Dorsal column-medial lemniscal pathway

The **first-order neurons** are located in the spinal ganglia. They send the peripheral processes to the proprioceptors and the tactile receptors. The central processes through the posterior root enter the spinal cord and ascend along the posterior funiculus of the same side towards the medulla oblongata, forming two fasciculi:

1. *Fasciculus gracilis* runs medially through all spinal cord levels. It transmits sensation from the lower spinal segments (T6 and below) — lower limbs and lower part of the trunk.
2. *Fasciculus cuneatus* joins the posterior funiculus in the upper thoracic and cervical segments lateral to the fasciculus gracilis. It conducts information from the upper spinal segments (T6 and above) — upper limbs and upper part of the trunk.

The **second-order neurons** lie in the *gracile* and *cuneate nuclei* of the medulla. Their axons (internal arcuate fibers) cross over to the opposite side, forming the *decussation of medial lemniscus (sensory decussation).* Rostral to the decussation a bundle of axons, called ***medial lemniscus***, passes along the midline through the medulla, then through the pons and midbrain to the thalamus.

The **third-order neurons** are located in the thalamus (ventral posterolateral nuclei, VPL). Their axons pass through the posterior limb of the internal capsule and terminate somatotopically in the primary somatosensory cortex — the ***postcentral gyrus*** and adjacent ***paracentral lobule*** (Fig. 47). Some axons end in the secondary somatosensory cortex in the parietal lobe posterior to the primary area.

LESIONS of the dorsal funiculus would cause a loss of proprioceptive sensation and discriminative touch in the ipsilateral part of the body below the level of the lesion. The inability to sense and localize body parts causes incoordination of voluntary movements — sensory ataxia. Loss of discriminative touch leads to inability to recognize objects by touch.

Lesions of the medial lemniscus above the decussation at the levels of the medulla and pons would cause similar symptoms but on the opposite side.

Injuries at the midbrain level and above, would affect all types of sense (proprioception, touch, pain, and temperature) on the opposite side of the body due to involvement of the spinothalamic fibers.

SPINOTHALAMIC PATHWAY

Spinothalamic pathway (syn. anterolateral pathway) comprises the **anterior** and **lateral spinothalamic tracts**, which are the main tracts of the **anterolateral system**[19] involved in the perception of pain, temperature and crude touch (Fig. 14, 67).

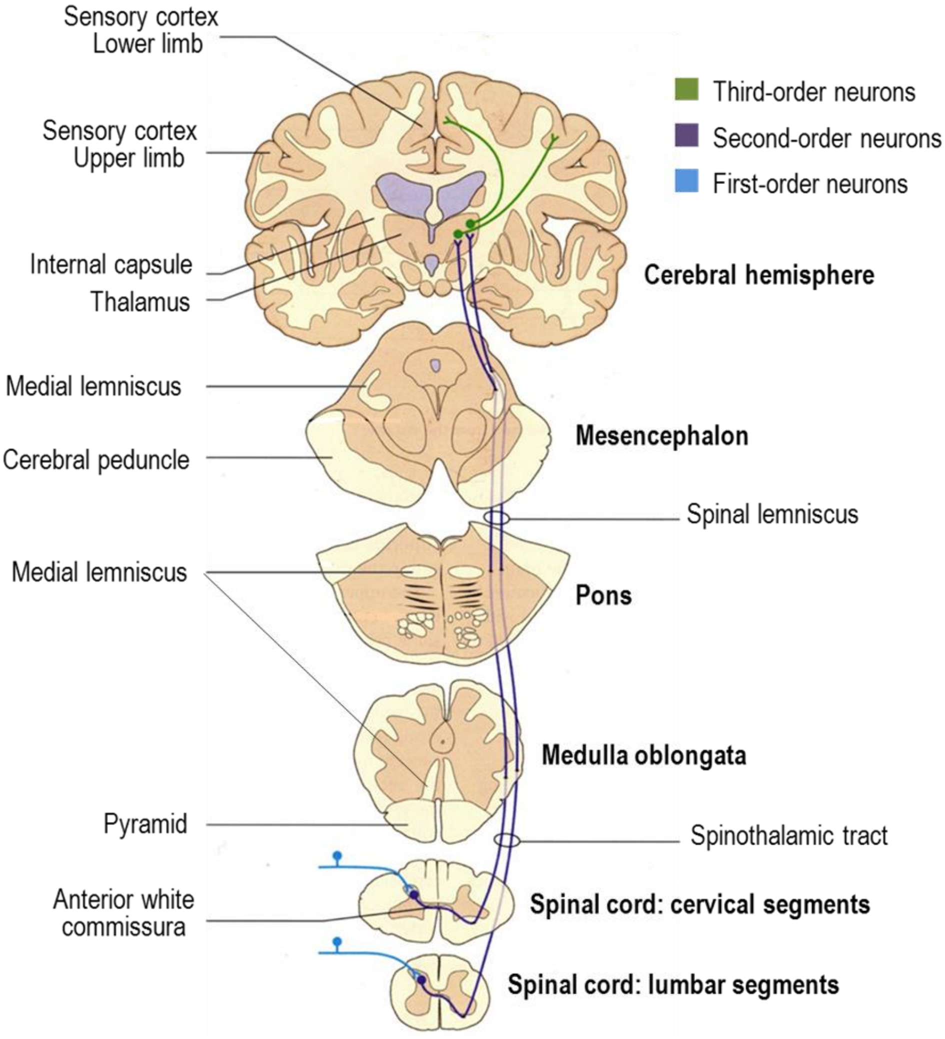

Fig. 67. Spinothalamic pathway

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[19] The anterolateral system is composed by the ascending tracts that occupy the anterolateral portion of the spinal cord white matter (from the anterior funiculus to the ventral part of the lateral funiculus). Besides the spinothalamic tracts, it comprises the spinotectal and spinoreticular tracts and some other fibers that split from the spinothalamic tract in the brain stem.

The spinothalamic pathway transmits exteroceptive impulses from the skin of the limbs, body, and neck:

– The smaller **anterior spinothalamic tract** conveys crude tactile sensation (not clearly localized) — light touch and pressure.

– The bigger **lateral spinothalamic tract** conveys pain and temperature sensation. It is important in perception of fast sharp well localized pain.

The **first-order neurons** of the spinothalamic tracts are located in the spinal ganglia. Their peripheral processes end by the skin receptors. The central processes enter the spinal cord via the posterior root to synapse on the interneurons of the posterior horn.

(Before entering the posterior horn, the axons form ascending and descending branches running up or down a few segments. The collection of these fibers forms the **dorsolateral tract of Lissaure** (Fig. 14), extending along the apex of the posterior horn throughout the length of the spinal cord.)

The **second-order neurons** lie in the posterior horn (marginal zone, substantia gelatinosa, and nucleus proprius). Their axons cross the midline in the *anterior white commissure* and ascend on the contralateral side of the spinal cord: the *anterior* spinothalamic tract — in the anterior funiculus, the *lateral* spinothalamic tract — in the lateral funiculus. In the medulla, both tracts form a single bundle of fibers — the **spinothalamic pathway**, also called the ***spinal lemniscus***, which passes through the brain stem to the thalamus. In the upper pons and midbrain, the spinal and medial lemnisci come close to each other and terminate together in the same thalamic nuclei.

The **third-order neurons** are located in the thalamus (in the VPL nuclei). Their axons pass through the posterior limb of the internal capsule and reach the primary somatosensory cortex — the **postcentral gyrus** (Fig. 47).

LESIONS: Unilateral destruction of the spinothalamic tract at the level of the spinal cord and the lateral side of the medulla leads to a deficit of pain and temperature sensation on the contralateral side of the body below the lesion. The tactile sensation, as well as vibration and body position sense, transmitted by the dorsal column pathway unilaterally, are preserved.

Lesion at the level of the midbrain, which affects both the spinothalamic fibers and the medial lemniscus, causes loss of all kinds of sensations on the opposite side of the body (accompanied by symptoms of damage to the cranial nerves nuclei).

ADVANCED: The spinotectal (spinomesencephalic) and spinoreticular tracts of the anterolateral system separate from the *spinothalamic fibers* in the brainstem (Fig. 14). The *spinotectal fibers* terminating in the midbrain colliculi, are involved in the reflex orientation of the head and eyes towards somatic stimuli (spinovisual reflexes). The fibers entering the periaqueductal gray are involved in the control of pain perception.

The *spinoreticular tract* transmits sensory information to the brain structures via the reticular formation (RF) of the brainstem. The RF neurons project to the thalamic nonspecific nuclei and the hypothalamus. The thalamic projections to the limbic cortex are concerned with the emotional perception of pain, and to the insula — with visceral reactions to pain. Pain stimuli transmitted by the spinoreticular tract are perceived as diffuse, dull, burning pain.

The spinothalamic and spinoreticular pathways also contain afferent fibers from internal organs that join these tracts at the level of the spinal cord.

SPINOCEREBELLAR PATHWAYS

Spinocerebellar pathways convey unconscious, mainly proprioceptive information, which is subconsciously processed, and allows the cerebellum to control balance, posture and coordinate movements. The direct pathways to the cerebellum form 2-neuron chains (Fig. 14, 68).

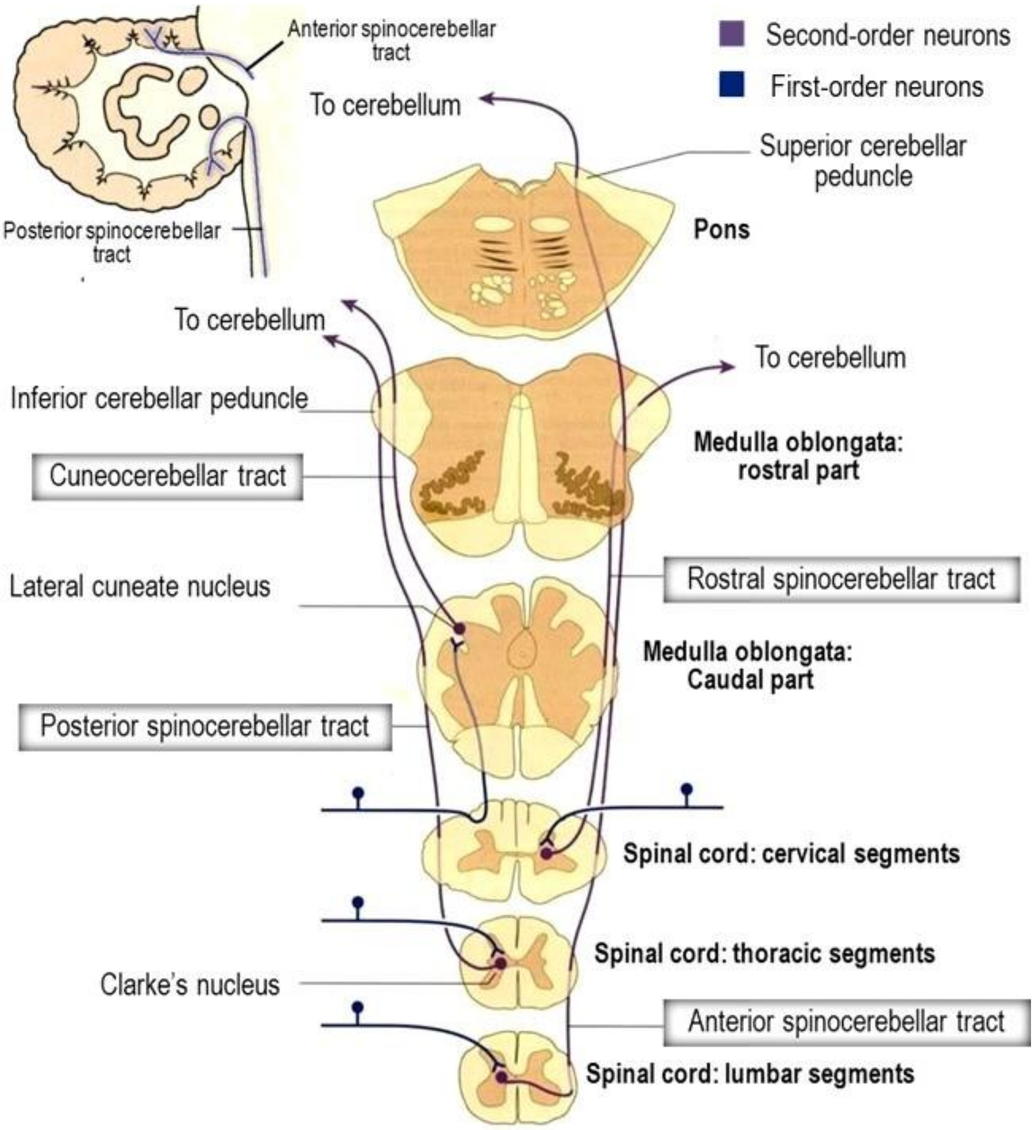

Fig. 68. Spinocerebellar pathways

The **posterior** and **anterior spinocerebellar tracts** transmit impulses from the trunk and lower limbs of the same side.

The **first-order neurons** lie in the spinal ganglia. The peripheral processes are connected with the proprioceptors in muscles and joints. The central processes via the dorsal root enter the spinal cord.

The **second-order neurons** lie in the gray matter of the spinal cord; their axons ascend towards the cerebellum along the periphery of the lateral funiculus:

– The **second-order neurons** of the *posterior spinocerebellar tract* (the most important and well defined) are located in the *posterior (dorsal) thoracic nucleus (Clarke's nucleus)* at the level of C8–L2 spinal segments. Axons of the second-order neurons ascend ipsilaterally in the posterior portion of the lateral funiculus of the spinal cord, pass through the medulla oblongata, enter the cerebellum via the *inferior cerebellar peduncle* and terminate in the vermis cortex.

– The **second-order neurons** of the *anterior spinocerebellar tract* are located in the intermediate gray matter (*T12–L5 spinal segments*). Their **axons** decussate via the *white anterior commissure* to the contralateral side and ascend in the anterior portion of the lateral funiculus, then pass through the medulla oblongata and pons, reach the midbrain, and turn back. In the superior medullary velum, most fibers decussate again and enter the cerebellum via the *superior cerebellar peduncles* to terminate in the vermis cortex. Hence, this pathway ends ipsilateral to the body part it represents.

LESIONS: Damage to the spinocerebellar pathways leads to the loss of unconscious proprioceptive information and affects control and correction of ongoing movements. This results in deficits of motor function (ataxia) — disturbances in gait, inability to perform smooth, directed, coordinated movements.

ADVANCED: The ***cuneocerebellar tracts*** is the main direct pathways to the cerebellum that carry proprioception from the upper limb and upper body (Fig. 68). The bodies of the **first-order neurons** are located in the spinal ganglia of the cervical spinal nerves (C2–C8). Their axons ascend to the medulla in the *fasciculus cuneatus* and end in the *lateral cuneate nucleus* (analogous to the Clarke's nucleus), located lateral to the cuneate nucleus. The **second-order neurons** of the lateral cuneate nucleus give rise to the *cuneocerebellar fibers*, which enter the inferior cerebellar peduncle and end ipsilaterally in the vermis.

SOMATOSENSORY PATHWAYS FROM THE FACE AND HEAD

Somatosensory pathways from the face and head (except the back of the head innervated by branches of the second and third cervical spinal nerves) transmit sensory information from skin of the face and head, mucous membranes of the oral and nasal cavities, palate, pharynx, and laryngeal vestibule, from the teeth, external and middle ear, conjunctiva and cornea of the eyes, proprioception from masticatory and facial muscles, extrinsic muscles of the eyeball and temporomandibular joint.

This information is transmitted to the CNS by cranial nerves, predominantly by the *trigeminal (V) nerve*, additionally by the *glossopharyngeal (IX)* and *vagus (X) nerves*, and *facial (VII) nerve* (from small area of the external ear).

The **first-order neurons** are located in the sensory ganglia of the above-mentioned cranial nerves. The peripheral processes reach the receptors; the central processes via the roots of the cranial nerves enter the brain stem and synapse on the neurons of the *trigeminal nuclei* (Fig. 69, 70). The fibers descending from their entry to the brainstem towards the spinal nucleus form a bundle, the *spinal trigeminal tract*, located lateral to the respective nucleus.

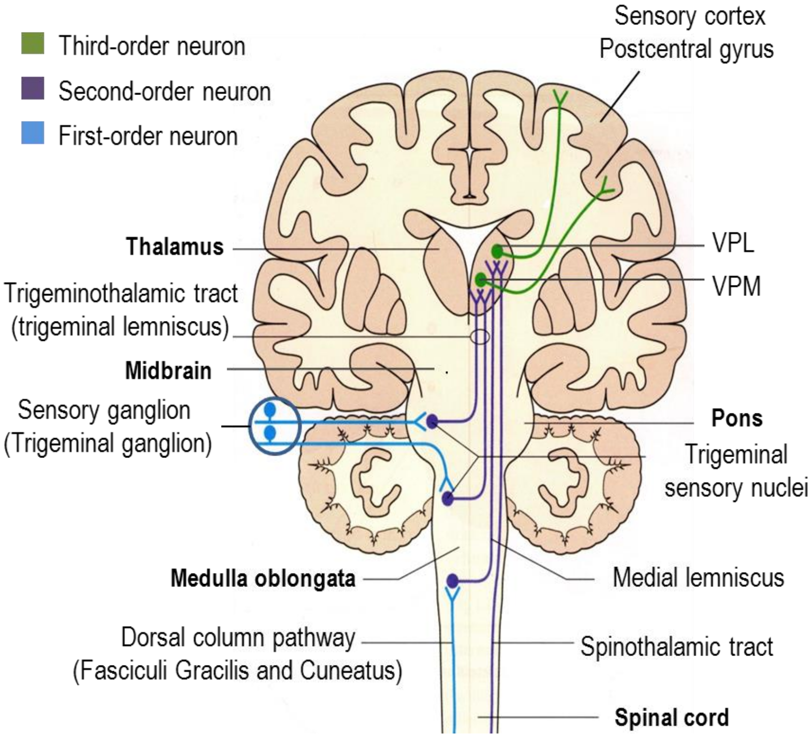

Fig. 69. Somatosensory pathways from the face and head and spinal sensory tracts of cortical direction (VPL — ventral posterolateral nucleus; VPM — ventral posteromedial nucleus)

The **second-order neurons** are located 1) in the *principle sensory nucleus* (*syn. pontine nucleus*), which processes discriminative touch and proprioception; and 2) in the *spinal trigeminal nucleus,* which processes pain, thermal and crude touch information.

Axons of the **second-order neurons** (all arising from the spinal nucleus, and most arising from the principle nucleus) decussate and form the contralateral **trigeminal lemniscus**, or **trigeminothalamic tract**, which ends in the thalamus.

The **third-order neurons** are located in the thalamic nuclei (mainly in VPM — ventral posteromedial nucleus). Their axons pass through the posterior limb of the internal capsule and terminate in the face area of the primary sensory cortex — the lower half of the *postcentral gyrus* (Fig. 47).

LESIONS: Unilateral damage to the brain stem that involves the trigeminal lemniscus at the level of the medulla and lower pons (where only crossing axons that arise from the spinal nucleus are located) would cause the loss of pain and temperature sense in the contralateral half of the face. Damage above this level (after axons of the pontine nucleus join) would affect the sense of touch and proprioception in face as well.

ADVANCED: The proprioceptive information is transmitted by the trigeminal nerve through the primary afferent neurons (first-order neurons) located in the *mesencephalic nucleus* of the trigeminal nerve (Fig. 70). Some axons of these neurons terminate in the pontine nucleus, others connect to the motor nucleus of the trigeminal nerve and take part in the monosynaptic stretch reflex (jaw jerk), which plays an important role in the chewing process.

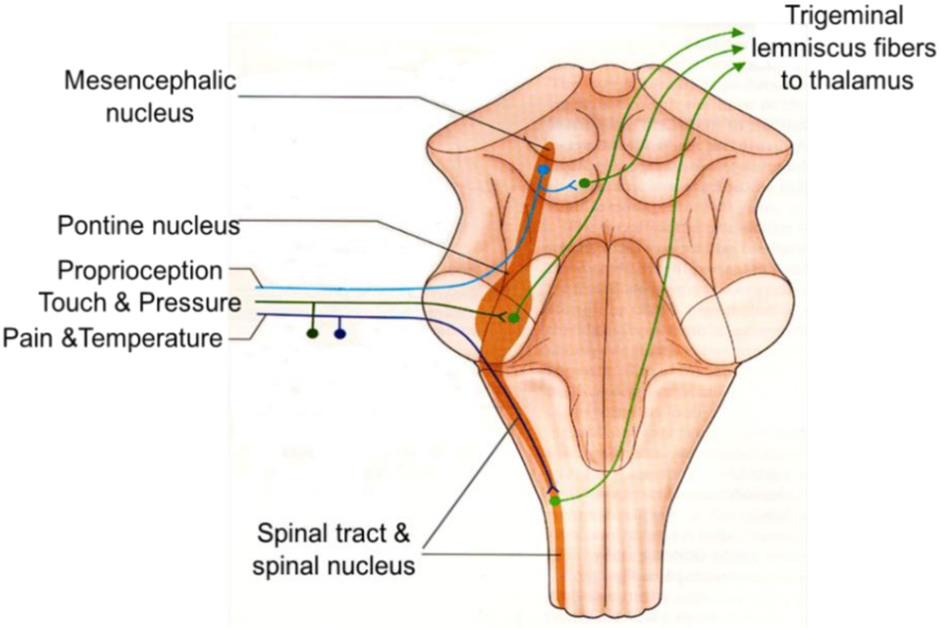

Fig. 70. Trigeminal sensory nuclei and their major connections

DESCENDING PATHWAYS

Descending or motor pathways send motor commands from the brain to the effectors (muscles and glands). The **somatic motor pathways** control activity of the skeletal muscles. One group of these pathways, often called the *pyramidal tracts,* originates in the cerebral cortex and conducts conscious voluntary commands to the skeletal muscles. Another group, referred to as the *extrapyramidal tracts,* originates in the motor centers of the brainstem and subconsciously controls automatic muscle activity. The **visceral motor pathways** transmit impulses from the centers of the autonomic nervous system located in the hypothalamus and brain stem to the autonomic neurons in the spinal gray matter and to the autonomic nuclei of the cranial nerves. They control the activity of the smooth muscles of the internal organs and vessels, myocardium, and glands secretion.

Motor pathways consist of two levels of neurons. The cell bodies of **first-order neurons** — **upper motor neurons**, are located in the brain. Their axons descend through the brainstem and spinal cord. The cell bodies of the **second-order neurons** — the **lower motor neurons**, are located in the motor nuclei of the anterior horns of the spinal cord or the motor nuclei of the cranial nerves in the brainstem. The axons of the lower motor neurons run from the spinal cord via the ventral roots and spinal nerves to the muscles of the trunk, neck and limbs; and from the brain stem through the cranial nerves to the muscles of the head (Fig. 71).

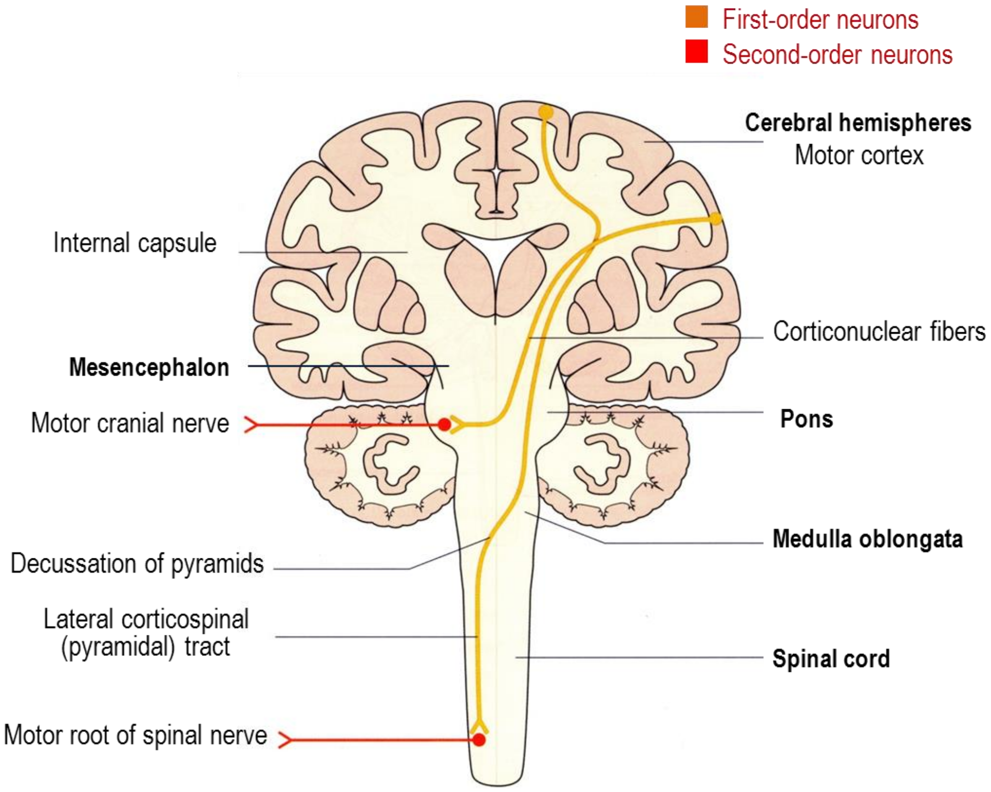

Fig. 71. Corticonuclear and corticospinal tracts

Upper motor neurons can synapse with lower motor neurons directly (as in the lateral corticospinal tract) or indirectly via **interneurons** (in most descending tracts). However, for simplicity, the interneuron is usually omitted in the description of motor pathways.

ADVANCED: The motor tracts are divided by their topography in the spinal cord into “lateral” and “medial” groups. The *lateral group* includes the *lateral corticospinal tract,* the *rubrospinal tract,* and some *reticulospinal fibers.* They descend in the lateral funiculus and terminate in the lateral motor nuclei of the anterior horn, which innervate the muscles of the limbs. They activate the flexor muscles and are especially important for the skillful movements of the fingers. The *medial group* includes the *anterior corticospinal*, *reticulospinal*, *vestibulospinal* and *tectospinal* tracts terminating mainly in the medial motor nuclei that innervate the antigravity muscles — axial muscles and extensors of the proximal muscles. These pathways are important for regulating balance, posture, and movement of the proximal limbs.

MOTOR PATHWAYS ORIGINATING IN THE CEREBRAL CORTEX (PYRAMIDAL TRACTS)

Motor pathways that originate in the cerebral cortex and provide conscious voluntary control over skeletal muscles are often called “pyramidal”, since most of their fibers pass through the pyramids of the medulla oblongata.

The *corticospinal* and *corticonuclear fibers* form three tracts (Fig. 14, 71, 72):

– The **corticonuclear tract**, often called the *corticobulbar tract* (the *bulb* generally refers to the medulla oblongata), controls the muscles of the head and some neck muscles;

– The **anterior corticospinal (pyramidal) tract** controls the axial muscles and voluntary movements of the trunk;

– The **lateral corticospinal (pyramidal) tract** controls the muscles of the limbs, and is primarily responsible for fine voluntary movements, such as precise skilled movement of the fingers.

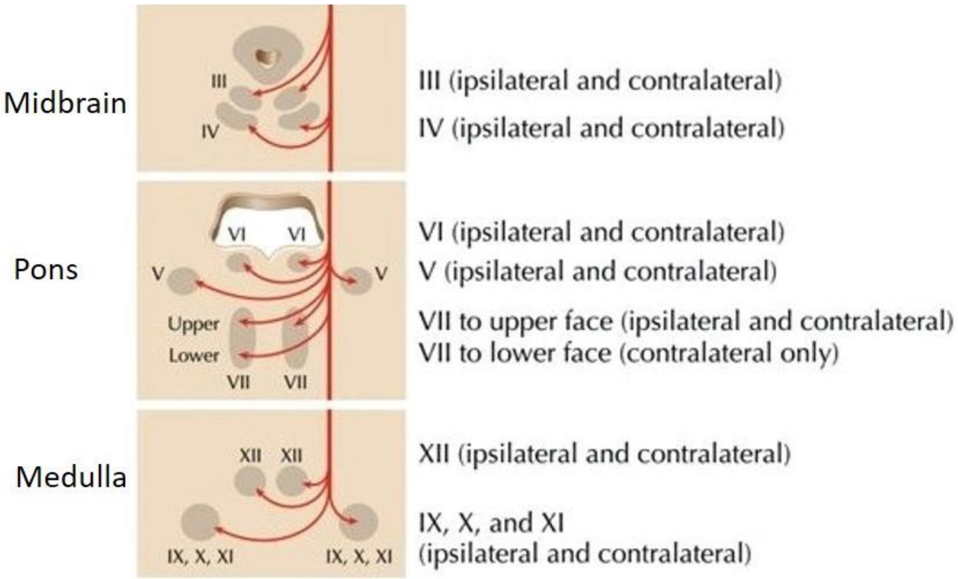

Fig. 72. Corticonuclear tract: termination of the upper motor neuron in the cranial nerve nuclei

The **first-order neurons** (pyramidal cells) of all three tracts are located in the primary motor cortex (in the fifth layer) — the *precentral gyrus* and *paracentral lobules,* and some of the neurons — in the secondary motor cortex, of the frontal lobe. In the precentral gyrus the pyramidal neurons are distributed in the somatotopic manner similar to that in the primary somatosensory cortex (Fig. 47).

Corticonuclear tract (Fig. 71, 72): Axons of the **first-order neurons** descend through the genu of the internal capsule and pass into the brain stem where they terminate at different levels in the nuclei of the cranial nerves. Most axons decussate just before reaching the nuclei, but some terminate on the ipsilateral side. Completely crossed axons end on neurons of the facial nucleus (CN VII), innervating the muscles of the lower half of the face.

The **second-order neurons** are located in the motor nuclei of the cranial nerves (CN III–VII, CN IX–XII). Their axons through the cranial nerves reach the corresponding muscles.

Corticospinal tracts (Fig. 73): Axons of the **first-order neurons** pass through the posterior limb of the internal capsule and descend in the ventral part of the brainstem to form the *pyramids* of the medulla oblongata. At the caudal end of the pyramids approximately 80–90 % of corticospinal fibers cross the midline via the **decussation of pyramids**. The crossed fibers form the **lateral corticospinal tract**, which descends in the lateral funiculus of the spinal cord and terminates on the motoneurons of the anterior horn.

The remaining uncrossed fibers form the **anterior corticospinal tract**, which descends in the anterior funiculus. Most of the fibers cross the midline at the segmental levels, passing through the *anterior white commissure*, and terminate in the anterior horn of the opposite side. Some fibers terminate on the same side.

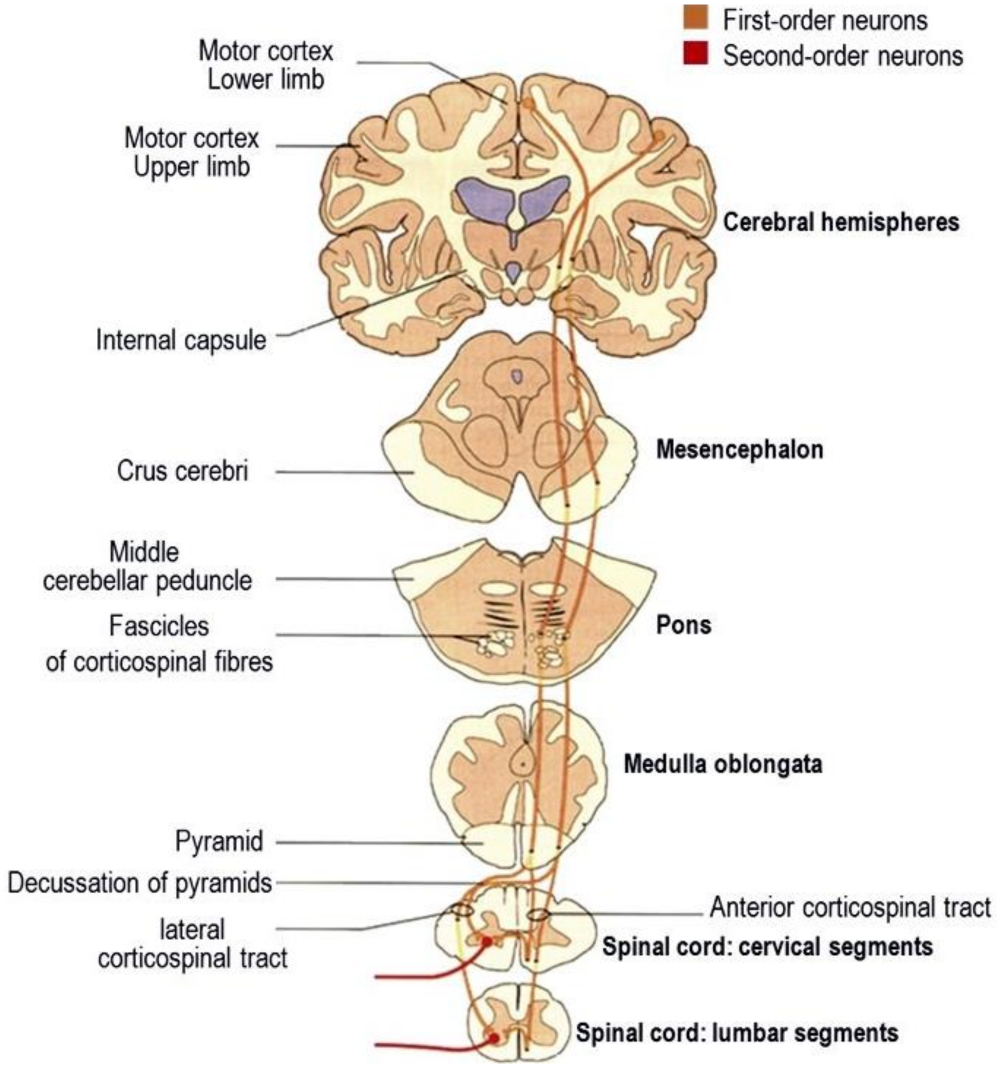

Fig. 73. Corticospinal tracts

Thus, the muscles of the trunk and the respiratory muscles are under the control of both hemispheres; while the muscles of the limbs are controlled by the contralateral cerebral hemisphere.

The **second-order neurons** of the corticospinal tracts are the motor neurons of the anterior horns, the axons of which pass through the spinal nerves to the skeletal muscles.

LESIONS: Lesions of the *corticospinal tracts* lead to weakening of muscles (paresis) or loss of voluntary movements (paralysis), which are limited to the muscles of the limbs (mainly distal ones), since the muscles of the trunk are under the bilateral control of the cerebral cortex. Damage above the level of the decussation — in the cerebral cortex (for example, in stroke) or in the internal capsule (in cerebrovascular disorders), affects movements on the contralateral side. An injury at the level of the spinal cord, below the decussation, which involves the lateral corticospinal tract, affects the ipsilateral muscles.

Unilateral lesions of the lower part of the precentral gyrus, where the *cortironuclear tract* originates, results in mild weakness of the head and neck muscles. This is due to the incomplete decussation of the corticonuclear fibers. Therefore, the vital functions, such as chewing and swallowing, are usually preserved. The exceptions are the muscles of the lower half of the face, which will be paralyzed on the contralateral side.

SUBCONSCIOUS MOTOR PATHWAYS (EXTRAPYRAMIDAL TRACTS)

“Extrapyramidal system” is a part of the motor system that provides subconscious control of muscle tone and movements, participates in reflexes, coordination of automatic movements, maintaining balance, posture and locomotion, takes part in voluntary movements (preparing, tuning and making them smoother).

The extrapyramidal system includes subcortical centers involved in motor functions and motor pathways originating in the centers of brain stem:

1. The *higher centers of the extrapyramidal system*, such as the basal nuclei, substantia nigra, subthalamic nuclei, cerebellum, and thalamus, modulate the motor activity indirectly.

2. The *motor centers of the brainstem*, such as the red nucleus, vestibular nuclei, reticular formation, etc., give rise to extrapyramidal motor pathways, which through lower motor neurons provide the direct control over skeletal muscles.

The largest **extrapyramidal tracts** are the *rubrospinal*, *vestibulospinal, reticulospinal* and *tectospinal* tracts (Fig. 14). The rubrospinal tract helps control the distal limb muscles that perform more precise movements; it activates the same motor neurons, which are controlled by the corticospinal tract and are responsible for contraction of the flexor muscles. The other tracts control muscle tone and gross movements of the neck, trunk, and proximal limb muscles activating neurons that control the extensors.

All of the above tracts comprise 2 neurons (Fig. 74).

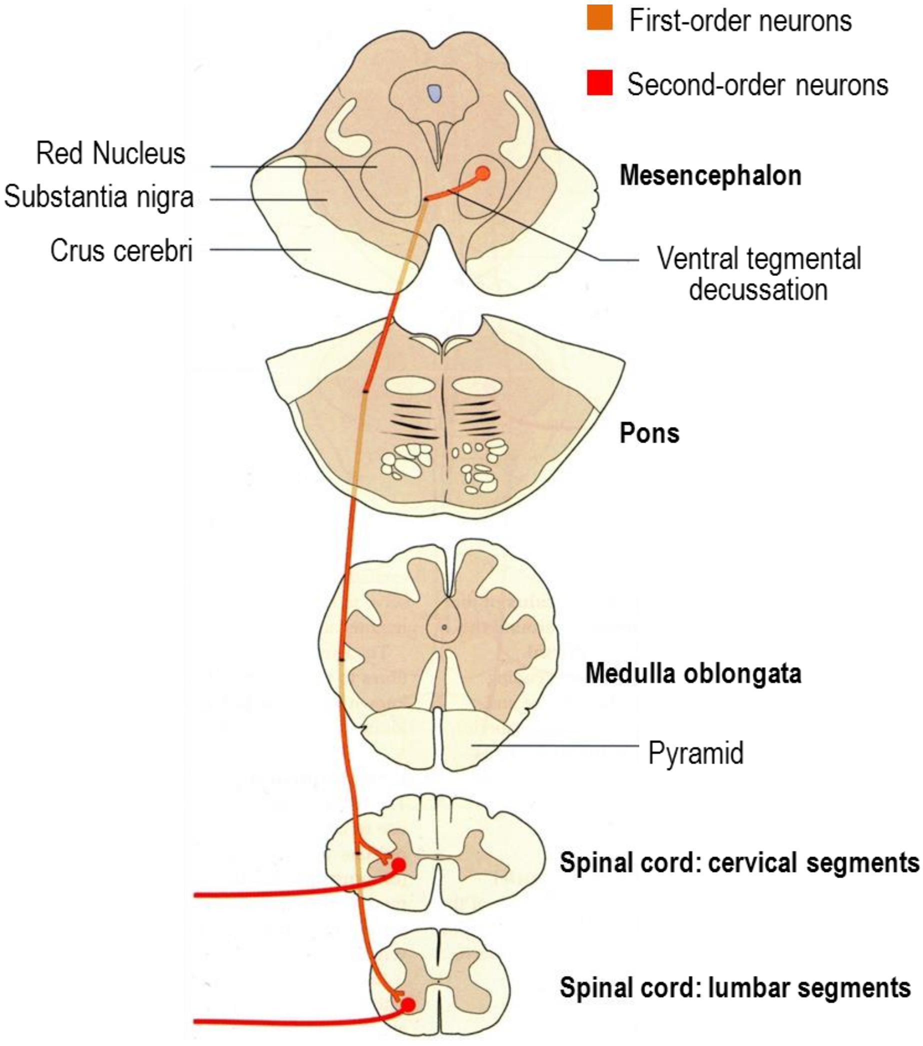

Fig. 74. Rubrospinal tract

The **first-order neurons** are located in the corresponding motor center of the brainstem, which is reflected in the name of a particular tract. Axons of the upper motor neurons (crossed or uncrossed) descend along the spinal cord in the anterior or lateral funiculus and connect (directly or indirectly — via interneurons) with the motor neurons of the spinal cord. Some axons terminate in the brainstem in the motor nuclei of the cranial nerves.

The **second-order neurons** (lower motor neurons) are located in the motor nuclei of the anterior horn or cranial nerves. Their axons reach the striated muscles of the head and body via the peripheral nerves — cranial or spinal.

The ***rubrospinal tract*** is one of the extrapyramidal tracts. It controls mainly the movements of the arm and hand by activating flexors, similar to the lateral corticospinal tract (Fig. 74).

The **first-order neurons** originate in the **red nucleus**. Their axons decussate ventrally within the midbrain and descend in the brainstem and then in the lateral funiculus of the spinal cord, medial to and overlapping with the lateral corticospinal tract. Most rubrospinal fibers terminate at the cervical and thoracic levels of the spinal cord on the motor neurons of the anterior horns. Some fibers end in the motor nuclei of the cranial nerves and are involved in the regulation of reflex movements of the masticatory and facial muscles.

The **second-order neurons** lie in the lateral motor nuclei of the anterior horns. Their axons terminate mainly in the muscles of the upper limb.

ADVANCED: The *red nucleus* plays an important role in mediating and coordinating voluntary movements due to the direct connection with the cerebral cortex, the cerebellum, and the RF. The red nucleus receives the direct input from the precentral gyrus (via corticorubral fibers) and transmits these signals to the skeletal muscles via the rubrospinal tract. Thus, the rubrospinal tract is an alternative route for voluntary motor commands to the distal muscles of the upper limbs, which can be important if the lateral corticospinal tract is damaged. A significant part of the red nucleus fibers connects with the RF of the brainstem and influences movements via the reticulospinal tracts as well.

The *reticulospinal tracts* originate in the **reticular formation** of the brainstem. The *medial reticulospinal tract* (uncrossed) arises in the **pons** and courses through the *medial longitudinal fasciculus* (MLF) to the anterior funiculus of the spinal cord. It activates mainly the motor neurons of the antigravity muscles (extensors), maintains complex posture, participates in reflex orienting movements, including eye movements.

The *lateral reticulospinal tract* (partially crossed) arises in the **medulla** and passes in the ventral part of the lateral funiculus to the anterior horns. Part of its fibers end in the lateral motor neurons of the anterior horn. These fibers, similar to the rubrospinal tract, activate proximal flexor muscles. The lateral reticulospinal tract regulates reflex activity, including many visceral functions, influences muscle tone and facilitates voluntary movements, coordinates automatic movements of locomotion and posture, modulates pain impulses.

The *lateral* and *medial vestibulospinal tracts* originate in the corresponding **vestibular nuclei** and relay information from the inner ear and the cerebellum. The larger *lateral vestibulospinal tract* (uncrossed) runs in the anterior funiculus throughout the spinal cord. It controls antigravity muscles (extensors) and corrects posture to maintains body balance during standing and moving. *The medial vestibulospinal tract* (partially crossed) is a part of the *medial longitudinal fasciculus* (MLF) of the brain stem, which further runs in the anterior funiculus of the cervical segments. Its fibers terminate in the nuclei of the CN III, IV, VI and anterior horns of the upper cervical segments that innervate the extrinsic muscles of the eyes and the neck muscles. This tract stabilizes position of the head when the body moves and coordinates the head and eye movements.

The *tectospinal tract* begins in the **tectum** of midbrain, in the **superior colliculi**. It forms decussation ventral to the cerebral aqueduct, runs through the brainstem close to the MLF projecting to the nuclei of the “oculomotor” nerves (CN III, IV, and VI). The remaining fibers descend in the anterior funiculus medial to the anterior pyramidal tract and terminate mainly in the upper cervical segments. The tract controls the tone of muscles of the neck, upper trunk, and shoulder girdle (extensors and rotators) and eyes position. It coordinates reflex movements of the eyes, head, and upper limbs in response to visual and auditory stimuli (so-called startle-reflex).

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CONTENTS

Учебное издание

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