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SOMATIC CONDUCTION PATHWAYS OF THE CENTRAL NERVOUS SYSTEM

Учебно-методическое пособие

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Предназначено для студентов 2-го курса медицинского факультета иностранных учащихся, изучающих дисциплину «Анатомия человека» на английском языке. Предлагаемые материалы могут быть использованы при изучении нервных болезней.

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GENERAL CHARACTERISTICS OF THE CONDUCTION PATHWAYS OF THE CENTRAL NERVOUS SYSTEM

Conduction tracts (pathways) of the central nervous system (CNS) are bundles of nerve fibers (usually axons), which transmit similar information, have common source of origins, direction and destination, and generally specific position in the white matter of CNS. Axons of the specific tracts are characterized by relatively uniform diameter, myelination and conduction velocity.

Depending on the size and shape the bundles of axons are called tracts, fascicles (Latin: *fasciculi*), fibers, loops (Latin: *lemnisci*), radiations.

Depending on the direction of tracts they can be divided into 3 categories: association, commissural and projection tracts/fibers.

Association tracts are formed by longitudinally oriented fibers that connect areas of the same side within a part of the brain or spinal cord.

In the cerebral hemispheres they connect different cortical areas of the same side: the *short* association fibers (*arcuate fibers)* connect the adjacent gyri; the *long* association fibers connect more distant areas of cortex and lie deeper in the white matter (e. g., *superior* and *inferior longitudinal fasciculi, uncinate fasciculus, cingulum*) (fig. 1).

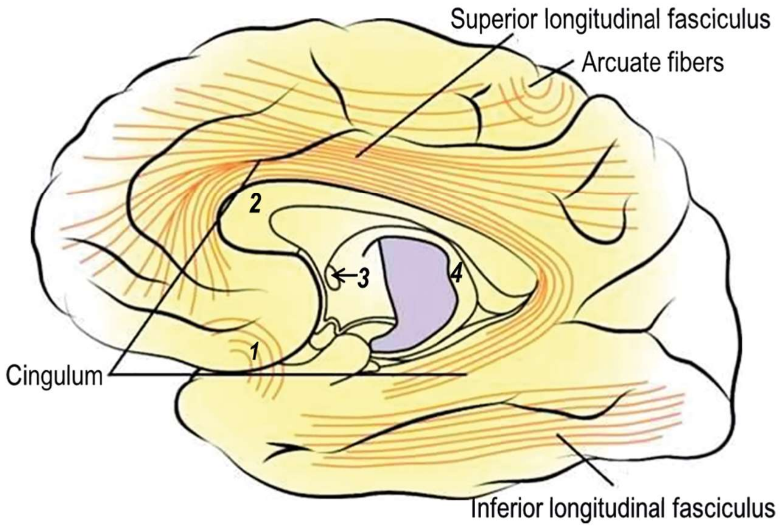

Fig. 1. Association and commissural tracts of the hemispheres:
1 — uncinate fasciculus; *2* — corpus callosum; *3* — anterior commissure; *4* — hippocampal commissure

Among the subcortical association tracts some are structurally separated bundles of fibers, such as the *fornix, stria terminalis, stria medullaris* (all are related to the limbic system). Others form numerous fascicles and tracts within the white matter of the brain, which interconnect the cerebellum, thalamus and nuclei of the brain stem (e. g., dentatorubral, dentatothalamic, rubro-olivary, olivocerebellar tracts).

In the spinal cord association (propriospinal) tracts — *anterior, lateral* and *posterior fasciculi proprii*, are located in the white matter of the corresponding funiculi next to the central gray matter (fig. 2). They serve for intersegmental connections and comprise ascending, descending, crossed and uncrossed fibers.

Commissural tracts are composed of transversally oriented fibers that connect the symmetrical parts of the brain or the opposite halves of the spinal cord (fig. 1).

The *corpus callosum* is the largest commissural tract linking the cerebral cortex of the left and right cerebral hemispheres. The *anterior commissure* is a small bundle of fibers that connects the right and left olfactory lobes and the limbic structures of the temporal lobes. The *hippocampal commissure,* aka, *commissure of the fornix*, connects the right and left hippocampal formations.

The *posterior commissure* is a small nerve fascicle in the posterior wall of the 3rd ventricle that connects the symmetrical small nuclei of the posterior thalamus and rostral part of the midbrain involved in the bilateral light reflex and eye responses to light.

The *habenular commissure* is a small fascicle anterior to the pineal gland (a part of the epithalamus) connecting the symmetrical habenular nuclei.

The *anterior spinal white commissure* connects the left and right sides of the spinal cord in the depth of the anterior median fissure; it contains fibers of the spinothalamic and anterior corticospinal tracts.

Projection tracts have vertical direction and connect different levels of the CNS.

The ***short tracts*** (fibers) connect the nerve centers within the brain, in particular, hemispheres with the thalamus and brain stem (e. g., corticopontine, corticorubral, thalamoparietal fibers). The ***long tracts*** connect the brain with the spinal cord in both directions. **Ascending, afferent tracts** transmit sensory information from the spinal cord to the brain. **Descending, efferent tracts** carry motor signals from the brain to the spinal cord (fig. 2).

The **long projection tracts (pathways)** are also defined in a wider sense as chains of neurons transmitting similar information all the way from receptors towards the nerve centers in the brain or from the brain to motor endings/effectors. In this sense a pathway comprises, additionally to the CNS structures, components of the peripheral nervous systems (PNS) linking the brain and the spinal cord with the rest of the body.

The sensory information received from the external and internal environments by receptors is conducted towards the CNS via the sensory nerves fibers, sensory ganglia and sensory roots. By passing through the spinal cord and brain, the sensory information reaches the nerve centers where it is processed (analyzed, interpreted or perceived) and an appropriate respond is created. The motor command initiated in the brain is conducted through the CNS and then the motor root and motor nerves/fibers of the peripheral nerve to reach the motor endings in the skeletal muscle or viscera.

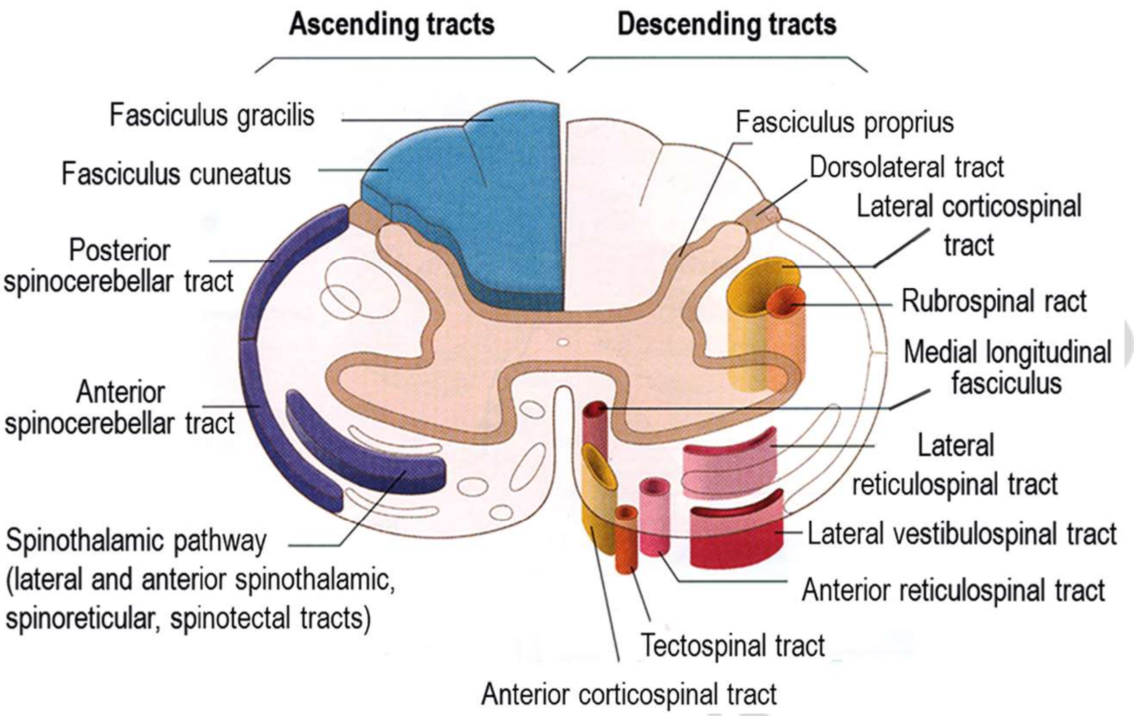

Fig. 2. Long and short (propriospinal) tracts in the transverse section through the cervical part of the spinal cord

The projection fibers associated with the cerebral cortex (except for the olfactory pathway) are arranged in a compact white matter structure at the base of the hemispheres — the *internal capsule*. Towards the cerebral cortex these fibers (both ascending and descending) become a fan-shaped radiating mass — *corona radiata.*

The **internal capsule** on the horizontal section of the hemisphere is V-shaped and has three parts: **genu** — the bend, **anterior** and **posterior limbs** (Latin: *crura*) (fig. 3). The *short afferent projection fibers* are found in each part of the internal capsule. They connect different nuclei of the thalamus with the corresponding cortical areas (e. g., thalamofrontal, thalamoparietal fibers) and with the basal nuclei (e. g., thalamostriate fibers). These fibers, often collectively called the *thalamocortical fibers*, compose the *thalamic radiations*.

The terminal part of the ***long afferent (sensory) pathways*** of cortical direction is a component of the thalamic radiation (*thalamoparietal fibers*) passing through the posterior limb of the internal capsule. The *acoustic* and *optic radiations* occupy the caudal end of the posterior limb (fig. 3).

The majority of the *short efferent fibers* originating in different lobes of the hemisphere form the *corticopontine tract* with its bigger part (*frontopontine fibers*) in the anterior limb. (Via the pontine nuclei the cerebral cortex communicates with the cerebellum.) Other fibers connect the cerebral cortex with the thalamus and nuclei of the brain stem — reticular formation, nucleus ruber, tectum of the midbrain (e. g., corticothalamic, corticorubral fibers).

The cortical ***long efferent (motor) pathways*** pass through the internal capsule as follows: in the genu — the *corticonuclear fibers* (to the head and neck); in the rostral part of the posterior limb — the *corticospinal fibers* (successively: to the upper limb, trunk and lower limb) (fig. 3).

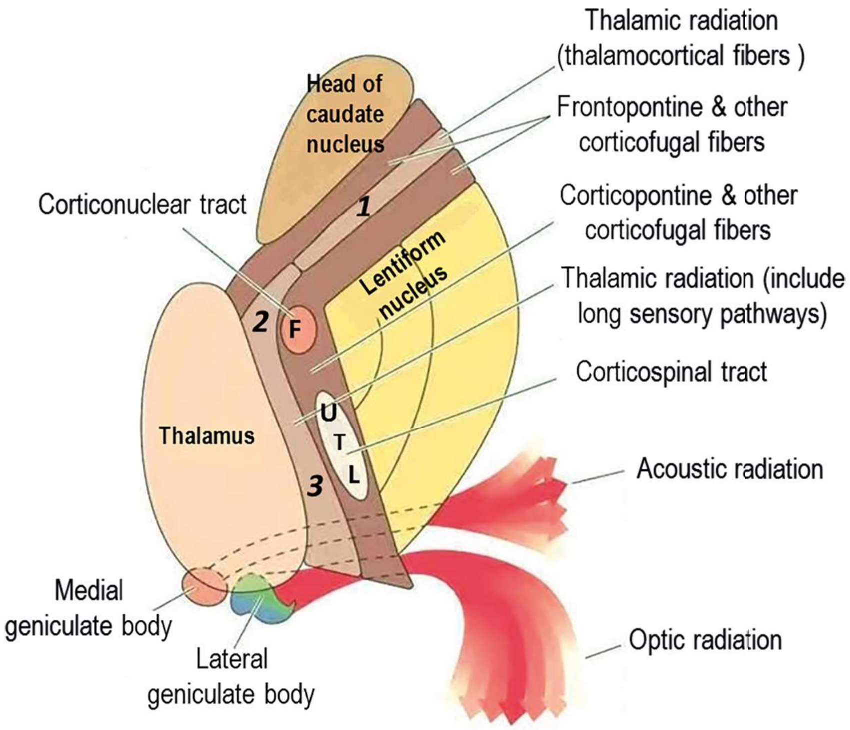

Fig. 3. Scheme of horizontal section through the internal capsule:
1 — anterior limb; *2* — genu; *3* — posterior limb; *F* — face; *U* — upper extremity; *T* — trunk; *L* — lower extremity

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.

Ascending pathways can be classified based on the location of receptors and the character (modality) of signals they convey as follows:

1. **Exteroceptive** and **proprioceptive**, commonly referred to as **somatosensory pathways**, conduct sensation from the «soma» (in Latin *soma* means body), i. e. from the receptors in the skin and locomotor apparatus:

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

– ***proprioreceptors*** are receptors located in muscles, muscle tendons, joints; they provide proprioception (information about changing in muscle length and tension, joint angle, which is integrated in the sense of the body parts position and movement), sensation of deep pressure and vibration.

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

3. **Pathways of special sensations** (optic, acoustic, vestibular, olfactory, and gustatory) carry signals from the different kinds of specific receptors in the sensory 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).

Some ascending pathways end in the cerebral cortex, and sensory signals conveyed by these tracts reach our conscious awareness. Other tracts end in subcortical centers (e. g., cerebellum) and the transmitted information is processed at the subconscious level.

While the sensory information from the body to the cerebellum (by the ***spinocerebellar tracts***) is conveyed by two-neuron pathways, the ***pathways of cortical direction*** are presented by the chains of at least three neurons. The **first-order neuron**, or primary afferent neuron (commonly pseudounipolar), is located outside the CNS — in the spinal ganglia (*syn.* dorsal root ganglia) or sensory ganglia of the cranial nerve. The axon of this neuron splits into two processes. The peripheral process serves as a «dendrite» and via the branch of the spinal or cranial nerve it connects with a receptor. The central process (axon) enters the spinal cord via the dorsal root of the spinal nerve, or enters the brain via the sensory root of the cranial nerve. The **second-order neuron** is located in the gray matter (commonly posterior horn nuclei) of the spinal cord, gracile and cuneate nuclei in the medulla oblongata, or sensory nuclei of the cranial nerves. The **third-order neuron,** the last neuron projecting in the cortex, is in the thalamus.

The somatosensory pathways that transmit sensation ***from the body*** through the spinal cord based on their morphological and physiological properties, functions, and topography are subdivided into 3 main groups:

– **dorsal (posterior) column-medial lemniscal system (pathways)** that comprises gracile and cuneate fascicles of the posterior funiculi of the spinal cord;

– **anterolateral system (pathways)** that 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 PATHWAY

Dorsal column-medial lemniscal (DCML) pathway (syn. *dorsal column pathway, fasciculi gracilis and cuneatus, fasciculi of Goll and Burdach, ganglio-bulbo-thalamo-cortical tract*) is concerned with conscious proprioception (muscle and joint sense, sense of body parts position and movement), vibration and pressure sensations, and discriminative tactile sense — fine touch[1].

This pathway conducts sensations from the mechanoreceptors located in the skin (exteroceptors), muscles and joints (proprioceptors) of the limbs, body, and neck. The fibers comprising this pathway are heavily myelinated, thick and topographically (somatotopically) organized. These allow for a fast and accurate assessment of the sensory stimuli — their localization, character, intensity and duration.

The DCML pathway, as its name suggests, ascends in the posterior funiculus (*syn.* dorsal column) of the spinal cord, where it comprises **fasciculus gracilis** and **fasciculus cuneatus**; in the brain stem it forms a bundle of fibers called **medial lemniscus** (fig. 2, 4).

The **first-order neurons** are located in the spinal ganglia. They send the peripheral processes to the proprioceptors and the tactile receptors in skin. Axons of the first-order neurons via the posterior root enter the spinal cord, posterior funiculus and ascend in two fascicles towards the medulla to synapse there on the second-order neurons. *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. *Fasciculus cuneatus* joins the posterior funiculus in the upper thoracic and cervical segments lateral to the fasciculus gracilis; it conducts information from upper spinal segments (T6 and above) — upper limbs and upper part of the trunk.

The **second-order neurons** form the *gracile* and *cuneate nuclei*. In the medulla their axons (internal arcuate fibers) cross over to the opposite side, forming the so called *sensory decussation (decussation of medial lemniscus)* After decussation a bundle of axons, called ***medial lemniscus***, passes the medulla, pons, midbrain, and terminates in the thalamus.

The **third-order neurons** are located in the thalamus (ventral posterolateral nuclei, VPL). Their axons pass via the posterior limb of the internal capsule (fig. 3), corona radiata, and terminate mainly in the primary somatosensory cortex of the parietal lobe — the superior half of the ***postcentral gyrus*** (in somatotopical projection called Penfild’s homunculus) (fig. 5). Some neurons project to the secondary somatosensory cortex of the posterior part of the parietal lobe.

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[1] 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 things by shape and texture.

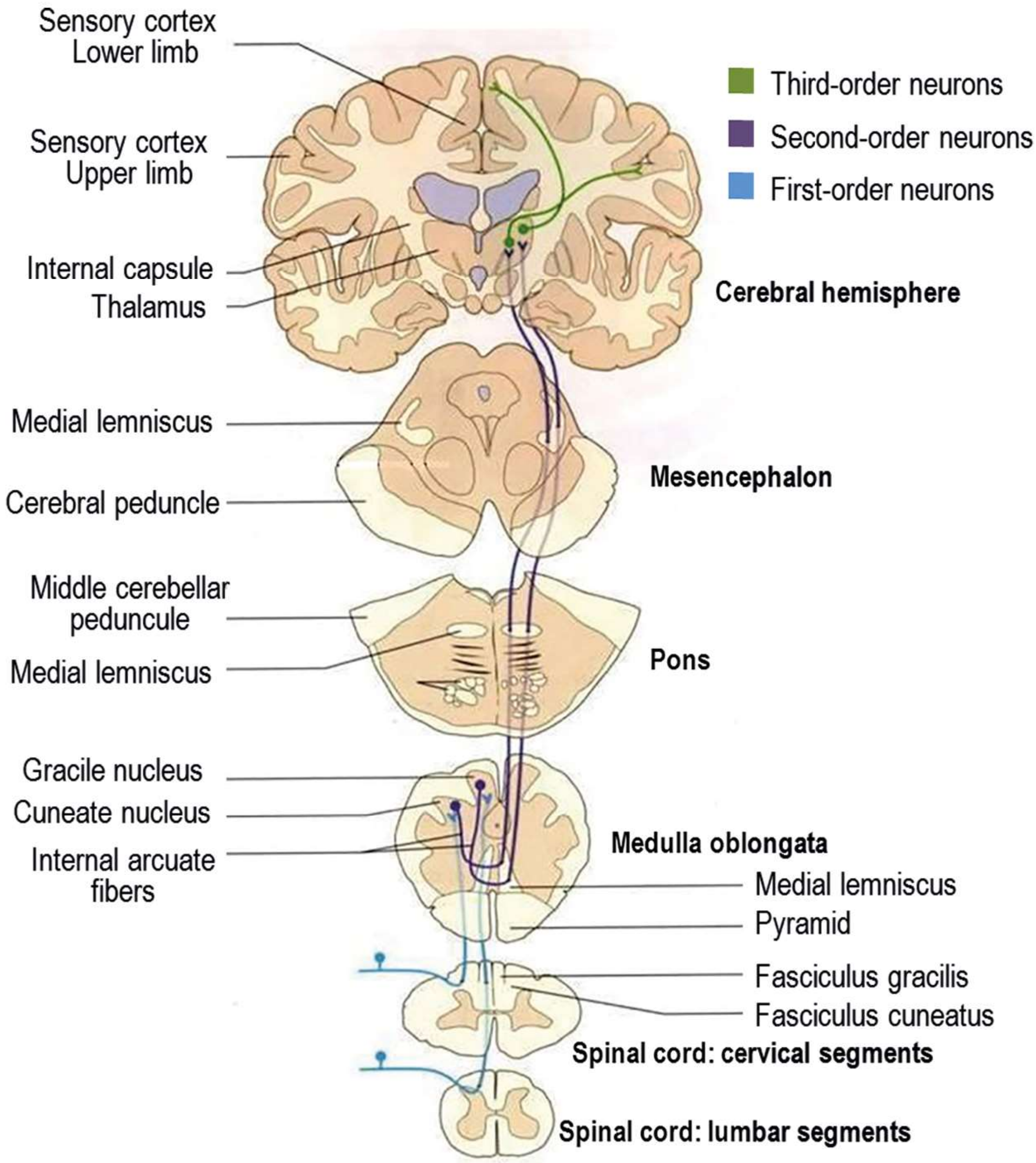
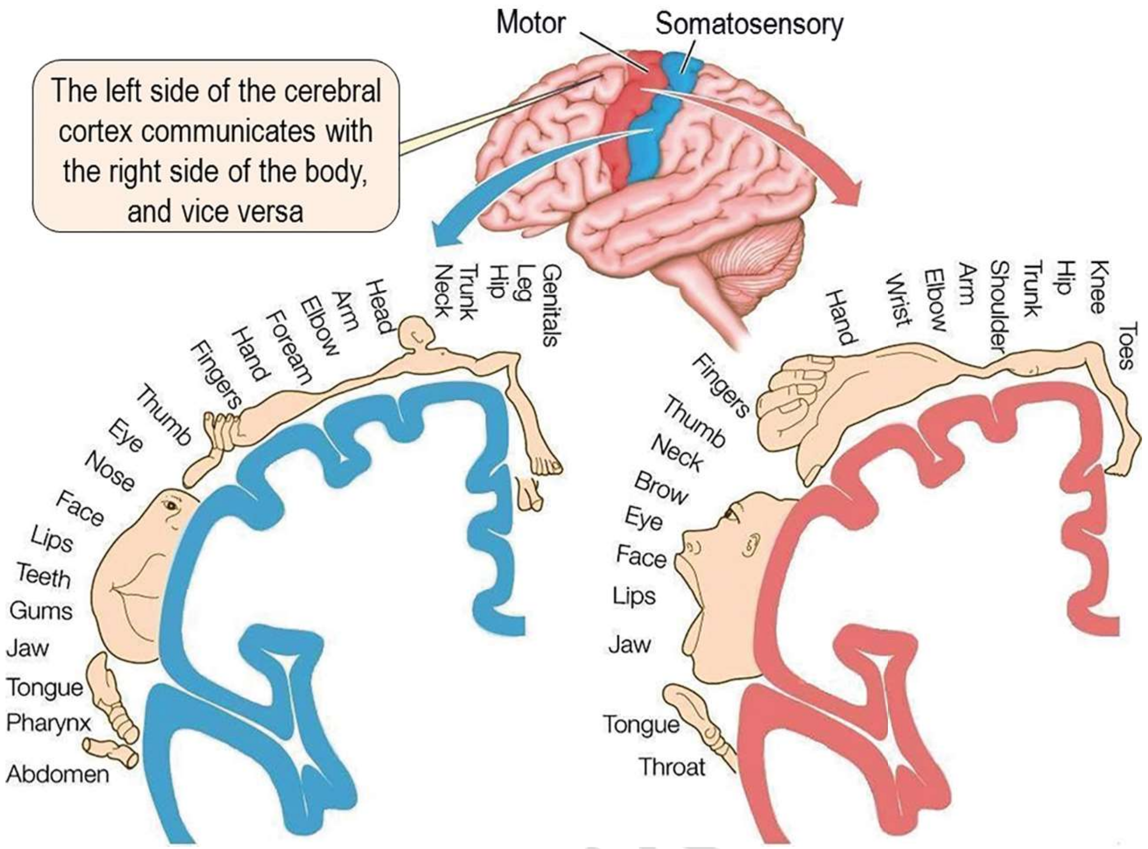


Fig. 4. Dorsal column-medial lemniscal pathway

Advanced information. Somatotopy, or topographic organization, is the point-for-point representation of an area of the body (its receptor or motor endings) in a particular structure of the CNS (in the gray or white matter). Examples of such somatotopic organization are the sensory and motor Penfield's homunculi in the cortex of the cerebral hemispheres, postcentral and precentral gyri, respectively. In these gyri the contralateral half of the body is represented as inverted, with the hand and face located inferiorly and the leg superiorly, with the foot and anogenital region on the medial surface of the hemisphere (in the paracentral lobule). Note, that the higher the density of the nerve endings in the periphery (e. g., in the hand) the larger an area of their cortical projection would be (fig. 5).



a ***b***

Fig. 5. Representation of the body parts in the precentral and postcentral gyri:
a — primary somatosensory cortex; *b* — primary motor cortex

Lesions. As the dorsal funiculus of the spinal cord transmits information from the same side of the body (ipsilateral), its destruction would cause a loss of proprioceptive sensation (sense of position), vibration and discriminative tactile sense in the ipsilateral part of the body below the level of the lesion. (The sense of crude touch, temperature and pain transmitted by spinothalamic tracts would be unaffected). Disability to sense and localize the body parts causes impaired coordination of voluntary movement — sensory ataxia. Loss of discriminative touch leads to loss of two-point discrimination and astereognosis, i. e. inability to recognize objects by touch.

A lesion of the medial lemniscus at the levels of the medulla oblongata (above the decussation) and pons would cause the symptoms similar to those occurred in lesions of the posterior funiculi, but on the side opposite (contralateral) to the damage.

Injuries to the medial lemniscus at the midbrain level, destruction of the thalamic neurons (of the VPL nuclei), or neurons of the somatosensory cortex would affect all types of sense (proprioception, touch, pain, and temperature) on the opposite side of the body.

SPINOTHALAMIC PATHWAY

Spinothalamic pathway (syn. *anterolateral pathway*) comprises the **anterior** and **lateral spinothalamic tracts,** which are the main tracts of the **anterolateral system**[2] involved in the perception of pain, temperature and crude touch (fig. 2, 6). The spinothalamic pathway transmits impulses predominantly from the exteroceptors, in particular, skin receptors of the limbs, body and neck. The smaller **anterior spinothalamic tract** conducts crude tactile sensation — light touch and pressure (it provides only crude awareness of localization and intensity of the tactile stimuli). The bigger **lateral spinothalamic tract** conveys pain and temperature sensation. Similar to the dorsal column pathway, it has somatotopical organization and is important in localizing pain and thermal stimuli and, in particular, in perception of fast sharp well localized pain.

The **first-order neurons** bodies 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 is the **dorsolateral tract of Lissaure** (fig. 2) extending along the apex of the posterior horn throughout the length of the spinal cord.)

The **second-order neurons** lie in the posterior horn[3]. Their axons decussate via the *anterior white commissure* and ascend on the contralateral side in the anterolateral part 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 join together (and with the spinotectal tract) to form a single bundle of fibers — the ***spinothalamic pathway*** (also called ***spinal lemniscus***). The spinal lemniscus runs via the brain stem to terminate in the thalamus.

The **third-order neurons** are in the thalamic nuclei (VPL). Their axons pass through the posterior limb of the internal capsule (fig. 3), corona radiata, and reach the primary somatosensory cortex **— postcentral gyrus** (fig. 5).

Advanced information. In the lower brain stem the spinal lemniscus remains separate from the medial lemniscus. It passes in the lateral parts of the medulla, then in the ventrolateral portions of the pons tegmentum, as the medial lemniscus stays closer to the midline (fig. 6). In the upper pons and the midbrain the spinal and medial lemnisci come close to each other and terminate together in the same thalamic nuclei.

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[2] 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.

[3] In the marginal zone — most dorsal part of the dorsal horn, in the substantia gelatinosa, and in deeper parts of the posterior horn, collectively known as the nucleus proprius.

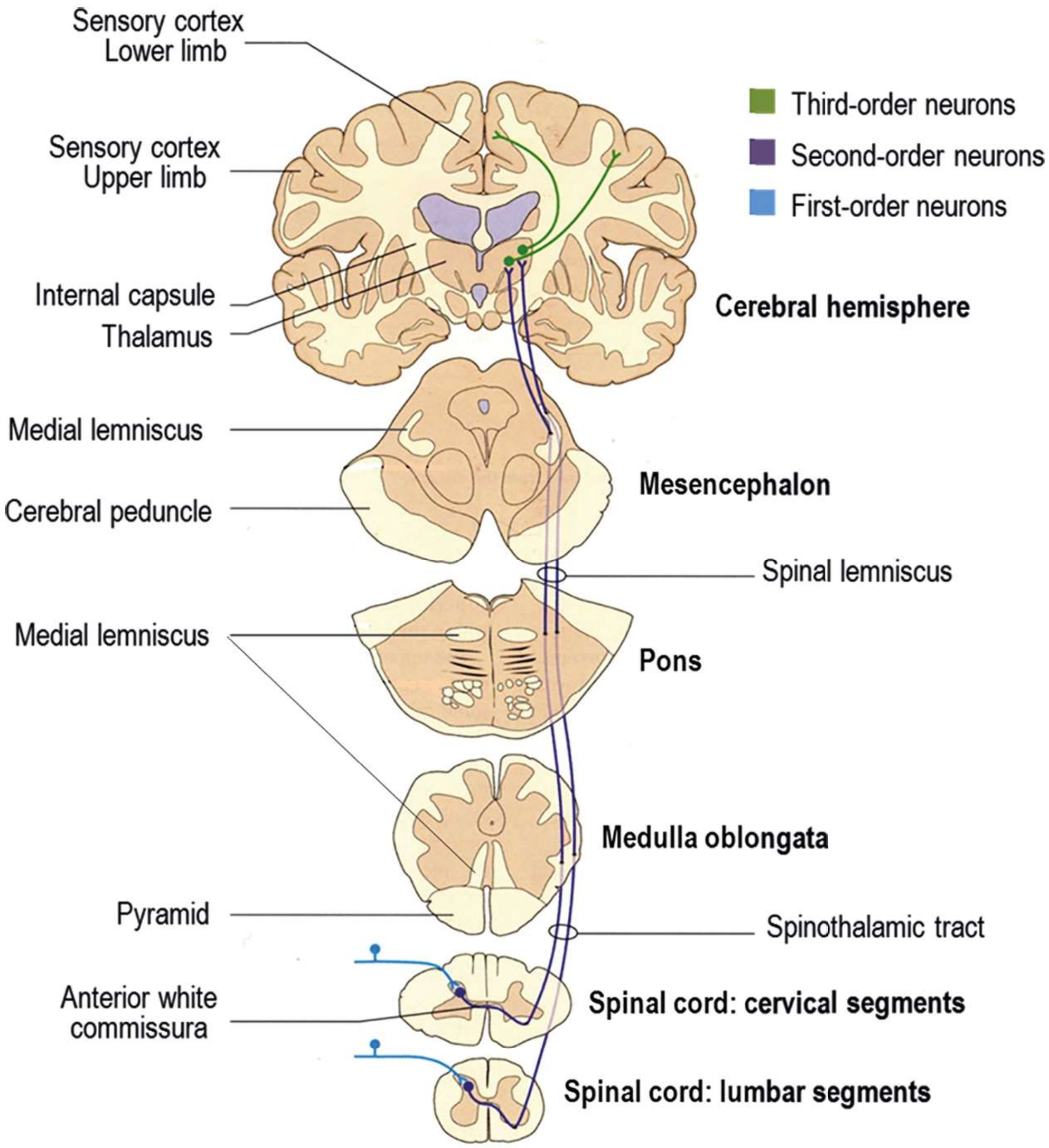

Fig. 6. Spinothalamic pathway

The *spinotectal tract (spinomesencephalic tract)* is a bundle of nerve fibers (axons of the *second-order neurons* of the posterior horn) ascending contralaterally in the lateral funiculus of the spinal cord ventral to the lateral spinothalamic tract (fig. 2). It separates from the *spinal lemniscus* in the upper brain stem and projects mainly to the tectum (colliculi) of the midbrain. The incoming sensory information contributes to reflex orientation of the head and eyes toward somatic stimuli (spinovisual reflexes). The fibers of this tract that project to the periaqueductal gray are thought to be involved in controlling pain perception (by the release of endorphins to the circulation).

The *spinoreticular tract* transmits somatosensory information (from the muscles, joints, and skin) to the brain structures via the reticular formation (RF) of the brain stem. Axons of the *second-order neurons* from the posterior horn of the spinal cord ascend in the white matter bilaterally along with the spinothalamic tract (fig. 2). They synapse on the neurons of the RF, which, in turn, project to the thalamus (predominantly to the nonspecific intralaminar nuclei) and to the hypothalamus. The intralaminar thalamic nuclei project mainly to the cingulate gyrus of the limbic cortex, involved with the emotional perception of pain, and insula, concerned with the visceral responses to pain.

Pain stimuli transmitted by the spinoreticular tract are caused mainly by chemical substances released from damaged tissue following noxious stimulation and perceived as diffuse (dull, burning) pain. Activation of the RF increases the level of conscience and alertness to damaging stimuli, causes reflex somatic and autonomic reactions to pain.

Presence of multiple pain pathways may explain the fact of returning pain after chordectomy (section of the lateral spinothalamic tract for the treatment of pain).

The two main pathways that carry nociceptive signals, the spinothalamic and spinoreticular tracts, contain also afferent fibers from viscera joining at the level of the spinal cord, as they do not form specific afferent pathways.

Lesions. Unilateral destruction of the spinothalamic tract at the level of the spinal cord (it may happen from damage of half of the spinal cord) 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 on this side are preserved («dissociated sensory loss») because they are transmitted by the dorsal column pathway unilaterally.

The same pattern of sensory loss (but affecting a large area — from the neck down) may occur when only the lateral side of the medulla is damaged with the spinothalamic tract passing here. (This damage is usually combined with the unilateral sensory deficit in the face due to involvement of the spinal trigeminal tract, described below.)

A lesion at the level of the midbrain, where the spinal and the medial lemnisci come close to each other, would impair both pathways and cause the loss of all senses on the opposite side of the body (accompanied by symptoms of damage to the cranial nerves nuclei).

A lesion of the posterior horn or anterior white commissure of the spinal cord would cause a deficit of pain and temperature sensation is the skin areas (dermatomes) corresponding to the affected spinal segments, but proprioception and discriminative tactile sensation remain.

SPINOCEREBELLAR PATHWAYS

Spinocerebellar pathways convey unconscious, mainly proprioceptive information, which is subconsciously processed, and allows the cerebellum to control muscle tone, posture, balance, and coordination of movements. The direct pathways to cerebellum form 2-neuron chains (fig. 2, 7). The largest, the **posterior** and **anterior spinocerebellar tracts**, transmit impulses from the trunk and lower limbs, mainly of the same side. They are of great importance in coordinating the movements of the lower limb muscles and maintaining the posture and balance of the body at rest and in motion.

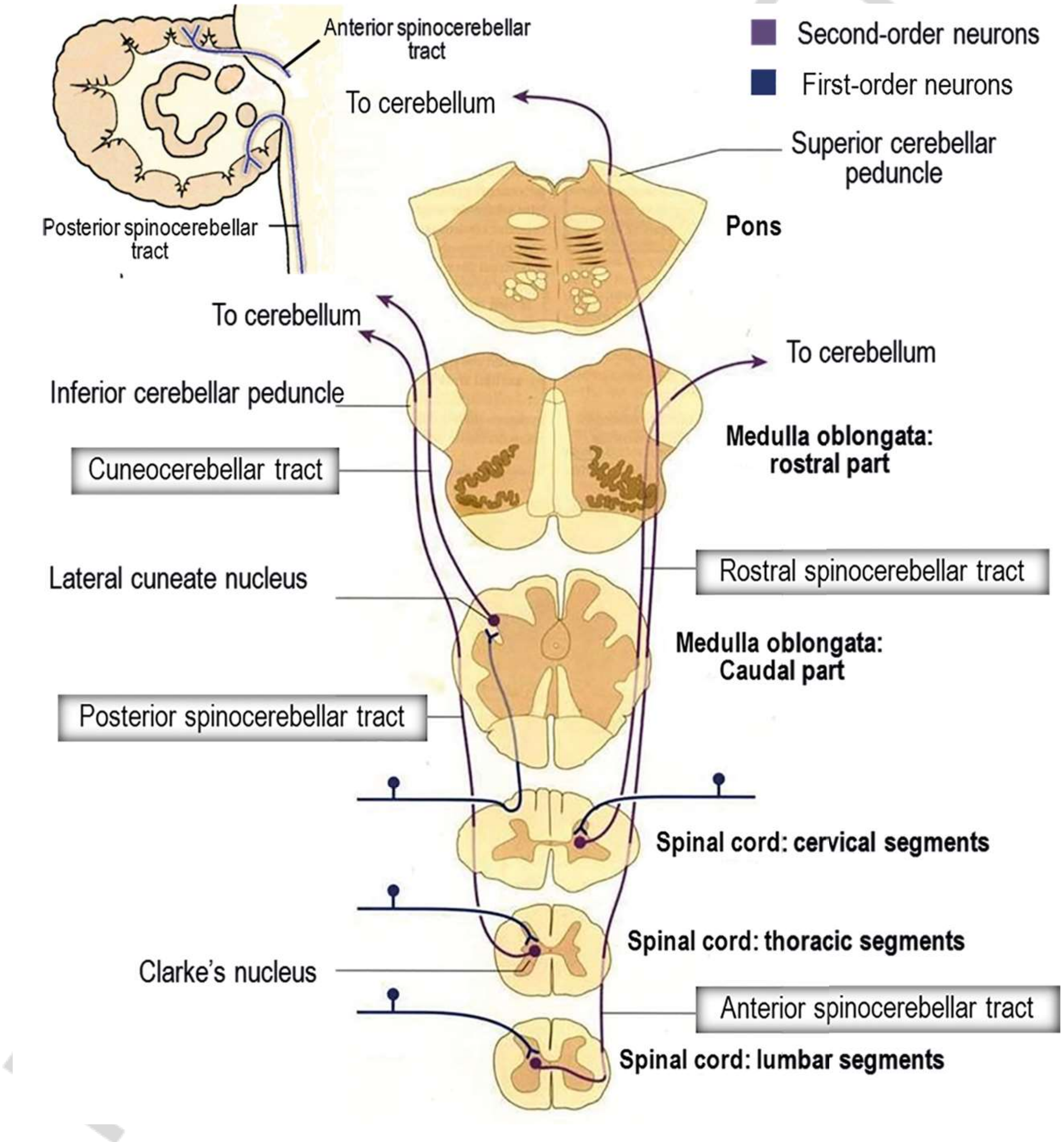

Fig. 7. Spinocerebellar pathways

The **first-order neurons** lie in the spinal ganglia. The peripheral processes are connected with the proprioceptors in muscles and joints. The axons pass via the dorsal root to the gray matter of the spinal cord, where they synapse with the second-order neurons. Axons of the **second-order neurons** 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 *dorsal horn nuclei* (*posterior thoracic nucleus, aka dorsal nucleus of Clarke*) at the level of C8-L2 spinal segments. **Axons** of the second-order neurons ascend ipsilaterally (on the same side) in the lateral funiculus of the spinal cord up to the medulla oblongata, enter the cerebellum via the **inferior cerebellar peduncle** and end in the vermis cortex.

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

Advanced information. The ***cuneocerebellar*** and ***rostral spinocerebellar tracts*** are direct pathways to the cerebellum that carry proprioception from the upper limb and upper body (fig. 7). The ***cuneocerebellar tract*** is bigger and complements the posterior spinocerebellar pathway. 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), 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.

The **rostral spinocerebellar tract**, less pronounced in humans, complements the anterior spinocerebellar pathway. Its **first-order neurons** synapse on the neurons of the posterior horn in the upper cervical segments of the same side. Axons of the **second-order neurons** pass in the lateral funiculus, adjacent to the spinocerebellar pathways, and enter the cerebellum via the superior and inferior cerebellar peduncles.

It is believed that the posterior spinal cerebellar and cuneocerebellar tracts are more differentiated in a functional sense. Thanks to the monosynaptic transmission of impulses between neurons, they carry information from each individual muscle, which is important for the rapid regulation of subtle movements of the limbs. The anterior and rostral spinocerebellar tracts transmit more general information from several muscle groups, which helps in controlling the position of the whole limb and the balance of the body during movement.

Lesions. Damage to the spinocerebellar pathways leads to the loss of unconscious proprioceptive information (about length of the muscles, degree of their stretching) and affects control and correction of ongoing movements. This results in deficits of motor function (ataxia) — inability to perform smooth, directed, coordinated movements (e. g., disturbances in gait, incoordination of arms movements). Lesion of the inferior cerebellar peduncle and/or the superior peduncle caudal to the decussation would result in the ipsilateral motor incoordination, whereas a lesion that occurs in the superior peduncle rostral to the decussation affects the contralateral side of the body.

Isolated lesions of the spinocerebellar pathways are uncommon. If the descending motor tracts are involved (e. g., in case of the spinal cord damage) the resulting muscle weakness or paralysis masks the coordination disorder. Some heredity diseases can cause degeneration of the spinocerebellar pathways and affect their function.

SOMATOSENSORY PATHWAYS FROM THE FACE (AND HEAD)

Somatosensory pathways from the face (and head) transmit information to the CNS via the cranial nerves V, IX, X and VII:

– predominantly via the *trigeminal (V) nerve* — from skin of the face, front part of the external ear and anterior scalp; conjunctiva; cornea; mucosal membranes of the oral and nasal cavities, including anterior 2/3 of the dorsum of tongue; teeth; dura mater of the anterior and middle cranial fossae; proprioception from masticatory and facial muscles, extrinsic muscles of the eyeball, and temporomandibular joint;

– via the *glossopharyngeal (IX) nerve* — from mucosa of the posterior 1/3 of the tongue, soft palate, tonsils, pharynx and middle ear;

– via the *vagus (X) nerve* — from the lower pharynx; laryngeal vestibule; dura mater of the posterior cranial fossae (sensory impulses from other organs supplied by the vagus are carried by the visceral fibers originating in the inferior ganglion of the vagus and ending in the solitary nucleus);

– via the *vagus (X),* together with the *facial (VII) nerve,* — from skin of the posterior parts of the auricle and external acoustic meatus, external surface of the tympanic membrane.

The **first-order (primary afferent) neurons** are located in the *sensory ganglia* of the above mentioned cranial nerves. The peripheral processes reach the receptors; the central processes (axons) via the roots of the cranial nerves enter the brain stem and synapse on the neurons of the *trigeminal nuclei* (fig. 8, 9).

The **second-order neurons** are located 1) in the pons — *pontine nucleus,* aka *main trigeminal nucleus* (processes discriminative touch and proprioception); and 2) in the medulla — *spinal trigeminal nucleus* (processes pain, thermal and crude touch information).

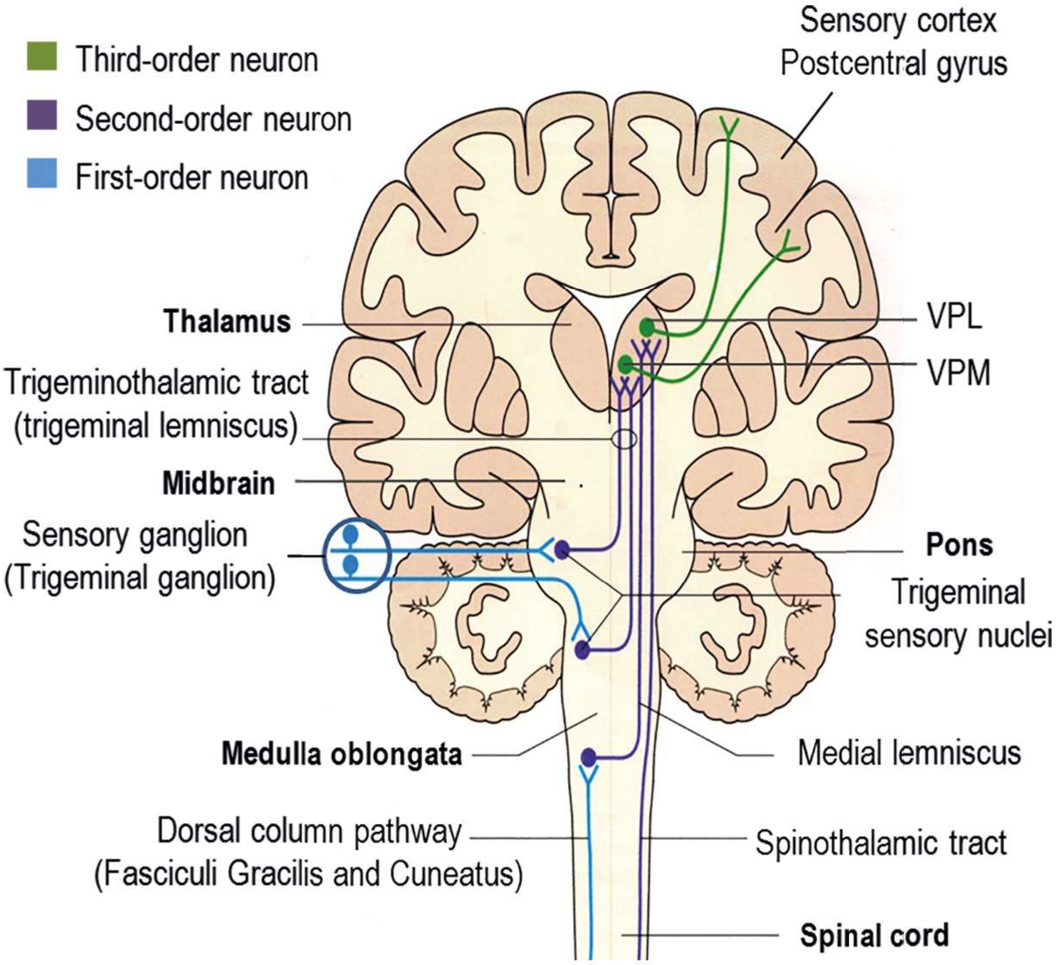

Fig. 8. Somatosensory pathways from the face and head and other sensory tracts of cortical direction (VPL — lateral ventral posterior nuclei; VPM — medial ventral posterior nuclei)

Most of axons of the **second-order neurons** decussate and form the contralateral ***trigeminal lemniscus,*** aka ***trigeminothalamic tract*** (it passes lateral and posterior to the medial lemniscus). The fibers of the trigeminal lemniscus terminate in the *thalamus.*

The **third-order neurons** are located in the thalamic nuclei. The **axons** of the third-order neurons ascend via the internal capsule to terminate mainly in the face area of the primary sensory cortex — the lower half of the *postcentral gyrus* (fig. 5).

Advanced information. Similar to the somatosensory pathways from the body the two main pathways for transmitting conscious information from the head and face can be distinguished:

1. The cranial homologue of the dorsal column-medial lemniscal pathway is the pathway of discriminative touch and proprioception, which includes the *pontine nucleus.* The axons of its *second-order neurons* decussate (a part of the fibers remains uncrossed; so it is unusual to lose all sensations on one side of the face from lesions of the brain) and terminate in the contralateral thalamus — in the me-

dial ventral posterior nuclei (VPM), where the face receptors are represented. The *third-order neurons* of the VPM nuclei project in the somatotopic manner to the primary sensory cortex — the lower half of the postcentral gyrus (fig. 5).

The proprioceptive information ***from the masticatory apparatus*** (masticatory muscles, temporomandibular joint, and periodontal ligaments) is transmitted to the *mesencephalic nucleus*, which is formed by the primary afferent unipolar neurons (fig. 9). The central processes of these neurons pass in several directions — some end in the pontine nucleus, others connect with the motor nucleus of the trigeminal nerve and take part in the monosynaptic stretch (jaw jerk) reflex that plays an important role in the process of chewing.

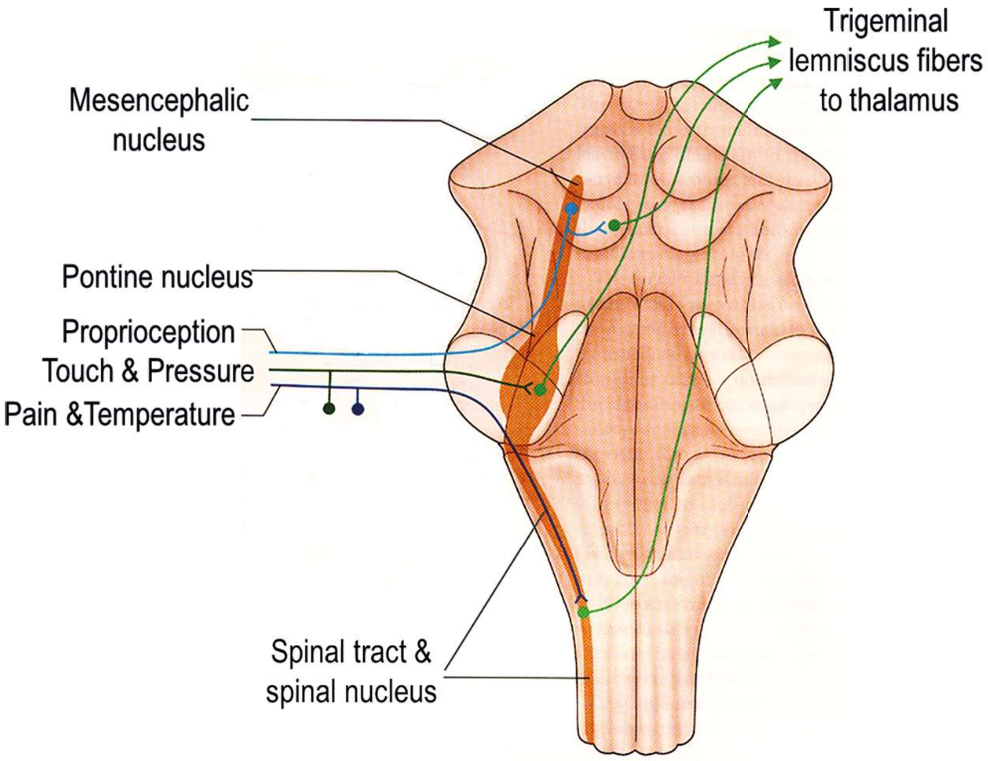

Fig. 9. Trigeminal sensory nuclei and their major connections

2. The homologue of the spinothalamic pathway comprises the *spinal trigeminal nucleus,* which extends from the lower pons to the upper segments (C3) of the spinal cord and receives pain, temperature (and crude touch) information (fig. 9, 10). Axons of the afferent (first-order) neurons descend from the trigeminal nerve entry to the brain towards the caudal end of the spinal nucleus lateral to it in a bundle, called the *spinal trigeminal tract*. The small rostral part of the nucleus receives information from the mouth, the caudal parts — from all other areas. Representation of the face and scalp in the spinal trigeminal nucleus is shown in the fig. 10. Accordingly, a lesion at a particular level of the spinal nucleus would produce pain and temperature sensation loss in the respective arcuate («onion-skin») area.

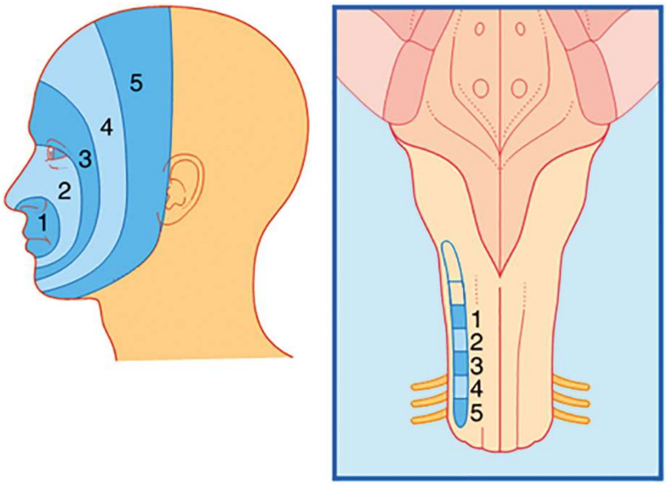

Fig. 10. Representation of the face in the spinal trigeminal nucleus

The axons of the *second-order neurons* of the *spinal trigeminal nucleus* decussate and pass to the thalamic nuclei. Those transmitting well localized (sharp) pain and temperature sensation terminate in the VPM nuclei, the neurons of which project to the primary somatosensory cortex. Other axons that transmit information of poorly localized stimuli and dull, aching pain end in the intralaminar nuclei of the thalamus and the reticular formation (their role is similar to that of the spinoreticular pathway). The intralaminar nuclei project diffusely into the cortical regions — mainly the limbic cortex and insula.

Lesions. The lesion of the spinal trigeminal tract (axons of the primary afferent neurons) interrupts signals from the trigeminal and other sensory ganglia and causes a unilateral (in the same half of the face) loss of pain and temperature sensation in the region that is supplied by the sensory nerve involved.

The lesion of the spinal trigeminal nucleus leads to similar sensory deficits. In case of damage to a part of the nucleus the sensory loss is limited by the respective arcuate («onion-skin») area (fig. 10), which does not correspond to the distribution of the trigeminal nerve branches in the skin.

Unilateral damage to the brain stem that involves the main trigeminal (pontine) nucleus decreases discriminative touch and proprioception on the contralateral half of the face but does not cause a complete loss of sensation, since not all fibers emerging from the nucleus decussate.

Destruction of the trigeminal lemniscus (trigeminothalamic tract) at the level of the medulla and lower pons would cause the loss of pain and temperature sense in the conralateral half of the face. Damage to the brain stem above this level (after axons of the pontine nucleus join) would affect the sense of touch and proprioception in face as well. Besides, a loss of all sensations in the contralateral side of the body occurs due to involvement of the spinal ascending sensory pathways — medial and spinal lemnisci, which come to close proximity with the trigeminal lemniscus at the level of the midbrain.

DESCENDING PATHWAYS

Descending or motor pathways send motor commands from the brain to the effectors. The *somatic motor pathways* end by motor endings in the skeletal muscles: those originating from the cerebral cortex, called the *pyramidal tracts,* conduct conscious voluntary commands; the tracts originating from subcortical motor centers, the *extrapyramidal tracts*, regulate involuntary muscle activity at the subconscious level. The *visceral motor pathways* connect centers of the autonomic nervous system in the brain with those in the spinal cord and control smooth muscles of internal organs and vessels, myocardium, secretion of glands.

The motor pathways have two levels of neurons. The cell bodies of the **first-order (upper-motor) neurons** are located in the gray matter of the brain: the cerebral cortex or subcortical motor centers. The cell bodies of the **second-order (lower-motor) neurons** are located in the *motor nuclei:* in the anterior horn of the spinal cord or in the brain stem — nuclei of the cranial nerves. Axons of the upper-motor neurons synapse with the lower-motor neurons directly (most axons of the lateral corticospinal tract) or indirectly (in the majority of descending pathways), by way of **interneurons**[4], also called internuncial neurons. Axons of the **lower-motor** neurons terminate on muscles. The axons pass from the spinal cord via the ventral roots and motor branches of the spinal nerves; or from the brain stem via the motor roots and branches of the cranial nerves.

Advanced information. The motor tracts are divided by their topography in the spinal cord and termination in the anterior horn nuclei into the «lateral» and «medial» groups. The **lateral group**, which comprises the *lateral corticospinal tract* and *rubrospinal tract*, descends in the lateral funiculus of the spinal cord and primarily influences motor neurons (and their interneurons) of the lateral aspects of the anterior horn. Axons of this cell group innervate muscles of limbs and chiefly the distal musculature that controls movements of digits. The **medial group** of the descending tracts, which includes the *reticulospinal, vestibulospinal* and *tectospinal tracts*, terminates largely on the medially situated motor neuron group (and their interneurons) that principally innervates the trunk musculature (axial and proximal limb muscles). In other words, the lateral group of tracts is of a great importance to skilled movements of the distal parts of extremities, especially fingers of the hand, whereas the medial group is important for regulating posture and movement of the proximal limb parts.

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[4] In this case an interneuron appears the second-order neuron and, hence, the motor pathway — a 3-neuron pathway. However, for simplification they usually describe the motor pathways as the 2-neuron pathways skipping interneurons.

Pyramidal tracts

Pyramidal tracts (*corticospinal* and *corticonuclear tracts*) originate in the cerebral cortex and provide conscious voluntary control over skeletal muscles. They are often called «pyramidal» because their fibers form pyramids of the medulla oblongata. There are three pyramidal tracts (fig. 11, 12):

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

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

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

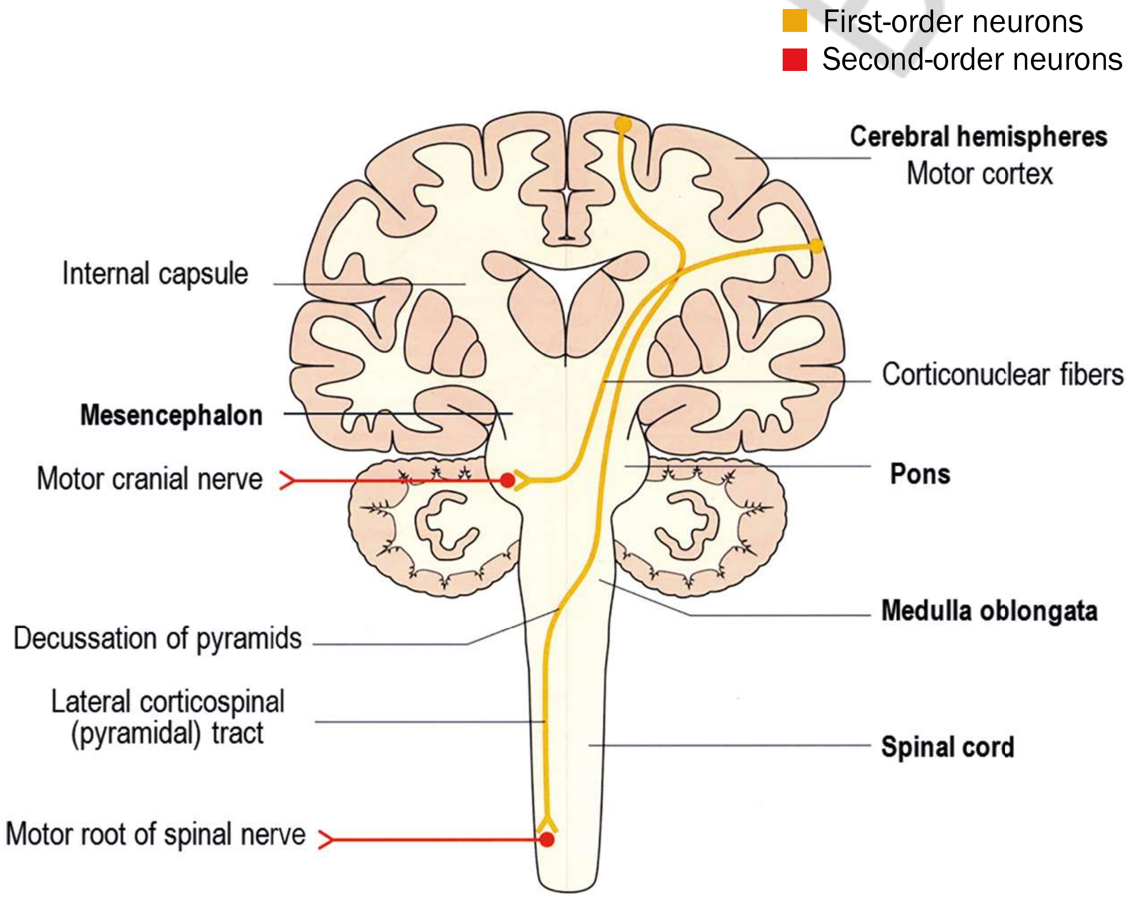

Fig. 11. Corticonuclear and corticospinal tracts

The **first-order neurons** (pyramidal cells) of the pyramidal tracts are located in the primary motor cortex (in the fifth layer of the grey matter) — the *precentral gyrus* and *paracentral lobules,* and some of the neurons — in the secondary motor cortex, the premotor area of the frontal lobe. In the precentral gyrus the pyramidal neurons are distributed in the somatotopic manner (motor homunculus) similar to that in the primary somatosensory cortex (fig. 5).

The ***corticonuclear tract*** (fig. 3, 11): Axons of the **first-order neurons** descend via the genu of the internal capsule and pass in the brainstem where at different levels they synapse on the *motor neurons* **(second-order neurons)**, which lie in the *motor nuclei of the cranial nerves* (III, IV, V, VI, VII, IX, XI, and XII). Most axons decussate just before they reach the nuclei, but some of them end on the ipsilateral side. The **second-order neurons** axons leave the brainstem with the cranial nerves and reach the corresponding muscles.

The ***corticospinal tracts*** (fig. 2, 3, 12): Axons of the **first-order neurons** converge to 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 lower border of the medulla approximately 80–90 % corticospinal fibers cross the midline via the *decussation of pyramids*. They form the ***lateral corticospinal tract*** that descends in the lateral funiculus of the spinal cord and terminates on the *motoneurons of the anterior horn nuclei*.

A smaller portion of the pyramidal fibers remains uncrossed and forms the ***anterior corticospinal tract*** descending in the anterior funiculus. Most fibers of this tract cross the spinal cord through the *anterior white commissure* to terminate in the contralateral motor nuclei of the anterior horn, but some fibers remain uncrossed and end in the anterior horn of the same side. Thus, the trunk muscles (especially respiratory muscles and the diaphragm) are under the control of both hemispheres; as the limbs muscles are controlled by the contralateral hemisphere of the brain.

The **second-order neurons** of the corticospinal tracts are the motor neurons[5] of the anterior horns of the spinal cord. Their axons pass through the ventral roots and the spinal nerves to end in the muscles.

Lesions. Lesions of the pyramidal tracts affect the upper motor neurons — their bodies in the motor cortex or axons that form the tracts, and lead to decrease (paresis) or loss (paralysis) of voluntary movements. These lesions are accompanied by increased muscle tone (spasticity of muscles, increased tendon reflexes, etc.) due to loss of inhibitory effect of the cortex on the motor neurons of the spinal cord.

Damage to the *corticospinal tract* is limited to muscles of limbs (primarily the distal muscles, but also muscles of shoulder and hip), since the body muscles are under the control of both hemispheres. Damage above the level of the decussation — in the cerebral cortex (e. g., in stroke) or internal capsule (cerebrovascular disorders), affects limbs movements on the conralateral side. Damage below the decussation, which involves the lateral corticospinal tract, affects the ipsilateral limb muscles.

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[5] Among the interneurons of the anterior horns receiving signals from the pyramidal tract there are cells that inhibit the activity of alpha-motoneurons. Thus, by stimulating or inhibiting the peripheral motoneurons activity, the pyramidal tracts are able to regulate both contraction and relaxation of muscles.

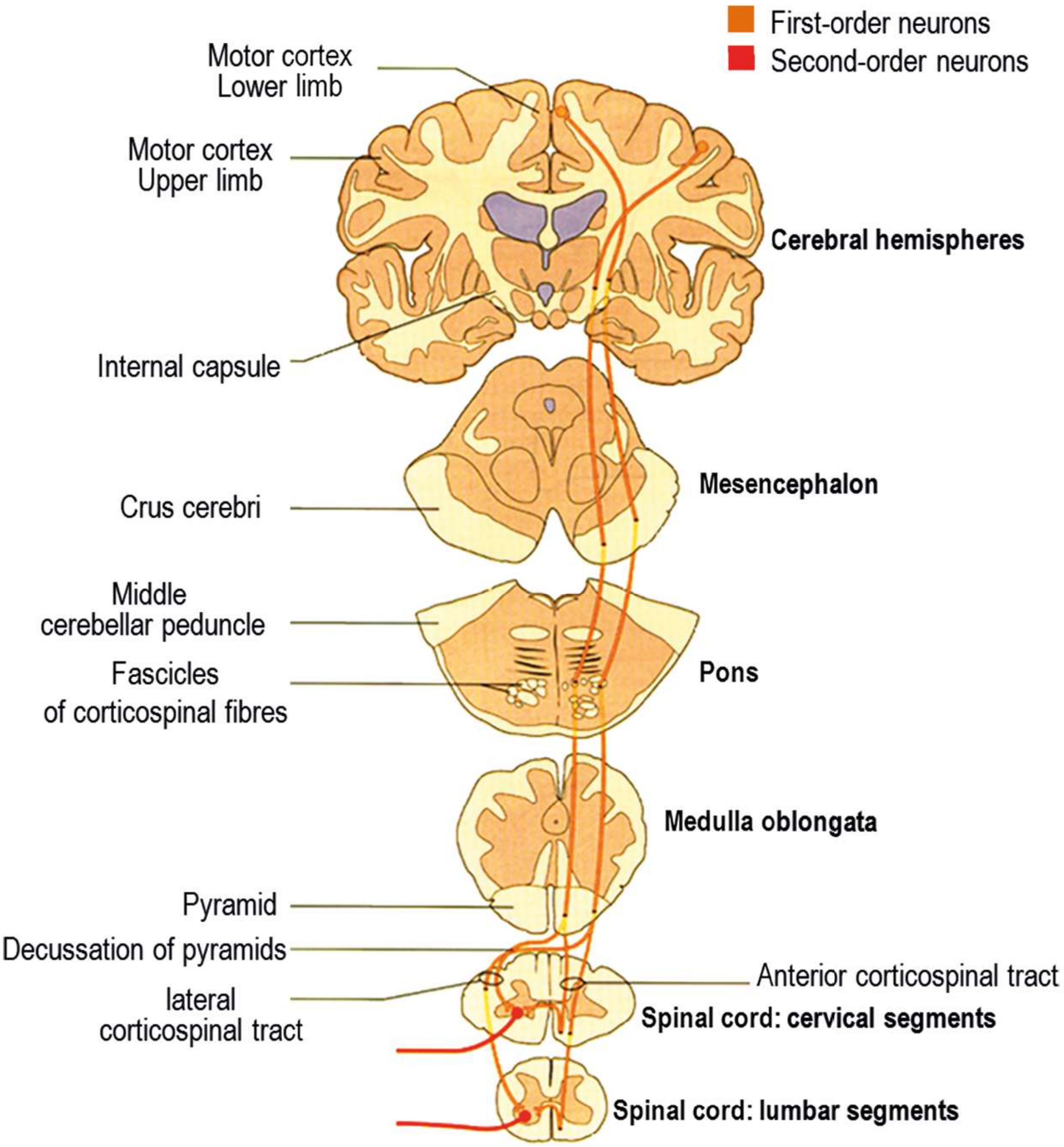

Fig. 12. Corticospinal tracts

The lesion of the lower motor neuron causes the so-called flaccid paralysis, accompanied by loss of muscle tone and reflexes and subsequent muscle atrophy.

Unilateral damage of pyramidal neurons in the lower part of the precentral gyrus or fibers of the *cortironuclear pathway* usually results in mild weakness of head and neck muscles. This is due to the bilateral input from the cerebral cortex to most cranial nerves (result of incomplete crossing of the corticonuclear fibers). Therefore, the vital functions, such as chewing, swallowing, are preserved.

The exceptions are the muscles of the tongue and the lower half of the face. The corticonuclear fibers that terminate in the motor nucleus of the XII cranial nerve innervating the tongue muscles, and on the motor neurons of the VII cranial nerve nucleus, which supply the oral muscles, decussate almost completely. A unilateral lesion of the pyramidal neurons controlling these muscles (e. g., in stroke) will result in spastic muscle paralysis on the contralateral side.

EXTRAPYRAMIDAL TRACTS

Extrapyramidal tracts are part of the **«extrapyramidal system»** that is responsible for involuntary movements: involved in reflexes, coordinate automatic movements of locomotion and posture, influences muscle tone, and participates in voluntary movements. It comprises 1) the centers in the brainstem, which are directly connected with motonerons, e.g., red nuclei, vestibular nuclei, reticular formation; and 2) the centers that modulate motor activity indirectly, such as cerebellum, basal nuclei, substancia nigra, subthalamic nuclei, thalamus, and different sensory areas of the cerebral cortex. The largest extrapyramidal tracts are the *rubrospinal, vestibulospinal, reticulospinal and tectospinal tracts* (fig. 2).

The **extrapyramidal tracts** have principally similar structure comprising 2 neurons (fig. 13, 14).

The **first-order neuron** is in the corresponding motor center of the brainstem; its axon (crossed or uncrossed) descends along the spinal cord in the anterior or lateral funiculus and connects (directly or indirectly — via an interneuron) with the motor neuron of the anterior horn. Some axons of **first-order neurons** terminate on the motor neurons in the brainstem.

The **second-order neurons** are the motor neurons located in the motor nuclei of the cranial nerves or anterior horn of the spinal cord; their axons reach the muscles of the head and neck, body and limbs within the peripheral nerves — cranial or spinal.

The ***rubrospinal tract*** controls muscle tone and movements of the limb muscles — activates flexors and inhibits extensors, similar to the lateral corticospinal tract (fig. 2, 13).

The **first-order neurons** originate in the **red nucleus**. Their axons decussate ventrally within the midbrain and descend in the brain stem 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 levels on the anterior horn motor neurons that control the movements of the arm and hand. Some axons of the **first-order neurons** end in the motor nuclei of the cranial nerves and are involved in the regulation of the reflex movements of the masticatory and facial muscles.

The **second-order neurons** lie in the lateral group nuclei of the anterior horn (or cranial nerves nuclei) and directly innervate muscles.

Advanced information. The red nucleus plays an important role in mediating and coordinating voluntary movements due to the direct connection with the cerebral cortex and the cerebellum. The red nucleus receives the direct input (corticorubral fibers) from the precentral gyrus and transmits signals from the cerebral cortex to the muscles. Thus, it is considered an alternative route for voluntary motor commands. In primate experiments the rubrospinal tract can assume almost all the functions of the corticospinal tract when the latter is destroyed (except for the finest individual movements of finders). It receives the direct input from the cerebellum. A significant part of the red nucleus fibers passes to the cerebellum, transmitting signals from the cerebral cortex, and to the reticular formation of the brain stem and participates in regulation of muscle tone together with other extrapyramidal tracts.

While the rubrospinal tract belongs to the lateral group of the motor pathways other extrapyramidal tracts belong to the medial group that regulates mainly the axial musculature and proximal limb muscles.

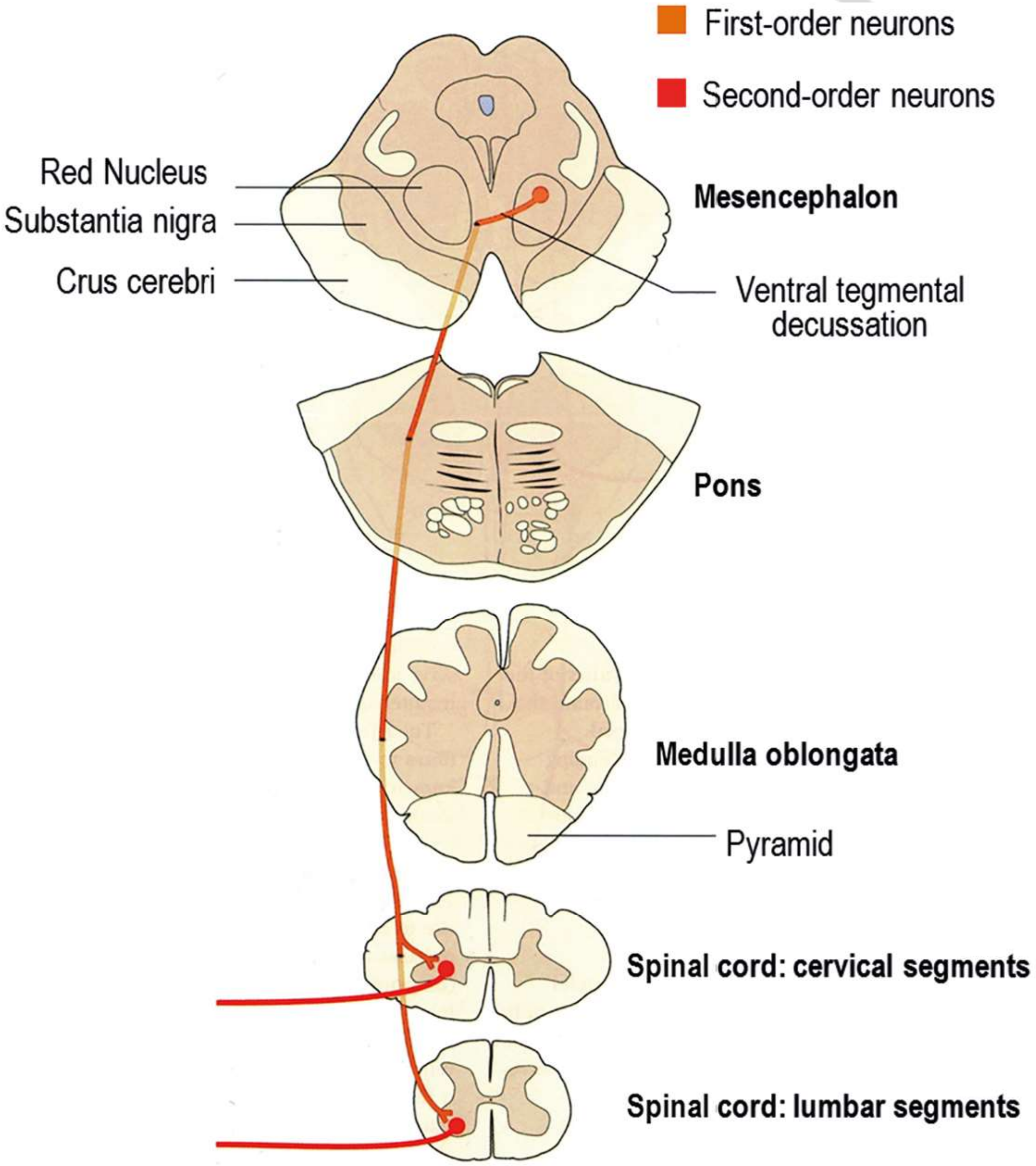

Fig. 13. Rubrospinal tract

The ***reticulospinal tracts*** (fig. 2) originate in the reticular formation (RF) of the brain stem, which integrates the proprioceptive and other sensory information with the signals coming from all motor centers of the brain (cortical and subcortical). Generated in the RF motor commands are transmitted to the muscles by the reticulospinal tracts, which are involved in many aspects of motor control — coordinate automatic movements of locomotion and posture, influence muscle tone and facilitate voluntary movements. They mediate autonomic functions, modulate pain impulses and reflex response to sensory stimuli as well.

The *medial reticulospinal tract* (uncrossed) arises from 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 and participates in reflex orienting movements.

The *lateral reticulospinal tract* (partially crossed) arises from the **medulla** and passes anteriorly in the lateral funiculus with part of the fibers ending on the lateral motor neurons of the anterior horn. The lateral reticulospinal tract, similar to the rubrospinal tract, serves as alternative to the corticospinal tract (by these tracts, via the RF and red nucleus, cortical neurons can control motor function). This tract facilitates voluntary movements (inhibits extensors and activates proximal flexor muscles) and coordinates movements associated with locomotion. Besides, it modulates the sensitivity to the sensory stimuli (including pain stimuli) that elicit flexor reflexes.

The ***vestibulospinal tracts*** control muscle tone to maintain balance of the body and position of head, they provide postural adjustment (righting reflexes) based on information coming to vestibular nuclei from the internal ear and cerebellum (fig. 2, 14).

The larger *lateral vestibulospinal tract* (uncrossed) originates in the lateral vestibular nucleus and runs in the anterior funiculus throughout the spinal cord. It controls axial and proximal limb muscles. By activating the antigravity muscles (extensors) it provides necessary compensatory postural correction (both at rest and when moving) to maintain balance of the body.

The *medial vestibulospinal tract* (partially crossed) originates in the medial vestibular nucleus, runs in the brain stem through the MLF giving collaterals to the nuclei of cranial nerves (III, IV, VI and XI). In the spinal cord it courses in the anterior funiculus up to the cervical and upper thoracic segments. This tract controls the muscles of the neck and extrinsic muscles of the eyes. It stabilizes head position when the body moves and coordinates the head and eye movements.

The ***tectospinal tract*** provides a reflex response, the so-called srartle-reflex, to sudden acoustic and optic stimuli (fig. 2). The tract begins in the superior colliculi of the midbrain quadrigeminal plate and forms decussation ventral to the cerebral aqueduct. It runs through the brainstem in close relation to the MLF projecting to the nuclei of the «oculomotor» nerves (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 of the spinal cord. This tract controls the tone of muscles (extensors and rotators) of the neck, upper trunk, and shoulder girdle and position of eyes to coordinate movements of the head and eyes in response to sudden light and sound stimuli.

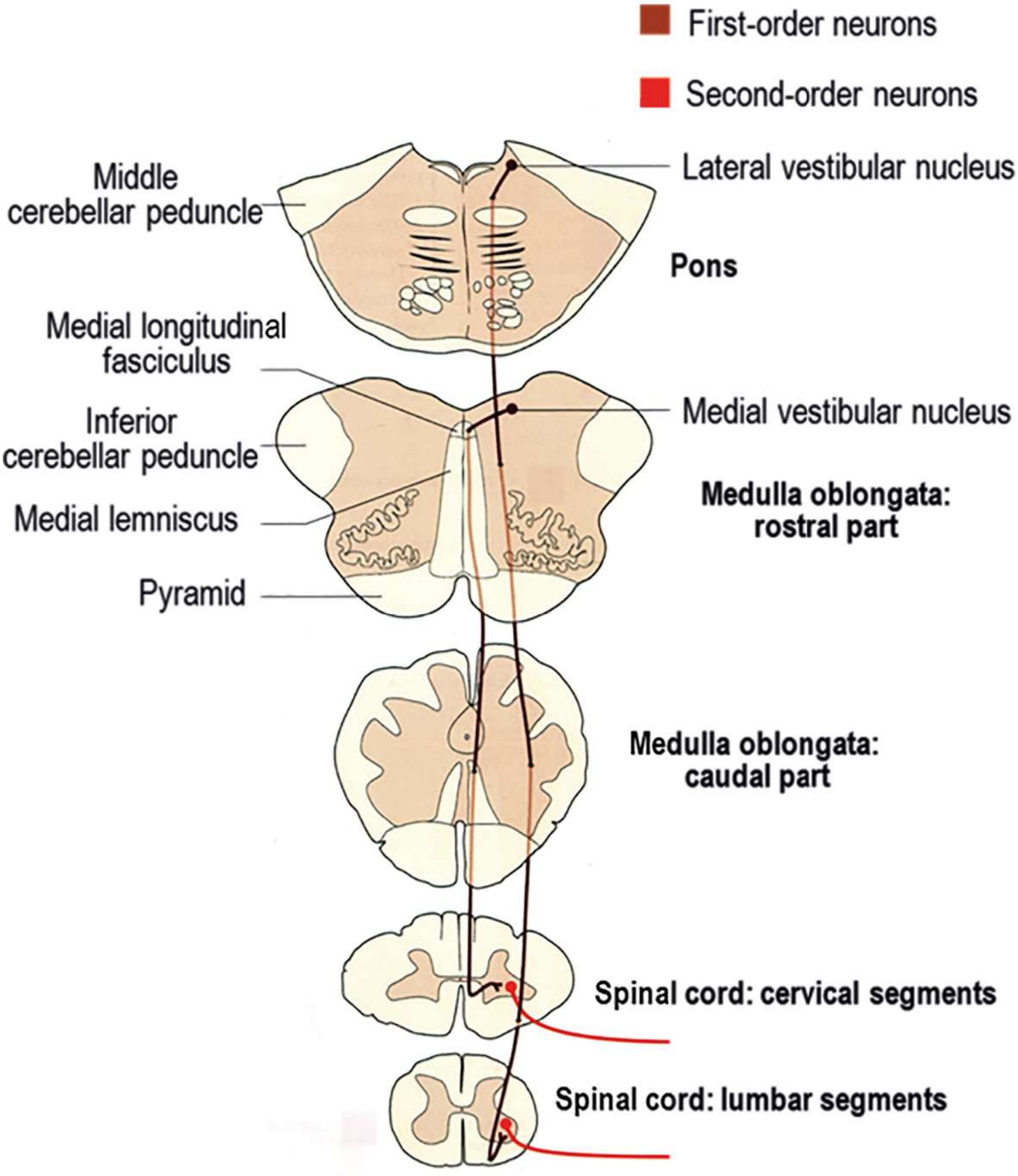

Fig. 14. Vestibulospinal tracts

Lesions of the extrapyramidal system can lead to a wide range of movement disorders, such as abnormally increased (hyperkinesis) or decreased (hypokinesia) muscular movements, tremor, loss of balance, and impaired (increased or decreased) muscle tone. Symptoms of extrapyramidal disorders significantly depend on the site and degree of damage and involvement of adjacent structures.

Damages to some extrapyramidal tracts are rather specific. For example, damage to the tectospinal tract leads to a deficit of the auditory and visual reflexes (quadrigeminal reflexes). Damage to the lateral vestibulospinal tract causes postural instability; typically a person would sway (particularly with eyes closed) and can fall when walking. The rubrospinal tract lesion causes a temporary slowness in movement (it is thought to play a role in movement velocity).

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