

## General Sensory Systems and Taste

### Introduction

Sensory pathways within the central nervous system connect primary afferents with specific parts of the contralateral cerebral cortex. These so-called lemniscal systems synapse in nuclei of the spinal cord and lower brain stem and in the sensory relay nuclei of the thalamus. Multisynaptic pathways through the reticular formation are arranged in parallel with the lemniscal systems. Descending pathways from the cerebral cortex, the central grey matter, the reticular formation and the raphe nuclei terminate in the main relay stations of the sensory projection systems. Protopathic systems, subserving pain and temperature and yielding ungraded, diffuse impressions of an all-or-none character, can be distinguished from epicritic systems concerned with the mediation of tactile and kinesthetic information of a discriminative type [164]. However, one should be cautious in attributing isolated functions to certain ascending pathways, which for all we know, may participate simultaneously in most sensory functions [1010].

Sensation from the trunk and limbs and that from the face are mediated by two different sets of sensory pathways. The posterior funiculus-medial lemniscus pathway subserves epicritic sensation from the trunk and limbs. Its primary afferents ascend in the posterior funiculus and synapse in the dorsal column nuclei. These nuclei are the origin of the medial lemniscus, which decussates in the caudal medulla and ascends, dorsal to the pyramid and along the ventral border of the tegmentum, to the thalamus. The sensory root (portio major) of the trigeminal nerve

is the first link in the epicritic pathway from the face. It synapses in the principal sensory nucleus of the trigeminal nerve and decussates at the level of the pons to join the medial lemniscus in its course to the thalamus. Epicritic systems are somatotopically organized, e.g. lamination of primary afferents in the posterior funiculus and representation of the body in the ventral posterior nucleus of the thalamus and in the primary and secondary somatic sensory cortex.

The protopathic pathways arise from the dorsal horn of the spinal grey matter and from the pars caudalis of the spinal nucleus of the trigeminal nerve. Both these relay nuclei have the same laminated structure. They receive thin primary afferents that conduct pain and temperature sensation and collaterals from thicker primary afferents that innervate mechanoreceptors. The spinothalamic tract is the protopathic pathway for the trunk and limbs. Its fibres decussate within the cord at the level of their origin from the dorsal horn and ascend in the anterolateral funiculus together with the spinoreticular and ventral spinocerebellar tracts. The lateral trigeminothalamic tract conveys pain and temperature sensation from the face. It decussates in the caudal medulla, at the level of its origin from the pars caudalis of the spinal trigeminal nucleus. Both the spinothalamic and the lateral trigeminothalamic tracts terminate, together with the medial lemniscus, in the ventral posterior nucleus of the thalamus. Their termination also includes adjoining parts of the intralaminar nuclei, the posterior group and the ventral lateral nucleus, where they overlap with other afferent systems.

Most of the relay nuclei, including the somatosensory cortex, give origin to descending systems, which reciprocate the ascending connections. A descending inhibitory pathway which selectively influences pain conduction in the dorsal horn and the pars caudalis of the spinal trigeminal nucleus includes the central grey matter and the raphe nuclei.

Primary afferents in the facial, glossopharyngeal and vagal nerves are the first link in the gustatory and general viscerosensory pathways. These fibres descend in the medulla oblongata in the solitary tract, which is medial to the spinal tract of the trigeminal nerve, near the floor of the fourth ventricle. They terminate in the nucleus of the solitary tract. Connections from this nucleus to the telencephalon are interrupted in the medial, parvocellular part of the ventral posterior nucleus of the thalamus. Another pathway from the solitary tract nucleus synapses in the parabrachial nuclei and bypasses the thalamus to reach the gustatory cortex in the parietal operculum and the insula. Telencephalic targets of the taste pathway include the lateral nucleus of the amygdala.

#### Primary Afferents and the Spinal Grey Matter (Figs. 123 and 124)

Most primary afferents enter the spinal cord through the dorsal roots. A certain number of unmyelinated fibres enter through the ventral roots [243], but their exact distribution remains unknown at present. Dorsal root fibres bifurcate on entering the cord. They segregate into thin myelinated (A $\delta$ ) and unmyelinated (C) fibres, which enter the lateral part of the dorsolateral fasciculus and cap the dorsal horn, and thicker myelinated (A $\alpha$ , A $\beta$  and A $\gamma$ ) fibres, which course through the posterior funiculus. Collaterals of these fibres enter the grey matter of the cord, where they terminate in the dorsal horn, the intermediate grey matter and the ventral horn.

Recent physiological and anatomical studies [115, 116, 178, 347] have generally con-

firmed Wall's [1472] observation of a physiological laminar arrangement of the input to the dorsal horn and the intermediate grey matter. The C- and A $\delta$ -fibres, which innervate most of the receptors responding to noxious stimuli (including the thermoreceptors and certain mechanoreceptors), terminate on marginal cells and in the superficial part of the substantia gelatinosa [729, 786, 787, 788, 1109]. A-fibres also terminate at the ventral border of the dorsal horn. Collaterals of thicker myelinated (A $\beta$  and A $\gamma$ ) fibres, innervating touch receptors in the skin, terminate in the deep layers of the substantia gelatinosa, the nucleus proprius and the adjoining intermediate grey matter. Visceral and somatic primary afferents also converge on cells in this region [125]. Joint afferents ramify in more ventral parts of the intermediate grey matter. The collaterals of the large calibre (A $\alpha$ ) myelinated fibres which innervate muscle spindles and Golgi tendon organs penetrate the ventral horn, where they terminate on motoneurons.

Most of the neurons that are contacted by primary afferents have long axons, which enter the funicular white matter; short axon cells are rare in the spinal grey matter [1214]. The great majority of small neurons in the substantia gelatinosa belong to an intrinsic system of the dorsal horn. It caps the dorsal horn as a thin cell layer, poor in myelin, located between the superficial marginal layer and the nucleus proprius. It contains the terminal arborizations of thin primary afferents, which contact relay cells of the marginal layer, and also the flame-shaped arborizations of thicker dorsal root fibres, which terminate on relay cells of the nucleus proprius. The substantia gelatinosa is often considered to be a site of interaction between the thin fibres that conduct pain and temperature and the larger cutaneous afferents from the dorsal root [681, 753, 970, 1003, 1473]. The microcircuitry of the substantia gelatinosa has not been completely resolved.

#### The Anterolateral System (Figs. 128 and 129)

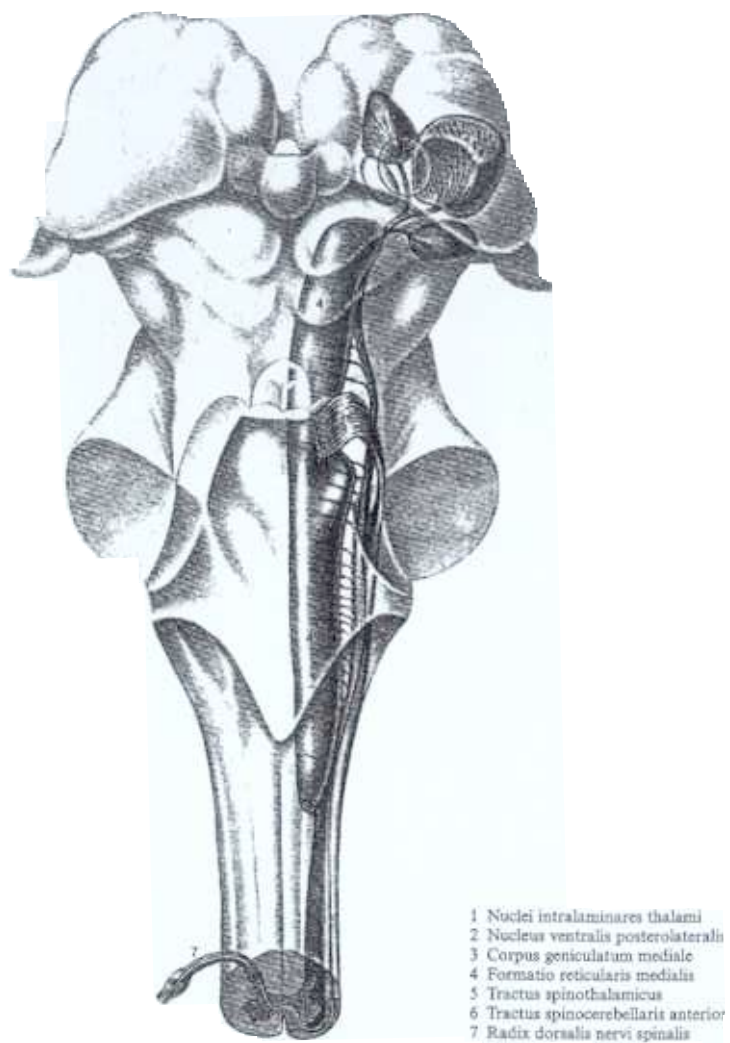
The anterolateral funiculus contains some of the main ascending fibre systems of the spinal cord. The spinothalamic tract, the protopathic pathway conducting pain and temperature from the spinal cord, originates from the cells of the marginal layer, from the nucleus proprius of the dorsal horn and from the intermediate grey matter (laminae I, IV, V, VI, VII and VIII of Rexed [1118]). Most spinothalamic fibres cross in the white commissure of the cord. Propriospinal and spinoreticular fibres arise from the same regions of the grey matter. However, these projections are bilateral and originate mainly in the intermediate grey matter. Fibres of the ventral (or anterior) spinocerebellar tract occupy the periphery of the anterolateral funiculus. Their origin partially overlaps with that of the propriospinal and spinoreticular systems [116, 272, 347, 1078, 1385, 1516, 1517, 1518]. The ascending fibres in the anterolateral fasciculus display a roughly somatotopic organization. Fibres originating from lower levels of the cord are located lateral to fibres from higher levels.

In the brain stem, the anterolateral fasciculus is located lateral to the reticular formation. Spinoreticular fibres terminate at different levels in the medial reticular formation. They are the first link in a multisynaptic pathway that has been postulated to ascend within the reticular formation and terminate mainly in the intralaminar nuclei of the thalamus. In addition, spinal fibres terminate in the central grey matter of the mesencephalon and in the deep layers of the mesencephalic tectum. At the level of the superior colliculus, most fibres of the spinothalamic and lateral trigeminothalamic tracts lie concentrated in a small bundle at the dorsal tip of the medial lemniscus.

The spinothalamic tract terminates in the posterolateral ventral nucleus, posterior group and certain intralaminar nuclei of the thalamus [110, 111, 138, 263, 682, 830, 852, 884, 886, 887]. In the posterolateral ventral

nucleus, the termination is somatotopically organized. In primates and humans, the fibres terminate in bursts or rod-like aggregates, overlapping the projections from the dorsal column nuclei. Rostrally, the termination of the spinothalamic tract extends to the junction with the ventral lateral nucleus, which also receives proprioceptive, vestibular and cerebellar afferents. Spinothalamic fibres terminate diffusely in the medial part of the posterior group, an ill-defined region of the thalamus located between the posterior ventral nucleus and the lateral nuclear group. The spinothalamic tract also terminates in a diffuse, non-somatotopic manner in some of the intralaminar thalamic nuclei, mainly the central lateral nucleus [935]. The projection to the intralaminar nuclei is partially bilateral: some of its fibres cross in the posterior commissure. Most of these intralaminar nuclei also receive projections from the reticular formation, the raphe nuclei and the cerebellum, some of which subserve motor rather than sensory functions. Hence, not all regions that receive spinothalamic fibres are part of a pain-conducting system.

Nociceptive units have been identified in the posterior ventral nucleus, the medial part of the posterior group, the nucleus submedialis and the zona incerta [48, 263, 401]. The lateral thalamus is concerned with the discriminative aspects of pain, the medial thalamus with the motivational and arousal aspects of a painful stimulus. Spinothalamic projections to the medial thalamus arise from the intermediate grey matter, together with the spinoreticular fibres, and from the marginal layer and nucleus proprius of the dorsal horn, together with the spinothalamic tract fibres to the lateral thalamus [116, 263, 400, 401, 1516].



g. 128. The anterolateral fasciculus. The position of the ascending spinal tracts and related nuclei a dorsal view (5/3 x)

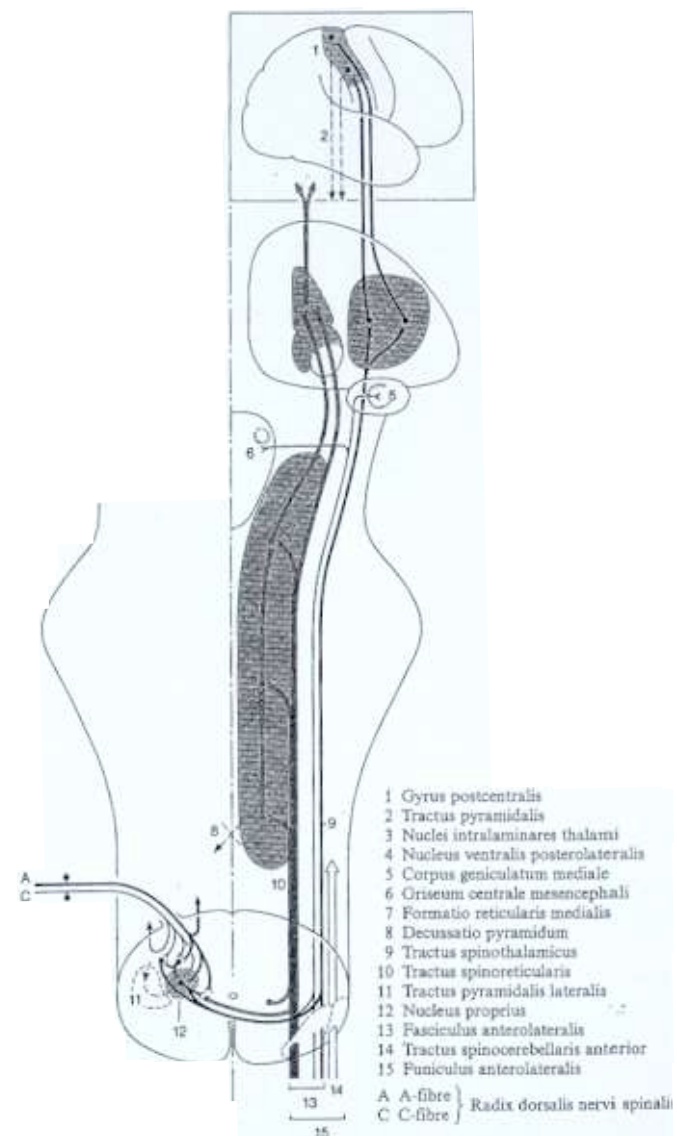


Fig. 129. The neuronal connections of the spinoreticular tract (darkly shaded) and of the spinothalamic tract (solid line)

### The Medial Lemniscus System (Figs. 130 and 131)

The first link in the epicritic conduction pathway from the cord comprises branches of thick myelinated dorsal root fibres that ascend in the posterior funiculus, where they are somatotopically organized, fibres from sacral and lumbar roots ascend medially in the gracile fascicle; those from cervical roots ascend laterally in the cuneate fascicle. A small contingent of thoracic fibres takes an intermediate position (Fig. 123). The gracile and cuneate fascicles terminate in corresponding dorsal column nuclei in the caudal end of the medulla oblongata. Along the course of the dorsal root fibres in the posterior funiculus, and at their termination in the dorsal column nuclei, the initial laminar pattern becomes reorganized so that fibres, from adjacent dorsal roots, that innervate the same cutaneous field are bundled together. As a result of this convergence the overlap between neighbouring dermatomes is eliminated, but the original laminar organization of the posterior funiculus becomes indistinct [1503].

Posterior funiculus fibres innervating the distal parts of the limbs terminate somatotopically in cell clusters which occupy the dorsal parts of the gracile and medial cuneate nuclei. In the ventral and rostral parts of these nuclei the somatotopic organization is much less precise. The posterior funiculus contains an important system of intrinsic fibres, originating from the nucleus proprius of the dorsal horn. These intrinsic fibres terminate in the ventral and rostral parts of the dorsal column nuclei [485, 1172]. Other fibres, which ascend in the posterolateral funiculus, terminate bilaterally in the ventral and rostral parts of the dorsal column nuclei, and also in a cell group (group Z [171]) located at the rostral end of the gracile nucleus, which serves as a spinothalamic relay nucleus for muscle afferents of the lower limb [13, 422, 1172]. A similar proprioceptive relay for the upper limb is located in the lateral cuneate nucleus [139], which mainly projects to

the cerebellum through the restiform body. Efferents from the diffusely organized ventral and rostral parts of the dorsal column nuclei are more widely distributed than efferents from the cell clusters in the dorsal parts of the nuclei. Both regions project to the contralateral thalamus, but the ventral and rostral parts also project to the cerebellum, the inferior olive and back to the dorsal horn [112, 135, 232, 395, 749].

From the gracile and the medial cuneate nuclei arise internal arcuate fibres. These cross the medial plane and ascend in the medial lemniscus to terminate in the posterolateral ventral nucleus, the posterior group, the magnocellular part of the medial geniculate body and the zona incerta [110, 111, 137]. The projection of the dorsal column nuclei to the posterolateral ventral nucleus is organized in a "core-and-shell" fashion. Tactile projections from the cell clusters of the dorsal column nuclei occupy the core of the nucleus and proprioceptive afferents terminate in the shell. The fibres of the medial lemniscus terminate in a series of parallel laminae, which extend anteroposteriorly, throughout the shell and the core of the nucleus. Each lamina represents a specific region of the body, but includes different sensory modalities along its anteroposterior axis [362, 636, 642, 1504].

### The Somatosensory Cortex

Different somatosensory areas have been distinguished in the cerebral cortex. The first (S1), which occupies the postcentral gyrus, consists of four cytoarchitectonic fields (3a, 3b, 1 and 2 of Brodmann [177]), which extend parallel to the central sulcus. The S1 cortex can be divided into narrow, regionally specific columns, which extend perpendicular to the central sulcus through all four cytoarchitectonic fields. The cortical columns receive their afferents from the thalamic cells located within the laminae of lemniscal fibres in the ventral posterior nucleus. The core of this nucleus projects to fields 3b and 1, the shell

to fields 3a and 2. Each of the four cytoarchitectonic fields of S1 therefore contains a complete representation of the body surface. Proprioceptive afferents from the shell region terminate in the anterior field (3a) and the posterior field (2), which surround the central tactile fields (3b and 1). The latter receive their thalamic projections from the core of the ventral posterior nucleus [362, 629, 635, 636, 642, 898, 959, 1316, 1504].

The ventral posterior nucleus also projects to the second somatosensory area (S2), which is located in the parietal operculum. Nociceptive projections to the somatosensory cortex have not been documented and painful sensations cannot be evoked by stimulation of the somatosensory cortex in humans [1064]; see however [36]. Nociceptive units are present at the level of the posterior ventral nucleus of the thalamus, and the projection of the medial part of the posterior group to the retroinsular cortex has been implicated in the transmission of pain in monkeys [190, 630], see also [1365].

### The Trigeminal System (Figs. 132 and 133)

Somatosensory fibres of the trigeminal nerve enter the pons in the sensory root (portio major) and are distributed to the principal sensory nucleus and the spinal trigeminal nucleus. A-fibres terminate in the principal sensory nucleus and in the different subdivisions of the spinal trigeminal nucleus (pars oralis, pars interpolaris and pars caudalis, [1027]). Thin A- $\delta$  and C-fibres descend in the spinal tract (which continues in the dorsolateral fasciculus of the dorsal horn) and terminate in the pars caudalis and upper cervical dorsal horn [283]. Fibres of the mandibular division of the trigeminal nerve descend in the dorsal part of the tract, whereas the ophthalmic division fibres occupy the ventral part. Fibres of the maxillary nerve occupy an intermediate position and descend less far caudally than the other two divisions [730, 1173].

Small somatosensory components of the facial, glossopharyngeal and vagal nerves also join the spinal trigeminal tract.

The pars caudalis of the spinal trigeminal nucleus consists of a layer of marginal cells, a substantia gelatinosa and a nucleus proprius, which are continuous with the same layers of the spinal dorsal horn. The A- and C-fibres of the spinal trigeminal tract and those of the spinal roots have essentially similar synaptic relations. As well, the afferent connections of the pars caudalis and the dorsal horn are essentially similar [189, 380, 528].

The epicritic and protopathic pathways from the trigeminal nerve arise from the rostral and caudal parts, respectively, of the trigeminal nuclear complex. Sjöqvist's tractotomy of the spinal tract at the level of the rostral border of the pars caudalis [730, 1257] therefore effectively abolishes pain and temperature sensibility in the ipsilateral face, leaving the tactile sense intact. The protopathic pathway from the trigeminal nerve, which joins the spinothalamic tract as the lateral trigeminothalamic tract, originates from the pars caudalis of the spinal trigeminal nucleus and crosses in the caudal medulla oblongata [1247]. The pars caudalis also gives rise to an intranuclear ascending system, which terminates in the principal sensory nucleus [189, 380, 585, 1049]. This system has been implicated in pain conduction from the face, by behavioural experiments which showed that a midsagittal cut at the level of the principal sensory nucleus is more effective in abolishing pain sensation in the face than a more caudal cut at the level of the pars caudalis [457]. The lateral trigeminothalamic tract ends in clusters of terminals in the contralateral posteromedial ventral nucleus of the thalamus, in the adjoining part of the posterolateral ventral nucleus, in the border region of these nuclei with the ventral lateral nucleus, in the posterior group, and bilaterally in some of the intralaminar nuclei [110, 189, 221, 380].

The ventral part of the principal sensory nucleus gives rise to the crossed epicritic pathway, which joins the medial lemniscus

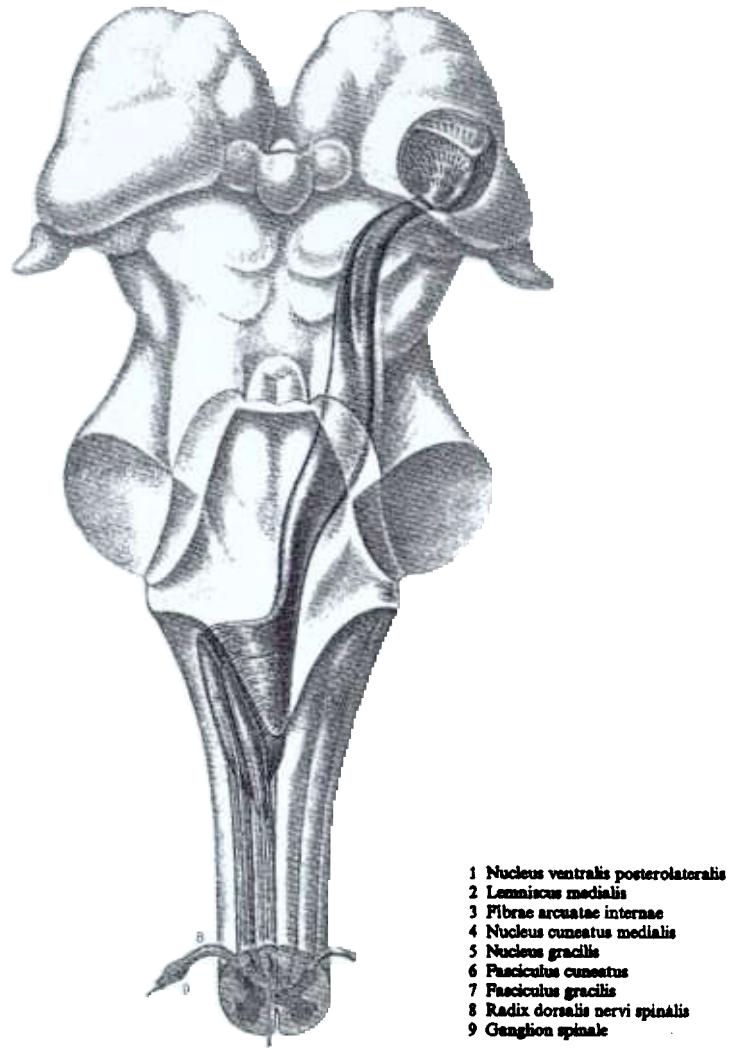


Fig. 130. The medial lemniscus. Position of tracts and nuclei in a dorsal view (5/3 x)

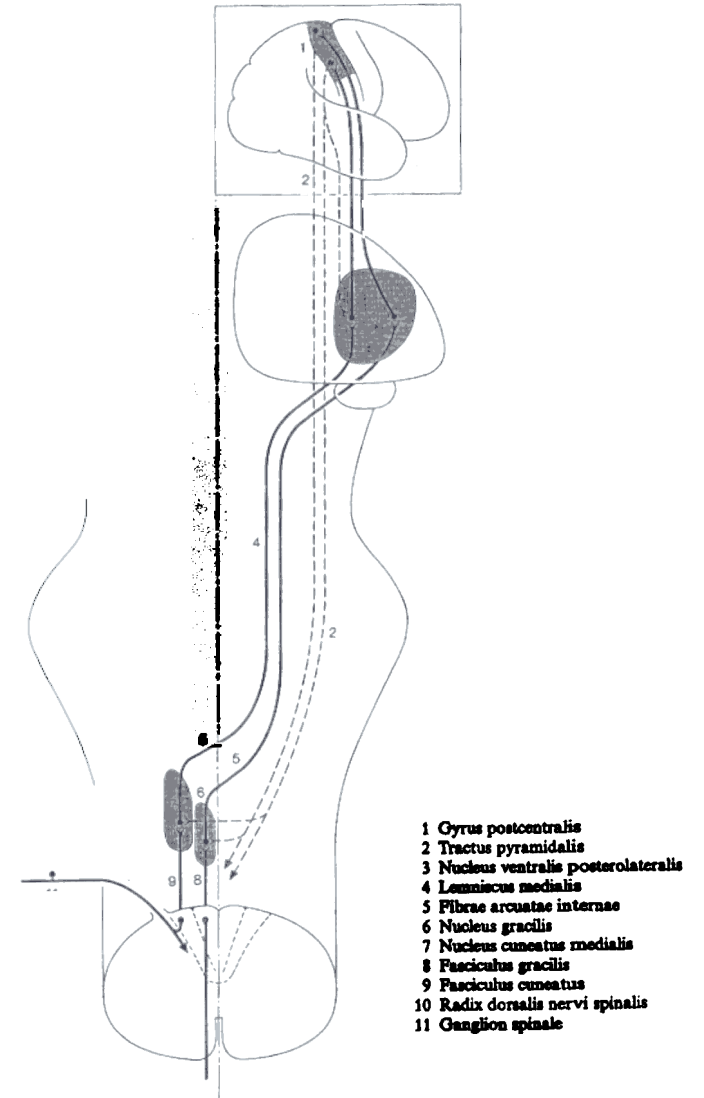
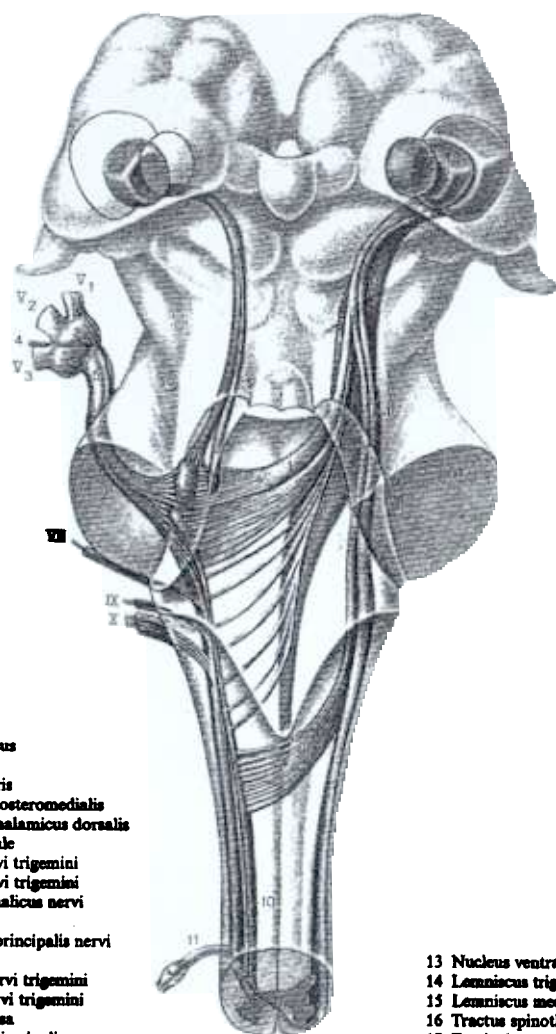


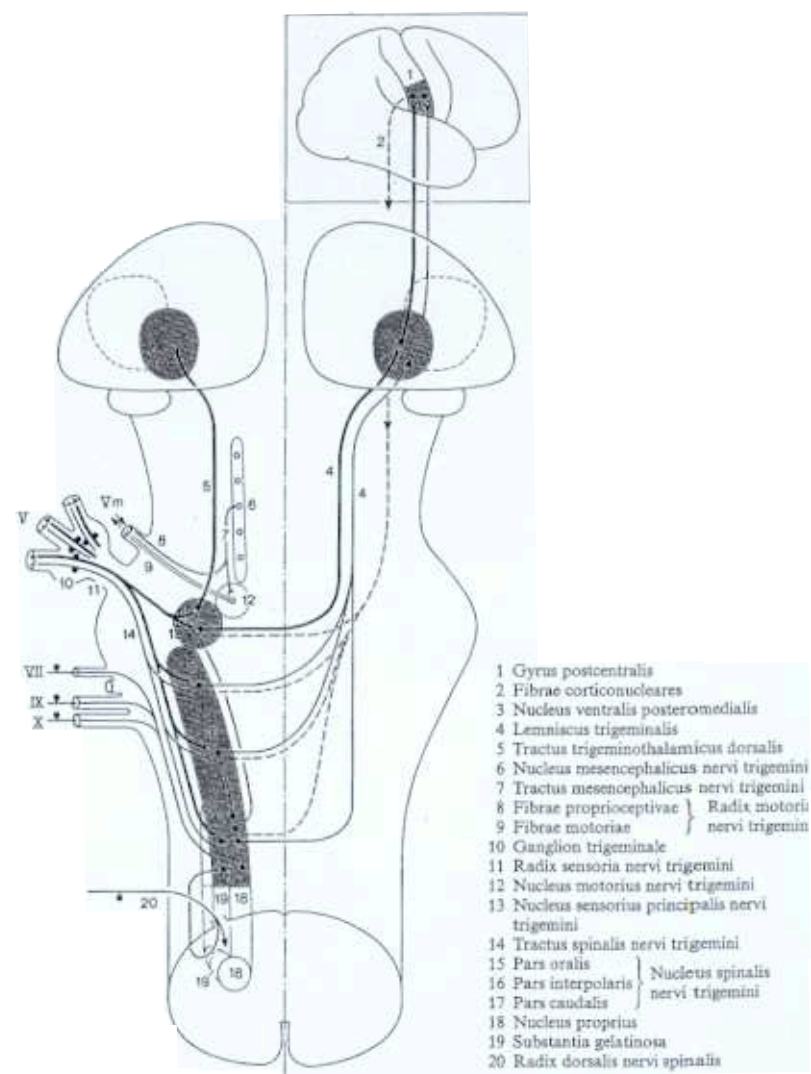
Fig. 131. The neuronal connections of the dorsal column nuclei and the medial lemniscus



- V<sub>1</sub> Nervus ophthalmicus  
 V<sub>2</sub> Nervus maxillaris  
 V<sub>3</sub> Nervus mandibularis  
 1 Nucleus ventralis posteromedialis  
 2 Tractus trigeminothalamicus dorsalis  
 3 Ganglion trigeminale  
 4 Radix motoria nervi trigemini  
 5 Radix sensoria nervi trigemini  
 6 Nucleus mesencephalicus nervi trigemini  
 7 Nucleus sensorius principalis nervi trigemini  
 8 Nucleus spinalis nervi trigemini  
 9 Tractus spinalis nervi trigemini  
 10 Substantia gelatinosa  
 11 Radix dorsalis nervi spinalis  
 12 Nucleus proprius

- 13 Nucleus ventralis posteromedialis  
 14 Lemniscus trigeminalis  
 15 Lemniscus medialis  
 16 Tractus spinothalamicus  
 17 Fasciculus tegmentalis ventralis  
 18 Tractus trigeminothalamicus lateralis

Fig. 132. The central connections of the trigeminal nerve. Position of nerves, tracts and nuclei in a dorsal view (5/3 ×). Roman numerals indicate the corresponding cranial nerves



- 1 Gyrus postcentralis  
 2 Fibræ corticonucleares  
 3 Nucleus ventralis posteromedialis  
 4 Lemniscus trigeminalis  
 5 Tractus trigeminothalamicus dorsalis  
 6 Nucleus mesencephalicus nervi trigemini  
 7 Tractus mesencephalicus nervi trigemini  
 8 Fibræ proprioceptivæ } Radix motorii  
 9 Fibræ motoriae } nervi trigemini  
 10 Ganglion trigeminale  
 11 Radix sensoria nervi trigemini  
 12 Nucleus motorius nervi trigemini  
 13 Nucleus sensorius principalis nervi trigemini  
 14 Tractus spinalis nervi trigemini  
 15 Pars oralis } Nucleus spinalis  
 16 Pars interparialis } nervi trigemini  
 17 Pars caudalis }  
 18 Nucleus proprius  
 19 Substantia gelatinosa  
 20 Radix dorsalis nervi spinalis

Fig. 133. The neuronal connections of the trigeminal nerve

as the trigeminal lemniscus. The uncrossed, dorsal trigeminothalamic tract arises from the dorsal part of the principal sensory nucleus [187, 865, 1262, 1382, 1539]. The trigeminal lemniscus terminates in the posteromedial ventral nucleus, where it overlaps with the projection of the lateral trigeminothalamic tract. The termination of the uncrossed trigeminothalamic tract in the cat differs from that of the crossed fibres and occupies the lateral part of the parvocellular portion of the posteromedial ventral nucleus, lateral to the gustatory subdivision of the nucleus [1538].

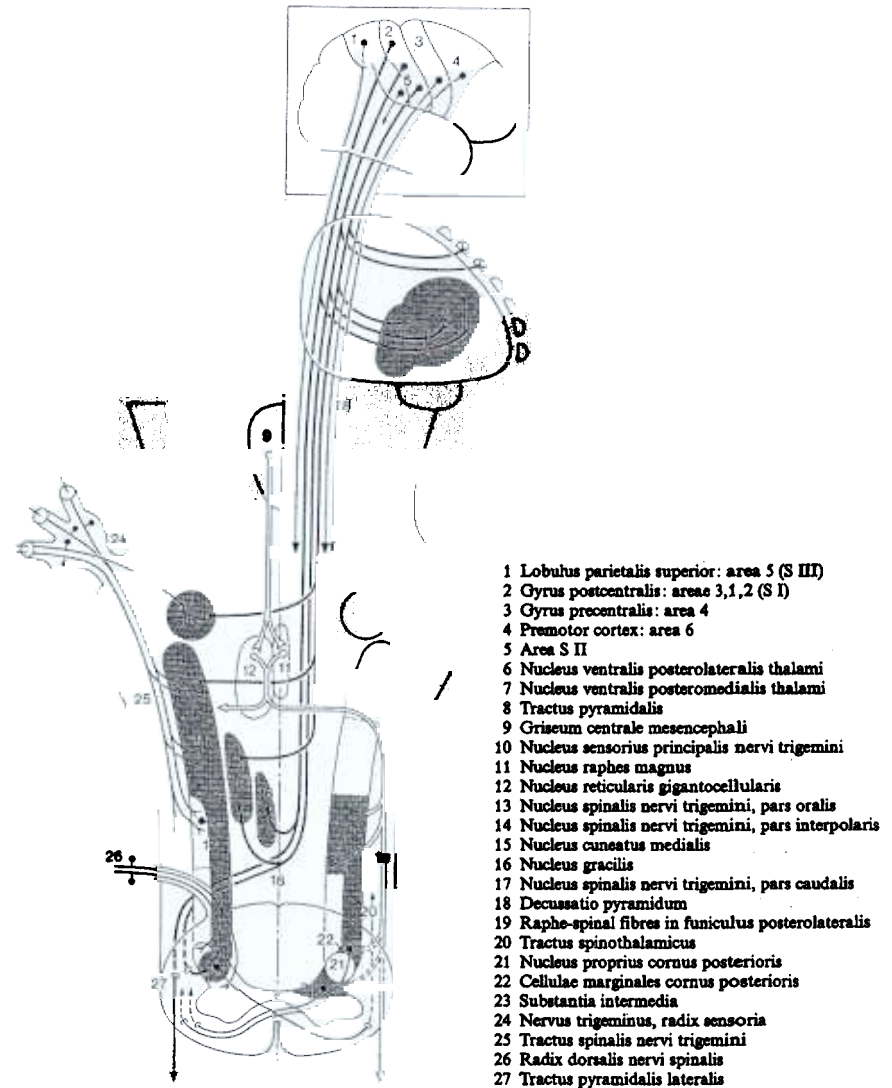
Investigations into the central nervous system of rodents have not been systematically considered in this chapter. An exception should be made for the discovery that in mice there is a discrete projection of the facial vibrissae to distinct cell aggregates in the fourth layer of the somatosensory cortex [1527]. This has promulgated a series of investigations which have improved our understanding of information processing in a sensory system [11, 100, 332, 484, 685].

Unlike to all other primary afferents, the proprioceptive muscle-spindle afferents, which enter the brain stem in the trigeminal nerve, arise from cells located within the central nervous system. These cells constitute the mesencephalic nucleus of the trigeminal nerve, located alongside the central grey matter of the mesencephalon. The axons of these cells descend in the mesencephalic tract of the trigeminal nerve, and have collaterals which terminate on the cells of the trigeminal motor nucleus. The main axons of the mesencephalic root, together with the axons of the motoneurons, constitute the portio minor of the trigeminal nerve. More distally, the portio minor is continuous with the mandibular division of the trigeminal nerve, which distributes both sensory and motor components to the muscles of mastication.

### Descending Connections to Somatosensory Relay Nuclei (Fig. 134)

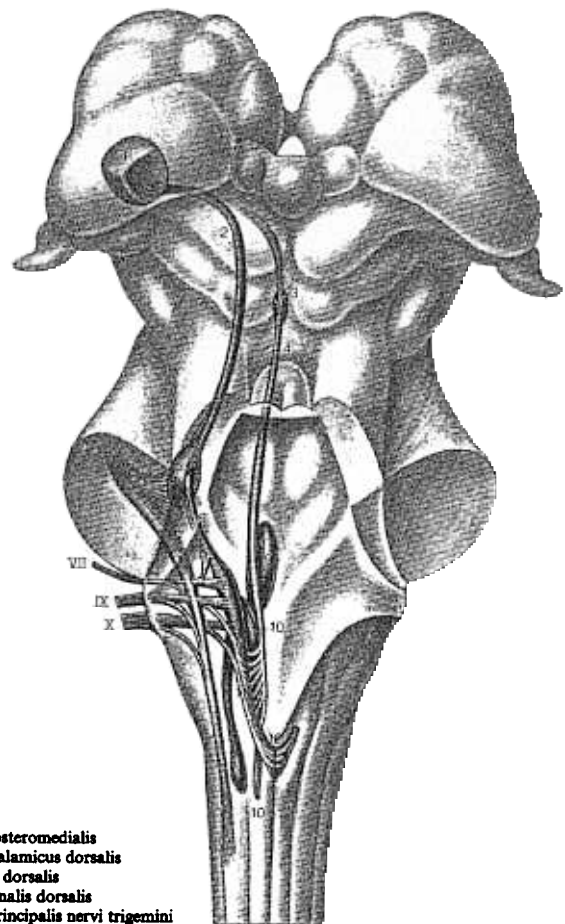
Descending fibres from the deep layers of pyramidal cells in the first and second somatosensory areas (S1 and S2) terminate somatotopically in the ventral posterior nucleus. A more extensive area including the adjoining part of the motor cortex in the precentral gyrus (area 4), the premotor cortex (area 6) and the sensory association area (area 5) in the superior parietal lobule contributes fibres that join the pyramidal tract and terminate in the contralateral sensory nuclei of the trigeminal nerve, the dorsal column nuclei and the dorsal horn [11, 13, 221, 259, 671, 738, 739, 740, 1366, 1488, 1489]. Descending fibres from the cortex preferentially terminate outside the clusters or laminae which contain the main sensory relay cells of the ventral posterior nucleus of the thalamus, the principal trigeminal sensory nucleus and the dorsal column nuclei. In the pars caudalis of the trigeminal spinal tract nucleus and the dorsal horn, the fibres terminate both in the deep layers and in the marginal zone or in the substantia gelatinosa [232].

Other descending systems, which originate from the raphe nuclei and the reticular formation of the pons and medulla oblongata, terminate on the cells that give rise to the spinothalamic and the lateral trigeminothalamic tracts in the spinal grey matter and in the pars caudalis of the trigeminal spinal tract nucleus. Fibres from raphe magnus nucleus, some of which are serotonergic, and from the adjoining reticular formation terminate bilaterally in the marginal layer, the substantia gelatinosa of the pars caudalis and dorsal horn and in the intermediate grey matter. This system inhibits both nociceptive and non-nociceptive units. The raphe-spinal system is often considered to be the final link in a descending pathway from the central grey matter of the mesencephalon, which mediates the analgesia produced by stimulation or opiates [81, 116, 312, 347, 401, 851, 1163]. The role of monoaminergic and peptidergic



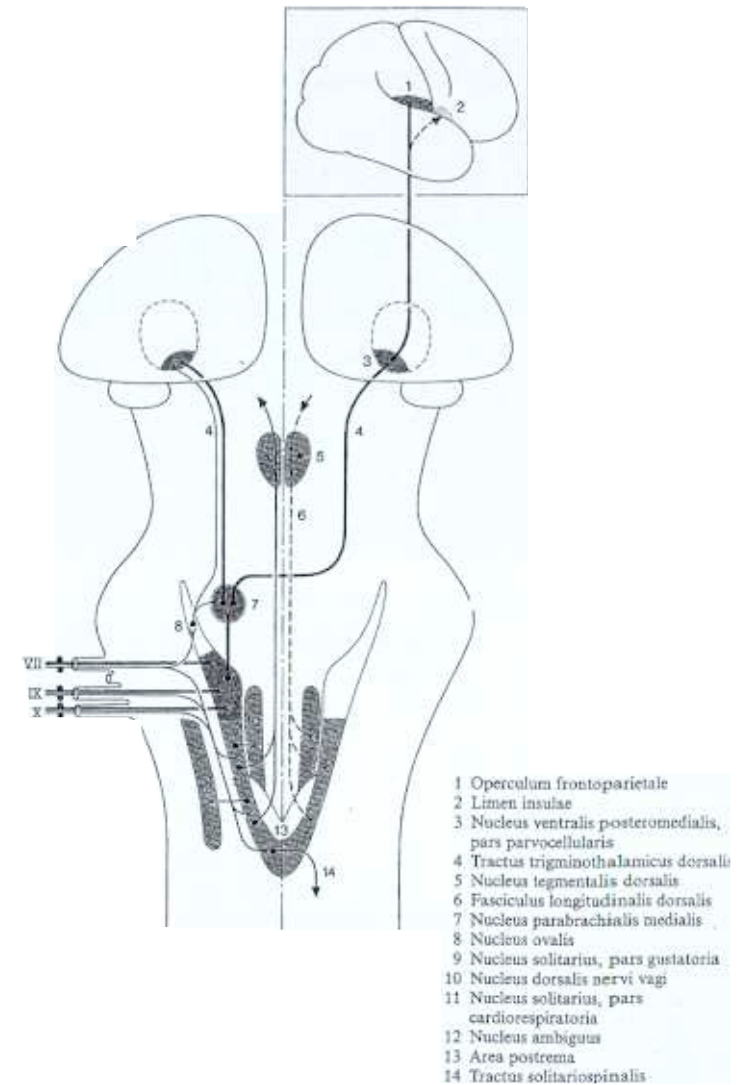
- 1 Lobulus parietalis superior: area 5 (S III)
- 2 Gyrus postcentralis: areas 3,1,2 (S I)
- 3 Gyrus precentralis: area 4
- 4 Premotor cortex: area 6
- 5 Area S II
- 6 Nucleus ventralis posterolateralis thalami
- 7 Nucleus ventralis posteromedialis thalami
- 8 Tractus pyramidalis
- 9 Griseum centrale mesencephali
- 10 Nucleus sensorius principalis nervi trigemini
- 11 Nucleus raphes magnus
- 12 Nucleus reticularis gigantocellularis
- 13 Nucleus spinalis nervi trigemini, pars oralis
- 14 Nucleus spinalis nervi trigemini, pars interpolaris
- 15 Nucleus cuneatus medialis
- 16 Nucleus gracilis
- 17 Nucleus spinalis nervi trigemini, pars caudalis
- 18 Decussatio pyramidum
- 19 Raphe-spinal fibres in funiculus posterolateralis
- 20 Tractus spinothalamicus
- 21 Nucleus proprius cornus posterioris
- 22 Cellulae marginales cornus posterioris
- 23 Substantia intermedia
- 24 Nervus trigeminus, radix sensoria
- 25 Tractus spinalis nervi trigemini
- 26 Radix dorsalis nervi spinalis
- 27 Tractus pyramidalis lateralis

Fig. 134. Descending systems to sensory relay nuclei



- 1 Nucleus ventralis posteromedialis
- 2 Tractus trigeminothalamicus dorsalis
- 3 Nucleus tegmentalis dorsalis
- 4 Fasciculus longitudinalis dorsalis
- 5 Nucleus sensorius principalis nervi trigemini
- 6 Nucleus ovalis
- 7 Tractus spinalis nervi trigemini
- 8 Nucleus solitarius
- 9 Nucleus prepositus hypoglossi
- 10 Nucleus dorsalis nervi vagi
- 11 Tractus solitarius
- 12 Obex
- 13 Nucleus ambiguus

Fig. 135. The tractus solitarius. Position of nerves, tracts and nuclei in a dorsal view (5/3 ×). Roman numerals indicate the corresponding cranial nerves



- 1 Operculum frontoparietale
- 2 Limen insulae
- 3 Nucleus ventralis posteromedialis, pars parvocellularis
- 4 Tractus trigeminothalamicus dorsalis
- 5 Nucleus tegmentalis dorsalis
- 6 Fasciculus longitudinalis dorsalis
- 7 Nucleus parabrachialis medialis
- 8 Nucleus ovalis
- 9 Nucleus solitarius, pars gustatoria
- 10 Nucleus dorsalis nervi vagi
- 11 Nucleus solitarius, pars cardiorespiratoria
- 12 Nucleus ambiguus
- 13 Area postrema
- 14 Tractus solitariospinalis

Fig. 136. The neuronal connections of the visceral afferent system. The nuclei of the special visceral afferent part of the system (taste) are darkly shaded



cell groups and pathways in regulating pain transmission is considered more fully in Nieuwenhuys' monograph on the chemical anatomy of the central nervous system [997].

The descending connections from the spinal tract nucleus of the trigeminal nerve [189, 191, 1165] and the ventral region of the dorsal column nuclei [221, 749] to the dorsal horn can be considered as part of an intranuclear pathway. Their function has not yet been elucidated.

### The Visceral Afferent Systems (Figs. 135 and 136)

Visceral afferent fibres and small contingents of somatosensory fibres enter the medulla oblongata in the facial, glossopharyngeal and vagus nerves. The somatosensory fibres join the spinal tract of the trigeminal nerve. The visceral afferents descend more medially, in the solitary tract, to terminate on the solitary nucleus. Special visceral afferents subserving taste terminate in the rostral, gustatory part of this nucleus. General visceral afferents descend more caudally to terminate in the caudal, cardiorespiratory part of the solitary nucleus and the area postrema. Some of these fibres cross-caudal to the obex and ascend for some distance in the contralateral solitary tract, others terminate in the ventral part of the lateral cuneate nucleus and in the dorsal nucleus of the vagus nerve [98, 656, 657, 1000]. Ascending root fibres of the facial nerve terminate in the oval nucleus, a rostral prolongation of the solitary nucleus located dorsal to the sensory nuclei of the trigeminal nerve [58, 98, 1120].

In humans, fibres from the dorsal trigeminothalamic tract originate from the oval nucleus and the principal trigeminal sensory nucleus. In rats and cats, the ascending taste pathway contains an extra synapse in the medial parabrachial nucleus. From here, fibres ascend ipsilaterally (and in the rat also bilaterally) in the region of the dorsal trigeminothalamic tract, to terminate in the medial

parvocellular part of the posteromedial ventral nucleus of the thalamus, in the amygdala and directly in the gustatory neocortex. The gustatory neocortex and the lateral nucleus of the amygdala are reciprocally interconnected. Both project to the parvocellular part of the posteromedial ventral nucleus [765, 766, 1001, 1007, 1008, 1538]. The cortical projection area for taste is found in the frontal and parietal operculum and in the limen insulae [105].

The dorsal longitudinal fascicle, located in the nucleus praepositus hypoglossi and the central grey matter, connects the caudal part of the solitary nucleus with the dorsal tegmental nucleus and more rostral structures [948]. Crossed, solitariospinal fibres descend from the caudal part of the nucleus [1383].

## Special Sensory Systems

### The Vestibular System (Figs. 137-140)

#### The Vestibular Nerve and Nuclei

The vestibular system provides information about the position and motion of the head in space. The receptive elements are the hair cells of the membranous labyrinth. These cells are located in the cristae ampullares of the semicircular canals and in the maculae of the utricle and the saccule. The first-order elements are bipolar neurons, the somata of which constitute the vestibular ganglion, located in the internal auditory meatus. The peripheral processes of these cells are distributed to the hair cells. The central processes of the bipolar cells constitute the vestibular part of cranial nerve VIII, which enters the brain stem at the level of the pontomedullary junction. Within the vestibular nuclear complex the fibres of the vestibular nerve bifurcate into short ascending and longer descending branches [597, 848]. The vestibular nuclear complex is situated beneath the floor of the lateral part of the fourth ventricle. It comprises four cell masses, the superior, lateral, medial and inferior (or descending) vestibular nuclei (Figs. 104-107). Most ascending branches of the vestibular nerve fibres terminate in the superior vestibular nucleus, but some ascend to the cerebellum (see below). The descending branches of the vestibular nerve constitute a conspicuous bundle in the inferior vestibular nucleus. The fibres in this bundle issue numerous transversely orientated collaterals, which pass to the inferior and medial vestibular nuclei [597, 848]. The large-celled lateral vestibular nucleus or nucleus of

Deiters receives only a few primary vestibular fibres, in its ventral part [207].

Although single vestibular nerve fibres have been observed to distribute their terminal branches to the superior, medial and inferior vestibular nuclei [597, 848] experimental studies have shown that individual receptor components of the labyrinth project preferentially to particular portions of the vestibular nuclear complex. Cells in the vestibular ganglion that innervate the cristae of the semicircular canals project primarily to the superior and medial vestibular nuclei, while those that innervate the maculae of the utricle and saccule have central terminations mainly in the inferior vestibular nucleus [207, 369, 1287].

Some primary vestibular fibres project beyond the vestibular nuclei to terminate ipsilaterally in the cerebellum, the reticular formation and the lateral cuneate nucleus.

The primary vestibulocerebellar fibres reach the cerebellum via the juxtarestiform body and terminate profusely in all parts of the nodulus and in the ventral folia of the uvula. Much smaller numbers of fibres reach the flocculus, deep folia of vermal lobules V and VI and the lingula. All primary vestibulocerebellar fibres terminate as mossy fibres in the granular layer of the cerebellar cortex [207, 706]. The vestibuloreticular fibres terminate in the parts of the gigantocellular reticular nucleus situated adjacent to the vestibular nuclear complex, and particularly in a cell group lying immediately caudoverentral to the abducens nucleus [207]. There is experimental evidence suggesting that this reticular cell group projects primarily to the contralateral abducens nucleus [372, 434,