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 caudoventral to the abducens nucleus [207]. There is experimental evidence suggesting that this reticular cell group projects primarily to the contralateral abducens nucleus [372, 434,
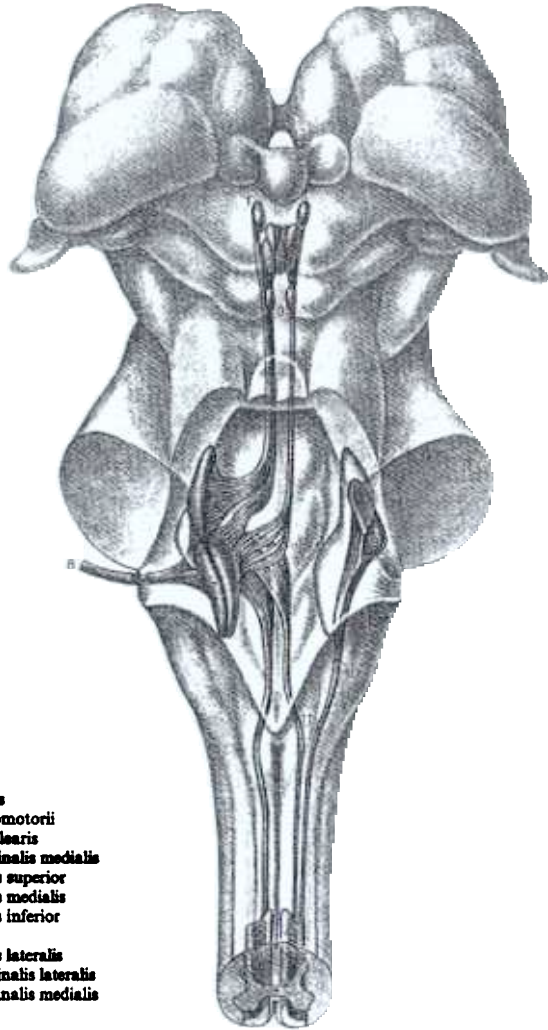
1 Nucleus interstitialis
2 Nucleus nervi oculomotorii
3 Nucleus nervi trochlearis
4 Fasciculus longitudinalis medialis
5 Nucleus vestibularis superior
6 Nucleus vestibularis medialis
7 Nucleus vestibularis inferior
8 Nervus vestibularis
9 Nucleus vestibularis lateralis
10 Tractus vestibulospinalis lateralis
11 Tractus vestibulospinalis medialis

Fig. 137. The vestibular system. Position of nerve, tracts and nuclei in a dorsal view (5/3 ×). The lateral vestibulospinal tract is shown on the *right*
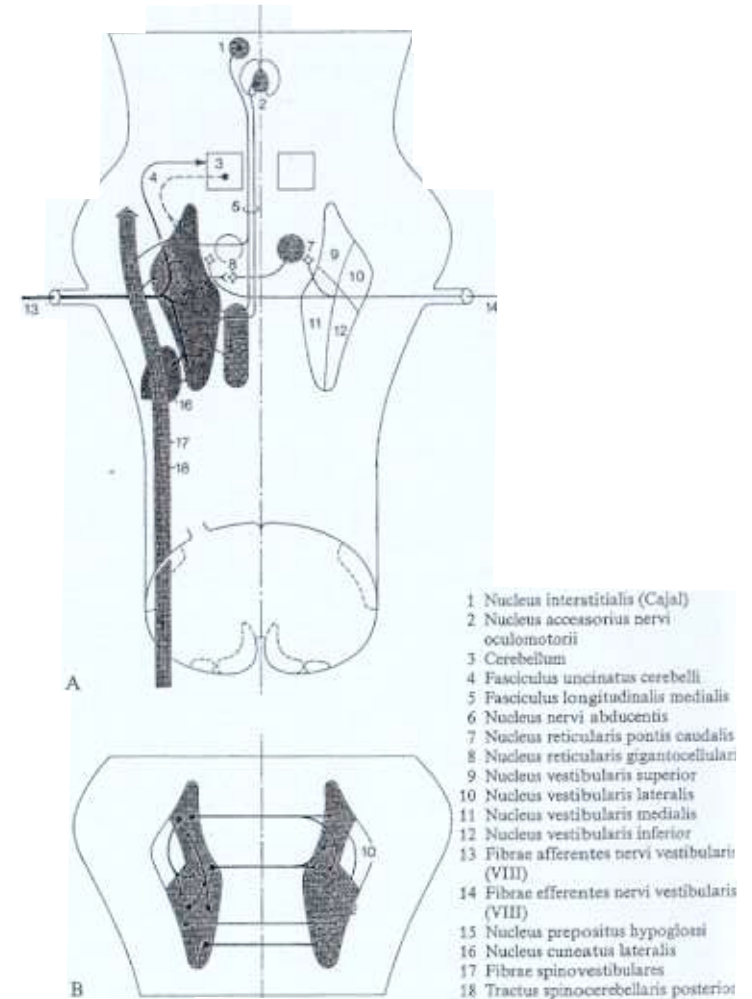
1 Nucleus interstitialis (Cajal)
2 Nucleus accessorius nervi
   oculomotorii
3 Cerebellum
4 Fasciculus uncinatus cerebelli
5 Fasciculus longitudinalis medialis
6 Nucleus nervi abducentis
7 Nucleus reticularis pontis caudalis
8 Nucleus reticularis gigantocellularis
9 Nucleus vestibularis superior
10 Nucleus vestibularis lateralis
11 Nucleus vestibularis medialis
12 Nucleus vestibularis inferior
13 Fibrae afferentes nervi vestibularis
   (VIII)
14 Fibrae efferentes nervi vestibularis
   (VIII)
15 Nucleus prepositus hypoglossi
16 Nucleus cuneatus lateralis
17 Fibrae spinovestibulares
18 Tractus spinocerebellaris posterior

Fig. 138 A, B. The connections of the vestibular system. A Afferent and efferent fibres of the vestibular nerve and central afferents of the vestibular nuclear complex. B Internuclear and commissural connections of the vestibular complex

837]. The primary vestibular fibres which pass to the lateral cuneate nucleus originate from macular regions and terminate in the rostrolateral portion of the nucleus.

It is noteworthy that the vestibular nerve, in addition to afferent fibres, also carries a number of efferent fibres. The latter arise from a group of neurons which is interposed between the abducens and the superior vestibular nuclei and lies embedded in the reticular formation. The projection to one labyrinth has a bilaterally symmetrical origin from the cell groups on each side of the brain stem [411]. In the cat about 20% of the efferent vestibular neurons give off axons which reach both labyrinths [289]. Goldberg and Fernandéz [411] have demonstrated that the efferent fibres have a predominantly exicitatory influence on the afferent activity in the vestibular nerve. They suggest that the efferent vestibular system functions to extend the dynamic range of the afferents during the large accelerations accompanying voluntary head movements.

Afferents to the Vestibular Nuclei

Apart from afferents from the vestibular ganglion the vestibular nuclei receive input from various other sources, among which are the cerebellum, the spinal cord, the nucleus praepositus hypoglossi and the interstitial nucleus of Cajal. The cerebellovestibular fibres arise from Purkinje cells located in the flocculonodular lobe, the uvula and the anterior lobe vermis, and from the fastigial nucleus [206, 216]. The vermis (nodulus and uvula) and the flocculus project in a complementary manner [1456] to the ipsilateral superior, medial and inferior vestibular nuclei. The principal afferents to the lateral vestibular nucleus are the axons of Purkinje cells which are located in a paramedian strip of the anterior lobe vermis (Fig. 166). Because of this, the lateral vestibular nucleus may be considered a ventrally displaced cerebellar nucleus. The cerebellovestibular fibres originating from the fastigial nucleus project bilaterally to the

inferior and lateral vestibular nuclei. Spinovestibular fibres, arising largely from caudal levels of the spinal cord, ascend ipsilaterally and terminate in the lateral vestibular nucleus and in the caudal parts of the medial and inferior vestibular nuclei [1093]. Furthermore, Carpenter and co-workers [206, 216] recently reported that in the cat the central cervical nucleus, a cell mass located in the intermediate grey matter of the spinal cord, projects to the contralateral inferior and superior vestibular nuclei. Cells located in the caudal half of the nucleus praepositus hypoglossi project to the inferior and medial vestibular nuclei, and these connections are partially reciprocated by efferents from those vestibular nuclei [206]. The only vestibular nuclear afferents descending from higher levels of the neuraxis arise from the interstitial nucleus of Cajal and from the midline visceral nuclei of the oculomotor complex (VOMC). The fibres emanating from the interstitial nucleus of Cajal descend in the medial longitudinal fascicle and terminate in the ipsilateral superior and medial vestibular nuclei, whereas those from the VOMC project to the medial and inferior nuclei [206, 216].

The vestibular nuclear complexes of the two sides are amply interconnected by commissural fibres (Fig. 138 B). The superior and medial nuclei send numerous fibres to their counterparts the opposite side [371]. Moreover, the medial nuclei project strongly to the contralateral superior nuclei, and vice versa. The inferior vestibular nucleus provides afferents to the opposite superior, medial and inferior nuclei [206]. Extensive internuclear connections between the individual nuclei of the vestibular complex have also been demonstrated [206, 216, 1162]. Experimental evidence thus indicates that the superior vestibular nucleus is reciprocally related to the medial and inferior nuclei.

Efferents from the Vestibular Nuclei

The vestibular nuclei distribute their efferents more widely in the neuraxis than any other special sensory system [206]. These efferents can be grouped as follows (Fig. 139):

1. Fibres passing to the cerebellum.
2. Projections to the spinal cord and to oculomotor centres.
3. Fibres ascending to the thalamus.

The secondary vestibulocerebellar fibres originate from the inferior, medial and superior nuclei and project to the ipsilateral nodulus, uvula and anterior lobe vermis and, bilaterally, to the flocculus. They terminate, like the primary vestibulocerebellar fibres, as mossy fibres in the granular layer of the cerebellar cortex [165, 206, 216]. Certain parts of the vestibular nuclear complex are able to influence the activity of cerebellar climbing fibres. However, this occurs via an indirect vestibulocerebellar pathway which is synaptically interrupted in the inferior olive. Vestibulo-olivary fibres originate from the inferior, medial and superior vestibular nuclei and terminate in specific parts of the inferior olive (in the cat these are the ipsilateral subnucleus β, and bilaterally the dorsomedial cell column and the caudal medial accessory olive [206, 207, 1177]. In view of the known topography of the olivocerebellar projections, it is likely that the climbing fibre-mediated vestibular information mainly influences the caudal vermis.

The projections to the spinal cord and oculomotor centres from the lateral vestibular nucleus form the lateral vestibulospinal tract, an ipsilateral, somatotopically organised bundle that descends in the lateral part of the anterior funiculus. Its fibres are distributed throughout the spinal cord, exerting facilitatory influences on spinal reflex activity and on extensor muscle tone. The remaining three vestibular nuclei discharge efferents into the medial longitudinal fascicle (MLF), a conspicuous bundle extending in a dorsomedial position throughout the brain stem. Caudally this bundle passes over into the an-

terior funiculus of the spinal cord. Fibres originating from the medial and inferior vestibular nuclei constitute a descending component of the MLF which is known as the medial vestibulospinal tract. Fibres from each of the two participating vestibular nuclei pass bilaterally to the cervical part of the spinal cord, where they make monosynaptic connections with motor neurons innervating the neck muscles [1015]. These connections form part of a set of reflex circuits by which the position and movements of the head are correlated with those of the eyes.

Fibres originating in the medial vestibular nucleus, which descend with the medial vestibulospinal tract, have also been observed to terminate in the contralateral central cervical nucleus. This nucleus receives dorsal root fibres conveying impulses from joint surfaces of the upper cervical vertebrae and projects crossed fibres to the superior and inferior vestibular nuclei as well as to the cerebellum [206].

The ascending vestibular contributions to the MLF originate mainly from the superior and medial vestibular nuclei. The fibres from the superior nucleus remain largely on the ipsilateral side, whereas those from the medial nucleus ascend bilaterally. Together these fibres constitute the vestibulomesencephalic projection. They terminate in the nuclei of the extraocular muscles, i.e. the abducens, trochlear and oculomotor nuclei, the interstitial nucleus of Cajal, and in the rostral interstitial nucleus of the MLF. The interstitial nucleus of Cajal gives rise to a small interstitiospinal tract that, by way of the MLF and the anterior funiculus, passes throughout the length of the brain stem and spinal cord.

The fibres that connect the vestibular nuclei with the oculomotor centres are links in elementary three-neuron reflex paths. The impulses conveyed by these paths help stabilise retinal images by producing eye movements compensatory for head movements. According to the recent experimental studies of Carpenter and co-workers [206, 216] all four vestibular nuclei project to the nuclei of the extraocular muscles. The main results
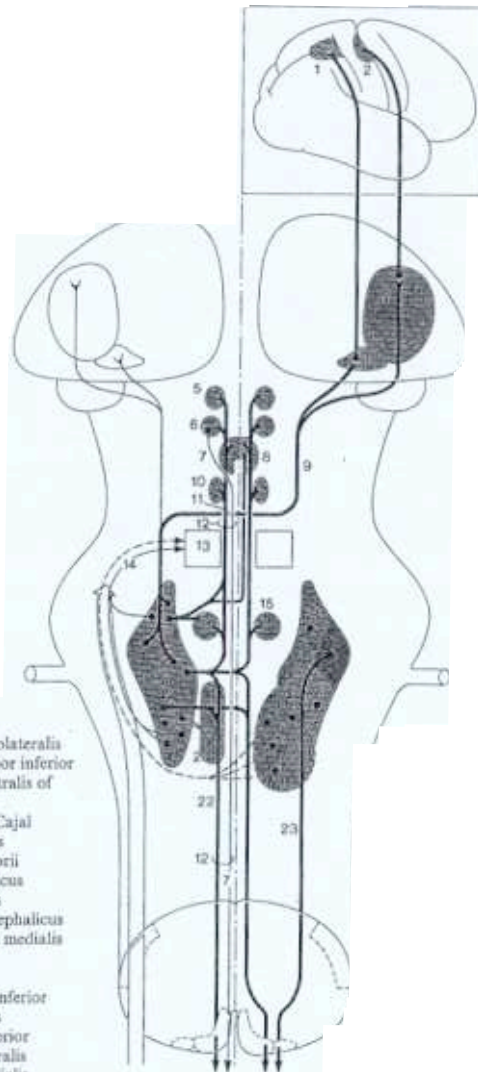
1 Area 2v
2 Area 3a
3 Nucleus ventralis posterolateralis
4 Nucleus ventralis posterior inferior
5 Nucleus interstitialis rostralis of
   the FLM
6 Nucleus interstitialis of Cajal
7 Tractus interstitiospinalis
8 Nucleus nervi oculomotorii
9 Tractus vestibulothalamicus
10 Nucleus nervi trochlearis
11 Tractus vestibulomesencephalicus
12 Fasciculus longitudinalis medialis
   (FLM)
13 Cerebellum
14 Pedunculus cerebellaris inferior
15 Nucleus nervi abducentis
16 Nucleus vestibularis superior
17 Nucleus vestibularis lateralis
18 Nucleus vestibularis medialis
19 Nucleus vestibularis inferior
20 Nucleus prepositus hypoglossi
21 Nucleus olivaris inferior
22 Tractus vestibulospinalis medialis
23 Tractus vestibulospinalis lateralis

Fig. 139. The connections of the vestibular system: efferent connections of the vestibular nuclei
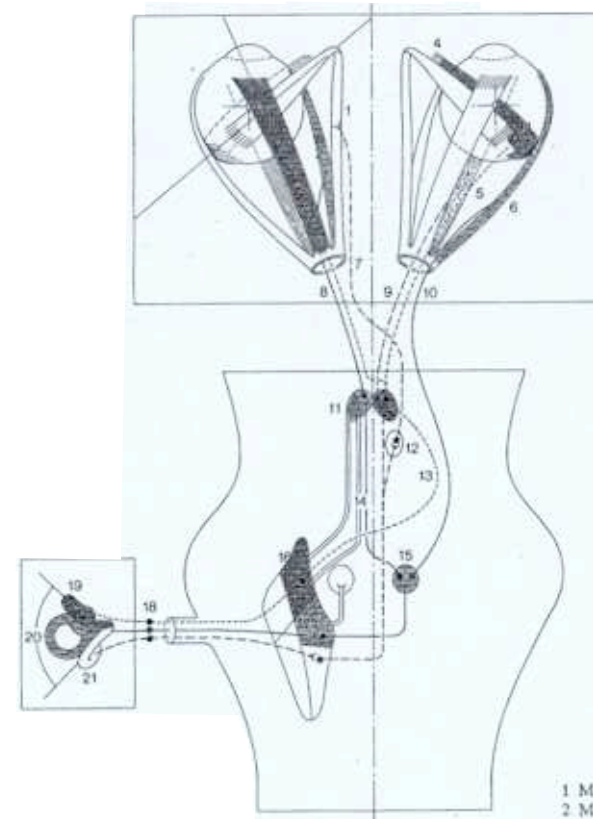
1 Musculus obliquus superior
2 Musculus rectus medialis
3 Musculus rectus superior
4 Musculus obliquus inferior
5 Musculus rectus inferior
6 Musculus rectus lateralis
7 Nervus trochlearis
8 Nervus oculomotorius sinister
9 Nervus oculomotorius dexter
10 Nervus abducens
11 Nucleus nervi III
12 Nucleus nervi IV
13 Pedunculus cerebellaris superior
14 Fasciculus longitudinalis medialis
15 Nucleus nervi VI
16 Nucleus vestibularis superior
17 Nucleus vestibularis medialis
18 Ganglion vestibulare
19 Canalis semicircularis anterior
20 Canalis semicircularis lateralis
21 Canalis semicircularis posterior

Fig. 140. Connections between the semicircular canals and the nuclei of the extraocular muscles. Excitatory connections are indicated in *black*; inhibitory connections with *open contours*. The synaptic relations of the inhibitory vestibuloocular relay cells are not indicated

of these studies may be summarised as follows. Projections from the medial vestibular nucleus supply both abducens nuclei and ascend bilaterally and asymmetrically in the MLF; crossed fibres project to the contralateral trochlear nucleus, the oculomotor complex and the interstitial nucleus of Cajal, while a small number of uncrossed fibres project exclusively to the oculomotor complex. The inferior vestibular nucleus issues exclusively crossed ascending fibres in the MLF, which terminate contralaterally in the trochlear nucleus and in the oculomotor complex. Ascending projections from the ventral part of the lateral vestibular nucleus terminate sparsely in the ipsilateral abducens nucleus, and substantially in the ipsilateral oculomotor complex. The superior vestibular nucleus projects via the MLF to the following ipsilateral centres: trochlear nucleus, oculomotor complex, interstitial nucleus of Cajal and nucleus of Darkschewitsch. Contralateral projections of the superior vestibular nucleus decussate in the isthmus region and terminate contralaterally in the oculomotor complex and, sparsely, in the trochlear nucleus, the interstitial nucleus of Cajal and the nucleus of Darkschewitsch. The manner in which impulses from the three semicircular canals influence, via the vestibular nuclear complex, the centres for the extraocular muscles, is indicated diagrammatically in Fig. 140.

Projections from the Vestibular Nuclei to the Cerebral Cortex

The pathways along which vestibular stimuli reach the level of "conscious experience" are still imperfectly known. However, there is evidence that sparsely scattered cells located within the superior, medial and lateral vestibular nuclei give rise to fibres which terminate in the thalamus. Most of these fibres ascend in the area of the ipsilateral lateral lemniscus. They then decussate in the isthmus region, after which they pass diffusely through the midbrain tegmentum and the fields of Forel. A smaller number of vestibu-

lothalamic fibres remains ipsilateral and follows the so-called ascending tract of Deiters, a bundle located immediately dorsolateral to the MLF. The vestibulothalamic fibres terminate bilaterally in the pars oralis of the ventral posterolateral nucleus (VPLo), the ventral posterior inferior nucleus (VPI) and the pars caudalis of the ventral lateral nucleus. In the monkey physiological experiments have revealed two separate vestibular cortical areas, area 2v at the rostral tip of the intraparietal sulcus and area 3a in the floor of the central sulcus. It seems likely that fibres originating in the VPLo represent the link in the vestibulocortical pathway to area 3a, and that the VPI is the source of the vestibular thalamocortical fibres terminating in area 2v [248, 360, 757, 840, 1017, 1112].

The Auditory System
(Figs. 141–143)

Auditory Centres

The central auditory system includes, in addition to several rhombencephalic cell masses, a mesencephalic, a diencephalic and a telencephalic centre (Fig. 141). The rhombencephalic cell masses are the cochlear nuclei, the nuclei together constituting the superior olivary complex and the nuclei of the lateral lemniscus.

The human cochlear nuclei are composed of a ventral and a dorsal nucleus, which are comparable though not identical in their cytoarchitecture to those of other mammals [938]. The ventral cochlear nucleus comprises a rostral area of spherical cells, a central area of multipolar and globular cells, a caudal area of so-called octopus cells and a laterodorsal cap of small neurons. The dorsal cochlear nucleus is well developed, but does not show the characteristic laminated pattern seen in other mammals.

The superior olivary complex is largely embedded in the trapezoid body, a large, transversely oriented fibre stream. It com-

prises the medial and lateral superior olivary nuclei and the nucleus of the trapezoid body. The medial and lateral superior olivary nuclei are elongated cell masses, the former of which is much better developed than the latter. The nucleus of the trapezoid body is, just as the lateral superior olivary nucleus, poorly developed in man [1029]. These three cell masses, i.e. the medial and lateral superior olivary nuclei and the nucleus of the trapezoid body, are surrounded by a zone containing small groups of cells that vary in size and shape. The latter cell groups are collectively designated as the periolivary nuclei. They were formerly believed to be involved only descending pathways. However, it has recently been established that the cell groups of the periolivary nuclei also give rise to ascending projections [3].

The nuclei of the lateral lemniscus constitute an elongated strand of cells which lies embedded in the fibre bundles of the lateral lemniscus as it ascends through the pontine tegmentum to the midbrain. Two nuclei, a ventral and a dorsal, can be distinguished. Experimental studies [407, 726, 1501] have shown that these nuclei represent important links in the ascending auditory pathway.
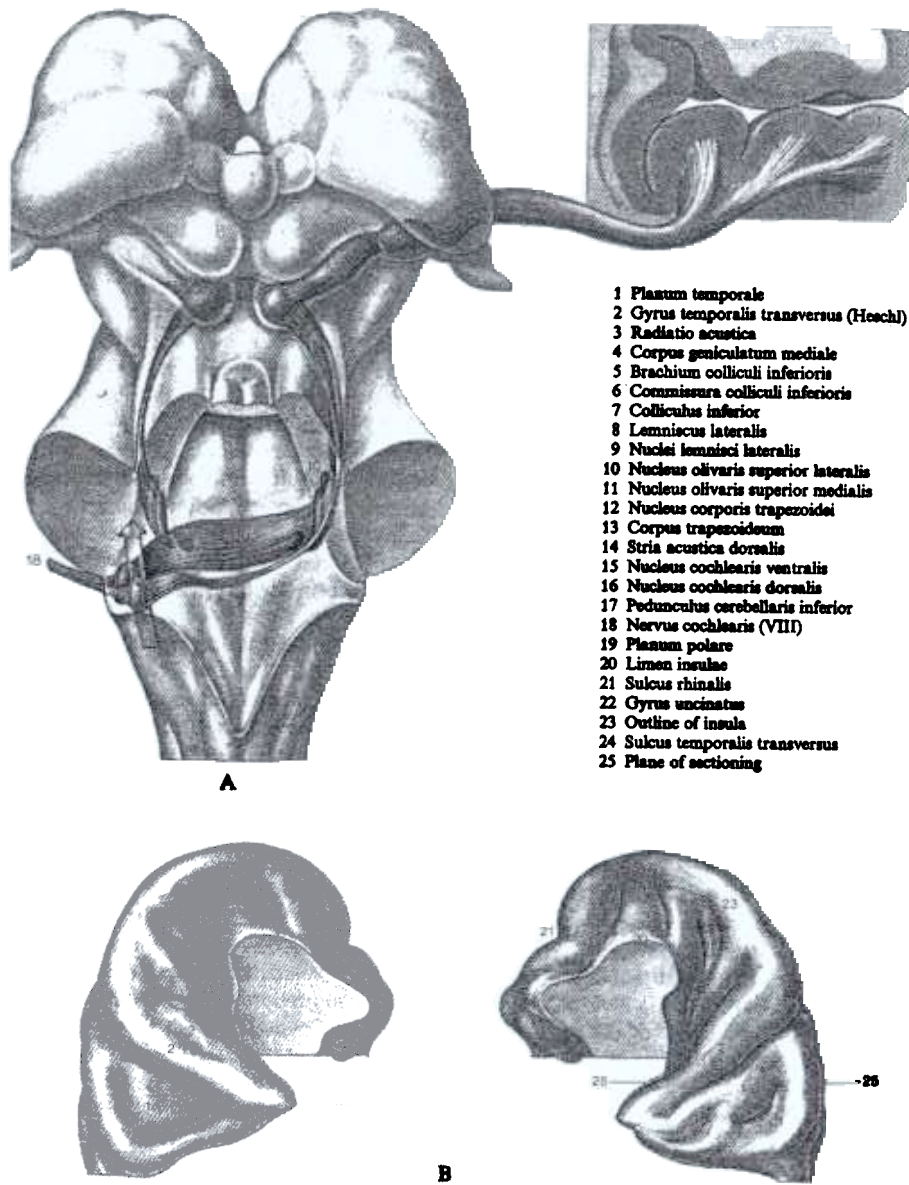
At the mesencephalic level the auditory system is represented by the inferior colliculus. This structure, which is a most important relay station in both the ascending and descending auditory projections, consists of a large, compact central nucleus and a more diffuse, mainly laterally situated zone of grey matter. The specific diencephalic nucleus for hearing is the medial geniculate body, which forms part of the dorsal thalamus. This nucleus comprises three main divisions, medial, dorsal and ventral. Part of the ventral division has a laminar organisation. The telencephalic auditory centre occupies the posterior portion of the cortex covering the upper surface of the temporal lobe.

Auditory Pathways

Figure 141 shows that the centres mentioned above are interconnected by distinct fibre streams. The cochlear nuclei give rise to two, more or less transversely orientated bundles, the trapezoid body and the dorsal acoustic stria. The trapezoid body crosses in the ventral part of the tegmentum. After having reached the lateral part of the pons, the bundle makes an abrupt rostral turn and continues as the lateral lemniscus.

The nuclei of the superior olivary complex and the cell mass bearing its name lie embedded in the trapezoid body. The dorsal acoustic stria passes over the inferior cerebellar peduncle. Arching ventrally, this bundle traverses the reticular formation to reach the region of the contralateral superior olivary complex where it continues into the lateral lemniscus. The bundle just mentioned is situated in the dorsolateral part of the pons and the caudal midbrain. It ascends to the inferior colliculus, in which most of its fibres terminate. The brachium colliculi inferioris, a prominent bundle visible on the surface of the midbrain, connects the inferior colliculus with the medial geniculate body. The inferior colliculi of both sides are, in addition, interconnected by commissural fibres. The final link in the auditory system is formed by the auditory radiation through which the medial geniculate body is connected with the cerebral cortex. Passing laterally, this radiation traverses the sublenticular portion of the internal capsule.

It is noteworthy that from the level of the inferior colliculus onwards the ascending auditory projection can be subdivided into a 'core' projection and a 'belt' projection [164]. The final target of the core projection is the primary auditory cortex, whereas the target of the belt projection is formed by the auditory cortical fields surrounding the primary auditory area. The core and belt projections include separate relay stations in the inferior colliculus and in the medial geniculate body. Within the inferior colliculus the central nucleus and the zona lateralis repre-

1 Planum temporale
2 Gyrus temporalis transversus (Heschl)
3 Radiatio acustica
4 Corpus geniculatum mediale
5 Brachium colliculi inferioris
6 Commissura colliculi inferioris
7 Colliculus inferior
8 Lemniscus lateralis
9 Nuclei lemnisci lateralis
10 Nucleus olivaris superior lateralis
11 Nucleus olivaris superior medialis
12 Nucleus corporis trapezoidei
13 Corpus trapezoideum
14 Stria acustica dorsalis
15 Nucleus cochlearis ventralis
16 Nucleus cochlearis dorsalis
17 Pedunculus cerebellaris inferior
18 Nervus cochlearis (VIII)
19 Planum polare
20 Limen insulae
21 Sulcus rhinalis
22 Gyrus uncinatus
23 Outline of insula
24 Sulcus temporalis transversus
25 Plane of sectioning

A

B

Fig. 141A, B. The auditory system. A Position of nerve, nuclei and tracts in a dorsal view (5/3).
The transverse gyrus of Heschl and the planum temporale have been drawn in the true position
relative to the brain stem and the thalamus; B Dorsal view of the temporal lobes, to show the position
of the transverse gyri of Heschl and the temporal plane (1/1 ×)

1 Planum temporale
2 Gyri temporales transversi
3 Radiatio acustica
4 Corpus geniculatum mediale, pars dorsalis
5 Corpus geniculatum mediale, pars ventralis
6 Corpus geniculatum mediale, pars medialis
7 Brachium colliculi inferioris
8 Colliculus superior
9 Colliculus inferior, zona lateralis
10 Commissura colliculi inferioris
11 Colliculus inferior, nucleus centralis
12 Nucleus lemnisci lateralis dorsalis
13 Nucleus lemnisci lateralis ventralis
14 Decussatio lemniscorum lateralium
15 Lemniscus lateralis
16 Nuclei periolivares
17 Nucleus olivaris superior medialis
18 Nucleus olivaris superior lateralis
19 Nucleus corporis trapezoidei
20 Corpus trapezoideum
21 Nervus cochlearis
22 Nucleus cochlearis ventralis
23 Nucleus cochlearis dorsalis
24 Stria acustica dorsalis

Fig. 142. The connections of the auditory system: ascending projections

A

B

1 Radiatio acustica
2 Colliculus inferior, zona lateralis
3 Colliculus inferior, nucleus centralis
4 Commissura colliculi inferioris
5 Decussatio lemniscorum lateralium
6 Nucleus lemnisci lateralis dorsalis
7 Lemniscus lateralis
8 Nuclei periolivares
9 Fasciculus olivocochlearis
10 Nervus cochlearis
11 Nucleus cochlearis ventralis
12 Nucleus cochlearis dorsalis

13 Fibres to m. tensor tympani
14 Radix motoria nervi trigemini
15 Nucleus motorius nervi trigemini accessorius
16 Nucleus motorius nervi trigemini
17 Nucleus olivaris superior lateralis
18 Nucleus nervi facialis
19 Nucleus nervi facialis, cellulae accessoriae
20 Fibres to m. stapedius
21 Nervus facialis

Fig. 143A, B. The connections of the auditory system. A commissural and descending connections
B pathways for the middle ear reflexes

sent the 'core' and 'belt' centres, respectively. The final link in the auditory core projection arises from the laminated portion of the ventral nucleus of the medial geniculate body, whereas the remaining divisions of that thalamic centre project to the belt area of the auditory cortex [201].

The primary auditory cortex corresponds roughly to the transverse gyrus of Heschl. Part of the belt area of the auditory cortex occupies the planum temporale, i.e. the region on the superior temporal plane lying posterior to the transverse gyrus and extending back to the end of the Sylvian fossa. There are considerable variations in the size and convolution of the supratemporal plane in the two hemispheres. Thus, Heschl's gyrus is usually solitary on the left, but double on the right side, and the left planum temporale is commonly much larger than the right [374, 376, 377]. These gross anatomical asymmetries may well represent the morphological substrate for language lateralisation [374].

The Ascending Auditory Projection

The primary neurons of the auditory system are the bipolar cells that constitute the spiral ganglion. Their peripheral processes make contact with the auditory receptors, i.e. the outer and inner hair cells in the organ of Corti. The central processes of the bipolar cells constitute the cochlear division of cranial nerve VIII, which enters the central nervous system just caudal to the vestibular division of the same nerve. The primary auditory fibers bifurcate immediately and are distributed to both the dorsal and the ventral cochlear nuclei. Within the cochlear nuclei these bifurcating fibers show profuse collateral branching and establish specific types of synaptic contacts with various types of neurons present in the cochlear nuclear complex.

Secondary auditory fibres originating from the dorsal cochlear nucleus constitute the dorsal acoustic stria and pass, via this bundle and via the lateral lemniscus, to the contralateral inferior colliculus e.g. [1024].

The other secondary auditory projection, the trapezoid body, arises from the ventral cochlear nucleus. Some of its fibres pass, like those of the dorsal auditory stria, directly to the inferior colliculus, but many other fibres are interrupted in one of the nuclei that lie embedded in the trapezoid body or in the nuclei of the lateral lemniscus. The following indirect channels are among those connecting the ventral cochlear nucleus with the inferior colliculus:

1. The spherical cells in the ventral cochlear nucleus project to the ipsilateral lateral superior olivary nucleus and to the medial superior olivary nucleus of both sides. Both superior olivary nuclei project in turn to the inferior colliculus [503]. The cells in the medial superior olivary nucleus are bipolar and orientated horizontally. From both the medial and the lateral pole of these cells a dendritic tuft arises. The laterally extending dendrites receive their input from fibres of the ipsilateral side, whereas the medially extending dendrites receive input from the contralateral side. This highly specific spatial organisation of afferents to cells in the medial superior olivary nucleus has to do with the role played by these cells in interpreting interaural differences in phase and intensity for localisation of sound.

2. The globular cells in the ventral cochlear nucleus project to the contralateral nucleus of the trapezoid body. The latter sends fibres to the ipsilateral lateral superior olivary nucleus, which in turn projects to the ipsilateral inferior colliculus [408, 1279]. There is physiological and morphological evidence to indicate that auditory information reaches the cerebellum via portions of the pontine nuclei. These portions receive corticopontine fibres originating from the auditory cortex and tectopontine fibres arising from the superior and inferior colliculi. The superior colliculus, it should be noted, receives fibres from the auditory cortex, as well as from the lateral zone of the inferior colliculus [164, 728]. Apart from the indirect pathways just discussed, the cerebellar auditory area re-

ceives a limited number of fibres arising directly from cells situated in different parts of the cochlear nuclear complex [561].

Fibres belonging to the acoustic system decussate in the median plane at various levels (Figs. 142, 143). The components of the dorsal acoustic stria and the trapezoid body have already been discussed. It should, however, be added that by way of these fibre systems several commissural connections between the right and left cochlear nuclear complexes are established [204].

1. The olivocochlear fascicle, or bundle of Rasmussen, is a fibre system originating from the periolivary nuclei. The fascicle consists largely of decussating fibres, which traverse the median plane, passing through the medullary reticular formation.

2. The commissure of the lateral lemniscus nuclei, also known as Probst's commissure, passes through the brachium conjunctivum and the most rostral part of the pontine tegmentum. It contains true commissural fibers between the right and left dorsal nuclei of the lateral lemniscus and fibers passing from those nuclei to the contralateral inferior colliculi [726].

3. The commissure of the inferior colliculus consists primarily of true commissural fibres interconnecting the two central nuclei [179], but also contains other fibres. These pass from the central nucleus and lateral zone of the inferior colliculus to the core and belt portions, respectively, of the medial geniculate body [33, 728].

4. The medial geniculate bodies are not joined by commissural connections, but the various auditory cortical areas of the two sides are reciprocally connected via the corpus callosum.

The Descending Auditory Projection

Parallel to the pathway from the organ of Corti to the auditory cortex, there is an uninterrupted chain of neurons conducting impulses in the opposite direction. The final link

in this descending system is formed by the olivocochlear bundle, which originates from the periolivary nuclei. Most of the fibres of this bundle decussate in the tegmentum. They enter the vestibular nerve and join the cochlear nerve via a vestibulocochlear anastomosis. After having entered the cochlea, they terminate in the organ of Corti. The higher links in the corticocochlear projection are constituted by (1) fibres passing from the primary auditory cortex to the lateral zone of the inferior colliculus, and (2) fibres descending (mainly ipsilaterally) to the periolivary nuclei. The exact site at which these fibres originate is unknown. Although the projections from the medial geniculate body to the auditory cortex are reciprocated by descending corticogeniculate fibres, the medial geniculate body is generally not considered to be a link in the corticocochlear projection. It is, however, worthy of note that Adams [2] has produced evidence to suggest that the medial geniculate sends fibres to the inferior colliculus.

The studies of Warr and collaborators [459, 1474, 1475, 1476, 1497] indicate that the olivocochlear bundle consists of two separate efferent systems, which differentially innervate the two types of hair cells situated in the organ of Corti. One system originates from large cells in the ventromedial part of the periolivary area. Their coarse axons project mostly to the contralateral cochlea, where they form large synaptic terminals at the bases of the outer hair cells. The other olivocochlear system arises from smaller neurons which are situated more laterally, in the vicinity of the lateral superior olivary nucleus. Unlike the large medial cells, these small elements project mostly to the ipsilateral cochlea and make "en passage" synapses with the primary afferent fibres, just beneath the inner hair cells. Adams [3] also reported the presence of two different types of olivocochlear neurons. However, he remained unable to confirm Warr's categorisation of these elements into medial and lateral groups. The olivocochlear neurons form a system by which the brain can influence its own audi-

tory input. Physiological experiments have shown that these neurons inhibit sensory outflow from the cochlea.

Apart from the corticocochlear path, two other descending auditory projections deserve brief mention. These projections, which arise from the inferior colliculus and from the periolivary nuclei, both terminate in the cochlear nuclei. As we have seen, the cochlear nuclei receive their main input from the cochlea, but do not send fibres back to that organ.

The colliculo-cochleonuclear projection consists of an ipsilateral component originating from the lateral zone of the inferior colliculus, and a bilateral component originating from the central nucleus. Both components terminate in the dorsal cochlear nucleus [249].

The periolivary cochleonuclear projection originates, as its name implies, from the cell groups situated in the periolivary area. These cell groups may well receive impulses from the ventral cochlear nuclei and from fibres descending from the inferior colliculus. Adams [3] mentions two groups of periolivary cells which impinge upon the cochlear nuclear complex, a lateral group of multipolar cells, whose members are located around the ipsilateral lateral superior olivary nucleus, and a medial group of small neurons situated ventral to the nucleus of the trapezoid body. This medial group projects bilaterally to the cochlear nuclei.

Auditory Reflex Pathways

The auditory cell masses in the brain stem serve not only as relay nuclei in ascending and descending projections, but also as reflex centres. Thus, efferents from the cochlear nuclei enter the reticular formation, where they synapse with neurons of the ascending reticular activating system. Impulses entering the reticular formation along this path give rise to the auditory evoked startle response. Fibres passing from the lateral zone of the inferior colliculus to the superior colliculus [9, 728] may be considered as important links

in the pathway providing for reflex turning of eyes and head in response to auditory stimuli. (It has already been mentioned that these fibres also form part of an auditory projection to the cerebellum).

Finally, pathways passing from the ventral cochlear nuclei to the motor nuclei of the trigeminal and facial nerves constitute reflex arcs that link the organ of Corti with the tensor tympani and the stapedius muscles. In response to sounds of high intensity, these muscles (Fig. 143B) contract reflexly and dampen the vibration of the ear ossicles. In this way the organ of Corti is protected from damage by excessive stimulation. Borg [144] provided experimental anatomical and physiological evidence that the reflex arcs indicated are closed by fibres passing from the ventral cochlear nucleus to regions of the ipsilateral and contralateral medial superior olivary nuclei, which in turn project to the tensor tympani and stapedius motoneurons in the motor trigeminal and facial nuclei. He considered it likely that the stapedius motoneurons also receive a direct projection from the ventral cochlear nucleus. Recent studies with the retrograde tracer technique [643, 674, 828, 923, 1236, 1276, 1356] have shown that the stapedius and the tensor tympani motoneurons both form separate cell groups, situated close to but clearly beyond the confines of the facial and motor trigeminal nuclei.

The Visual System

The Visual Pathway (Figs. 144 and 145)

The visual pathway begins at the retina, a thin, transparent lamina of tissue that is ontogenetically derived from the wall of the diencephalon. The retina is a laminated structure that contains photoreceptor cells, neurons and glia. The photoreceptors, i.e. the rods and cones, constitute the outer layer of the retina. Impulses from the photoreceptors are transmitted to bipolar cells that form an intermediate zone. The bipolar cells represent