direct projection which passes from the A1 group to the magnocellular parts of the paraventricular nucleus and to the supraoptic nucleus [1207].

Finally, it should be mentioned that the medullary noradrenergic cell groups have been implicated in the control of various anterior pituitary hormones, including growth hormone, luteinizing hormone and ACTH [942, 1487]. Given the fact that the activity of the anterior pituitary is regulated by neurosecretory processes in the median eminence, it is noteworthy that noradrenergic fibres originating from the cell groups mentioned are involved in three different projections leading to that structure, one direct and two indirect. The direct projection originates from cell group A1. The indirect projections are constituted by fibres arising from the A1 and A2 groups which terminate in the infundibular nucleus and in the parvocellular division of the paraventricular nucleus. Both of the latter centres project to the median eminence [1207].

As regards the *projections ascending from the adrenergic cell-groups C1 and C2* it has already been mentioned that fibres originating from these cell groups join the longitudinal catecholamine bundle, with which they ascend through the brain stem and enter the hypothalamus. These fibres give rise to terminal fields in a considerable number of centres, among which are the griseum centrale of the rostral rhombencephalon and mesencephalon, the locus coeruleus, some thalamic midline nuclei and the dorsomedial and paraventricular hypothalamic nuclei, the latter of which shows a high density of terminals [356, 530, 1164]. Little is known about the central actions of the adrenergic neurons. The dense innervation of the paraventricular nucleus suggests that adrenalin might be involved in oxytocin and vasopressin secretion, and the innervation of the dorsomedial hypothalamic nucleus indicates a possible influence on food intake.

The cholinergic cell-groups Ch5 and Ch6, which are situated in the rostral part of the lateral pontine tegmentum (Fig. 154C) give rise to an ascending bundle, the dorsal pathway of Shute and Lewis [1246]. This fibre system, which projects upon the superior colliculus and several thalamic centres, has been considered an integral part of the ascending reticular system [905, 907].

Cerebellum

(Figs. 160–166)

Introduction

Transverse fissures of differing depth divide the cerebellum into lobes, lobules and folia. Paramedian sulci, which are deepest in the posterior lobe, separate the vermis from the hemispheres (Figs. 16–18). The subdivision of the cerebellum has evolved from studies of its comparative anatomy and development [141, 762, 763, 764, 1458]. It is covered by a three-layered cortex and contains the deep cerebellar nuclei within its central white matter. Afferent systems terminate both in the cortex and in the deep nuclei; Purkinje cell axons connect the cortex with the deep cerebellar and certain vestibular nuclei; the main efferent pathways take their origin from the deep nuclei. A caudal zone of the cerebellum, consisting of the flocculus and the nodule, maintains important afferent and efferent connections with the vestibular and oculomotor systems. It is known as the vestibulocerebellum (Fig. 162).

The main neurons of the cerebellar cortex, with their afferent and efferent fibre connections, are arranged in two perpendicular planes. Purkinje cell dendritic arbors are oriented parasagittally, and the Purkinje cells which project to particular deep cerebellar nuclei are grouped together in parasagittal zones (Fig. 162). Each of these zones, and the deep cerebellar or vestibular nucleus to which it projects, receives a projection from a subdivision of the contralateral inferior olive. These olivocerebellar fibres terminate as climbing fibres on the dendrites of the Purkinje cells. The deep nuclei are reciprocally connected with the inferior olive through monosynaptic and multisynaptic nucleo-olivary pathways (Figs. 163, 164).

Most cerebellar afferents terminate as mossy fibres on granule cells of the cerebellar cortex, which in turn contact Purkinje cells. The axons of the granule cells (the parallel fibres) course transversely through the superficial layer of the cerebellar cortex. Mossy fibres originate from various nuclei in the spinal cord and brain stem. The terminations of mossy-fibre systems usually include both vermis and hemisphere and are often delimited by transverse fissures (Fig. 161). This transverse disposition of the mossy fibre afferents is further enhanced by the transverse orientation of the parallel fibres.

Each half of the cerebellar vermis is bilaterally connected with the vestibular nuclei and the pontine and bulbar reticular formation through direct corticovestibular fibres and the medial (fastigial) nucleus with its efferent tracts. The cortex of the hemisphere projects to the interposed and dentate nuclei (Fig. 164). These nuclei which give rise to the superior cerebellar peduncle, an important ascending pathway, which decussates in the mesencephalon and terminates in the red nucleus and thalamus. Through the ventral lateral nucleus of the thalamus, the cerebellar hemisphere is connected with the motor cortex. The influence of the cerebellar hemisphere on motoneurons and interneurons is therefore mediated through the corticobulbar, corticospinal, the rubrobulbar and rubrospinal tracts. Since both these sets of pathways are crossed, lesions of the cerebellar hemisphere result in ipsilateral loss of motor coordination (Figs. 119, 120).

Cortex and Central Nuclei

The surface of the cerebellum is covered by a cortex that presents a uniform, three-layered histological structure throughout its extent [1037]. These layers are, passing from superficial to deep, the cell-poor molecular layer, the monolayered Purkinje layer and the granular layer. The cerebellar cortex presents a lattice structure, with some of its main elements oriented in two perpendicular planes [157]. The profusely branching, flattened dendritic trees of the Purkinje cells extend into the molecular layer, where they are oriented perpendicular to the direction of the transverse fissures. The deepest layer consists of numerous small granule cells. The axons of these cells ascend to the molecular layer where they dichotomise and run parallel to the transverse fissures, through the Purkinje cell dendritic trees with which they make excitatory synapses. The neurotransmitter of the parallel fibres is probably glutamate (see [997] for a review of the chemical anatomy of the cerebellar cortex).

In all layers there are different types of short axon cells, which close feed-forward or feed-back inhibitory circuits. Golgi cells are located in the granular and Purkinje layers. Their dendrites extend into the molecular layer and receive excitatory synapses from parallel fibres. Their axonal plexus ramifies in the granular layer and forms inhibitory, GABA (gamma-amino-butyric acid)-ergic synapses with the dendrites of the granule cells. Basket and stellate cells are found in the molecular layer. Both are contacted by parallel fibres and form inhibitory synapses with dendrites of the Purkinje cells. Basket cells are so-called because their axons ramify around the primary dendrites and somata of the Purkinje cells, and terminate in a plume shape around the initial segment of the Purkinje-cell axon. GABA has been implicated as the neurotransmitter for both basket and stellate cells, but for the stellate cells taurine is still a likely candidate [997].

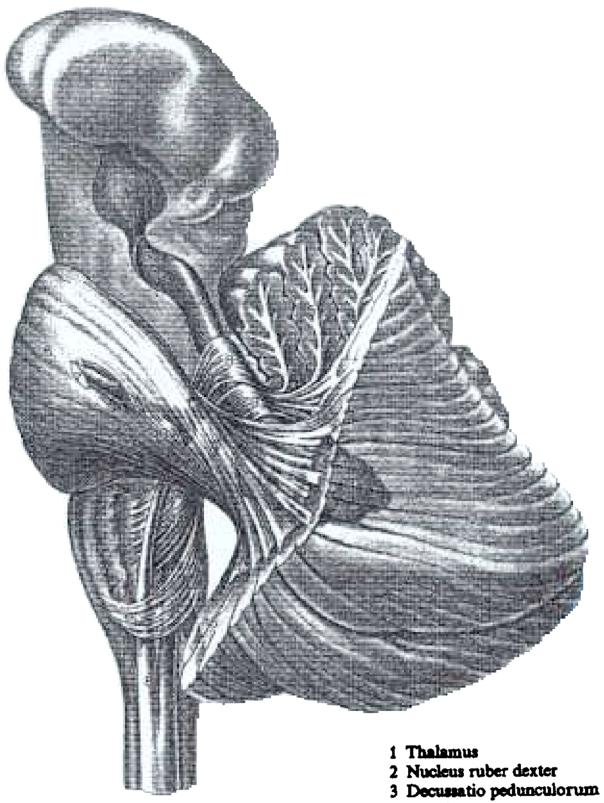
The deep cerebellar nuclei, to which most of the Purkinje cells project, are located in the central white matter close to the ventricular surface. Four nuclei are distinguished (Figs. 103–105): the medial fastigial nucleus, the globose and emboliform nuclei (corresponding to the posterior and anterior interposed nuclei of lower mammals [1019, 1486] and the dentate (lateral cerebellar) nucleus [228]. The fastigial nucleus is continuous with the globose nucleus and the emboliform nucleus is connected with the dentate. Purkinje cell axons pass ventrally between these two groups of nuclei, to terminate in the vestibular nuclei.

Types of Afferent and Intrinsic Connections

Afferent, intrinsic and efferent cerebellar connections can be distinguished. Cerebellar afferents enter the cerebellum from the pons via the middle cerebellar peduncle, and from the spinal cord and the medulla oblongata via the inferior cerebellar peduncle (Fig. 160).

Cerebellar afferents can be subdivided according to their mode of termination in the cerebellar cortex, into mossy fibres and climbing fibres [200, 1037]. Mossy fibres branch profusely and terminate with large endings (the mossy fibre rosettes) each of which contact a number of granule cell dendrites. These complex synapses, which also include the GABA-ergic terminals of the Golgi cells, are known as the cerebellar glomeruli. The mossy fibres constitute a strongly diverging system. One mossy fibre contacts many granule cells; one granule cell synapses with hundreds of Purkinje cells [962, 1039]. Mossy fibres originate from different sources in the pons, the medulla oblongata and the spinal cord. Their neurotransmitters are not known.

Climbing fibres are the terminal arborisations of the olivocerebellar fibres [295]. Olivocerebellar fibres branch preferentially in the parasagittal plane [54, 325]. Each olivocerebellar fibre provides climbing fibres to approximately ten Purkinje cells [926]; each



1 **Thalamus**
2 **Nucleus ruber dexter**
3 **Decussatio pedunculorum cerebellarium superiorum**
4 **Pedunculus cerebellaris superior**
5 **Vermis cerebelli**
6 **Pons**
7 **Nervus trigeminus**
8 **Tractus spinocerebellaris anterior**
9 **Pedunculus cerebellaris inferior**
10 **Pedunculus cerebellaris medius**
11 **Nucleus dentatus**
12 **Hemispherium cerebelli**
13 **Nucleus olivaris inferior dexter**
14 **Tractus olivocerebellaris**
15 **Fibrae arcuatae externae**
16 **Tractus cuneocerebellaris**
17 **Tractus spinocerebellaris posterior**

Fig. 160. The pedunculi of the cerebellum in a lateral view (3/2 ×)

Purkinje cell receives a single climbing fibre. The climbing fibres terminate with serial synapses on the smooth, primary-to-tertiary dendrites of the Purkinje cell. The distal portions of the Purkinje cell dendritic tree, the spiny branchlets, receive synaptic contacts from the parallel fibres. Collaterals of the olivocerebellar fibres have been observed to contact the inhibitory interneurons in the molecular layer and to terminate with mossy fibre rosettes on granule cells [859, 1037], but these contacts have not yet been experimentally verified. Connections of this type may subserve the long term depression of Purkinje cells which follows the excitation of these elements (the complex spike) by a climbing fibre [244]. Studies on the selective uptake and retrograde transport of physiologically inert D-aspartate strongly suggest that aspartate is the neurotransmitter in the climbing fibre pathway [1511].

Other types of afferent, which cannot be classified as mossy or climbing fibres, have recently been identified in the cerebellar cortex using cytochemical techniques. Serotoninergic fibres from the raphe nuclei, and noradrenergic fibres from the locus coeruleus, have been found in all layers of the cortex. They appear as a reticulum or as stray fibres in the granular layer, as a plexus in the Purkinje layer, and as transversely or radially oriented fibres in the molecular layer [5, 121, 997]. Fibres with the same appearance and distribution have recently been shown to arise from the hypothalamus [300]. All types of afferent fibres provide collaterals to the deep nuclei. Intrinsic connections consist of the Purkinje cell axons, which connect the cortex with the deep cerebellar and vestibular nuclei. Purkinje cell axons give off collaterals which terminate on neighbouring Purkinje cells, mainly those lying in the same parasagittal strip. Purkinje cells are inhibitory, the majority containing GABA as a neurotransmitter and many containing other neuroactive substances, e.g. the amino acid taurine and the peptide motilin [229, 481, 591, 600, 853].

Terminations of Mossy Fibre Systems

Mossy fibres connect motor centres at all levels of the central nervous system with the cerebellum. Primary afferents project to the cerebellum through the posterior spinocerebellar, central cervical, cuneocerebellar and trigeminocerebellar tracts. Interneurons in the intermediate grey matter of the spinal cord give rise to the anterior and rostral spinocerebellar tracts. Subcortical motor centres such as the vestibular nuclei, the superior colliculus and the red nucleus are connected with the cerebellum, either directly or through mossy fibre systems which relay in the reticular formation. The pontocerebellar fibres are the final link in the cerebrocerebellar pathway, which also provides the cerebellum with an efferent copy of the activity in the corticospinal and corticobulbar tracts.

Most mossy fibre systems terminate bilaterally in restricted regions of vermis and hemispheres, which are sometimes bordered by certain constant interlobular fissures (Fig. 162; [424, 612, 764, 1468]). Root fibres of the vestibular nerve terminate ipsilaterally in the nodule and the adjacent part of the uvula. A few terminate in the most ventral lobules of the anterior lobe and their termination in the flocculus is uncertain [167, 207, 706, 713]. Secondary vestibulocerebellar fibres also terminate in the flocculonodular and anterior lobes, but their termination is bilateral and covers a more extensive area than the primary vestibulocerebellar projection [165, 712].

Several spinocerebellar mossy fibre paths have been distinguished (Fig. 161). The posterior spinocerebellar and cuneocerebellar tracts are uncrossed, but the anterior spinocerebellar and rostral spinocerebellar tracts cross within the spinal cord [1033]. The posterior spinocerebellar tract arises from Clarke's thoracic nucleus and from neighbouring cells in the dorsal horn and ascends in the superficial part of the posterolateral funiculus [864, 1077, 1078, 1266]. It transmits proprioceptive and exteroceptive signals

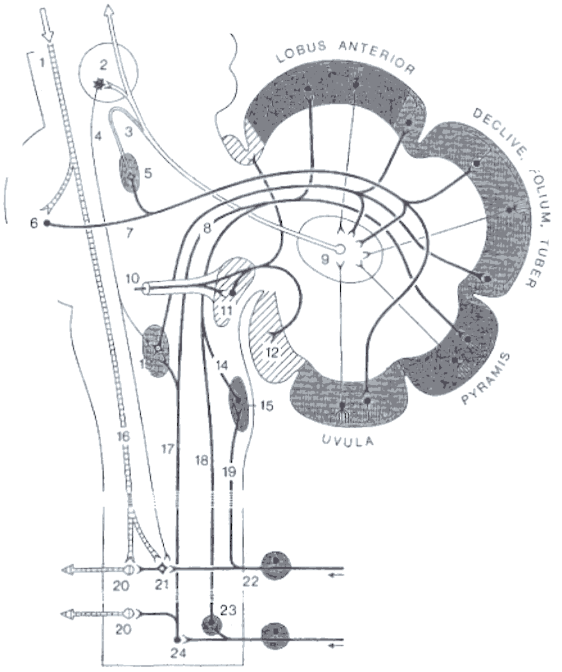
from the lower limb. Its forelimb equivalent is the cuneocerebellar tract, from the lateral cuneate nucleus and the adjoining part of the medial cuneate nucleus [395, 429, 613, 1477].

The anterior spinocerebellar tract arises at lumbar levels of the cord, from different cell groups in the substantia intermedia and from the spinal border cells [864, 1077, 1266]. Its fibres decussate in the ventral commissure and ascend superficially in the ventrolateral funiculus. According to Lundberg [326, 827], certain components of the anterior spinocerebellar tract originate as collaterals from spinal interneurons. This property distinguishes the anterior tract from the posterior spinocerebellar and cuneocerebellar tracts, which mainly transmit information about external events. An equivalent, partially crossed pathway arises from the cervical enlargement [1078, 1514, 1515]. This rostral spinocerebellar tract should be distinguished from the spinocerebellar fibres which arise from the central cervical nucleus located in the substantia intermedia of the upper cervical cord [272, 866, 867, 1512, 1513]. This nucleus receives primary input from neck muscles and is under a strong vestibular influence. Dorsally located spinocerebellar fibres of the posterior tract reach the cerebellum through the restiform body. The more ventrally located spinocerebellar fibres of the anterior, rostral and central cervical tracts pass rostral to the entrance of the trigeminal nerve and reach the cerebellum via the superior cerebellar peduncle.

Spinocerebellar and cuneocerebellar fibres terminate bilaterally in the anterior lobe and in the pyramis and the adjoining gracile lobule of the posterior lobe (Figs. 161, 162; [429, 430]). Spinocerebellar projections predominate in the cortex in the deep parts of the interlobular fissures, the exteroceptive components of the tracts terminating more superficially than the proprioceptive components [323]. A somatotopic pattern of termination can be discerned in the medial part of the hemisphere the pars intermedia [610, 611, 612, 613]. Here the hindlimb components terminate ventral to the forelimb components [5, 324]. Mossy fibres from all subdivisions of the spinal trigeminal nucleus terminate in still more dorsal regions [584, 1528, 1541]. In the vermis, a mediolateral somatotopic pattern prevails. The central cervical spinocerebellar projection is mainly represented in the most ventral part of the anterior lobe, where it overlaps with primary and secondary vestibulocerebellar and (more caudal) spinocerebellar afferent projections [866, 867].

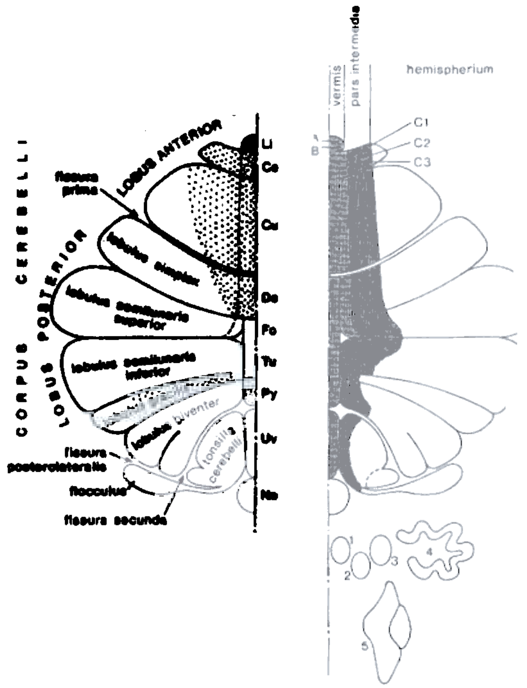
Most reticulocerebellar fibres originate from the nuclei of the lateral and anterior funiculi, located in the caudal medulla oblongata [242]. The nucleus of the lateral funiculus (lateral reticular nucleus) is located within, and receives terminations from, the ascending fibres of the ground bundle of the lateral funiculus [731] and the descending fibres of the rubrospinal tract [1441]. The nucleus of the anterior funiculus (paramedian reticular nucleus) is located adjacent to the medial longitudinal fascicle and the lateral vestibulospinal tract, and receives collateral terminations from both. Reticulocerebellar fibres enter the cerebellum through the restiform body. Those of the nucleus of the anterior funiculus reach the restiform body as external arcuate fibres, which pass ventral in the raphe and through and ventral to the pyramid [193]. The terminations of the reticulocerebellar fibres overlap with those of the spinocerebellar and vestibulocerebellar systems, but probably spread more widely in the hemisphere.

Pontocerebellar fibres constitute the largest contingent of mossy fibres. They originate bilaterally from the pontine nuclei [168, 1156], which receive dense, somato-topically organized projections from the entire cerebral cortex [122, 173, 409, 1508]. Another contingent of pontocerebellar fibres arises from the pontine tegmental reticular nucleus, which is located in the ventromedial tegmentum. It receives projections from the entire neocortex in addition to a recurrent pathway from the deep cerebellar nuclei via the descending branch of the superior cerebellar peduncle [45, 170, 1380, 1381]. Other afferent



1 Pedunculus cerebri
2 Nucleus ruber
3 Pedunculus cerebellaris superior, ramus descendens
4 Tractus rubrospinalis
5 Nucleus reticularis tegmenti pontis
6 Nuclei pontis
7 Pedunculus cerebellaris medius
8 Pedunculus cerebellaris inferior
9 Nuclei centrales cerebelli
10 Nervus vestibularis (VIII)
11 Nuclei vestibulares
12 Lobus flocculonodularis
13 Formatio reticularis myelencephali
14 Tractus cuneocerebellaris
15 Nucleus cuneatus lateralis
16 Nucleus pyramidalis
17 Tractus spinocerebellaris anterior
18 Tractus spinocerebellaris posterior
19 Funiculus posterior
20 Cellulae motorae cornus anterioris
21 Substantia intermedia
22 Radix dorsalis nervi spinalis
23 Nucleus thoracicus
24 "Bordercell" of anterior horn

Fig. 161. The afferent connections of the cerebellum I: distribution of the mossy fibre systems



Li	Lingula cerebelli
Ce	Lobulus centralis
Cu	Culmen
De	Declive
Fo	Folium vermis
Tu	Tuber vermis
Py	Pyramis vermis
Uv	Uvula vermis
No	Nodulus

1 Nucleus fastigii
2 Nucleus globosus
3 Nucleus emboliformis
4 Nucleus dentatus
5 Nuclei vestibulares

Fig. 162. The cerebellar cortex, unfolded in one plane showing the nomenclature of cerebellar lobules and fissures and the fields of termination of the mossy fibre systems on the left side and the organization of the corticonuclear and corticovestibular projection on the right side. Pontocerebellar fibres (*open contours*), spino- and cuneocerebellar fibres (*dotted*) and vestibulocerebellar fibres (*hatched*). Corticonuclear projection zones and their target nuclei are indicated with the same shadings

projections to the basal and tegmental pontine nuclei originate from the tectum, the spinal cord and the dorsal column nuclei. Pontocerebellar fibres terminate in all cerebellar lobules, with the possible exception of the nodule [666]. In the vermis and the pars intermedia, where their terminations overlap with the spinocerebellar projections, they terminate preferentially in the superficial parts of the lobules. This overlap mainly concerns the pontocerebellar projections which transmit information from the sensorimotor cortex to the "spinal" regions of the cerebellum, and the exteroceptive components of the spinocerebellar tracts, which also terminate in more superficial parts of the cortex. The pontocerebellar and spinocerebellar projections to these lobules display an identical somatotopic organization [709, 1106, 1107, 1397].

In the vermis, pontocerebellar projections preponderate in the declive, folium and tuber. This part of the vermis corresponds to the classical visual projection area of the cerebellum [10, 1267]. The pontocerebellar projection to this central part of the vermis transmits information from the tectum, which reaches the pontine nuclei through the tectopontine tract [535] from the striate cortex and from the visual association areas [122, 398]. In lower mammals dense visual pontine projections also reach the uvula and the adjoining paraflocculus (the biventral lobule of man [185]). Projections to the flocculus preferentially originate from the pontine tegmental reticular nucleus [393]. In most of the hemisphere the pontocerebellar projection is the only known afferent system of mossy fibres, with the possible exception of the monoaminergic afferents, which have not yet been studied in great topographical detail [121].

Recently, connections of the limbic system with the cerebellum have been demonstrated. These connections take their origin from the hypothalamus and the central grey matter [299, 300, 467]. The fibres ramify and terminate in all layers of the cortex, mainly in the vermal and paravermal areas. Mossy fibres have also been shown to arise as collaterals from the relay cells of all the deep cerebellar nuclei. This projection is relatively sparse, and it displays roughly the same parasagittal organization as the olivocerebellar climbing fibre projection [425, 876, 1377].

The termination of the vestibulocerebellar, spinocerebellar and reticulocerebellar mossy fibres in the granular layer is discontinuous. These mossy fibres terminate in parasagittally arranged clusters which alternate with empty strips [331, 732, 1210, 1461, 1531]. It seems likely that these empty strips are occupied by the mossy fibres of other systems which terminate in the same region. Pontocerebellar fibres to the hemisphere terminate diffusely. Only in the vermis do they show a mediolateral periodicity similar to that of the other mossy fibre systems. Mossy fibre systems issue collaterals to the deep nuclei. Most of these collaterals seem to come from afferents arising from the paramedian reticular nucleus and the pontine tegmental reticular nucleus [329, 393]. In addition, the anterior interposed nucleus receives a collateral projection from the rubrospinal tract [166, 575].

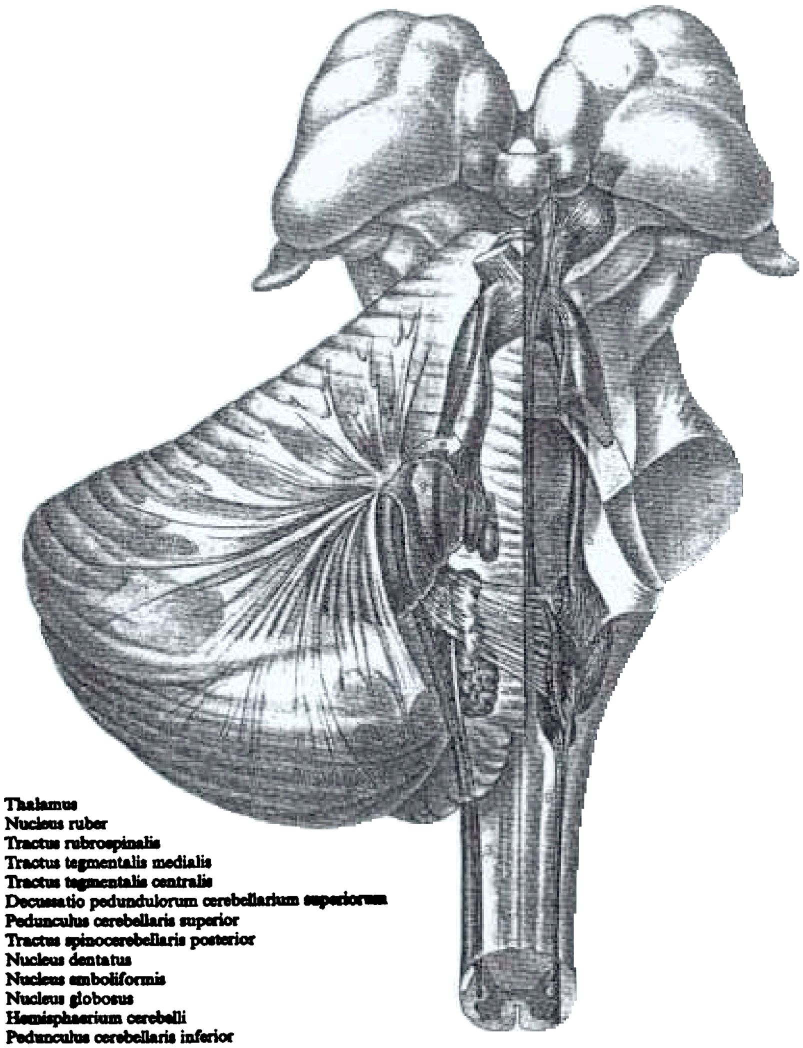
Functional Zones: Organization of the Olivocerebellar Climbing Fibre System and the Corticonuclear Projection

Corticonuclear and corticovestibular fibres originate as Purkinje-cell axons from longitudinal zones in the cerebellar cortex. These zones extend perpendicular to the interlobular fissures. The corticonuclear fibres from each of these zones occupy separate compartments in the cerebellar white matter and terminate in a single deep cerebellar or vestibular nucleus [469, 610, 611, 1457, 1459, 1460, 1462]. The vermis of the anterior lobe contains the symmetrically disposed A- and B-zones. The medial A-zone is connected with the ipsilateral fastigial nucleus and the medial vestibular nucleus; the lateral B-zone projects to Deiters' lateral vestibular nucleus. The A-zone extends into the posterior lobe, where it includes almost the entire vermis. The B-zone continues in the lobulus simplex (lobule VI of Larsell) immediately behind the primary fissure, but is absent more caudally. The medial part of the hemisphere, which corresponds to the pars intermedia of Jansen and Brodal [610, 611, 612], can be subdivided into three C zones, which project to the nucleus interpositus. The medial (C1) and lateral (C3) zones are connected with the emboliform (or anterior interposed) nucleus. The intermediate (C2) zone projects to the globose (or posterior interposed) nucleus. The major, lateral part of the hemisphere contains the two D1- and D2-zones, which project to the ventrolateral, parvocellular and dorsomedial, magnocellular subdivisions of the dentate nucleus. The C1 and C3 zones are present in the anterior lobe and the paramedian (gracile) lobule. The C2-zone and the D1- and D2-zones extend through all the lobules of the cerebellar hemisphere. Longitudinal zones, which are present in the flocculus and which project to the vestibular nuclei and/or the dentate nucleus, replace the D-zones in this part of the cerebellum.

Climbing fibres originate from the contralateral inferior olive and reach the cerebellum via the inferior cerebellar peduncle. They show a mediolateral disposition, similar to the intrinsic connections between the cerebellar cortex and the deep nuclei (Figs. 163 and 164). The corticonuclear and olivocerebellar projections will therefore be discussed together. The terminal fields of the climbing-fibre paths from subdivisions of the inferior olive constitute narrow, parasagittal zones which coincide with the corticonuclear projection zones. The olivocerebellar fibres which terminate as climbing fibres in a particular zone also send collaterals to its deep cerebellar target nucleus. Climbing fibre zones extend perpendicular to the lobular projection fields of the mossy fibre systems [55, 161, 169, 174, 175, 261, 322, 394, 452, 453, 1202, 1506]. Fibres from the caudal parts of both accessory olives terminate in the contralateral vermis. These caudal parts of the accessory olives receive afferent connections from the contralateral substantia intermedia and the base of the dorsal horn of the entire spinal cord [53], the dorsal column nuclei and the spinal trigeminal nucleus [135, 658, 933, 934]. Purkinje cells of the A-zone (in the medial half of each hemivermis), which project to the fastigial nucleus and the medial vestibular nucleus, receive climbing fibres from the caudal part of the medial accessory olive. The Purkinje cells of the B-zone, which project to Deiters' lateral vestibular nucleus [40], occupy the lateral half of the vermis. They receive their climbing fibres from the caudal pole of the dorsal accessory olive. Collaterals of these olivocerebellar fibres terminate in the deep cerebellar or vestibular nucleus which receives the Purkinje cell axons from their target zone in the cortex, i.e. climbing fibres to the A-zone contribute collaterals to the fastigial nucleus and those to the B-zone to Deiters' lateral vestibular nucleus.

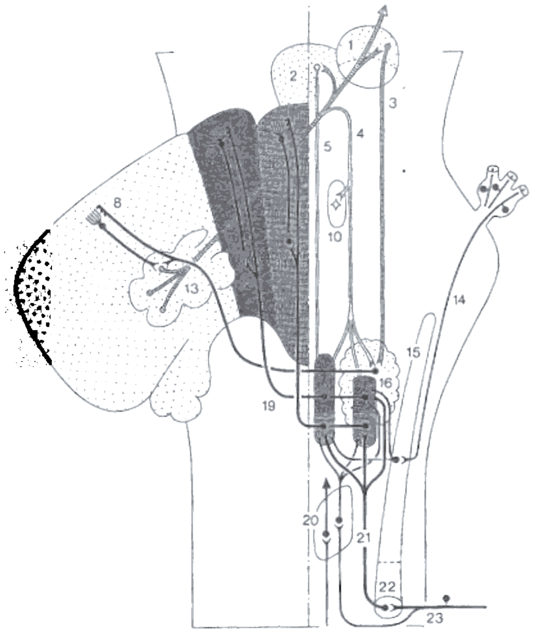
Olivocerebellar fibres to the pars intermedia take their origin from the rostral halves of both accessory olives. Within the pars intermedia they terminate in the three interdigitating C-zones, which in turn project to the anterior and posterior interposed nuclei. These nuclei receive collaterals from the olivocerebellar fibres that terminate in the pars intermedia. The rostral halves of the dorsal and medial accessory olives differ in their afferent connections. The rostral and caudal parts of the dorsal accessory olive share somesthetic connections from the spinal cord and the brain stem, whereas the rostral half of the medial accessory olive is dominated by connections from the rostral central grey matter containing the Darkschewitsch' nucleus. These connections descend in the medial tegmental tract, within the medial longitudinal fascicle [193, 1020].

Fibres from the principal olive terminate in the D-zones, which occupy the lateral part of the hemisphere [1155], and in the dentate nucleus, which is the main recipient of the corticonuclear projection from the hemisphere [394]. The principal olive receives the central tegmental tract from the parvocellular part of the red nucleus [1178, 1304, 1469].



1 Thalamus
2 Nucleus ruber
3 Tractus rubrospinalis
4 Tractus tegmentalis medialis
5 Tractus tegmentalis centralis
6 Decussatio pedunculorum cerebellarium superiorum
7 Pedunculus cerebellaris superior
8 Tractus spinocerebellaris posterior
9 Nucleus dentatus
0 Nucleus emboliformis
1 Nucleus globosus
2 Hemisphaerium cerebelli
3 Pedunculus cerebellaris inferior
4 Tractus olivocerebellaris
5 Nucleus olivaris inferior
6 Amiculum olivae
7 Nucleus olivaris accessorius dorsalis
8 Nucleus olivaris accessorius medialis
9 Tractus spino-olivaris

ig. 163. The olivocerebellar circuits. Position of tracts and nuclei in a dorsal view (5/3 ×). The cerebelum was split in the midline and the right half removed



1 Nucleus ruber
2 Griseum centrale mesencephali
3 Tractus tegmentalis centralis
4 Pedunculus cerebellaris superior, ramus descendens
5 Tractus tegmentalis medialis
6 Vermis cerebelli
7 Hemispherium cerebelli, pars intermedia
8 Hemispherium cerebelli, pars lateralis
9 Pedunculus cerebellaris superior
10 Nucleus reticularis tegmenti pontis
11 Nucleus fastigii
12 Nuclei globosus et emboliformis (interpositus)
13 Nucleus dentatus
14 Tractus spinalis nervi trigemini
15 Nucleus spinalis nervi trigemini
16 Nucleus olivaris inferior
17 Nucleus olivaris accessorius dorsalis
18 Nucleus olivaris accessorius medialis
19 Tractus olivocerebellaris
20 { Nucleus cuneatus lateralis
Nucleus cuneatus medialis
Nucleus gracialis
21 Tractus spino-olivaris
22 { Cornu posterius
Substantia intermedia
23 Radix dorsalis nervi spinalis

Fig. 164. The afferent connections of the cerebellum, the climbing fibers and the afferent connections of the inferior olive

The origin of the projections to the inferior olive from the mesodiencephalic junction is not restricted to the Darkschewitsch nucleus and the parvocellular red nucleus [502], but also includes parts of the central grey matter and the mesencephalic tegmentum, and visual centres such as Cajal's interstitial nucleus of the medial longitudinal fascicle [1031, 1074]. The targets of these descending projections to the inferior olive, which also include a projection from the superior colliculus [359, 515, 535, 619], also involve those parts of the caudal medial accessory olive which send climbing fibres to the visual receptive area in the vermis of the posterior lobe [10]. Direct projections from the cerebral cortex to the inferior olive are scarce [1176]. Cortical control of the olivary complex is mostly effectuated through the intermediacy of the red nucleus and other preolivary centres in the brain stem [37, 38, 39]. Finally it should be pointed out that some parts of the inferior olive receive a serotoninergic projection from the raphe nuclei [689, 1509].

The similarity in the topographical organization of the corticonuclear and olivocerebellar projections is enhanced by the existence of reciprocal connections between the deep cerebellar nuclei and the subdivisions of the inferior olive from which they receive their collateral projections [228, 440, 658, 1314, 1378]. Direct, reciprocal nucleo-olivary fibres originate from a special population of small GABA-ergic neurons of the deep nuclei [106, 117, 992]. The projections of the interposed and dentate nuclei (to the contralateral red nucleus and the nucleus of Darkschewitsch) and the central and medial tegmental tracts form strong feed-back loops which follow the same topographical pattern.

The Vestibulocerebellum

The afferent and efferent connections of the vestibulocerebellum set this structure apart from the remainder of the cerebellum. Originally it was defined as the flocculonodular lobe, the region which receives primary vestibular root fibres and projects preferentially to the vestibular nuclei [762]. Recently it was shown that the primary vestibular projection is mostly limited to the nodule [706, 758, 759], and that the flocculus is dominated by visuomotor afferents. The common feature of both subdivisions of the vestibulocerebellum is therefore their efferent projection to the vestibular nuclei, rather than their common input. The nodule and flocculus project to the vestibular nuclei, but their Purkinje cell axons terminate in different, complementary regions [44, 466, 759, 1456].

The vestibulocerebellum has been implicated in the regulation of compensatory, vestibulo-ocular, optokinetic and neck reflexes, all of which pass through the vestibular nuclear complex [600]. The flocculus receives information about retinal slip from the nuclei of the accessory optic system [535, 1254], through mossy and climbing fibres which originate in the pontine tegmental reticular nucleus [393] and the dorsal cap of the medial accessory olive, respectively [18, 392, 758]. This makes the flocculus particularly well equipped to influence eye movements. Indeed, it has been shown to be essential for the execution of smooth visual pursuit [1551].

Efferent Pathways

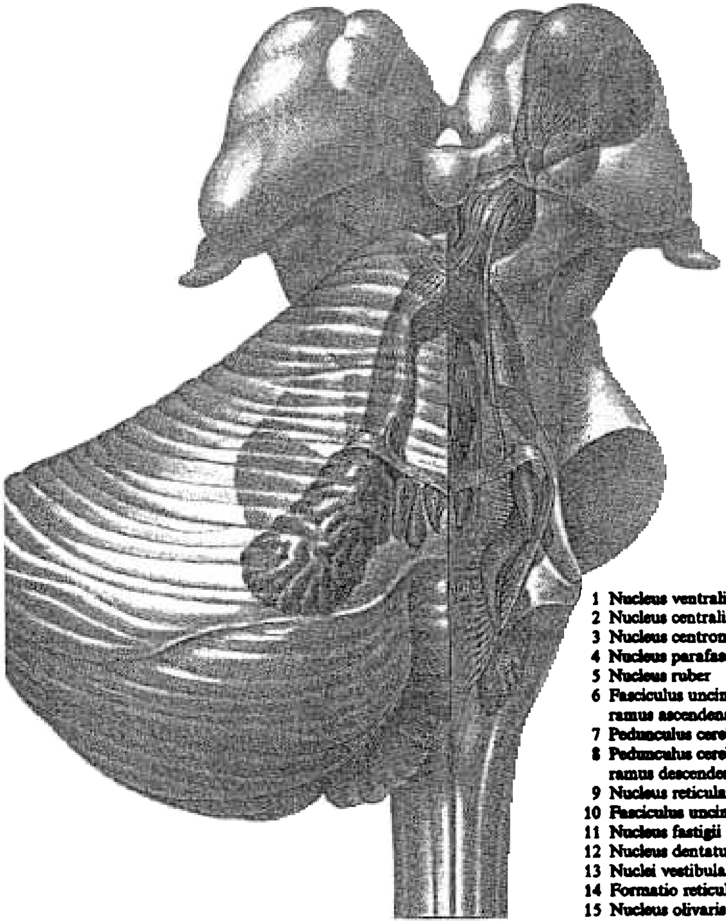
The main efferent pathways from the cerebellum arise from the deep cerebellar nuclei (Figs. 165 and 166). The fastigial nucleus gives rise to the uncinate fascicle, which decussates within the cerebellum, in the cerebellar commissure, and to the uncrossed, direct fastigiobulbar tract. The uncinate fascicle passes over the superior cerebellar peduncle to enter the vestibular nuclei from the lateral side. The direct fastigiobulbar fibres enter the vestibular nuclei from the dorsal side, in the lateral wall of the fourth ventricle. Through these two pathways the fastigial nucleus is bilaterally connected with the medial and descending vestibular nuclei and the medial reticular formation of the pons and medulla oblongata [86]. Some fibres of the fastigial nucleus reach the spinal cord [863]. An ascending bundle of fibres, derived from the uncinate fascicle, courses dorsomedial to the superior cerebellar peduncle and subsequently dorsal to the central tegmental tract, to terminate in the lateral tegmentum of the mesencephalon and the deep layers of the superior colliculus. In the diencephalon, its fibres terminate in the intralaminar nuclei and in the ventral medial and ventral lateral nuclei. Some of its fibres recross in the tectal commissure and in the massa intermedia.

The dentate and interposed nuclei give rise to the superior cerebellar peduncle, which decussates in the caudal mesencephalon. Here fibres of the globose (posterior interposed nucleus), fastigial and dentate nuclei terminate in the central grey matter, the deep layers of the superior colliculus and in the pretectum [525, 669]. The superior cerebellar peduncle surrounds and traverses the red nucleus. Fibres from the emboliform nucleus (anterior interposed nucleus) terminate in the caudal magnocellular part of the red nucleus, fibres from the dentate in its rostral parvocellular part [61, 351]. Beyond the red nucleus, fibres of the superior cerebellar peduncle enter the thalamus through the subthalamus, where some of them terminate in the zona incerta.

Fibres from all of the cerebellar nuclei terminate in the thalamus on the caudal part of the ventral lateral nucleus (VLc, [629]), which projects to the motor cortex in the frontal lobe. Rostral portions of the cerebellar nuclei project to the lateral part of the ventral lateral nucleus, which contains the representation of caudal parts of the body. Caudal parts of the cerebellar nuclei project to medial parts of the ventral lateral nucleus, which contains the representation of rostral body parts [60, 62, 629]. Thalamic projections from the different cerebellar nuclei terminate in alternating sheets or rods, which show only very little overlap [1369]. According to many authors the area of cerebellothalamic projection also includes rostral parts of the ventral lateral nucleus, the adjoining ventral anterior nucleus and the ventral medial nucleus. These differences of interpretation are more apparent than real; they can be largely reduced to what Mehler [888] has called "atlas semantics" because the descriptions by different authors of the areas to which the cerebellothalamic fibres are distributed are rather similar [43, 86, 111, 501, 659, 1280, 1313]. In the caudal part of the ventral lateral nucleus the cerebellar projections overlap with the terminations of the spinothalamic system [60, 61, 62, 111]. They remain, however, segregated from the pallidothalamic and the nigrothalamic projections as well as from and the terminations from the medial lemniscus [587, 629, 659].

The cerebellum, especially the fastigial and dentate nuclei, provides one of the main afferent systems of the intralaminar nuclei. Cerebellar fibres terminate in the parafascicular nucleus and the central lateral nucleus. Through the intralaminar nuclei the cerebellum is connected with the striatum and the cortex of the frontal and parietal lobes. Within the intralaminar nuclei, the cerebellar afferents overlap with spinothalamic, reticulothalamic, pallidothalamic and nigrothalamic projections. Connections from the deep cerebellar nuclei to the oculomotor nuclei come from the cells of the so-called group Y [171, 216, 439], an aggregation of cells located ventral to the dentate nucleus, in the floccular peduncle, which probably belongs to the superior vestibular nucleus.

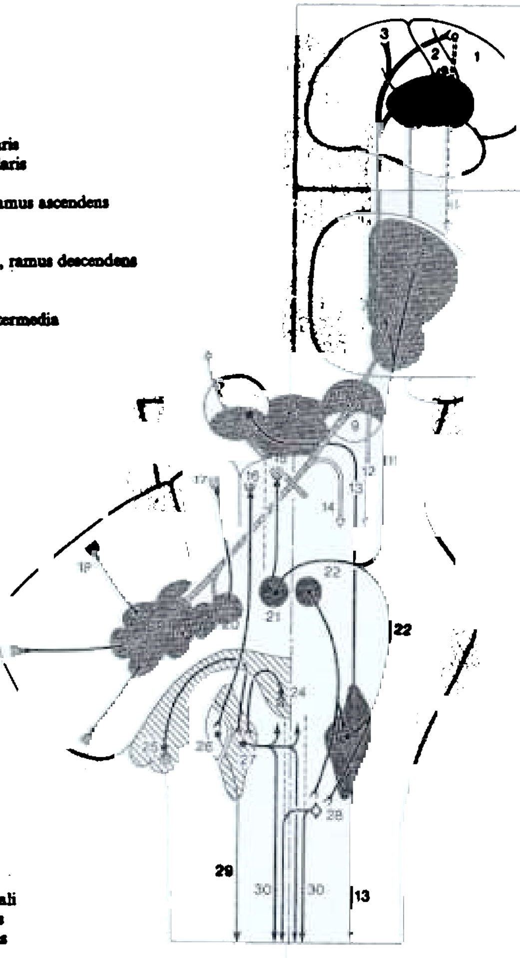
Ultimately each hemivermis is bilaterally connected with the spinal cord, through the fastigial nucleus and the vestibulospinal and reticulospinal tracts in the medial longitudinal fascicle. Connections between the hemisphere and the cord from the interposed nuclei include the superior cerebellar peduncle



1 Nucleus ventralis lateralis
2 Nucleus centralis lateralis
3 Nucleus centromedianus } Nuclei intralaminares
4 Nucleus parafascicularis
5 Nucleus ruber
6 Fasciculus uncinatus cerebelli, ramus ascendens
7 Pedunculus cerebellaris superior
8 Pedunculus cerebellaris superior, ramus descendens
9 Nucleus reticularis tegmenti pontis
10 Fasciculus uncinatus cerebelli
11 Nucleus fastigii
12 Nucleus dentatus
13 Nuclei vestibulares
14 Formatio reticularis myelencephali
15 Nucleus olivaris inferior

Fig. 165. The efferent connections of the cerebellum. Position of tracts and nuclei in a dorsal view (5/3 ×). The cerebellum was split in the midline and the right half removed

1 Lobus frontalis
2 Motor cortex (area 4)
3 Lobus parietalis
4 Striatum
5 Tractus pyramidalis
6 Nucleus ventralis lateralis
7 Nuclei intralaminares
8 Nucleus ruber, pars parvocellularis
9 Nucleus ruber, pars magnocellularis
10 Griseum centrale mesencephali
11 Fasciculus uncinatus cerebelli, ramus ascendens
12 Tractus tegmentalis centralis
13 Tractus rubrospinalis
14 Pedunculus cerebellaris superior, ramus descendens
15 Vermis cerebelli, A-zone
16 Vermis cerebelli, B-zone
17 Hemispherium cerebelli, pars intermedia



18 Hemispherium cerebelli, pars lateralis
19 Nucleus dentatus
20 Nuclei globosus et emboliformis (interpositus)
21 Nucleus fastigii
22 Fasciculus uncinatus cerebelli
23 Nuclei vestibulares
24 Nodulus
25 Flocculus
26 Nucleus vestibularis lateralis
27 Nuclei vestibulares medialis, superior et inferior
28 Formatio reticularis myelencephali
29 Tractus vestibulospinalis lateralis
30 Fasciculus longitudinalis medialis

Fig. 166. The efferent connections of the cerebellum

and the rubrospinal tract. The connection, starting from the interposed and dentate nuclei, comprises the superior cerebellar peduncle, the ventral lateral nucleus of the thalamus, the motor cortex and the pyramid. Because the superior cerebellar peduncle and the rubrospinal and pyramidal tracts cross, each cerebellar hemisphere is ultimately connected with the ipsilateral half of the spinal cord.

Function and Malfunction of the Cerebellum

Lesions of the cerebellum result in a loss of motor coordination, known as cerebellar ataxia [403]. There is loss of precision in muscle contraction; movements overshoot or undershoot (dysmetria). Loss of coordination and dysmetria also affect speech (cerebellar dysarthria) and ocular movements. Changes in muscle tone, usually hypotonia, are frequently seen. An explanation of the role the cerebellum plays in motor coordination is still lacking. The laterality and localization of symptoms are usually in accordance with the known anatomy of the input and output channels of the cerebellum. Bilateral, axial ataxia dominates with lesions of the vermis. The limbs are more affected with damage to the ipsilateral hemisphere, and vestibular and oculomotor symptoms result from diseases that affect the vestibulocerebellum. However, the correlation between symptoms and the topography of lesions remains rather crude, and clinical manifestations of lesions which damage a single cerebellar zone or a single deep cerebellar nucleus have not yet been described.

Mossy fibres provide the main drive for the coordinating activity of the cerebellum, but it is not known how an appropriate cerebellar output is generated. Mossy fibre systems generally terminate over wide areas of the cerebellar cortex, and their mediolateral spread is further enhanced by the parallel fibres, the axons of the granular cells on which they terminate. Mossy fibres are therefore in a position to modulate the activity in many different longitudinal cortical zones and their efferent nuclear channels simultaneously.

Climbing fibres, which have a powerful, excitatory action on Purkinje cells, but a very low firing rate, contribute little to the overall discharge of the Purkinje cells. The organization of the olivocerebellar climbing fibre system closely mimics the organization of the cerebellar efferent system. Each part of the inferior olive monitors a particular output channel. Climbing fibres may serve as a level-setting, gating or learning device, which changes the efficacy of the input to Purkinje cells from mossy and climbing fibres [14, 600, 858].

Thalamocortical and Corticothalamic Connections

(Figs. 167–169)

The Thalamus: Its Parts and Peduncles

The thalamus is a nuclear complex located in the wall of the diencephalon, caudal to the interventricular foramen. During development, part of the medial wall of the hemisphere adheres to the dorsal thalamic surface (lamina affixa). Consequently the thalamus becomes located in the floor of the central part of the lateral ventricle. Laterally the external medullary lamina separates the thalamus from the internal capsule. The reticular nucleus of the thalamus is located between the external medullary lamina and the internal capsule. This nucleus is penetrated by bundles of thalamocortical and corticothalamic fibres that become detached from the internal capsule and enter the thalamus. Ventral to the thalamus, the reticular nucleus continues into the zona incerta of the subthalamus. The reticular nucleus and zona incerta belong to the ventral thalamus, together with the ventral nucleus of the lateral geniculate body. The main mass of the thalamus is known as the dorsal thalamus. The terms dorsal and ventral thalamus are derived from their relative position in the lateral diencephalic wall during development [291, 512]. Fibres from the superior cerebellar peduncle and the globus pallidus (Fig. 173) pass through the ventral portion of the external medullary lamina between the thalamus and the zona incerta to end in the anterior part of the thalamus.

Corticothalamic and thalamocortical fibres that become detached from the corona radiata and the internal capsule and enter the thalamus at its rostral and caudal poles and along its dorsal surface are termed the thalamic peduncles. As Fig. 169 shows, these peduncles are medial to the long corticofugal pathways which descend to the brain stem and the spinal cord. The anterior thalamic peduncle breaks away from the anterior limb of the internal capsule, and its fibres form a reciprocal connection with the prefrontal and orbitofrontal parts of the cortex and the cingulate gyrus. The superior and posterior thalamic peduncles diverge from the posterior limb of the internal capsule, and their fibres form a two-way connection between the thalamus and the central parietal and occipitotemporal areas. The inferior thalamic peduncle reaches the thalamus at its ventromedial side, medial to the posterior limb of the internal capsule. It contains fibres connecting the thalamus and the orbitofrontal, insular and temporal cortices and the basal prosencephalon. Amygdalothalamic fibres enter the inferior thalamic peduncle from the ventral amygdalofugal pathway (cf. Figs. 193, 194 and 201).

The nomenclature of the thalamic nuclei in the present work (see also Figs. 24 and 25) is derived from Walker [1471], Olszewski [1028]. Jones' [629] recent monograph on the thalamus contains a complete and authoritative review of thalamic morphology and connections. The curved internal medullary lamina divides the thalamus into the medial thalamic nucleus and the ventral and lateral groups of thalamic nuclei. Caudally the ventral group is replaced by the medial geniculate body, which together with the lateral geniculate body, belongs to the metathalamus. The posterior group of nuclei is located in the caudal part of the thalamus, in an area