thalamic reticular nucleus. Other substantial subcortical efferents pass from the visual cortex to the pretectal region and the superior colliculus.

The pretectal region or complex is immediately rostral to the superior colliculus at the level of the posterior commissure. According to a recent analysis in the monkey [579], this complex can be subdivided into five different cell groups: the optic tract nucleus, the pretectal olivary nucleus and the medial, anterior and posterior pretectal nuclei. Fibres from the retina pass to the pretectal region, predominantly to the contralateral side. The pretectal olivary nucleus and the optic tract nucleus receive dense bilateral projections, whereas the posterior and medial pretectal nuclei are more sparsely innervated by the retina [113, 579]. The involvement of the pretectal complex in visual reflexes and eye movements will be considered below. Suffice it to mention here that:

1. The rodent equivalent of the medial pretectal nucleus contains cells which represent the source of a (mainly contralateral) centrifugal projection to the retina [598, 599].

2. Elements in the optic tract nucleus form a relay in pathways connecting the retina with the cerebellum. Fibres originating from the latter nucleus have been traced in the rat and rabbit to the following three "precerebellar" nuclei: the reticular nucleus of the pontine tegmentum, the pontine nuclei, and the dorsal cap of the inferior olivary nucleus [535, 1367]. Fibres connecting the posterior pretectal nucleus with the caudal dorsal accessory olive have been described in the cat [1].

The Accessory Optic System

The so-called accessory optic system (AOS) is a number of primary optic fibres which deviate from the optic tract at various levels and project to three small mesencephalic cell masses, the dorsal, lateral and medial terminal nuclei of the AOS (cf. [1255]). The largest contingent of these fibres is known as the

superior fasciculus of the accessory optic tract. This fascicle descends from the main optic tract between the superior colliculus and the medial geniculate body, proceeds superficially over the cerebral peduncle, and terminates ventromedially near the exit of the oculomotor nerve. There are three terminal nuclei:

1. The dorsal terminal nucleus is ventral to the rostral portion of the superior colliculus, close to where the superior fascicle of the accessory optic tract emerges. It merges with the optic tract nucleus, one of the pretectal cell masses.

2. The lateral terminal nucleus is ventrocaudal to the medial geniculate body, at the dorsal edge of the cerebral peduncle.

3. The medial terminal nucleus is in the mediobasal portion of the midbrain, close to the medial margin of the substantia nigra. The three terminal nuclei receive their retinal input principally from the contralateral eye. It has long been assumed that the medial terminal nucleus is lacking in primates (e.g. [1373]); however, its presence has recently been demonstrated in two primate species [1484].

The terminal nuclei of the accessory optic tract are reciprocally connected with the nucleus of the optic tract. This is of functional interest because the AOS and the optic tract nucleus are both involved in processing direction-selective visual information [535, 1254].

In rodents and cats, the terminal nuclei of the accessory optic tract, along with the nucleus of the optic tract, have been shown to project differentially to the dorsal cap of the inferior olive. This part of the inferior olive sends climbing fibres to the vestibulocerebellum, i.e. the flocculonodular lobe [535, 846, 1358, 1470]. Physiological experiments have shown that the AOS is intimately involved in visual-vestibular interaction, playing an important role in processing and distributing visual signals subserving compensatory eye and head movements [1254].

Visual Reflexes

The light reflex, i.e. constriction of the pupil on illumination of the eye, is mediated by a reflex arc that involves the following links (Fig. 146):

a) Axons of retinal ganglion cells which pass via the optic nerve and tract to the pretectal region, particularly the olivary pretectal nucleus [158, 1384].

b) Axons of pretectal neurons, projecting to the accessory oculomotor (Edinger-Westphal) nuclei of both sides [103].

c) Axons of the parasympathetic preganglionic neurons of the accessory oculomotor nuclei, which pass with the oculomotor nerves to the ciliary ganglia, where they synapse.

d) Postganglionic neurons whose axons innervate the sphincter pupillae muscle of the iris.

The pretectal efferents to the ipsilateral accessory oculomotor nucleus provide for the direct pupillary light reflex, those to the contralateral nucleus for the consensual pupillary light reflex.

In addition to the response to light, pupillary constriction also occurs following the initiation of ocular convergence. The neural pathway for this convergence-induced pupillary constriction is believed to be independent of that for light-induced pupillary constriction, since the two reflexes are dissociated in certain clinical conditions (the Argyll Robertson sign). The centre for pupillary dilatation is located in the intermediolateral cell column of the upper thoracic cord. The preganglionic sympathetic fibres originating from this so-called ciliospinal centre ascend through the sympathetic trunk and synapse in the superior cervical ganglion with postganglionic elements. The axons of the latter accompany the branches of the internal carotid artery and traverse the ciliary ganglion before they innervate the dilatator pupillae muscle of the iris.

Fibres descending through the lateral part of the medulla oblongata and of the spinal

cord synapse in the sympathetic ciliospinal centre. The origin of these fibres is unknown.

The pathway for the accommodation reflex, i.e. increase in the curvature of the lens for near vision, is (as far as its mesencephalic centres and efferent limb are concerned) closely comparable to the pathway for the light reflex. In both pathways the pretectal region, the accessory oculomotor nucleus and the ciliary ganglion are successive relay stations. However, the afferent limb of the accommodation reflex includes the visual cortex and is thus much longer and much more complex than that of the light reflex (Fig. 147). The final link on the efferent side of the accommodation pathway is formed by the postganglionic fibres to the ciliary muscle.

Eye Movements

Eye movements are effected by the coordinated activity of the six extraocular muscles. These muscles are innervated by the third, fourth and sixth cranial nerves, the nuclei of which are located in the medial part of the pontine and mesencephalic tegmentum. We still lack a coherent picture of the central neural mechanism for the control of eye movements; however, the following features of the circuitry involved are well established:

1. The abducens and oculomotor nuclei contain, in addition to motoneurons, "premotor" neurons, which provide reciprocal internuclear pathways [71, 434, 439, 838] (Fig. 148A: open circles). Axons of internuclear neurons in the abducens nucleus cross the midline and ascend in the contralateral medial longitudinal fasciculus (MLF) to the oculomotor complex, where they selectively excite motoneurons of the contralateral medial rectus muscle [195, 520, 877, 969, 1284, 1285]. This "six-to-three pathway" is essential for adduction of the eye in horizontal conjugate gaze. Lesions of the MLF between the abducens and oculomotor nuclei produce the syndrome of internuclear ophthalmoplegia. The internuclear neurons innervating the
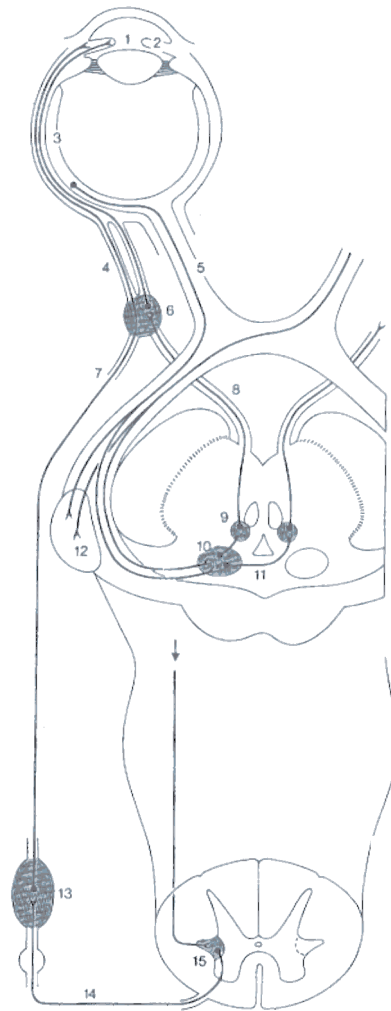
1 Pupilla
2 Iris
3 Retina
4 Nervi ciliares breves
5 Nervus opticus
6 Ganglion ciliare
7 Ramus sympathicus
8 Nervus oculomotorius
9 Nucleus accessorius nervi
   oculomotorii
10 Regio pretectalis
11 Commissura posterior
12 Corpus geniculatum laterale
13 Ganglion cervicale superius
14 Ramus communicans
15 Centrum ciliospinale

Fig. 146. The visual system II: the neural reflex arcs of the visual system; the pupillary light reflex
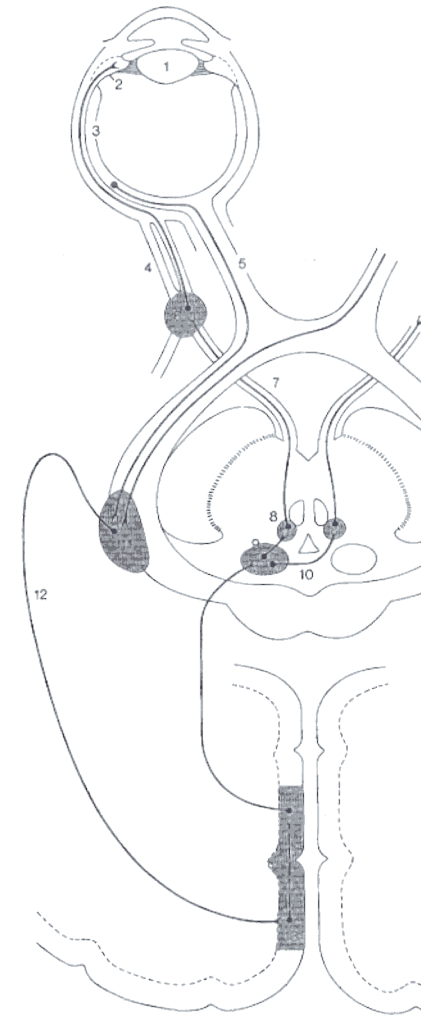
1 Lens crystallina
2 Corpus ciliare
3 Retina
4 Nervi ciliares breves
5 Nervus opticus
6 Ganglion ciliare
7 Nervus oculomotorius
8 Nucleus accessorius nervi
   oculomotorii
9 Regio pretectalis
10 Commissura posterior
11 Corpus geniculatum
   laterale
12 Radiatio optica
13 Area striata

Fig. 147. The visual system II: the neural reflex arcs of the visual system; the accomodation reflex

medial rectus motoneurons are affected, so that during attempted gaze to the contralateral side, the adducting eye shows a paresis [71, 504, 877].

2. Physiological and clinical evidence suggests that a group of cells located in the *paramedian pontine reticular formation (PPRF)*, which forms part of the oral and caudal pontine reticular nucleus (Fig. 153), plays a crucial role in the control of rapid (saccadic) conjugate eye movements [690, 1285]. The PPRF projects to the abducens nucleus of both sides [198, 434]. Physiological experiments have shown that the fibres passing to the ipsilateral abducens nucleus activate motoneurons and internuclear neurons [432, 505], whereas those passing to the contralateral abducens nucleus exert an inhibitory action [432]. The PPRF also projects to the ipsilateral prepositus hypoglossal nucleus and to the ipsilateral rostral interstitial nucleus the MLF (RIMLF). Both nuclei send fibres to the oculomotor nucleus. The fibres passing from the PPRF the RIMLF ascend close to, but outside, the MLF [1218]. Afferents to the PPRF include:

(a) bilateral projections from the frontal eye fields, discussed below;

(b) projections from the contralateral superior colliculus;

(c) ipsilateral projections from numerous brain-stem centres such as the interstitial nucleus of Cajal, the mesencephalic reticular formation, the vestibular nuclei and the nucleus prepositus hypoglossi [777, 1218].

The PPRF is also called the "pontine gaze centre". A unilateral lesion of this centre leads to a loss of all rapid eye movements towards the ipsilateral side. A bilateral rostral PPRF lesion produces horizontal gaze palsy with intact vertical gaze, but a bilateral caudal PPRF lesion leads to total loss of rapid eye movements in both the horizontal and the vertical plane [505].

3. The *vestibular nuclear complex* sends a massive bilateral projection to the nuclei of the extraocular muscles [206, 373] (Fig. 139).

This projection is organised so that the ipsilateral connections are inhibitory and the contralateral connections are excitatory [69, 71]. These connections form part of the vestibulo-ocular reflex pathways, which help stabilise the visual image on the retina by producing compensatory eye movements in response to head movements.

The different vestibulo-ocular pathways always address pairs of synergistic muscles from the two eyes, which exert their actions in one of the three planes of the semicircular canals ([427], Fig. 140). Through these pathways excitation and inhibition of two opposite canals by a movement of the head in space, leads to a conjugate (compensatory) eye movement in the opposite direction. Movements in the plane of the horizontal canals are effectuated through crossed, excitatory connections from the medial vestibular nucleus to the abducens nucleus, which innervates the lateral rectus muscle, and the internuclear pathway which recrosses to terminate on medial rectus motoneurons in the ipsilateral oculomotor nucleus [206, 370, 372, 522, 760, 839, 1546]. The vertical canals are excited by a movement of the endolymphe away from the ampullae. Excitation of a posterior canal leads, through a crossed excitatory pathway in the medial longitudinal fascicle from the medial vestibular nucleus to the trochlear and oculomotor nuclei, to contraction of the ipsilateral superior oblique and the contralateral inferior rectus muscles [373, 426, 518, 519, 521]. Excitation of an anterior canal results in contraction of the ipsilateral superior rectus (which is innervated from the contralateral oculomotor nucleus [1098] and the contralateral inferior oblique muscles. This excitatory connection relays in the superior vestibular nucleus and/or the portion of this nucleus located within the floccular peduncle (the group Y of Brodal and Pompeiano [171] and passes through the superior cerebellar peduncle [1532]. The ipsilateral inhibitory pathways ascend in the medial longitudinal fascicle. Those to the abducens nucleus take their origin from the medial vestibular nucleus; the inhibitory connections from

the vertical canals relay through the superior vestibular nucleus.

4. As its name implies the *nucleus prepositus hypoglossi (prepositus nucleus)* is situated directly in front of the hypoglossal nucleus (Fig. 127). It occupies a periventricular position, immediately adjacent to the MLF (Figs. 105, 106). This nucleus sends fibres to all of the external eye muscle nuclei, both ipsilateral and contralateral, and therefore has to be considered an important "preoculomotor" centre ([70, 373, 439, 837]; Fig. 148 B). Particularly dense projections are directed to the contralateral abducens nucleus and the ipsilateral medial rectus subdivision of the oculomotor nucleus [875].

The prepositus nucleus receives afferents from the frontal eye fields of both sides [774], the ipsilateral interstitial nucleus of Cajal [218], the rostral interstitial nucleus of the MLF [874] and the nucleus of the optic tract [535]. It entertains reciprocal connections with the ipsi- and contralateral vestibular complex, particularly the medial, inferior and ventrolateral nuclei, the PPRF and the cerebellum [44, 710, 875, 1467, 1545].

Apart from the various extraocular motor nuclei, the following cell masses receive inputs from the prepositus nucleus: the contralateral inferior olive, the contralateral superior colliculus and pretectum, and several thalamic nuclei including the intralaminar and ventrolateral nuclei [711, 875]. It is noteworthy that the vestibular nuclei also project to these thalamic centres.

It has been established that, as far as excitation and inhibition are concerned, the afferents from the vestibular complex to the prepositus nucleus are organised similarly to the vestibulo-oculomotor projections [69]. Moreover, the activity of nearly every neuron studied in the prepositus nucleus appears to be correlated with the position and movements of the eyes [814, 874]. McCrea and Baker [874, 875] have pointed out that the afferents from the prepositus nucleus arise chiefly from regions in the brain which are directly involved in the supranuclear control of eye and head movements, and that most

of the targets of the prepositus projections contain neurons whose activity is related to eye movements. They suggest that the function of the prepositus nucleus may be to generate an efference copy of oculomotor activity, and to distribute this signal to centres in the brain stem which are involved in various aspects of gaze control.

5. The *interstitial nucleus of Cajal*, which is situated in the rostral part of the mesencephalic tegmentum (Fig. 98), also represents a preoculomotor centre (Fig. 149). This nucleus receives afferents from the pretectal region, the superior colliculus and the vestibular nuclei [21, 206, 736]. Cortical afferents emanating from the frontal eye field have also been described [65]; cf, however [779]. The efferents of the interstitial nucleus pass to the oculomotor and trochlear nuclei of both sides, to the ipsilateral medial vestibular nucleus and to the spinal cord. The fibres to the contralateral oculomotor and trochlear nuclei pass via the posterior commissure [206, 1285]. The coarse fibres which descend to the spinal cord constitute the small interstitiospinal component of the MLF.

6. The *rostral interstitial nucleus of the medial longitudinal fascicle, or MLF (RIMLF)* is situated rostral to the interstitial nucleus of Cajal in the transition zone between the midbrain and the diencephalon. This centre is directly involved in the generation of fast vertical eye movements [196, 197]. The RIMLF receives afferents from the frontal eye field and the superior vestibular nucleus, and is reciprocally related with the PPRF [196, 779]. Cells of the RIMLF have predominantly ipsilateral projections to the oculomotor nucleus, particularly to the motoneuron subgroups of the vertical eye muscles [197, 1285]. Clinicopathological evidence indicates that Parinaud's syndrome (vertical gaze paralysis) results from damage to the RIMLF or its efferent fibres [1089].

7. The *superior colliculus* has a laminar structure consisting of alternate grey and white layers (Figs. 98, 99). From superficial to deep, these layers are:
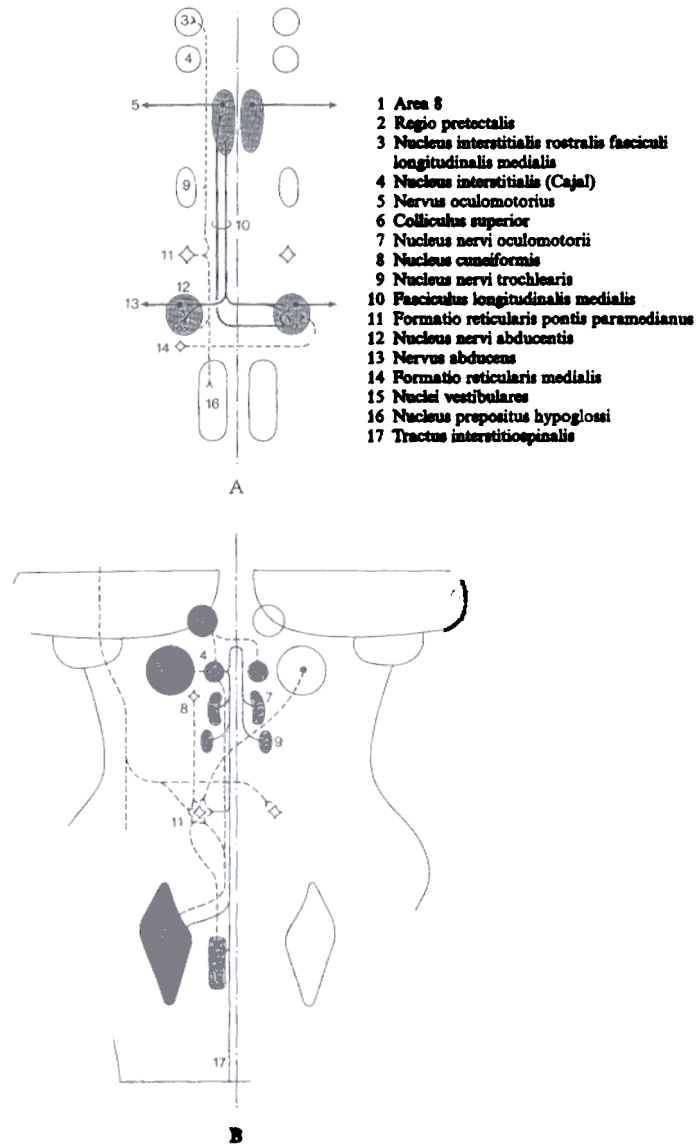
1 Area 8
2 Regio pretectalis
3 Nucleus interstitialis rostralis fasciculi
  longitudinalis medialis
4 Nucleus interstitialis (Cajal)
5 Nervus oculomotorius
6 Colliculus superior
7 Nucleus nervi oculomotorii
8 Nucleus cuneiformis
9 Nucleus nervi trochlearis
10 Fasciculus longitudinalis medialis
11 Formatio reticularis pontis paramedianus
12 Nucleus nervi abducentis
13 Nervus abducens
14 Formatio reticularis medialis
15 Nuclei vestibulares
16 Nucleus prepositus hypoglossi
17 Tractus interstitiospinalis

1 Area 8
2 Nuclei intralaminares thalami
3 Nucleus ventralis lateralis thalami
4 Nucleus tractus opticus
5 Regio pretectalis
6 Nucleus interstitialis rostralis fasciculi
  longitudinalis medialis
7 Nucleus interstitialis (Cajal)
8 Colliculus superior
9 Nucleus nervi oculomotorii
10 Nucleus nervi trochlearis
11 Formatio reticularis pontis paramedianus
12 Cerebellum
13 Nucleus nervi abducentis
14 Nuclei vestibulares
15 Nucleus prepositus hypoglossi
16 Nucleus olivaris inferior

Fig. 148A, B. The visual system III: The oculomotor pathways. A intrinsic connections and efferents of the paramedian pontine reticular formation (PPRF); B afferents of the PPRF and connections of the interstitial nucleus of Cajal. N.b.: Afferent connections are indicated with *interrupted lines* and efferent connections with *continuous lines*
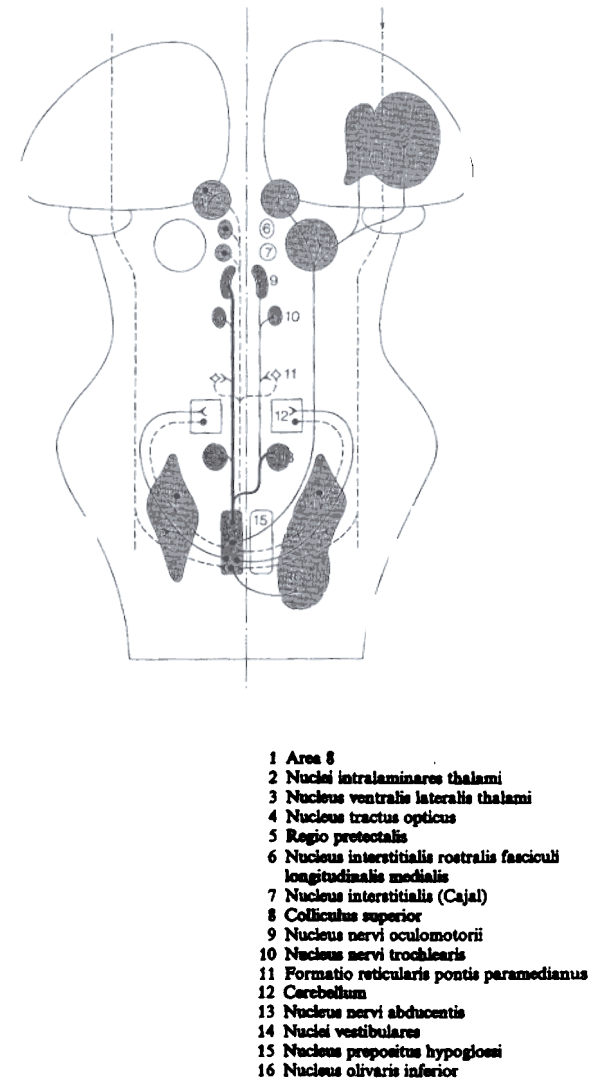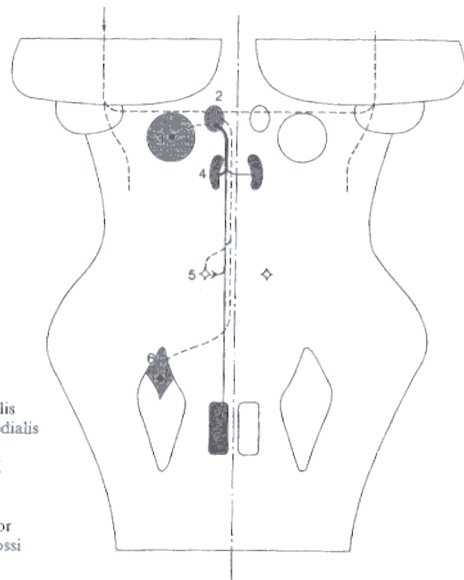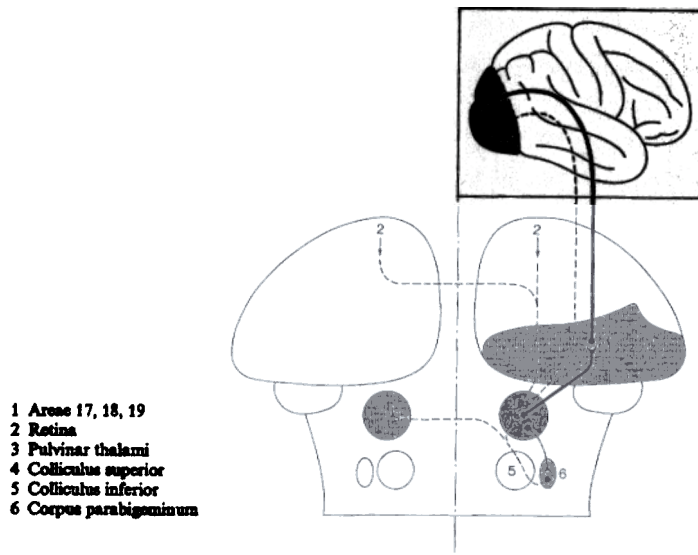
Fig. 149. The visual system III: The oculomotor pathways: the connections of the prepositus hypoglossi nucleus. N.b.: afferent connections are indicated with *interrupted lines* and efferent connections with *continuous lines*
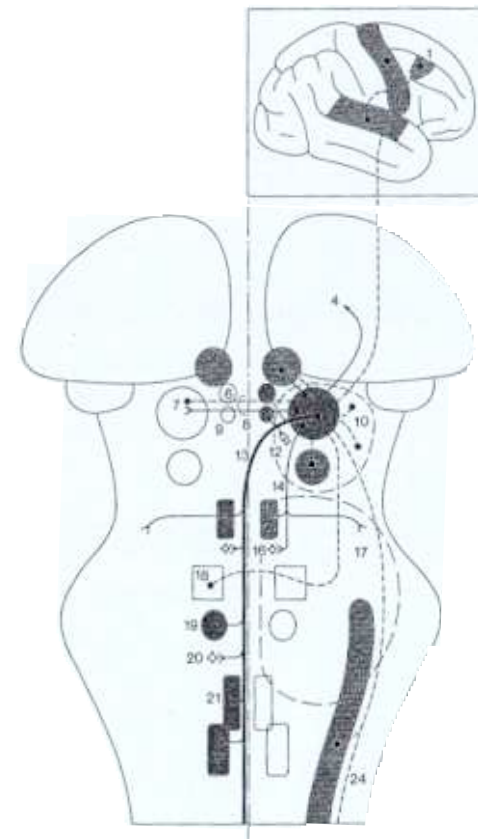
1 Area 8
2 Nucleus interstitialis rostralis
  fasciculi longitudinalis medialis
3 Colliculus superior
4 Nucleus nervi oculomotorii
5 Formatio reticularis pontis
  paramedianus
6 Nucleus vestibularis superior
7 Nucleus prepositus hypoglossi

Fig. 150. The visual system III: The oculomotor pathways: the connections of the rostral interstitial nucleus of the MLF. N.b.: afferent connections are indicated with *interrupted lines* and efferent connections with *continuous lines*

1 Areas 17, 18, 19
2 Retina
3 Pulvinar thalami
4 Colliculus superior
5 Colliculus inferior
6 Corpus parabigeminum

Fig. 151. The visual system III: The oculomotor pathways: the connections of the superficial zone of the superior colliculus. N.b.: afferent connections are indicated with *interrupted lines* and efferent connections with *continuous lines*

1 Area 8
2 Area 4
3 Area 22
4 Nucleus ventralis anterior
  Nucleus ventralis lateralis
  Nucleus lateralis dorsalis } thalami
  Nucleus medialis
  Nucleus parafascicularis
5 Regio pretectalis
6 Nucleus interstitialis rostralis fasciculi
  longitudinalis medialis
7 Colliculus superior
8 Commissura colliculi superioris
9 Nucleus interstitialis (Cajal)
10 Substantia nigra, pars reticulata

11 Colliculus inferior
12 Nucleus cuneiformis
13 Tractus tectobulbaris medialis
14 Tractus tectobulbaris lateralis
15 Nucleus reticularis tegmenti pontis
16 Nucleus reticularis pontis
17 Nuclei pontis
18 Cerebellum
19 Nucleus nervi abducentis
20 Nucleus reticularis myelencephali
21 Nucleus olivaris accessorius medialis
22 Nucleus prepositus hypoglossi
23 Nucleus spinalis nervi trigemini
24 Tractus spinotectalis

Fig. 152. The visual system III: The oculomotor pathways: the connections of the deep collicular zone. N.b.: afferent connections are indicated with *interrupted lines* and efferent connections with *continuous lines*

1. The mainly fibrous stratum zonale
2. The stratum griseum superficiale
3. The stratum opticum
4. The stratum griseum medium
5. The stratum album medium or stratum lemnisci
6. The stratum griseum profundum
7. The stratum album profundum

On the basis of connections and functions the superior colliculus can be partitioned into a superficial zone and a deep zone. The superficial zone, which consists of layers 1–3, receives primarily visual afferents and gives rise to ascending fibres. The deep zone, which encompasses layers 4–7, receives heterogeneous multimodal inputs and sends descending fibres to centres in the brain stem and spinal cord.

The visual afferents of the superior colliculus orginate in part from both eyes and in part from the ipsilateral visual cortex. The retinal fibres pass via the optic tract and reach the superior colliculus via its brachium (Figs. 15, 144, 145), to enter the stratum opticum [96]. The cortical fibres, which arise from areas 18 and 19 as well as 17, appear to be topographically organised [363]. They also enter the superior colliculus via its brachium, but pass mainly into the stratum zonale. Physiological experiments have shown that the superficial collicular zone contains a retinotopic map of the contralateral homonymous halves of the visual field, so that central visual regions are represented rostrally, peripheral regions caudally, upper visual regions medially and lower regions laterally.

The superficial collicular zone gives rise to a large, topographically organised projection to the pulvinar thalami, which arises from neurons situated in a cytoarchitectonically distinct sublamina of the stratum griseum superficiale [572, 1056]. The superficial zone also gives rise to a substantial ipsilateral projection to the corpus parabigeminum (Fig. 101), a structure which has regionally organised bilateral projections back to the superior colliculus [73, 477].

The deep collicular zone receives a variety of afferent projections, including: (a) fibres

originating from several non-visual cortical areas, e.g. the motor cortex (area 4), the frontal eye field (area 8) and the auditory cortex (area 22) [304, 363, 778]; (b) auditory fibres arising from the inferior colliculus; (c) somatosensory spinotectal and trigeminotectal fibres; (d) a highly ordered projection from the pars reticulata of the substantia nigra [435]; and (e) fibres from the fastigial nucleus [86]. It is also worth mentioning that commissural fibres connect the deeper grey layers of the two superior colliculi, and that these deeper layers are also reciprocally related to the pretectal region [113].

The deep collicular zone gives rise to ascending fibres which terminate within several dorsal thalamic centres, including the ventral anterior, ventral lateral, lateral dorsal, medial and parafascicular nuclei [477]. These ascending fibres presumably represent collaterals from axons which, after having descended into the tegmentum of the midbrain, pass caudally towards the rhombencephalon and the spinal cord [431]. The descending collicular fibres constitute two bundles, the larger contralateral medial tectobulbospinal tract or predorsal fascicle and the smaller direct lateral tectobulbar tract [476]. In the tegmentum of the midbrain the efferents of the deep collicular layers issue fibres to the interstitial nucleus of Cajal, the rostral interstitial nucleus of the MLF and the mesencephalic reticular formation (Fig. 99) and descend near the median raphe just ventral to the MLF. Some of these fibres continue to cervical spinal segments, occupying a position in the medial part of the anterior funiculus. The crossed tectobulbospinal tract issues fibres to numerous rhombencephalic areas, including the reticular nucleus of the pontine tegmentum, the dorsolateral pontine grey matter, the pontine and medullary medial reticular formation (particularly the PPRF), the medial accessory olive, the abducens nucleus and the nucleus praepositus hypoglossi. The tectospinal fibres terminate in laminae VI and VII of the cervical grey matter. The fibres of the direct tectobulbar tract descend laterally to those of the predorsal fascicle. These fibres

terminate mainly in the reticular nucleus of the pontine tegmentum, the dorsolateral pontine grey matter and the pontine reticular formation [431, 476].

An orderly representation of the visual world, as present in the superficial collicular zone, has also been found in the deeper zone. The auditory space and the surface of the body are also represented in an orderly manner in the deeper zone of the superior colliculus; these representations or maps are topographically aligned with each other as well as with the visual map. Thus, the collicular visual, auditory and somatosensory maps are all in spatial register (for review cf. [573, 1286]. The relationships between these various sensory representations should not be thought of as entirely static (e.g. only valid for the situation in which the eyes occupy the primary orbital position). In the monkey a shift in eye position produces a corresponding shift in the auditory map [615]. However, it is hard to grasp how the collicular representation of an inherently dynamic body surface could become and remain aligned with the representation of the visual world.

One of the principal functions of the superior colliculus is to participate in the control of orienting responses, i.e. the steering of rapid combined movements of eyes, head and body towards external stimuli. For visual stimuli such an orienting response leads to bringing the image of an object onto the fovea centralis. Following this location or "foveation" another important function of the colliculus, tracking of the object, comes into operation. The movements of eyes, head and body involved in orientation are under the control of various premotor centres, among which are the rostral interstitial nucleus of the MLF, the interstitial nucleus of Cajal, the PPRF, the internuclear neurons in the abducens nucleus, the nucleus praepositus hypoglossi, the pontine and medullary reticular formation and neurons in the medial part of the cervical spinal grey matter. The efferent cells in the deeper zone of the superior colliculus receive and integrate the sensory (visual, auditory, and somatosensory) stimuli

which reach this zone and have, via their axons, direct access to the various premotor centres mentioned above [897]. In other words this set of neurons constitutes an "interface" by which sensory signals are transformed into commands for orientation responses [573]. This "interface" is in turn under the control of the corpus striatum via the nigrocollicular projection, the cerebellum via the fastigiocollicular projection and the frontal eye field via corticotectal fibres. It is noteworthy that the eye and head movements are topographically represented in the deep collicular zone, and that this "motor" organisation is, reportedly, in register with the sensory representations in this zone [573, 1286].

The superior colliculus is not the only centre which relays cerebellar influence on the orienting response. Without going into details, the dorsolateral parts of the basal pontine nuclei and the reticular nucleus of the pontine tegmentum (both of which also receive fibres from the cerebral cortex and the pretectal region) constitute the first link in a tectopontocerebellar mossy fibre projection, which terminates in lobules VI and VII and in the flocculus (lobule X). The same cerebellar cortical areas receive a climbing fibre projection from certain parts of the medial accessory olive. These parts are dominated by the superior colliculus via the crossed tectobulbar tract. The vestibular nuclei occupy a prominent position among the premotor centres which are influenced by the cerebellum.

8. One of the cell masses in the pretectal complex, *the optic tract nucleus* is an essential station in the subcortical pathway mediating horizontal optokinetic nystagmus [245].

9. A small cortical area situated in the posterior part of the middle frontal gyrus, which roughly corresponds to *area 8 of Brodmann*, is involved in the initiation of the orienting response as well as of voluntary eye movements, not dependent on visual stimuli ('scanning'). The initial part of the pathway from this frontal eye field to the nuclei of

the extraocular muscles is formed by fibres that terminate in the pretectal region, the superior colliculus, the PPRF and the prepositus hypoglossal nucleus [736, 773, 774, 778, 1218]. Direct connections with the rostral part of the oculomotor nuclear complex have also been reported [772].

10. A large *occipital cortical field*, roughly corresponding to areas 17, 18 and 19, plays a role in controlling eye movements induced by visual stimuli ('pursuit movements'). This occipital eye field, like the frontal eye field, sends efferents to the superior colliculus and the pretectum [72, 1403].

Ascending Reticular Systems

The Reticular Formation
(Figs. 153, 154)

The area which occupies the central portion of the brain stem is known as the reticular formation. Throughout most of its extent this area is occupied by aggregations of loosely arranged cells of different types and sizes, and the fibre systems that pass through its territory are likewise mostly diffusely organised. The term reticular formation refers to the fact that the dendrites of the cells in this area are arranged in bundles that together form a net-like pattern [1211]. The traversing fibre systems pass through the interstices of this network. The reticular formation is surrounded by cranial nerve nuclei and relay centres and also by the long ascending (lemniscal) and descending fibre systems of the brain stem. Caudally the reticular formation is continuous with the intermediate grey matter or substance, of the spinal cord; rostrally it continues into the intralaminar nuclei of the thalamus and into certain aggregations of subthalamic cells, among which the zona incerta may be mentioned. On both cytoarchitectonic and functional grounds the reticular formation can be divided into three longitudinal columns or zones [162]: (1) a median and paramedian zone, which consists of the raphe nuclei, (2) a medial zone which contains many large cells, and (3) a lateral, largely parvocellular zone. Figure 153 shows that a sharp boundary between the medial and lateral zones can only be drawn at the levels of the pons and the rostral medulla oblongata.

The Raphe Nuclei

The raphe nuclei include the nucleus raphes pallidus, the nucleus raphes obscurus, the nucleus raphes magnus, the nucleus raphes pontis, the nucleus centralis superior and the nucleus raphes dorsalis. Studies with the aid of histofluorescence and immunohistochemical techniques have revealed that many cells in these nuclei contain the indolamine serotonin. Because the raphe nuclei are not entirely congruent with the various aggregations of serotoninergic neurons, Dahlström and Fuxe [279, 280] introduced a new classification of the indolamine-containing cells in the brain stem of the rat, distinguishing nine cell groups numbered B1-B9. Most of these cell groups have also been recognised in primates [343, 344, 564]. In the following synopsis of the raphe nuclei the description of these centres as presented by Taber et al. [1349] and Braak [153] will be harmonised as much as possible with the subdivision introduced by Dahlström and Fuxe.

The nucleus raphes pallidus, in the ventral medulla oblongata, borders ventrally on the pyramidal tracts. It corresponds largely to cell-group B1 of Dahlström and Fuxe. Serotoninergic neurons within the superficial arcuate nuclei may be considered as a ventrolateral extension of the B1 group [421, 1258]. The nucleus raphes obscurus (Fig. 107), which corresponds to cell group B2, is situated at the same level as the nucleus raphes pallidus, but occupies a more dorsal position. The nucleus raphes magnus is found in the caudal pons (Figs. 104–107). Many of the serotoninergic neurons of group B3 are situated within its confines. The rather small