Chapter 11
The Cerebrocerebellar System

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Abstract The cerebellum has massive reciprocal interconnections with the cerebral cortex and with cerebral subcortical structures that complement its interconnections with the spinal cord and brainstem. The major cerebrocerebellar link is mediated by the feedforward/afferent corticopontine projections and mossy fibers emanating from the pontocerebellar projections, and the feedback/efferent cerebellothalamic and thalamocortical projections. These highly arranged connections link sensorimotor, associative and limbic regions of cerebral cortex with the cerebellum and the intervening pontine nuclei and thalamus in a topographically precise manner. The cerebellum also has reciprocal links with the basal ganglia and hypothalamus, and with structures in the limbic circuit. In addition to these mossy fiber afferents to cerebellum, the inferior olive receives indirect input from motor and associative regions of the cerebral cortex by way of the red nucleus and zona incerta, and it conveys these inputs to cerebellum via climbing fibers. The cerebrocerebellar pathways are organized into segregated loops of information processing and stand in contrast to the cerebellar cortical architecture that is essentially uniform. Knowledge of cerebrocerebellar circuits is critical to understanding theories of the cerebellar contribution to motor and nonmotor function, and to the diagnosis and management of patients with lesions in these pathways.

Keywords Cerebellum • Cerebral • Anatomy • Connections • Projections • Neural circuits • Corticopontine • Pontocerebellar • Cerebellothalamic • Thalamocortical • Pons • Thalamus • Olive

The cerebellum has massive reciprocal interconnections with the cerebral hemispheres. The cerebrocerebellar circuit consists of a two-stage feedforward, or afferent limb, and a two-stage feedback, or efferent limb. The feedforward limb synapses in the nuclei of the basis pontis, and comprises the corticopontine projections and the pontocerebellar pathway. The feedback limb originates in the deep cerebellar

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nuclei (DCN) with an obligatory synaptic step in thalamus; the thalamocortical projection forms the final stage of this feedback system. The cerebral cortex communicates mostly with the contralateral cerebellum. Cerebral cortex projects to the ipsilateral pons, pontocerebellar fibers cross to the other side of the pons and course though the middle cerebellar peduncle to the contralateral cerebellum. The cerebellar feedback travels via the superior cerebellar peduncle, decussates in the brachium conjunctivum, and terminates in the contralateral thalamus; the thalamocortical projection is ipsilateral. This chapter provides an overview of the connectional anatomy of the cerebrocerebellar circuit derived from tract tracing studies in animal models, mostly the monkey, with a particular focus on the feedforward limb of the circuit. Further details and discussion of important earlier studies can be found in the references cited here.

11.1 The Feedforward Limb of the Cerebrocerebellar System

Corticopontine projections arise from neurons in layer Vb (Glickstein et al. 1985), and course in the anterior limb of the internal capsule from prefrontal regions, and in the sagittal stratum and/or posterior limb of the internal capsule from posterior regions (Schmahmann and Pandya 1992, 1997a, 2006). They course above and then medial to the lateral geniculate nucleus before descending into the cerebral peduncle where prefrontal fibers are most medial, premotor and motor cortices occupy its middle third, and parietal, temporal and occipital fibers are in the lateral third (Schmahmann and Pandya 1992, 1997a). The relative size of the cerebral peduncle comprised of fibers derived from association cortices is larger in human than monkey, reflecting evolutionary expansion (Ramnani et al. 2006).

11.1.1 Patterns of Termination in the Pons

Each cortical area gives rise to topographically arranged terminations in a unique mosaic of patches around the neurons of the basis pontis, distributed within transverse and rostrocaudal dimensions. Terminations interdigitate with each other but do not overlap.

11.1.2 Neurons of the Basis Pontis

Pontine neurons in monkey are arranged in nuclei according to location and cytoarchitecture. These are the dorsal tier (the dorsomedial, dorsal, dorsolateral and extreme dorsolateral nuclei), intermediate tier (median, paramedian, intrapeduncular and peri-peduncular, and lateral nuclei), and a ventral pontine nucleus (Nyby and Jansen 1951; Schmahmann and Pandya 1989). The nucleus reticularis tegmenti pontis (NRTP), is immediately adjacent to the dorsal tier nuclei. In human, these architectonic features are less persuasive (Schmahmann et al. 2004a).

11.1.3 Corticopontine Projections

Projections from motor cortices terminate preferentially in the caudal half of the pons, in close proximity to traversing corticofugal fibers (Nyby and Jansen 1951; Brodal 1978; Wiesendanger et al. 1979; Hartmann-von Monakow et al. 1981; Schmahmann et al. 2004b). Projections from the face region of the supplementary motor area (SMA) are most medial. Projections from the ventral precentral gyrus (M1 face representation) are also medial, but lateral to those from SMA-face. M1 hand projections are in medially placed curved lamellae in mid and caudal pons. Dorsal trunk projections are in medial and ventral locations, ventral trunk/hip projections encircle the peduncle in the caudal pons, and projections from the foot representation are heaviest caudally in laterally placed curved lamellae (Schmahmann et al. 2004b) (Fig. 11.1). Corticopontine projections from the sensory cortex also terminate mostly in the caudal half of the pons (Brodal 1978; Brodal and Bjaalie 1992).

Motor topography is apparent in the human pons as shown in structure-function correlations in patients with stroke (Schmahmann et al. 2004a) (Fig. 11.2). Face movement and articulation are in rostral and medial basilar pons, hand coordination and dexterity are medial and ventral in rostral and mid-pons, and arm coordination is represented ventral and lateral to the hand. Leg coordination is in the caudal half of the pons, with lateral predominance. Gait is represented in medial and lateral locations throughout the rostral-caudal extent of the pons.

The pons receives heavy projections from multiple cerebral association areas (Fig. 11.3).

- Prefrontal projections to pons arise mostly in dorsolateral and dorsomedial prefrontal cortices from areas concerned with attention as well as with conjugate eye movements (area 8), the spatial attributes of memory and working memory (area 9/46d), planning, foresight, and judgment (area 10), motivational behavior and decision making capabilities (areas 9 and 32), and from areas considered to be homologous to the language area in human (areas 44 and 45). Terminations are in the medial pons in its rostral third, favoring the median, paramedian, dorsomedial and medial part of the peripeduncular pontine nuclei (Schmahmann and Pandya 1995, 1997b).

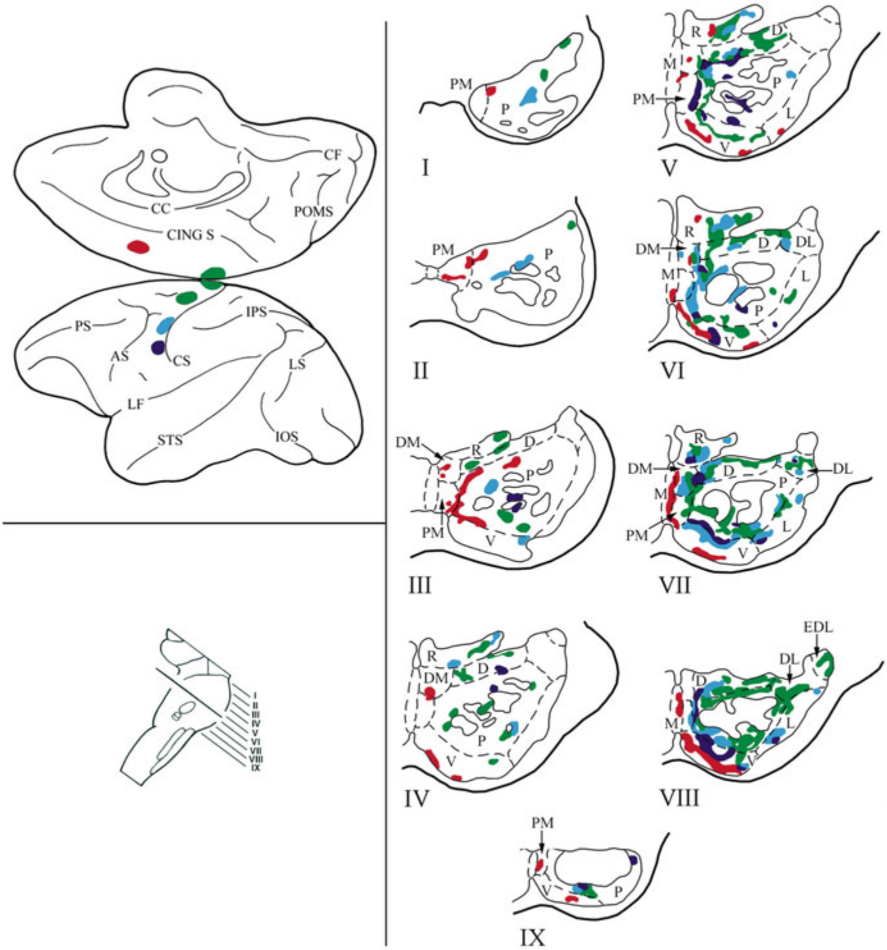

Fig. 11.1 Composite color coded summary diagram of projections to the basis pontis from motor and supplementary motor cortices in the rhesus monkey. Injection sites in the cerebral cortex (*top left*) are shaded in *solid colors*. The corresponding termination patterns in the nine rostro-caudal levels of the pons taken at the level shown in the brainstem view (*lower left*), are represented by similarly colored regions. SMA – *red*; Trunk and Leg – *green*; Hand – *light blue*; Face-Hand overlapping area – *dark blue*. The terminations are predominantly in the caudal half of the pons, each cortical area projecting to a unique subpopulations of neurons within the pons. The SMA projections are most medial, and the face, hand, and leg projections are progressively more laterally situated (From Schmahmann et al. 2004b)

- Posterior parietal projections arise from both gyral and sulcal cortices including the multimodal caudal regions. Inferior parietal lobule projections to pons are predominantly rostral, those from superior parietal lobule distribute throughout the rostro-caudal extent of the pons. Parietal projections are mostly in the intermediate and lateral sectors of the pons, with topographic organization deter-

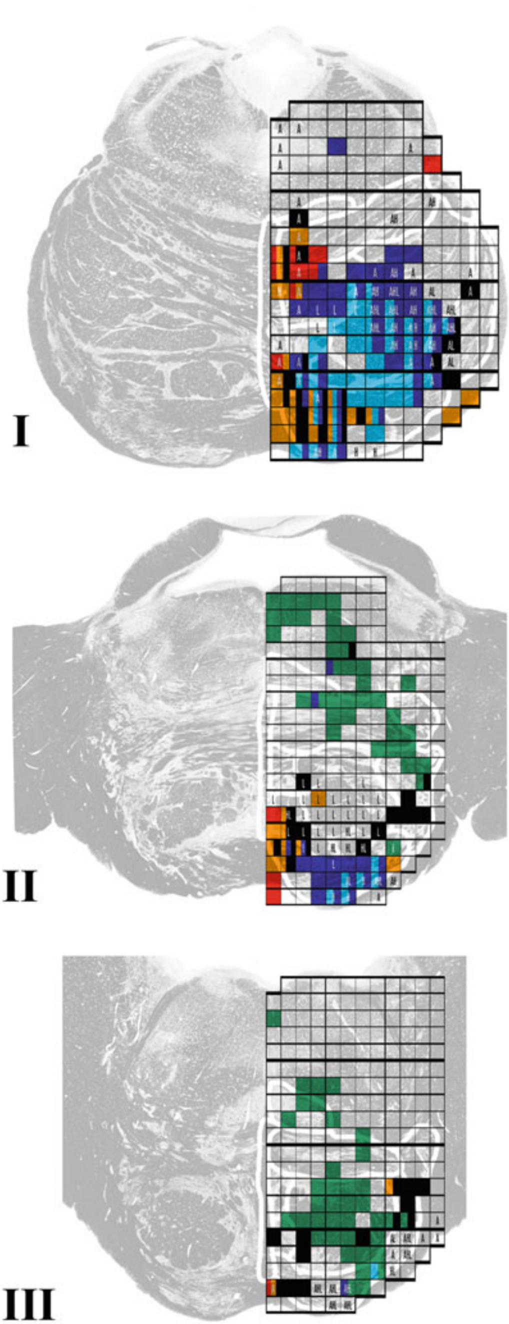

Fig. 11.2 Color-coded composite summary diagram to illustrate the topographic map of motor representations in the human pons derived from analysis of ischemic stroke in the basis pontis. Pontine levels I through III from rostral to caudal pons. Face – *red*; dysarthria – *orange*; hand dexterity – *dark blue*; arm dysmetria – *light blue*; leg dysmetria – *green*; gait – *black*. *A* arm strength, *H* hand strength, *L* leg strength (From Schmahmann et al. 2004a)

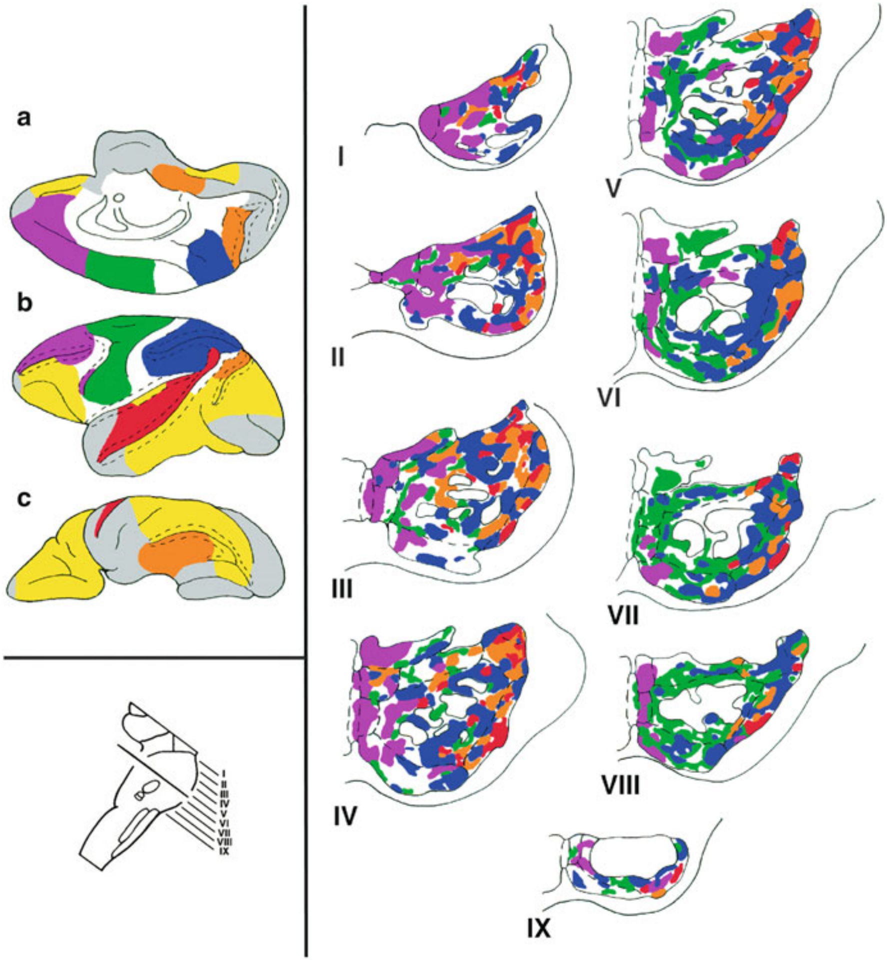

Fig. 11.3 Color-coded summary diagram illustrating the distribution within the nuclei of the basis pontis (levels I–IX) of the rhesus monkey of projections derived from association and paralimbic cortices in the prefrontal (*purple*), posterior parietal (*blue*), temporal (*red*), and parastriate and parahippocampal regions (*orange*), and from motor, premotor and supplementary motor areas (*green*). The medial (**a**), lateral (**b**) and ventral (**c**) surfaces of the cerebral hemisphere are shown above. Cerebral areas that have been shown to project to the pons by other investigators using either anterograde or retrograde tracers are depicted in *white*. Areas that have no pontine projections (according to anterograde and retrograde studies) are shown in *yellow*; those with no pontine projections according to retrograde studies are in *gray. Dashed lines* on the hemispheres represent sulcal cortices. *Dashed lines* in the pons represent pontine nuclei, and *solid lines* demarcate corticospinal fibers (From Schmahmann 1996)

mined by their site of origin (May and Andersen 1986; Schmahmann and Pandya 1989).

- Temporal lobe projections arise from the multimodal regions of the cortex of the upper bank of the superior temporal sulcus, the superior temporal gyrus and

supratemporal plane, and terminate in lateral and dorsolateral pontine regions (Schmahmann and Pandya 1991, 1992).
- Parastriate cortices at the dorsomedial and dorsolateral convexity, as well as the posterior parahippocampal gyrus, project to the lateral and dorsolateral pontine regions (Schmahmann and Pandya 1993).
- Rostral cingulate projections are directed to the medial pontine nuclei, the caudal cingulate to more lateral regions (Vilensky and Van Hoesen 1981; Schmahmann and Pandya 2006).
- Pontine projections arise also from the anterior insular cortex (Glickstein et al. 1985).

There is a dichotomy in the corticopontine projections according to the dorsal versus ventral streams of cognitive processing (Schmahmann and Pandya 1997a). Visual areas concerned with visual motion and the peripheral visual field (the “where” pathway) project to pons (dorsal part of the prelunate gyrus, caudal lower bank of the cortex in the superior temporal sulcus, polymodal convergence zones in the lower bank of the cortex in the intraparietal sulcus, and paralimbic parts of the caudal inferior parietal lobule). Cortical regions concerned with visual feature discrimination and the central visual field (the “what” pathway) do not have pontine projections (ventral prelunate gyrus, rostral lower bank of the superior temporal sulcus, middle and inferior temporal gyri, lateral aspects of the posterior parahippocampal gyrus). In the frontal lobe, pontine projections arise from the dorsolateral and dorsomedial prefrontal cortices that are concerned with spatial features of working memory, but not from the ventral prefrontal and orbitofrontal cortices that are part of the ventral stream of cognitive operations (Pandya et al. 2015). These anatomic arrangements suggest that the cerebellum plays a role in spatial awareness, and in attentional, executive, auditory and linguistic functions subserved by the dorsal stream of cognitive processing. They complement the cerebellar conections with the cingulate gyrus, posterior parahippocampal gyrus, and with subcortical limbic structures (discussed below) that form part of the anatomical basis of the cerebellar role in emotional processing.

11.1.4 Pontocerebellar Projections

Pontocerebellar fibers course to the contralateral cerebellum by first running horizontally in a focused aggregate toward the midline. They then fan out in multiple directions to travel in most of the transverse pontocerebellar fiber bundles across the entire extent of the opposite side of the basis pontis at approximately the same rostrocaudal level. They then regroup in the middle cerebellar peduncle before entering the cerebellum (Schmahmann et al. 2004c). This anatomical arrangement has clinical implications for the phenomenon of ataxic hemiparesis arising from lesions of the basis pontis in patients (Fisher and Cole 1965; Schmahmann et al. 2004a) (Fig. 11.4).

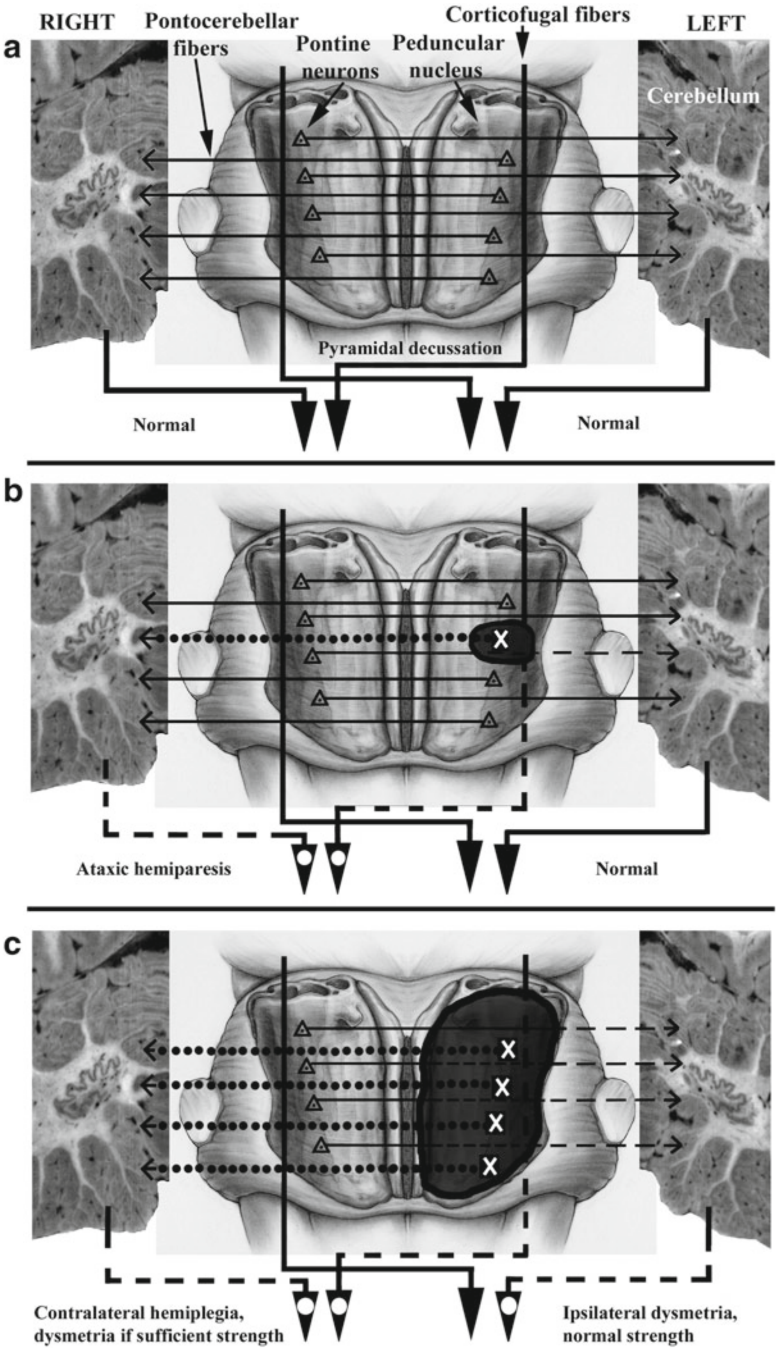

Fig. 11.4 Schematic diagram of the motor consequences of basis pontis infarction. A ventral view of the monkey pons is shown with the median, paramedian and peduncular pontine nuclei represented. Partial views of coronal sections of human cerebellum are seen on either side. (**a**) Normal arrangement, showing the pontine neurons, pontocerebellar fibers, and descending corticofugal

Neurons in the caudal pons project mainly to the cerebellar anterior lobe, and the intrapeduncular nucleus projects to vermal lobule VIIIB (Brodal and Walberg 1977). Thus the anterior lobe (particularly lobules IV and V) and paramedian lobule (lobule VIII) which contain sensorimotor representations of the upper and lower extremities (Snider and Stowell 1944; Snider 1952), receive afferents from pericentral motor and sensory cortices. The dorsolateral pontine region and the NRTP project to lobule VIII and IX (dorsal paraflocculus, uvula) and the vermal visual area in lobule VII. Neurons in the dorsomedial nucleus also project to the vermal visual area (Brodal 1979).

The rostral pons receives input from cerebral association areas, and is linked with the cerebellar posterior lobe. Medial parts of the rostral pons project to crus I, and neurons in the medial, ventral, and lateral pons send their axons to crus II (Brodal 1979). Crus I therefore receives inputs from premotor and prefrontal cortices, crus II is linked with posterior parietal areas, but also with prefrontal cortices (Kelly and Strick 2003). These anatomical observations are consistent with conclusions derived from earlier physiological studies (Allen and Tsukuhara 1974).

The pattern of divergence and convergence in the corticopontine and pontocerebellar pathways suggests that information from functionally diverse parts of the cerebral cortex and subcortical nuclei are brought together and integrated in the cerebellar cortex (Brodal and Bjaalie 1992; Schmahmann 1996).

11.2 The Feedback Limb of the Cerebrocerebellar System

11.2.1 The Cerebellar Corticonuclear Microcomplex

Apart from the vestibulocerebellum (lobule X – flocculus and nodulus, and the vermal part of lobule IX – uvula), that projects directly to the vestibular nuclei, efferents from the cerebellum are conveyed exclusively through the DCN (Voogd 2004). The cerebellar cortex projects to the DCN with a medio-lateral topography (Haines et al. 1997). Midline cortex projects to medial nuclear regions (fastigial nucleus), lateral hemisphere to the lateral/dentate nucleus, and intervening cortex to the interpositus nucleus (nucleus interpositus [NI] posterior, equivalent in human to globose nucleus, and NI anterior to emboliform nucleus).

Fig. 11.4 (continued) pathways to spinal cord. (**b**) Anatomical and clinical consequences following a small lesion in the basis pontis (*shaded black area*). Some pontine neurons are destroyed (marked by X), and the pontocerebellar fibers emanating from the lesioned neurons are affected (*dotted lines*). Pontocerebellar fibers arising from neurons in the contralateral hemipons are interrupted by the lesion (*dashed lines*), as are the descending corticofugal fibers (*heavy dashed lines*). (**c**) Large pontine lesions (*shaded black area*) destroy many pontine neurons and descending corticofugal fibers, and interrupt most of the pontocerebellar fibers traveling through the lesion from the normal hemipons (From Schmahmann et al. 2004c)

11.2.2 Cerebellothalamic Projections

The superior cerebellar peduncle (SCP) carries efferents from the DCN; fibers from the NIP are situated most medially, NIA fibers are intermediate, and dentate fibers are most lateral (Voogd 2004). Ascending axons from the fastigial nucleus course medially adjacent to the SCP. Each cerebellar nuclear region projects to three to seven rostrocaudally oriented rod-like aggregates within a dorsoventral curved lamella in the thalamus (Thach and Jones 1979).

Cerebellar projections from the DCN are directed to motor thalamic nuclei (pars oralis of the ventral posterolateral nucleus – VPLo, the caudal and pars postrema aspects of the ventrolateral nucleus – VLc and VLps, and nucleus X); intralaminar nuclei (including the central lateral, paracentral, paraventricular, and centromedian-parafascicular nuclei); and the medial dorsal thalamic nucleus in its paralaminar parts – the laterally situated pars multiformis (MDmf) and more caudal pars densocellularis (MDdc). Fastigial and lateral/dentate nucleus projections to thalamus are directed to motor, intralaminar and medial dorsal nuclei. Interpositus nucleus projections terminate in motor related ventrolateral and ventral anterior nuclei (Jones 2007; Ilinsky and Kultas-Ilinsky 1987; Schmahmann 1996).

11.2.3 Thalamocortical Projections

Motor thalamic nuclei project to motor-related cortices, as well as to multimodal association cortices in the temporal lobe (from VLc and VLps), posterior parietal cortex (from VLc, VLps, VPLo and nucleus X), and the prefrontal cortex (from VLc, VPLo and nucleus X). The cerebellar-recipient MDmf and MDdc thalamic nuclei project to prefrontal cortices (area 8, area 46 at both banks of the principal sulcus, and area 9), as well as to the cingulate gyrus, posterior parietal cortex, and multimodal parts of the superior temporal sulcus. Further, the intralaminar nuclei (notably centralis lateralis and paracentralis) project widely throughout the hemispheres to associative and paralimbic cortices in the cingulate and parahippocampal gyrus (see Schmahmann 1996; Schmahmann and Pandya 1990, 1997b).

11.2.4 Cerebrocerebellar Loops

Transynaptic viral tracing studies reveal that primary motor cortex is reciprocally connected with vermal and hemispheric lobules IV–VI, and lobules VIIB and VIIIA; whereas dorsolateral prefrontal cortex areas 46 and 9 are linked with crus II of the cerebellar posterior lobe (Kelly and Strick 2003). The DCN projections back to the cerebral cortex are also topographically arranged (Middleton and Strick 1994; Dum and Strick 2003). Primary motor cortex receives projections via thalamus from the dorsal part of the dentate nucleus (microgyric, large cells, phylogenetically older) at mid rostrocaudal levels, and from the caudal portions of the AIN – which contain neurons activated by arm movement (Thach 1978; Van Kan et al. 1993). Premotor cortex receives input from the mid-rostrocaudal part of the dentate, ventral to the M1 projecting neurons. Frontal eye field projecting neurons are located in the caudal third of the dentate that is correlated with saccadic eye movements. And the prefrontal cortex (areas 46 and 9) receives projections from the ventral part of the dentate nucleus (macrogyric, small cells, phylogenetically newer) mostly in its middle third rostrocaudally. Projections to the posterior parietal cortex arise from neurons in the ventral and lateral parts of the dentate nucleus (Dum et al. 2002).

11.3 Other Cerebral Hemisphere Connections with Cerebellum

11.3.1 Basal Ganglia

The cerebellum and basal ganglia are anatomically interconnected. Motor and non-motor domains of the subthalamic nucleus project by way of the pons to motor and non-motor regions of the cerebellar cortex (Bostan et al. 2010), and DCN projections via thalamus are directed back to sensorimotor and associative territories of the putamen and caudate nucleus (Hoshi et al. 2005). This has clinical relevance, for example, in the phenomenon of dystonia that occurs in some patients with cerebellar lesions (Batla et al 2015).

11.3.2 Inferior Olive

The inferior olivary complex receives afferents via the central tegmental tract from the magnocellular division of the red nucleus (RNmc) linked with the precentral motor cortex, and from the parvicellular red nucleus (RNpc) linked with the supplementary motor cortices, the postcentral gyrus, and area 5 in the superior parietal lobule (Cintas et al. 1980; Saint-Cyr and Courville 1980). It also receives projections from the zona incerta which is linked with motor as well as with association and limbic cortices in the rostral cingulate cortex, posterior parietal cortex and dorsolateral and medial prefrontal regions (Shah et al. 1997). The inferior olive is the sole source of climbing inputs to the cerebellum. The olivocerebellar system is discussed in Chap. 8.

11.3.3 Hypothalamus

Posterior and dorsal hypothalamic regions project medially, dorsomedially and laterally within the caudal third of the pontine nuclei (Aas and Brodal 1988). Histaminergic neurons of the tuberomammillary nucleus in the posterior hypothalamus, the dorsomedial and ventromedial nuclei, and the periventricular zone terminate diffusely in the cerebellum. The ventromedial, dorsomedial and dorsal hypothalamic nuclei are linked with the cerebellar anterior lobe, and the lateral and posterior hypothalamic areas are linked with both anterior and posterior lobe (Haines and Dietrichs 1984). The DCN convey cerebellar projections back to the contralateral hypothalamus.

11.3.4 Mammillary Body

The medial mammillary nucleus (implicated in Korsakoff's amnestic syndrome) projects ventromedially at all rostrocaudal levels of the pontine nuclei (Aas and Brodal 1988). The lateral mammillary and supramammillary nuclei project directly to cerebellar anterior and posterior lobes.

11.3.5 Septal Nuclei, Hippocampus, and Amygdala

These regions important for memory and emotion are also interconnected with the cerebellum (Anand et al. 1959; Harper and Heath 1973; Snider and Maiti 1976). In addition, there are reciprocal connections between cerebellum and brainstem serotonin, norepinephrine and dopaminergic nuclei that have widespread projections to cerebral cortex (Dempsey et al. 1983; Marcinkiewicz et al. 1989).

Tract tracing studies in animal models thus reveal the rich complexity of cerebrocerebellar communications. Different areas of the cerebral cortex – motor, associative and limbic, are reciprocally linked with the cerebellum via anatomical circuits, or closed loops, which demonstrate topographic precision at each stage of the feedforward and feedback limbs. These anatomical connections are the essential substrates that enable cerebellar contributions to movement, cognition, emotion and autonomic control.

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