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The Brain

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NOTE:

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The links look like this: (Fig. 18–1).

The brain (*encephalon*) and spinal cord constitute the central nervous system. Twelve pairs of cranial nerves (*nervi craniales*) emerge from the brain and exit the cranial cavity to innervate the head, certain neck muscles, and viscera of the thoracic and abdominal cavities. Terms such as body, colliculus, peduncle, pyramid, lobe, gyrus and folium, are used to refer to various elevations of the brain surface.

Brain tissue is composed of billions of neurons and glial cells that form **gray matter** (substantia grisea) and **white matter** (substantia alba). Localized accumulations of gray matter are designated **nuclei**, and the gray matter covering the surface of the cerebrum or cerebellum is

called **cortex.** Concentrations of myelinated axons form white matter, which generally can be subdivided into **tracts** or fasciculi or striae. Regions (in the brain stem) where white and gray matter mix together are designated **reticular formation** (formatio reticularis).

The brain develops from three enlargements of the rostral end of the embryonic neural tube. The enlargements become the **forebrain** (*prosencephalon*), **midbrain** (*mesencephalon*), and **hindbrain** (*rhombencephalon*) (Table 18–1). Subsequently the forebrain and hindbrain differentiate further, producing five primary divisions of the brain: **telencephalon, diencephalon, mesencephalon, metencephalon**, and **myelencephalon** (Fig. 18–1).

The brain may also be divided into three large regions: **cerebrum, cerebellum**, and **brain stem** (Fig. 18–2=2). The cerebrum is the telencephalon, the cerebellum is the dorsal part of the metencephalon, and the brain stem encompasses the remaining primary divisions. *This chapter is organized to present first the brain stem, then the cerebrum, and finally the cerebellum.*

THE BRAIN STEM

The brain stem occupies the fossae of the floor of the cranial cavity, caudal to the optic canals. All of the cranial nerves arise from the brain stem, except for olfactory nerves (including those to the vomeronasal organ). The rostral end of the brain stem is connected to the cerebrum by internal capsule, a mass of myelinated axons. The brain stem is connected to the cerebellum by axons within three cerebellar peduncles. Caudally, the brain stem is continuous with the spinal cord.

A ventral view of the brain stem reveals the primary brain divisions that compose it and the cranial nerves that emerge from it (Fig. 18–3=3). The **medulla oblongata** (*myelencephalon*) is the most caudal region. It is distinguished by bilateral longitudinal bands of white matter, the

pyramids, that parallel the ventral midline. Seven cranial nerves (CN VI-XII) arise from the medulla oblongata. A transversely running trapezoid body demarcates the rostral extent of the medulla.

Rostral to medulla oblongata, the **pons** *(ventral metencephalon)* is distinguished by transverse fibers along its ventral surface. The trigeminal nerve (CN V) connect to the pons. Rostral to the pons, the ventral surface of the **midbrain** *(mesencephalon)* features a median interpeduncular fossa between bilateral cerebral peduncles. The ventral surface of each peduncle is capped by the white matter called **crus cerebri**. The oculomotor nerve (CN III) and the trochlear nerve (CN IV) arise from the midbrain, the latter exits from the dorsal surface.

The ***diencephalon*** is the rostral extent of the brain stem. Its ventral surface features mamillary bodies caudally, **optic chiasm** (*chiasma opticum*) rostrally and, between these, an infundibulum connecting the brain stem to the hypophysis. Rostral to the optic chiasm, optic nerves (CN II) runs to the eyeball.

Brain divisions are also evident in a dorsal view of the brain stem (Fig. 18–4=4). The dorsal surface of the medulla oblongata and pons features a rhomboid fossa (*fossa rhomboidea*), which is the floor of the fourth ventricle. Paired rostral and caudal colliculi mark the dorsal surface of the midbrain. Bilaterally, the diencephalon features a prominent thalamus and, more caudally, a metathalamus composed of medial and lateral geniculate bodies.

CRANIAL NERVE NUCLEI OVERVIEW. Neurons associated with cranial nerves are found at all levels of the brain stem. Individual cranial nerve nuclei form interrupted longitudinal columns that extend from the midbrain caudally, even entering the spinal cord (Fig. 18–5).

Afferent cranial nerve nuclei contain interneurons and projection neurons and receive

synaptic input from primary afferent axons in cranial nerves. General visceral afferent axons collect in the **solitary tract** (*tractus solitarius*) and synapse in the **nucleus of the solitary tract** (*nucleus tractus solitarii*). The rostral end of the nucleus also receives special visceral afferent axons conveying taste.

Somatic afferent axons entering from the trigeminal nerve segregate by modality. Pain and temperature axons form the **spinal tract of the trigeminal nerve (***tractus spinalis n. trigemini)* and synapse in the **nucleus of the spinal tract of V**. (*nucleus tractus spinalis n. trigemini)*. Axons conveying touch synapse in the **pontine sensory nucleus of the trigeminal nerve** (*nucleus sensibilis pontinus n. trigemini*). Unipolar cell bodies of proprioceptive primary neurons migrate into the brain and form the **nucleus of the mesencephalic tract of V** (*nucleus tractus mesencephalici n. trigemini*).

Efferent cranial nerve nuclei contain somatic efferent or visceral preganglionic neurons. The somatic and visceral nuclei form separate columns. Also, there are two separate somatic nuclear columns. Eye and tongue muscles are innervated by nuclei found dorsomedially in the brainstem. Striated muscles derived from pharyngeal arch myotomes (jaw, face, pharynx, larynx, esophagus and some neck muscles) are innervated by somatic efferent nuclei positioned ventrolaterally in the brainstem (previously these somatic efferent nuclei were labeled “special visceral efferent”). *Individual cranial nuclei will be described in more detail per brain stem region.*

RETICULAR FORMATION OVERVIEW. In addition to distinct regions formed by gray matter nuclei and white matter tracts, the brainstem features extensive areas of **reticular formation** (*formatio reticularis*) where gray and white matter are mixed together. Neurons of the reticular formation give rise to reticulospinal tracts, to thalamic projections that alert the cerebral

cortex, to cerebellar relay sites, and to visceral relay and premotor nuclei. Anatomically individual reticular formation nuclei are relatively indistinct but collectively they form three longitudinal zones: lateral and medial zones bilaterally and unpaired raphe nuclei located along the midline (Fig. 18–6).

Many neurons within unpaired **raphe reticular nuclei** *(nuclei raphe)* release serotonin as a neuromodulator that affects mood and pain sensitivity. Raphe nuclei in the pons and midbrain send axons rostrally, influencing the limbic system and affective behavior. The ***nucleus raphe magnus*** of the medulla oblongata plays an endogenous analgesia role. Activated by axon input from midbrain periaqueductal gray matter, the nucleus directs axons caudally to block nociceptive pathway transmission in the spinal cord dorsal horn via enkephalinergic interneurons (Beitz, 1992).

The medial nuclei of the reticular formation contain large neurons that give rise to reticulospinal tracts. Axons from the *gigantocellular reticular nucleus* of the medulla oblongata form the **lateral** (medullary) **reticulospinal tract** *(tractus reticulospinalis lateralis).* Magnocellular neurons of the caudal pontine reticular nucleus give rise to the **medial** (pontine) **reticulospinal tract.**

The lateral nuclei of the reticular formation contain small (parvocellular) neurons. The nuclei are functionally diverse. They receive spinal input and activate reticulospinal neurons. They are involved in forebrain arousal (ascending reticular activating system). They project to the cerebellum. And many of the reticular nuclei scattered along the brain stem are involved processing visceral information (Fig. 18–7). Some visceral nuclei have a relay role, receiving visceral input and projecting their output to other visceral nuclei. Some visceral nuclei have a premotor role, their axons drive preganglionic neurons in visceral efferent nuclei.

The Medulla Oblongata

The **medulla oblongata** (myelencephalon) contains of gray matter nuclei, white matter tracts, and mixed gray/white reticular formation. The nuclei may be categorized as cranial nerve nuclei, relay nuclei for sensory pathways, cerebellar projection nuclei, and reticular formation nuclei. White matter includes cranial nerve axons, axonal connections with the cerebellum, and tract axons traversing and terminating in the medulla oblongata.

THE SPINOMEDULLARY JUNCTION. The caudal extent of the medulla oblongata has some features resembling the spinal cord, with which it is continuous (Fig. 18–8). In a transverse section, one can see a central canal, superficial white matter, laterally expanded central gray matter, a ventral median fissure, and a dorsal median sulcus and septum. A dominant feature of the spinomedullary junction is the **pyramidal decussation** (*decussatio pyramidum*).

Each **pyramid** (*pyramis*) consists of myelinated axons that originate from neuronal cell bodies in the cerebral cortex. Axons within the pyramids go to the medulla oblongata (corticonuclear and corticoreticular axons) or to the spinal cord (corticospinal axons). The axons synapse on interneurons that regulate both efferent neurons (motor units) and projection neurons (cranial projecting pathways) (Davidoff, 1990; Hammond, 1986).

Most corticospinal axons turn dorsally and cross the midline (pyramidal decussation) to reach the dorsal half of the contralateral lateral funiculus, where they project caudally as the **lateral corticospinal tract.** A minority of axons delay decussation until they terminate in spinal gray matter; these run in the ipsilateral lateral corticospinal tract or in the ventral funiculus as the **ventral corticospinal tract.** The decussation of pyramidal axons and other caudally projecting tracts explains why one side of the brain controls voluntary movement in the contralateral side of the body.

Dorsally at the midline, *fasciculus gracilis* axons terminate in the ***nucleus gracilis***. Further laterally, *fasciculus cuneatus* axons terminate in the **medial cuneate nucleus** (*nucleus cuneatus medialis*) (Fig. 18–8). The fasciculi are composed of cranial branches of primary afferent axons associated with encapsulated receptors located in skin or in muscles, tendons, and joints. The nuclei relay sensory information from primary afferent neurons to neurons in the thalamus. Axons from the nuclei decussate as **deep arcuate fibers** (*fibrae arcuatae profundae*), and project rostrally as **medial lemniscus** (*lemniscus medialis*).

The fasciculus cuneatus and medial cuneate nucleus are concerned with discriminative touch and kinesthesia (sense of position and movement) from the thoracic limb and neck. Kinesthesia is relayed by neurons located ventrally in the medial cuneate nucleus.

The fasciculus and nucleus gracilis are concerned with discriminative touch from the caudal half of the body. Neurons situated medial and rostral to the nucleus gracilis are referred to as **nucleus Z**. Kinesthesia from the caudal half of the body reaches nucleus Z through a spinomedullary tract. Most kinesthetic input is from collateral branches of the dorsal spinocerebellar tract; only scant input arrives via the fasciculus gracilis (Hand, 1966).

Lateral to fasciculus cuneatus, the **spinal tract of the trigeminal nerve** (*tractus spinalis n. trigemini*) is visible (Fig. 18–8). It is superficial to the **nucleus of the spinal tract of the trigeminal nerve** (*nucleus tractus spinalis n. trigemini*). The tract is composed of small, myelinated and nonmyelinated axons from neuronal cell bodies located in the trigeminal ganglion, plus a minority of somatic afferent axons from the vagus, glossopharyngeal, and facial nerves. The nucleus is divisible into rostral, interpolar, and caudal parts. The tract and nucleus extend into the first two cervical segments of the spinal cord overlapping with dorsolateral fasciculus, marginal nucleus, and substantia gelatinosa.

Axons constituting the spinal tract of the trigeminal nerve convey noxious, temperature, and crude touch information from the face and nasal and oral cavities, including the teeth. Within the tract, axons from the dorsal face (ophthalmic division of the trigeminal nerve) travel ventrally, and those from the ventral face (mandibular division) travel dorsally. The nucleus has a comparable somatotopic organization. Additionally, the nasal and oral cavities are represented in rostral regions of the nucleus, while the surrounding perimeter of the face is represented caudally.

CAUDAL HALF OF THE MEDULLA OBLONGATA. The **olivary nucleus** (*nucleus olivaris*) is a prominent feature of the caudal medulla oblongata (Fig. 18–9). It is located dorsolateral to the pyramid and lateral to the medial lemniscus; it presents a distinctive serpentine profile in the ventrolateral medulla. The nucleus receives axonal input from the cerebellum, from the cerebral cortex via the pyramids, and from the red nucleus and periaqueductal gray matter via the central tegmental tract. Dorsal and medial accessory olivary nuclei receive afferents from the spinal cord.

Efferent axons from the olivary nuclei decussate and reach the cerebellum via the **caudal cerebellar peduncle** (*pedunculus cerebellaris caudalis*). Olivocerebellar fibers climb along dendritic trees of Purkinje (piriform) neurons in the cerebellar cortex and intensely activate small, localized regions of cortex for adjusting movement and posture. Other nuclei that project to the cerebellum terminate as mossy endings on granule neurons that diffusely influence the cerebellar cortex.

The **lateral cuneate nucleus** (*nucleus cuneatus lateralis*) is situated most dorsally in the medulla oblongata. It receives proprioceptive input from the thoracic limb and neck via the fasciculus cuneatus. Axons from the nucleus form **superficial arcuate fibers** (*fibrae arcuatae*

superficiales). The fibers merge with the dorsal spinocerebellar tract to form the *caudal cerebellar peduncle*, located at the dorsolateral margin of the medulla oblongata (Fig. 18–10=9). The dorsal spinocerebellar tract conveys proprioceptive information from the caudal half of the body.

The **fourth ventricle** is located in the medulla oblongata and pons. Caudally, the region where the fourth ventricle narrows to a point is called the ***obex***. Immediately rostral to the obex, the wall of the ventricle is formed by the ***area postrema***, a densely vascularized gray matter that has fenestrated capillaries and serves as an emetic center (activated by apomorphine). As one of the circumventricular organs, it is a region that lacks a blood brain barrier.

The floor of the fourth ventricle, designated **rhomboid fossa** (*fossa rhomboidea*), has a **median sulcus** (*sulcus medianus*) (Fig. 18–4=4). Bilaterally, a ***sulcus limitans*** marks the transition from floor to wall; also, it is the demarcation between the embryonic alar and basal plates. The **roof of the fourth ventricle** (*tegmen ventriculi quarti*) is formed by the **tela choroidea** (*tela choroidea ventriculi quarti*) a layer of ependyma and pia mater that attaches to the medullary wall along a line, called **tenia of the fourth ventricle** (*tenia ventriculi quarti*).

Rostrally, tela chroidea that connects to rostral cerebellar peduncles and contains trochlear nerve axons, constitutes **rostral medullary velum (***velum medullare rostrale).* Caudally the **caudal medullary velum (***velum medullare caudale),* forms the roof of the fourth ventricle. Tela chroidea of the caudal medullary velum gives rise to two longitudinal proliferations of blood vessels, forming the **choroid plexuses** of the fourth ventricle (*plexus choroideus ventriculi quarti*). The paired choroid plexuses produce cerebrospinal fluid.

Some cerebrospinal fluid enters the central canal, but most of it flows outward to the subarachnoid space, exiting the fourth ventricle bilaterally through a **lateral recess** (*recessus*

lateralis) that leads to a **lateral aperture** (*aperturae laterales*). The recess and aperture are located immediately caudal to the caudal cerebellar peduncle. Some choroid plexus extends through the lateral recess and aperture to secrete directly into the subarachnoid space (Fig. 18–11).

The **motor nucleus of the hypoglossal nerve** (*nucleus motorius n. hypoglossi*) is evident dorsally beside the midline (Fig. 18–9). Axons from the nucleus run ventrally and then angle through the lateral region of the olivary nucleus. They leave the medulla oblongata as roots of the hypoglossal nerve and innervate muscles of the tongue (somatic efferent axons).

The **parasympathetic nucleus of the vagus nerve** (*nucleus parasympathicus n. vagi*) is located dorsolateral to the hypoglossal nucleus. Preganglionic parasympathetic visceral efferent axons from the nucleus run laterally to join the vagus nerve and innervate thoracic and abdominal viscera. Rostrally, two small nuclei of this cell column contribute axons to the glossopharyngeal and facial nerves (Fig. 18–9). The parasympathetic nucleus of the glossopharyngeal nerve (*nucleus parasympatheticus n. glossopharyngei*) innervates parotid and zygomatic salivary glands. Further rostrally, the parasympathetic nucleus of the facial nerve (*nucleus parasympatheticus n. facialis*) innervates mandibular and sublingual salivary glands and nasal, palatine and lacrimal glands .

The ***nucleus intercalates***, positioned between the hypoglossal and the parasympathetic nuclei, sends axons to the cerebellum. It receives input from vestibular nuclei and is involved in holding vertical gaze position (Munro 1988).

The **solitary tract** (*tractus solitarius*) is distinct dorsolateral to the parasympathetic nucleus of the vagus (Fig. 18–9). The tract contains axons from visceral afferent cell bodies located in distal ganglia of the vagus and glossopharyngeal nerves and the geniculate ganglion of

the facial nerve. The axons synapse in the **nucleus of the solitary tract** (*nucleus tractus solitarii*). Caudally, right and left nuclei merge dorsal to the central canal, forming a *commissural nucleus.*

The nucleus of the solitary tract contains interneurons and projection neurons concerned with reflexes and sensation from the auditory tube, pharynx, larynx, esophagus, trachea, and other thoracic and abdominal viscera. The rostral end of the nucleus receives taste (special visceral afferent) input from three nerves: vagus (pharynx and larynx), glossopharyngeal (caudal third of tongue), and facial (rostral two-thirds of tongue).

The **nucleus ambiguus** is a column of sparse neurons located ventral to the nucleus of the spinal tract of the trigeminal nerve (Fig. 18–9). Except for some visceral efferent neurons that innervate the heart (Figs. 18–7), the nucleus ambiguous contains somatic efferent neurons. Via vagus and glossopharyngeal nerves, the neurons send axons to striated muscles of the pharynx, larynx, and esophagus.

A caudal continuation of the ambiguus cell column extends through the cervical spinal cord as the **motor nucleus of the accessory nerve** *(nucleus motorius n. accessorii* (Fig. 18–5). Its axons form the spinal root of the accessory nerve, which innervates certain muscles of the neck (cleidocephalicus, mastoid part of sternocephalicus, omotransversarius, and trapezius). The **accessory nerve** has a cranial root that arises from the caudal pole of the nucleus ambiguous. The root immediately joins the vagus nerve and eventually becomes recurrent laryngeal nerve.

The **lateral reticular nucleus** (*nucleus reticularis lateralis*), also referred to as *nucleus of the lateral funiculus* (*nucleus funiculi lateralis*), is located lateral to the olivary nucleus (Fig. 18–9). It receives input from the red nucleus and the spinal cord. Its axons join superficial arcuate fibers to reach the cerebellum via the caudal cerebellar peduncle.

LEVEL OF THE FACIAL NUCLEUS. The **motor nucleus of the facial nerve** (*nucleus motorius n. facialis*) is located ventrally in the medulla oblongata (Fig. 18–11). The nucleus contains somatic efferent neurons that innervate muscles of facial expression. Neurons are topographically arranged within the nucleus: rostral to caudal positioned neurons innervate rostral to caudal muscles, dorsal neurons innervate ventral muscles, and vice versa (Berman, 1968).

Axons from the facial nucleus stream dorsally and collect in a bundle that arcs, from medial to lateral, dorsally around the abducent nucleus, before proceeding ventrolaterally to exit passing through the trapezoid body (Fig. 18–5). The loop, located dorsal to the abducent nucleus, is referred to as the **genu of the facial nerve** (*genu n. facialis*).

The facial nerve also contains visceral efferent and afferent fibers. The **parasympathetic nucleus of the facial nerve** (*nucleus parasympathicus n. facialis*) is located caudal to the genu of the facial nerve. The nucleus is a rostral satellite of the parasympathetic column that supplies the glossopharyngeal and vagus nerves. Preganglionic cell bodies of the nucleus innervate neuronal cell bodies of postganglionic axons that supply lacrimal, nasal and palatine glands, and the mandibular and sublingual salivary glands. Special visceral afferent axons in the facial nerve convey taste from the rostral two-thirds of the tongue. The axons join the solitary tract and terminate in the rostral pole of its nucleus.

The facial nerve has a small contingent of general somatic afferent fibers that supply the concave surface of the auricle of the ear (Whalen and Kitchell, 1983). These axons join the spinal tract of the trigeminal nerve.

White matter at the lateral edge of the medulla oblongata constitutes the **caudal cerebellar peduncle** *(pedunculus cerebellaris caudalis)* (formerly restiform and juxtarestiform

bodies). The axons of the peduncle pass deep to the acoustic stria and turn abruptly dorsad to join the cerebellum (Fig. 18–10=9). The lateral recess of the fourth ventricle is located immediately caudal to the abrupt turn of the peduncle (Fig. 18–11).

Vestibular nuclei (*nuclei vestibulares*) produce a bulge in the wall of the fourth ventricle. The **caudal vestibular nucleus** *(nucleus vestibularis caudalis)* is situated medial to the caudal cerebellar peduncle, and the **medial vestibular nucleus** *(nucleus vestibularis medialis)* is located medial to the caudal nucleus. More rostrally, the **lateral vestibular nucleus** *(nucleus vestibularis lateralis)* is positioned dorsal to the caudal nucleus, and further rostrally, the **rostral vestibular nucleus** *(nucleus vestibularis rostralis)* can be found. Both the lateral and the rostral nuclei are shifted dorsally, among axons of merged cerebellar peduncles (Fig. 18–11).

The vestibular nuclei receive axons from the vestibular nerve, cerebellum, and spinal cord. The nuclei project to the cerebellum (via the caudal cerebellar peduncle), to motor nuclei of extrinsic eye muscles for vestibulo-ocular reflexes (via the medial longitudinal fasciculus), and to the spinal cord for vestibular reflexes concerned with the position of the head and body (via, respectively, ventral and lateral vestibulospinal tracts).

A prepositал nucleus *(nucleus prepositus n. hypoglossi)* is located medial to the medial vestibular nucleus. It extends from the nucleus intercalatus to the level of the genu of the facial nerve. The nucleus is functionally involved in eye movement (Berman, 1968).

ROSTRAL END OF THE MEDULLA OBLONGATA. Features of the rostral medulla oblongata include the trapezoid body and attachments of cranial nerves VI, VII, and VIII (Fig. 18–12). The **vestibulocochlear nerve** (CN VIII) is a combined nerve, composed of special proprioceptive axons that innervate the vestibular membranous labyrinth (vestibular nerve) and the special somatic afferent axons that innervate the cochlea duct (cochlear nerve).

The vestibular membranous labyrinth responds to linear and angular acceleration of the head, and the vestibular nerve conveys that information to the vestibular nuclei and the cerebellum.

The cochlea duct is the sense organ for hearing. Cochlear nerve axons synapse in both **ventral** and **dorsal cochlear nuclei.** The two nuclei merge into a single mass at the lateral margin of the medulla oblongata, but the dorsal nucleus forms a superficial prominence, the **acoustic tubercle** (*tuberculum acousticum*). Axons from the dorsal cochlear nucleus (and possibly vestibular nerve axons) form a transverse band, the **acoustic stria** (*stria acustica*), on the dorsal surface of the caudal cerebellar peduncle. Axons from the ventral cochlear nucleus form the **trapezoid body** (*corpus trapezoideum*), a large band of transverse fibers at the ventral surface of the rostral medulla oblongata.

Axons from cochlear nuclei project to both sides of the brain; however, the majority of them decussate. Many of the axons terminate in two nuclei that also project to both sides of the brain: The **dorsal nucleus of the trapezoid body** (*nucleus dorsalis corporis trapezoidei*) is prominent immediately dorsal to the trapezoid body. It has a twisted, encapsulated appearance (Fig. 18–12). The nucleus is important in sound localization and it triggers reflex contraction of middle ear muscles. The dorsal nucleus also gives rise to efferent axons that run in the vestibulocochlear nerve to inhibit receptor cells of the cochlear duct (Goldstein, 1980). **Ventral nuclei of the trapezoid body** (*nuclei ventrales corporis trapezoidei*) are neuronal cell bodies scattered among the axons of the trapezoid body.

Axons from nuclei of the trapezoid body and from cochlear nuclei project rostrally in the **lateral lemniscus** (*lemniscus lateralis*), toward the caudal colliculus. Some axons of the lemniscus synapse in **nuclei of the lateral lemniscus** (*nucleus menisci lateralis*), located along the lemniscus in the pons and midbrain.

The **genu of the facial nerve** can be seen in the rostral medulla oblongata (Fig. 18–12). Axons from the gunu run ventrolaterally between the dorsal nucleus of the trapezoid body and the nucleus of the spinal tract of V to exit as the facial nerve root. The **motor nucleus of the abducent nerve** (*nucleus motorius n. abducentis*) is located ventral to the genu of the facial nerve. Its somatic efferent axons extend ventrally and exit just lateral to the pyramid (Fig. 18–12). The abducent nerve innervates lateral rectus and retractor bulbi muscles of the eye.

The Pons

The pons consists of a dorsal part, designated *tegmentum*, and a ventral part that features **transverse pontine fibers** (*fibrae pontis transversae*) (Fig. 18–13). The pontine fibers run along the ventral surface of the pons and form the contralateral **middle cerebellar peduncle** (*pedunculus cerebellaris medius*). The pontine axons arise from contralateral **pontine nuclei** (*nuclei pontis*), gray matter immediately deep to the transverse fibers surrounding longitudinal axons of the ventral pons. The longitudinal axons belong to the **corticopontine tract** (*tractus corticopontinus)* and the **pyramidal tract** (*tractus pyramidalis*). The corticopontine axons and collateral branches of pyramidal axons synapses on neurons of the pontine nuclei.

The **pontine tegmentum** (*tegmentum pontis*) resembles medulla oblongata, including presence of a fourth ventricle. The roof of the fourth ventricle is formed by rostral medullary velum. The walls and floor of the ventricle are lined by a layer of gray matter (Fig. 18–14). This periventricular gray matter contains neuromodulatory cholinergic neurons (tegmental laterodorsal nucleus). **Parabrachial nuclei**, associated with the rostral cerebellar peduncle, are important visceral relay nuclei (Fig. 18–13). The **locus ceruleus** (*nucleus ceruleus*) is a collection of neuromodulatory adrenergic neurons located at the medial border of the rostral cerebellar peduncle (Fig. 18–14). Axons from locus ceruleus are distributed widely within the

brain and go to the spinal cord; they release norepinephrine.

The **trigeminal nerve** (CN V) joins the pons (Fig. 18–13). From neuronal cell bodies located in the trigeminal ganglion, central axons of nociceptive and thermoreceptive neurons turn caudally as they enter the pons along the caudal surface of the middle cerebellar peduncle. The axons form the **spinal tract of the trigeminal nerve (***tractus spinalis n. trigemini*) and synapse in gray matter medial to the tract, in the **nucleus of the spinal tract of V**. (*nucleus tractus spinalis n. trigemini).* Axons from the nucleus go to motor nuclei of cranial nerves for reflex activity, or they decussate and proceed as a trigeminothalamic tract to the thalamus.

Primary afferent axons that convey discriminative touch terminate in the **pontine sensory nucleus of the trigeminal nerve** (*nucleus sensibilis pontinus n. trigemini*). Axons from the nucleus decussate and project rostrally, medial to the medial lemniscus, as the trigeminal lemniscus. For kinesthesia, unipolar cell bodies of proprioceptive primary afferent neurons are located within the midbrain instead of in the trigeminal ganglion (an exception to the rule that primary afferent neuronal cell bodies are found in ganglia in the peripheral nervous system). The unipolar cell bodies form the **nucleus of the mesencephalic tract of V** (*nucleus tractus mesencephalici n. trigemini*). The **mesencephalic tract of V** (*tractus mesencephalicus n. trigemini*) consists of axons traveling between the trigeminal nerve and the nucleus.

The **motor nucleus of the trigeminal nerve** (*nucleus motorius n. trigemini*) contains somatic efferent neurons that innervate chiefly muscles of mastication. It is situated medial to the pontine sensory nucleus, axons of the mesencephalic tract of V pass between the two nuclei (Fig. 18–13). Axons from the motor nucleus form a motor root that joins the mandibular nerve from the trigeminal nerve.

NEUROMODULATION OVERVIEW. Neuromodulation refers to the relatively

prolonged influence of acetycholine, norepinephrine, dopamine, or serotonin on neuronal circuits. Whether the neuromodulation is excitatatory or inhibititory depends on the distribution of receptor types on target neurons. The receptors are metabotropic and release second messengers. Most neuromodulation nuclei are found in the midbrain and pons. The nuclei are small but axons from the nuclei are highly branched and widely distributed to broad regions of brain and spinal cord. (Fig. 18-15).

For example, the *locus ceruleus* of the pons distributes axons broadly within the brain and spinal cord and releases norepinephrine. In the spinal cord, norepinephrine enhances motor neuron excitability and suppresses spinothalamic synaptic transmission. Locus ceruleus neurons cease firing during REM sleep and during canine narcoleptic episodes, both associated with absence of muscle tone. In the brain, norepinephrine affects mood and enhances arousal. The locus ceruleus receives input from prefrontal cortex, hypothalamus, and raphe nuclei.

The dopamine released by the *substantia nigra pars compacta* of the midbrain impacts basal nuclei circuits that control movement. Dopamine can increase or decrease excitability depending on which dopamine receptor is present on the target neuron. The dopamine that is released by neurons of the midbrain *ventral tegmental area* affects brain circuits active during reward conditions.

The serotonin released by *raphe nuclei* generally has an inhibitory effect. It blocks synaptic transmission in nociceptive pathways and it impacts mood (most antidepressive drugs target brain serotonin receptors). The acetylcholine released by midbrain neurons of the *pedunculopontine nucleus* and *laterodorsal temental nucleus* is widely distributed to the thalamus and impacts motivation and alertness including sleep and wakeful status. The *basal nucleus* of the rhinencephalon distributes acetylcholine broadly to alert the cerebral cortex.

The Midbrain

The midbrain contains the **mesencephalic aqueduct** (*aqueductus mesencephali*), which links the fourth ventricle of the hindbrain with third ventricle of the diencephalon. Periaqueductal gray matter (PAG) surrounds the aqueduct (Fig. 18-16). The tectum (roof) of the midbrain is formed by paired rostral and caudal colliculi. The midbrain ventral to the tectum and aqueduct, is formed by paired cerebral peduncles. From dorsal to ventral, each peduncle has three regions: tegmentum, substantia nigra, and crus cerebri. Trochlear and oculomotor cranial nerves emerge from the midbrain.

Periaqueductal gray (*substantia grisea centralis*), which surrounds the aqueduct, has a high concentration of opiate receptors. The periaqueductal gray (PAG) gives rise to an endogenous analgesia system that enables the brain to suppress pain. The analgesia is produced by norepinephrine and serotonin release, which blocks synaptic activation of projection neurons by primary afferent neurons. PAG axons go to the spinal cord and to two neuromodulatory nuclei that also that project to the spinal cord: locus ceruleus (norepinephrine) and raphe nuclei (serotonin) (Beitz, 1992).

PAG neurons play a role relaying visceral information to and from the forebrain. The *dorsal longitudinal fasciculus* (*fasciculus longitudinalis dorsalis*) courses within the ventral PAG and conveys axons from the hypothalamus to parasympathetic nuclei of cranial nerves. Also, the *dorsal tegmental nucleus (nucleus tegmenti dorsalis)* is located within the PAG. It has limbic connections (mamillary, habenular, accumbens and septum), involving the PAG in affective behavior.

At the lateral margin of the PAG, the *mesencephalic tract of the trigeminal nerve* leads to the the *mesencephalic nucleus of the trigeminal nerve*. The nucleus consists of aligned unipolar

cell bodies belonging to proprioceptive primary afferent neurons. Further laterally, ventrally directed tectospinal/tectonuclear axons and dorsally directed trochlear nerve axons are evident (Fig. 18-16).

The **tectum** of the midbrain (*tectum mesencephali*) features paired caudal and rostral colliculi and their respective commissures (Fig. 18–17=17). The commissural axons are inhibitory. Caudal and rostral colliculi reflexly orient the eyes, ears, and head toward the source of a novel auditory/visual stimulus, respectively. A ***pretectal region*** anterior to the rostral colliculus controls the pupillary light reflex.

The **caudal colliculus** (*colliculus caudalis*) is gray matter situated caudally in the tectum (Fig. 18-16). It receives axons from the **lateral lemniscus** (*lemniscus lateralis*), ***commissure of the caudal colliculi*** *(commissural colliculorun caudalium*), medial geniculate body, auditory area of the cerebral cortex, and the cerebellum. Axons from the caudal colliculus project to the *medial geniculate body* via the **brachium of the caudal colliculus** (*brachium colliculi caudalis*), located on the lateral surface of the midbrain (Fig. 18-16). Also the caudal colliculus sends axons to *nuclei of the lateral lemniscus* and to the cerebellum. For reflex orientation toward the source of a sound, axons from the caudal colliculus go to the rostral colliculus, where tectospinal and tectonuclear pathways originate.

The **rostral colliculus** (*colliculus rostralis*) has neurons arranged in superficial, intermediate and deep layers (Fig. 18–18). The superficial neurons are organized retinotopically, receiveing axons from both the optic tract and visual cortex via the **brachium of the rostral colliculus** *(brachium colliculi rostralis)*. The deep neurons, which receives auditory and spinal axons (spinomesencephalic tract) are somatotopically organized. The intermediate layer gives rise to the tectonuclear and tectospinal axons that leave the colliculus for orientation reflexes and

saccadic eye movements (Grantyn, 1989). The rostral colliculus controls eye position by directing horizontal and vertical gaze centers located in reticular formation of the pons and midbrain, respectively.

Tectonuclear tract (*tractus tectonucleares***)** axons go to the facial nucleus for ear movements and join the **medial longitudinal fasciculus** *(fasciculus longitudinalis medialis)* for eye movements. Tectospinal fibers (for head movement) join the **medial tectospinal tract** and **lateral tectotegmentospinal tract** .

The **pretectal region** (including pretectal nuclei and nucleus of the optic tract) is located anterior to the rostral colliculus and lateral to the caudal commissure at the mesencephalon-diencephalon junction (Fig. 18–19). The region is involved in reflex regulation of pupil size in response to light. Optic tract axons arrive via the brachium of the rostral colliculus. The parasympathetic oculomotor nucleus constricts pupil size during the pupillary light reflex. Pupillary dilation that is emotionally driven involves the lateral tectotegmentospinal tract that travels to preganglionic sympathetic neurons in the spinal cord.

The **caudal commissure** (*commissura caudalis*) conveys decussating axons between pretectal regions, including the prestitial nucleus (nucleus of the caudal commissure), which also receives optic tract axons. Most decussating axons are concerned with the pupillary light reflex, although some axons in the commissure connect midbrain tegmental nuclei.

Below the tectum, each **cerebral peduncle** (*pedunculus cerebri*) consists of *tegmentum*, *substantia nigra*, and *crus cerebri*. **Crus cerebri** refers to the white matter along the ventral surface of the midbrain (Fig. 18–18). It consists of corticospinal, corticopontine, corticonuclear, and corticoreticular axons that arise from neuron cell bodies in the cerebral cortex. The axons travel through the internal capsule to reach the crus cerebri. Some axons leave the crus cerebri to

terminate in the midbrain and pons. Other axons proceed through the ventral pons and continue within pyramids of the medulla oblongata.

The *fossa interpeduncularis* is the area between bilateral crura on the ventral surface of the midbrain. The *substantia perforata caudalis* refers to the area where vessels enter the fossa. The *sulcus medialis cruris cerebri* runs along the medial margin of each crus. The **transverse crural tract** (*tractus cruralis transversus*), also called basal optic tract, refers to the small band of axons from the brachium of the rostral colliculus that cross the surface of the crus cerebri rostral to the oculomotor nerve (Fig. 18–17=17). The axons terminate in a nucleus located medial to substantia nigra; axons from the nucleus proceed to the oculomotor nucleus and tectum (Berman, 1968).

The gray matter immediately dorsal to the crus cerebri is **substantia nigra.** It has compact and reticulated parts that are functionally quite different (Fig. 18–18). The *pars compacta*, the larger more dorsal component, receives axons from the cerebral cortex, basal nuclei, and thalamus. It projects axons to basal nuclei of the striatum (accumbens, caudate, putamen). The *compact substantia nigra* and the adjacent *ventral tegmental area* contain dopaminergic neurons that neuromodulate basal nuclei circuits by targeting excitatory and inhibitory dopamine receptors. The net effect is movement facilitation. (In humans, Parkinson's disease results from the loss of dopamine neurons in the substantia nigra.)

The *pars reticulata* of the substantia nigra contains spontaneously active, inhibitory, GABAergic neurons that, along with the endopeducular neurons, serve as output for basal nuclei circuits. Pars reticulata axons project to the thalamus, tectum, and red nucleus. In particular, they provide basal nuclei control of saccade eye movements.

The **interpeduncular nucleus** (*nucleus interpeduncularis*) is evident as a round profile

located ventrally in the interpeduncular fossa (Fig. 18-16). The nucleus receives input from limbic structures via the medial nucleus of the *habenula* and the *fasciculus retroflexus*. The interpeduncular nucleus projects to midbrain raphe nuclei that release serotonin in connection with forebrain neuromodulation that impacts mood.

The **midbrain tegmentum** (*tegmentum mesencephali*) contains the red nucleus and nuclei associated with the reticular formation, cranial nerves, neuromodulation, and the mesencephalic locomotor region. The **mesencephalic reticular formation** receives axonal input from spinoreticular and spinothalamic tracts and gives rise to the ascending axons responsible for maintaining awake status in the ipsilateral cerebral cortex (reticular alerting system). The axons run in the *central tegmental tract* to intralaminar thalamic neurons.

The **pedunculopontine nucleus**, located caudally in the midbrain tegmentum, contain cholinergic neuromodulatory neurons that contribute to forebrain arousal, including EEG arousal during REM sleep. The nucleus contiains other neurons that, along with the adjacent **cuneiform nucleu**s, constitue a mesencephalic locomotor region. Stimulation of these neurons evokes stepping locomotor patterns.

The **central tegmental tract** (*tractus tegmenti centralis*) runs through the core of the brain stem (Fig. 18–18). It conveys information rostrally from the reticular formation to the thalamus and subthalamus. It conveys information caudally from the caudal diencephalon and midbrain to the olivary nucleus. The caudally directed axons in the tract arise collectively from zona incerta, parasympathetic oculomotor nucleus, periaqueductal gray, midbrain reticular formation, and red nucleus.

The **motor nucleus of the trochlear nerve** (*nucleus motorius n. trochlearis*) consists of somatic efferent neurons positioned adjacent to the midline immediately ventral to

periaqueductal gray matter in the caudal midbrain (Fig. 18-16). Axons from the nucleus course laterally, dorsally, and caudally along the margin of the periaqueductal gray matter. They enter the dorsal pons, decussate in the rostral medullary velum, exit dorsal to the rostral cerebellar peduncle and pass rostroventrally along the side of the mesencephalon. The trochlear nerve innervates only the contralateral dorsal oblique muscle of the eye.

The **motor nucleus of the oculomotor nerve** (*nucleus motorius n. oculomotorii*) is situated rostral to the trochlear nucleus (Fig. 18–18). It consists of somatic efferent neurons that innervate extrinsic muscles of the eye (dorsal rectus, medial rectus, ventral rectus, and ventral oblique) and the m. levator palpebrae superioris. Visceral efferent neurons, located dorsomedial to the somatic neurons, constitute the **parasympathetic nucleus of the oculomotor nerve** (*nuclei parasympathici n. oculomotorii*). These preganglionic neurons send axons to the ciliary ganglion, the sources of postganglionic axons to the ciliary body (for lens accommodation) and iris (for pupil constriction). Axons from both somatic and visceral oculomotor nuclei join; they course ventrally and exit medial to the crus cerebri as oculomotor nerve roots.

Certain tegmental nuclei (*nuclei tegmenti*) are referred to as accessory oculomotor nuclei because of their proximity and functional relationship to the oculomotor nucleus. These include the interstitial, prestitial, and precommissural nuclei.

The **red nucleus** (*nucleus ruber*) reputedly has a rostral, small-cell region (*pars parvicellularis*) and a caudal, large-cell region (*pars magnocellularis*). In carnivores, the nucleus has small, medium and large cell regions which overlap, rostral to caudal (Massion, 1967). The ipsilateral motor cortex projects axons to the red nucleus to drive voluntary movement (Fig. 18–20). Basal nuclei influence the red nucleus via axons from the substantia nigra reticulata.

The population of small neurons located rostrally in the red nucleus receives input from

the contralateral lateral (dentate) nucleus of the cerebellum and from the somatosensory neocortex (Pong, Horn and Gibson 2002). The neurons project ipsilaterally to the ventrolateral thalamic nucleus and to the olivary nucleus via the central tegmental tract (Onodera and Huicks 2009).

The population of medium cells in the red nucleus also receive axonal input from the contralateral lateral (dentate) nucleus of the cerebellum (Pong 2008). Axons from these medium projection neurons join the rubrospinal tract and terminate in the cervical spinal cord, for head movement (Fig. 18–20). Also, as rubronuclear tract axons, they innervate cranial nerve nuclei to elicit facial movements (Pong, Horn and Gibson 2002).

The caudal, large-cell region of the red nucleus is somatotopically organized (Holstege and Tan, 1988). It receives afferent axons from the contralateral interpositus nucleus of the cerebellum and the ipsilateral motor cortex, including collateral branches of corticospinal axons. Corticorubral projections from the forelimb cortical area are twice as numerous as those from hindlimb area (Ipekchyan, 2008). Axons of the large projections neurons of the red nucleus move limb joints via the rubrospinal tract. Collateral branches of rubrospinal axons synapse in the **lateral reticular nucleus** (*nucleus reticularis lateralis*) which projects to the cerebellum. Also, rubrospinal neurons send reciprocal axons to the interpositus nucleus.

The **rubrospinal tract** (*tractus rubrospinalis*) is the main tract for voluntary movement in the dog (Brooks, 1986). Rubrospinal axons decussate immediately and proceed through the contralateral brainstem and spinal cord, within the dorsal half of the lateral funiculus. The axons terminate at all segments of the spinal cord. Via interneurons, the axons excite flexor and inhibit extensor motor units to the limbs (Massion, 1967). (Damage to the red nucleus produces moderate extensor hypertonia in an intact dog. In the absence of a forebrain, red nucleus

destruction results in decerebrate rigidity.)

The Diencephalon

The diencephalon forms the rostral extent of the brain stem. It is connected bilaterally to each cerebral hemisphere by a mass of corticopedal and corticofugal projection axons collectively termed the internal capsule (Fig. 18–21). The diencephalon can be divided into five regions: metathalamus, thalamus, subthalamus, hypothalamus, and epithalamus.

The **third ventricle** (*ventriculus tertius*) is a narrow chamber separating right and left halves of the diencephalon, except where the **interthalamic adhesion** *(adhesio interthalamica)* occupies the center of the ventricle (Fig. 18–22=14). The interthalamic adhesion contains thalamic nuclei but not commissural axons. The third ventricle communicates caudally with the mesencephalic aqueduct. Bilaterally a dorsolateral **interventricular foramen** (*foramen interventriculare*) allows the third ventricle to communicate with the lateral ventricle.

The rostral wall of the third ventricle is formed by **lamina terminalis** *(lamina terminalis grisea*). Combined ependyma and pia mater, constituting **tela choroidea** (*tela choroidea ventriculi tertii*), forms the roof of the third ventricle and gives rise to paired choroid plexuses. Each plexus in the third ventricle continues as the choroid plexus of a lateral ventricle. The lateral attachment of the thin ventricular roof along thalamus, is referred to as *tenia thalami.* Ventrally, the third ventricle exhibits an **optic recess (***recessus opticus),* between the optic chiasm and the lamina terminalis; a **neurohypophyseal (infundibular) recess** (*recessus neurohypophysis*), located within the infundibulum of the neurohypophysis; and an **inframamillary recess** *(recesses inframamillaris)*, rostroventral to the mamillary bodies (Fig. 18–22=14).

The third ventricle contains several **circumventricular organs**, areas where the blood

supply is enriched, the blood-brain barrier is reduced (fenestrated capillaries), and ependymal cells assume glandular or baroreceptor/chemoreceptor roles: The **subcommissural organ** (*organum subcommissurale*) refer to thickened secretory ependyma located ventral to the caudal commissure (Fig. 18–19). The **subfornical organ** (*organum subfornicale*) is located ventral to the fornix (Akert et al., 1961); it controls salt intake behavior (Hiyama et al., 2004). Other secretory/sensory cells are found in the lamina terminalis (*organum vasculosum laminae terminalis griseae*) and in the ventricular wall of the hypothalamus (*organum vasculosum hypothalami*). (An additional circumventricular organ (*area postrema*) is located at the caudal end of the fourth ventricle.)

The diencephalons is commonly divided into four topographic regions: thalamus, metathalamus, hypothalamus, epithalamus, and subthalamus:

THE THALAMUS. The thalamus is closely linked to the cerebral cortex, via reciprocal connections. Thalamic projections to the cerebral cortex provide background cortical excitation to maintain wakefulness, convey ascending tract information concerning sensory modalities (except olfaction), and deliver input affecting emotional/affective behavior. Thalamocortical circuits are essential for movement. The circuits involves cerebellar and basal nuclear input to thalamic nuclei that, in turn, project to motor cortices.

Typically, individual thalamic nuclei contain excitatory projection neurons and inhibitory interneurons. In the canine thalamus, eighteen nuclei have been histologically distinguished and arranged into several defined groups (Salazar et al., 1989) (Fig. 18-23).

An **external medullary lamina** (*lamina medullaris thalami externa*) separates the **reticulate thalamic nucleus** (*nucleus reticulatus thalami*) from the other thalamic nuclei (Fig. 18–21). The reticulate nucleus is unusual. Its projection neurons are inhibitory and they target

other thalamic nuclei rather than cerebral cortex. Input to the reticulate nucleus comes from collateral branches of thalamic axons projecting to the cerebral cortex, also from collateral branches of reciprocal axons originating in the cerebral cortex (layer VI). The collateral branches excite reticulate neurons that, in turn, inhibit projection neurons within the source thalamic nuclei (Willis, 1985).

An **internal medullary lamina** (*lamina medullaris thalami interna*) divides thalamic nuclei into rostral, lateral and medial nuclear groups (Berman and Jones, 1982; Salazar et al., 1989). Additionally, the lamina contains **intralaminar thalamic nuclei** (*nuclei intralaminares thalami*) arranged in a rostral group (central medial, paracentral, and central lateral nuclei) and a caudal group (centrum medianum and parafascicular nuclei). Intralaminar nuclei project axons broadly to superficial layers of cerebral cortex and provide background excitation that keeps the cerebral cortex awake and alert (Steriade and Llinas, 1988). The nuclei are activated by ascending axons from the midbrain reticular formation. Intralaminar nuclei also receive input from cholinergic brainstem neurons, cerebral cortex, cerebellum, basal nuclei, and spinal cord. The centrum median nucleus projects to the putamen basal nucleus.

Three nuclei (rostral dorsal, rostral medial, and rostral ventral) comprise **rostral thalamic nuclei** (*nuclei rostrales thalami*) (Fig. 18-24). This nuclear group is associated with affective behavior and has reciprocal connections with the cingulate gyrus of the limbic system. Axonal input comes from the hippocampus via the fornix and from the mamillary body via the mamillothalamic tract.

The **lateral thalamic nuclei** (*nuclei laterales thalami*) may be subdivided into dorsocaudal and ventral groups. The dorsocaudal group includes: **lateral dorsal nucleus** (*nucleus lateralis dorsalis*), **lateral caudal nucleus** (*nucleus lateralis caudalis*), and the

pulvinar nucleus (*nucleus pulvinaris*). The lateral dorsal nucleus has connections similar to rostral thalamic nuclei and thus seems to have an affective behavior role. The lateral caudal and pulvinar nuclei are involved in selective visual attention. They receive input from the retina, tectum, and primary visual cortex. They project to visual association areas of the cerebral cortex (Berman and Jones, 1982).

Four nuclei constitute the ventral group of lateral thalamic nuclei: The **ventral rostral nucleus** (*nucleus ventralis rostralis*) receives inhibitory input from basal nuclei circuits (via the endopeduncular nucleus and substantia nigra reticulata). The nucleus projects axons predominantly to the supplementary motor cortex and the premotor cortex. The **ventral lateral nucleus** (*nucleus ventralis lateralis*) receives excitatory input from cerebellar nuclei and projects axons primarily to the motor cortex (Sakai et al, 1993). These two thalamic nuclei participate in voluntary movement selection and execution, via circuits involving motor cortices, basal nuclei, and cerebellar nuclei (Brooks, 1986). The **ventral medial nucleus** (*nucleus ventralis medialis*), situated surrounding the mammillothalmic tract, receives axonal input from basal nuclei and the cerebellum and projects axons to superficial laminae of motor-related cortices (Kosmal, 1986 and Sakai et al, 1993).

The **ventral caudal nucleus** (*nucleus ventralis caudalis*) relays information from cutaneous and proprioceptive receptors to primary and secondary somesthetic areas of the cerebral cortex. The nucleus is distinguished by the axon bundles that penetrate it. The lateral part of the nucleus (pars lateralis) receives axonal input from the body via the medial lemniscus. The medial part (pars medialis) receives axonal input from the face via the trigeminal lemniscus. Neurons at the medial edge of the nucleus receive taste information. Spinothalamic tract axons terminate within a transition region between the ventral caudal and the ventral lateral thalamic

nuclei, on neurons that respond to large receptive fields, multiple modalities, and noxious stimulation (Bessen and Chaouch, 1987; Willis, 1986).

The **dorsomedial thalamic nucleus** (*nucleus dorsomedialis thalami*) receives input from the hypothalamus, amygdala, endopeduncular nucleus, and prefrontal cortex. The nucleus projects output to the prefrontal cortex, which is anatomically defined as cortex receiving projections from the dorsomedial thalamic nucleus. (The prefrontal cortex is essential for planning motivated behavior.)

Paraventricular thalamic nuclei (*nuclei paraventriculares thalami*) are midline nuclei found along the wall of the third ventricle and in the interthalamic adhesion. These nuclei (reuniens, rhomboid, paratenial, and paraventricular nuclei) are functionally diverse (Berman and Jones, 1982). They project to the hypothalamus, hippocampal formation, and nucleus accumbens. Thus they are involved in affective behavior.

THE METATHALAMUS. The metathalamus consists of medial and lateral geniculate bodies (nuclei), which function like thalamus but are specialized for hearing and vision, respectively (Fig. 18–19).

The **medial geniculate body** (*corpus geniculatum mediale*) comprises the caudal extent of the diencephalon (Fig. 18–4=4). It is attached to the lateral surface of the midbrain and covered dorsally by brachium of the rostral colliculus. When sectioned, the geniculate body presents a round profile, designated **medial geniculate nucleus** (*nucleus geniculatus medialis*). Ventral magnocellular neurons in the nucleus project to primary auditory cortex; dorsal parvocellular neurons project to auditory association cortex. Primary and association auditory areas of the cerebral cortex are essential for pattern recognition and sound-significance interpretation. Projection axons reach the neocortex via the **acoustic radiation** (*radiatio*

acustica) of the internal capsule.

The *brachium of the caudal colliculus* conveys auditory axonal input to the medial geniculate nucleus. Most of the axons in the brachium originate from the *caudal colliculus*, the *lateral lemniscus* contributes the remaining axons. Neurons are tonotopically organized within the medial geniculate nucleus (as they are in most nuclei of the auditory pathway). At the level of the medial geniculate nucleus, the intensity of different tones can be distinguished but not temporal relationships (Mountcastle, 1980). Axons from auditory cortex (layer VI axons and layer V collateral branches) reciprocally feed back to the medial geniculate nucleus.

The **lateral geniculate body** (*corpus geniculatum laterale*) is located dorsal, rostral, and slightly lateral to the medial geniculate body (Fig. 18–19). The **lateral geniculate nucleus** (*nucleus geniculatus lateralis*) contains excitatory (glutaminergic) projection neurons and inhibitory (GABAergic) interneurons (typical for thalamic nuclei). The nucleus receives axons from the visual cortex and the optic tract. Retinal axons from large ganglion cells (size/direction vision) and axons from small ganglion cells (detail/color vision) synapse on separate population of geniculate projection neurons, as does a third type of ganglion cell associated with the *tapetum lucidum* and dim vision.

The lateral geniculate nucleus has dorsal and ventral parts. The *ventral part* (*pars ventralis*) is smaller and has reciprocal connections with the rostral colliculus and pretectal region; it also projects to the suprachiasmatic nucleus of the hypothalamus.

The *dorsal part* (*pars dorsalis*) of the canine lateral geniculate nucleus has neuron cell bodies arranged in six layers plus a medial interlaminar nucleus (Lee, Kim, Lee 1999). Right and left eyes terminate in alternate cell layers. From superficial to deep, layers 1, 3, 5 receive axons from the contralateral eye, remaining layers receive ipsilateral eye input. Superficial layers

receive axons from both large and small ganglion cells, deeper layers from just large ganglion cells, and deepest layers receive the dim vision axons. The latter also synapse in the medial interlaminar nucleus which exhibits four vertical layers.

The lateral geniculate nucleus has a rostrolateral "hilus" through which axons of the **optic radiation** (*radiatio optica*) reach the internal capsule and travel to and from the visual cortex. The lateral geniculate nucleus connects mainly with the primary visual cortex (the pulvinar thalamic nucleus connects heavily with visual association cortex).

The **retina** and **optic nerve** (*nervus opticus*) originate from the diencephalon during embryonic development and, histologically, they are central nervous system. Axons from ganglion cells of the retina comprise the optic nerve which begins at the optic disc of the eye (where the axons become myelinated). Approximately 75 per cent of axons in the canine optic tract decussate at the **optic chiasm** (de Lahunta, 1983). From the chiasm, axons continue as **optic tract** (*tractus opticus*) and terminate in the *lateral geniculate nucleus* (Fig. 18–17=17). Some axons leave the optic tract to form the **brachium of the rostral colliculus** *(brachium colliculi rostralis)***,** which contributes axons to the rostral colliculus, pretectal region, and *transverse crural tract* on the lateral surface of the midbrain.

THE HYPOTHALAMUS. The hypothalamus is situated ventral to the thalamus and medial to the subthalamus. It occupies the floor and the wall of the third ventricle (Figs. 18–22=22, Fig. 18-24). A *sulcus hypothalamicus* along the ventricular wall delineates the dorsal boundary of the hypothalamus. The ventral surface of the diencephalon shows only hypothalamic structures: *optic chiasm* rostrally, *tuber cinereum* at the level of the hypophysis, and bilateral *mamillary bodies* caudally (Fig. 18–3=3).

The ***tuber cinereum*** is the swollen region of the ventral hypothalamic surface. It gives

rise to an **infundibulum** with an attached **neural lobe** (*lobus nervosus*). Together these constitute the **neurohypophysis**. The neurohypophysis and the adenohypophysis that surrounds it comprise the ***hypophysis*** (pituitary gland). The infundibulum itelf may be subdivided into a root *(radix)* that arises from the tuber cinereum, a *pars cava* that contains the infundibular recess of the third ventricle, and a distal *pars compacta* that joins the neural lobe.

By controlling the hypophysis, the hypothalamus supervises endocrine secretion. Hypothalamic neurons of two nuclei (paraventricular & supraoptic) send axons directly into the neurohypohysis where they each release vasopressin and oxytocin hormones. Other nuclei send axons to the tuber cinereum where various releasing hormones are secreted and captured by hypothalamic capillaries. Hypothalamic-hypophyseal portal veins convey the releasing hormones to the adenohypophysis where they selectively trigger specific pituitary cells to secrete particular hormones.

The hypothalamus is involved in maintaining homeostasis, including blood electrolytes/osmolarity, body temperature, feeding/drinking behavior, and circadian cycling plus the sleep/awake cycle. Some hypothalamic neurons are sensitive to constituents in circulating blood (osmolarity, electrolytes, hormones, glucose, and temperature). Neurons of the rostral hypothalamus are concerned with lowering body temperature, and those in the caudal hypothalamus with conserving heat. Lesions damaging these areas would cause hyperthermia and hypothermia, respectively.

The hypothalamus plays a major role in displaying affective behavior. It contributes to behavioral expressions associated with rage, escape, pleasure, reproductive behavior, and response to stress. The hypothalamus controls the autonomic nervous system. It participates in regulation of cardiovascular, respiratory, gastrointestinal, and urinary organs. Stimulation

applied rostrally in the hypothalamus generally produces parasympathetic responses; caudal stimulation evokes sympathetic activity.

The hypothalamus has widespread brain connections. It receives axons from the optic tract. Axons arrive from the limbic system via the ***fornix*** (hippocampus) and ***stria terminalis*** (amygdala). The prefrontal cortex, septal region and olfactory nuclei contribute axons to the **medial forebrain bundle** (*fasciculus medialis telencephali*), which courses through the lateral hypothalamus and continues on, even to the level of the spinal cord. Hypothalamic axons to visceral efferent nuclei in the brain stem travel through the **dorsal longitudinal fasciculus** (*fasciculus longitudinalis dorsalis*). Hypothalamic commissural axons connect right and left sides. Reciprocal hypothalamic connections with the thalamus and midbrain are present, particularly via tracts involving the mamillary body.

The hypothalamus may be divided sagittally into lateral and medial zones plus a periventricular layer along the ventricular wall. The periventricular layer contains axons that connect the hypothalamus to the thalamus and brainstem. Some periventricular neurons trigger hormone release from the adenohypophysis via axons that run to the tuber cinereum. The majority of hypothalamic nuclei are in the medial sagittal zone. The lateral zone has fewer nuclei but more axon tracts (Fig. 18-25).

The hypothalamus is commonly divided into three transverse regions: a caudal region that includes the mamillary body; an intermediate (tuberal) region at the level of the tuber cinereum; and a rostral region that is dorsal to the optic chiasm and bounded rostrally by lamina terminalis. (The rostral region includes preoptic nuclei derived embryologically from the telencephalon.) Within the hypothalamus, loose collections of neurons are considered an “area” and more dense, discrete neuron clusters are recognized as “nuclei.” Hypothalamic nuclei per

transverse region include the following (Fig. 18-25):

Preoptic nuclei (*nucleus preopticus lateralis, nucleus preopticus medialis, nucleus preopticus medianis, and nucleus preopticus periventricularis*) are the most rostral hypothalamic nuclei (Fig. 18-26). They are associated with parasympathetic activity, including micturition and erection. The ***nucleus hypothalamicus rostralis*** is involved in body temperature reduction (panting, sweating, etc.). The **suprachiasmatic nucleus** (*nucleus suprachiasmaticus*), located dorsal to the optic chiasm, beside the midline, receives retinal input and controls circadian rhythms (e.g., body temperature, sleep/wakefulness, hormone levels, etc.).

The **paraventricular nucleus** (*nucleus paraventricularis*) and **supraoptic nucleus** (*nucleus supraopticus*) are located at the level of the optic chiasm. Axons from these nuclei form a **paraventriculohypophyseal tract** (*tractus paraventriculohypophsialis)* and a **supraopticohypophyseal tract** (*tractus supraopticohypophysialis)*. Axons of both tracts pass through the infundibulum to terminate in the neural lobe of the neurohypophysis. Neurons of both nuclei produce vasopressin (ADH) and oxytocin hormones. The hormones are packaged in secretory vesicles, actively transported along microtubules, and stored in axon terminals. Following secretion in response to arriving action potentials, the hormones are taken up by blood circulating within fenestrated capillaries.

The **intermediate hypothalamic region**, where the tuber cinereum is located, contains the **infundibular** or **arcuate nucleus** (*nucleus infundibularis*), **lateral tuberal nuclei** (*nuclei tuberis laterales*) and **periventricular nuclei**. These nuclei send axons to the tuber cinereum where the axons secrete peptides that are transported by blood to the adenophypophysis where they trigger hormone release. Some of the axons constitute a *tractus tuberohypophysialis* that secretes releasing hormones within the infundibulum.

The medial zone of the intermediate region contains a **dorsomedial hypothalamic nucleus** (*nucleus hypothalamicus dorsomedialis*) and a **ventromedial hypothalamic nucleus** (*nucleus hypothalamicus ventromedialis*). The latter is concerned with satiety, and lesions affecting it result in voracious appetite leading to hyperphagia and obesity. The adjacent **lateral hypothalamic nucleus** and area act as a feeding center. Damage causes anorexia and weight loss.

The caudal hypothalamic region features the **mamillary body** (*corpus mamillare*), visible at the caudoventral surface of the diencephalon. The body is composed of a large medial nucleus (*nucleus mamillaris medialis*) and a small lateral nucleus (combined *nucleus mamillaris lateralis and nucleus mamillaris cinereus*). The medial nucleus consists of small neurons organized into several subnuclei; the lateral nucleus has large neurons in two subnuclei (Fig. 18–21).

Mamillary nuclei receive axons from the hippocampus via the fornix, and they project axons to the rostral group of thalamic nuclei via a prominent **mamillothalamic tract** (*tractus mamillothalamicus*). Damage to the tract or to mamillary nuclei results in impaired working memory (diencephalic amnesia) (Vann and Aggleton, 2004). Reciprocal connections with midbrain tegmental nuclei are conveyed by the **mamillotegmental tract** (*tractus mamillotegmentalis*) and the **mamillary peduncle** (*pedunculus mamillaris*).

Additional nuclei of the caudal hypothalamus include several that project to mamillary nuclei: *nucleus periventricularis caudalis*, *nucleus supramamillaris*, and *nucleus premamillaris*. The *nucleus perifornicalis* refers to neurons surrounding the column of the fornix. The **caudal hypothalamic nucleus** drives sympathetic activity.

THE EPITHALAMUS. The epithalamus includes the pineal gland and the habenula

with its associated tracts. The **pineal gland** (*glandula pinealis*) is small in the dog (Fig. 18–4=4; Fig. 18–22=18). It is a midline endocrine gland situated between the habenular nuclei and the caudal commissure, extending caudally from the pineal recess of the third ventricle. The gland is composed of pinealocytes and glial cells contained within connective tissue trabeculae derived from meninges. Having fenestrated capillaries, the pineal gland lacks a blood brain barrier.

Pinealocytes secrete melatonin which promotes sleep and suppresses hypothalamic secretion of gonadotropin releasing hormone, causing suppression of sexual development. Melatonin production is inhibited by darkness and exhibits circadian rhythm. The gland is innervated by postganglionic sympathetic axons from cell bodies in the cranial cervical ganglion. The postganglionic neurons are activated in response to optic tract axonal input to the suprachiasmatic nucleus of the hypothalamus. The nucleus projects to the midbrain and, via the tectotegmentospinal tract, it reaches sympathetic preganglionic neurons in the spinal cord. Reciprocal connections between the pineal and habelula also exist.

The **habenula** is located caudally in the diencephalon, on the dorsomedial border of the thalamus (Fig. 18–21). Right and left habenulae are connected by a **habenular commissure** (*commissura habenularum*). The habenula is composed of medial and lateral **habenular nuclei** (*nuclei habenulares*), each having four subnuclei (Janklewicz, 1967). The medial nucleus has mainly limbic connections. The lateral nucleus is inhibited by basal nuclei.

The **habenular stria** (*stria habenularis thalami*), which courses along the dorsomedial margin of the thalamus (Fig. 18-24), conveys axons to habenular nuclei from basal nuclei, hypothalamus, and the rhinencephalon (septum, amygdala, and preoptic area). Axons from habenular nuclei travel via the ***fasciculus retroflexus*** (formerly habenulointerpeduncular tract) to the interpeduncular nucleus, to serotonergic raphe nuclei and to dopaminergic nuclei (substantia

nigra compacta and ventral tegmental area).

The habenula suppresses movement via inhibition of dopamine release. During adversity, the habenula exhibits neuronal activity linking the limbic forebrain with serotonergic and dopaminergic brainstem nuclei that neuromodulate brain function in relation to emotional status (pain, stress, reward, sleep, etc.). The habenula is involved in threat-induced movement freeze (dopamine effect) and in the movement atonia associated with REM sleep (serotonin effect).

THE SUBTHALAMUS. The subthalamus is the diencephalic region ventral to the thalamus and lateral to the hypothalamus. It contains the zona incerta, subthalamic nucleus, and white matter fields that border these nuclei (three H fields of Forel). The white matter fields are composed of basal nuclei axons traveling to thalamic nuclei or the red nucleus. *Note:* The endopeduncular nucleus may be included with the subthalamus (Nomina Anatomica Veterinaria 2005) or with the cerebrum. In this chapter it described with the cerebrum.

The **zona incerta** appears as a ventromedial extension of the thalamic reticulate nucleus, bounded dorsally by the axons of field H_1 (of Forel) and ventrally by field H_2 (Fig. 18–21). Via spontaneously active inhibitory neurons, the zona incerta suppresses activity in ventral caudal thalamic nuclei that relay sensory information to the neocortex. Pain behavior is a consequence of zona incerta damage. Brainstem cholinergic neurons (pedunculopontine nucleus) suppress zona incerta inhibition during activation of brainstem ascending alerting pathways.

The **subthalamic nucleus** *(nucleus subthalamicus)* is situated in the caudal diencephalon, ventromedial to the zona incerta, dorsomedial to the crus cerebri, and rostral to substantia nigra (Fig. 18–21). It contains inhibitory interneurons and excitatory projection neurons. Axons from prefrontal and motor cortices excite subthalamic neurons.

In response to cortical input, the subthalamus suppresses unwanted movements by

exciting the inhibitory neurons of endopeduncular nucleus. Premature movements result from damage to the subthalamus. An indirect basal nuclear pathway involving globus pallidus inhibition of subthalamic neurons is sensitive to dopamine and cholinergic neuromodulation. The subthalamic nucleus may play a pacemaker role within movement control circuits, since it fires spontaneous bursts of action potentials with regular frequency.

THE CEREBRUM

The **cerebrum** consists of paired cerebral hemispheres, derived from the embryonic telencephalon. A **cerebral transverse fissure** (*fissura transversa cerebri*) separates the cerebrum from the cerebellum. A **cerebral longitudinal fissure** (*fissura longitudinalis cerebri*) (Fig. 18–27=25; Fig. 18–28=35) separates right and left hemispheres except where they are connected across the midline by lamina terminalis and commissural axons of the corpus callosum, rostral commissure, hippocampus and fornix. The ***lamina terminalis***, once the rostral end of the embryonic neural tube, forms the rostral wall of the third ventricle (*lamina terminalis grisea*). The rostral commissure decussates in the lamina terminalis (*lamina terminalis alba*).

CEREBRAL HEMISPHERE. Each hemisphere is composed of surface gray matter, designated **cerebral cortex** *(cortex cerebri),* underlying **cerebral white matter** (Fig. 18–32=32), deep accumulations of gray matter called **basal nuclei,** and a **lateral ventricle** filled with cerebrospinal fluid (Fig. 18–29). The ventral region of the hemisphere is called the ***rhinencephalon*** because of its olfactory role (Fig. 18–30). Many **limbic system** structures (emotion and affective behavior conmponents) are within the rhinencephalon.

The surface of each cerebral hemisphere features elevated bands, called gyri (*gyri cerebri*), separated by grooves, called sulci (*sulci cerebri*). Generally, the name of a *gyrus* is the

same as its adjacent *sulcus* (Fig. 18–30; Fig. 18–31=28). The rostral end of the hemisphere is called the **frontal pole** (*polus rostralis*), and the caudal end is called the **occipital pole** (*polus caudalis*). The hemispheric region deep to the frontal bone can be referred to as the frontal lobe. Lobe terminology could be applied in relation to the parietal, occipital, and temporal bones; however, these lobar designations lack functional utility in the dog.

Three kinds of cerebral cortex (*pallium*) are distinguished per hemisphere. **Archicortex (***archipallium***)** is associated with the hippocampus (a component of the rhinencephalon). **Paleocortex (***paleopallium***)**, also found in the rhinencephalon, has three layers. **Neocortex (*neopallium*)**, the predominant cortex of the cerebrum, has six layers. The term **isocortex** refers to neocortex and **allocortex** refers to all the other types, including transitions among the above types.

The white matter of each cerebral hemisphere, consists of myelinated axons categorized as association, commissural, or projection axons (Fig. 18–33=33; Fig. 18–34=34). **Association axons** connect cortical regions within the same hemisphere. They are differentiated as long vs short. **Commissural axons** cross the midline, connecting the two hemispheres via the corpus callosum for the neocortex and the rostral commissure for the rhinencephalon. Viewed in a bisected brain, the **corpus callosum** presents an elongate trunk region (***truncus corporis callosi*)** that has a blunt caudal end **(*splenium*)** and a rounded rostral end **(*genu*)** that continues ventrally **(*rostrum*)** (Fig. 18–35=29). The divergence of the commissural axons dorsal to the lateral ventricle constitutes the *corpus callosum radiation* (*radiatio corporis callosi*).

Projection axons either enter the neocortex (corticopedal), typically from the thalamus, or they exit the neocortex (corticofugal) to terminate in the basal nuclei, brainstem, or spinal cord (Fig. 18–36=19). Projections axons run in the **internal capsule** (*capsula interna*) or in the

external capsule (*capsula externa*), the latter also contains rostral commissure axons (Fig. 18-26). The term ***centrum semiovale*** refers to the region of central white matter where radiations from the corpus callosum and internal capsule converge. ***Corona radiata*** refers to the collective white matter extensions that radiate from the centrum semiovale into individual cortical gyri.

The **lateral ventricle** (*ventriculus lateralis*) within each cerebral hemisphere communicates with the third ventricle through an **interventricular foramen** (*foramen interventriculare*) (Fig. 18-26). Each lateral ventricle has a choroid plexus that passes through the interventricular foramen and continues along the roof of the third ventricle. Each choroid plexus arises from tela choroidea (combined pia mater and ependyma) having a linear attachment called ***tenia choroidea*** or ***tenia fornicis*** (pending attachment location). Choroid plexuses are the source of cerebrospinal fluid.

The lateral ventricle is extended rostroventrally by a **rostral horn** (*cornu rostrale*) and caudoventrally by a **temporal horn** (*cornu temporale*) (Fig. 18–35=29). Typically, the rostral horn loses its connection to the olfactory ventricle (recess) located within the olfactory bulb and peduncle of the rhinencephalon (Fitzgerald, 1961).

THE RHINENCEPHALON. Rhinencephalon refers to the ventral region of each cerebral hemisphere. It is phylogenetically old and concerned with olfaction, memory formation, and emotional behavior. The rhinencephalon is separated from neocortex by rostral and caudal parts of the **lateral rhinal sulcus** (*sulcus rhinalis lateralis)* along the lateral surface of the cerebral hemisphere (Fig. 18–30). A **medial rhinal sulcus** *(sulcus rhinalis medialis)* separates the olfactory peduncle from the neocortical of the straight gyrus along the medial surface of the hemisphere.

The rhinencephalon has three defined parts: a **basal part** *(pars basalis rhinencephali)*,

consisting of the olfactory bulb and the superficial ventral portion of the hemisphere; a **septal part** *(pars septalis rhinencephali)*, composed of structures that rostrally form the medial wall of the lateral ventricle; and a **limbic part** *(pars limbica rhinencephali)*, strickly defined as being the hippocampus. The term **Limbic System** refers to circuits of neocortical, rhinencephalic, and brainstem components involved in memory, emotions, and affective behavior. It includes structures from all three parts of the rhinencephalon.

OLFACTORY PATHWAYS. The olfactory pathway starts with bipolar special visceral afferent neurons located in the **olfactory mucosa**. The neurons have long cilia embedded in olfactory mucus. The cilia have receptors that are sensitive to odorants trapped by the mucus. Nonmyelinated axons from the bipolar neurons collect into bundles that pass through the cribriform plate as **olfactory nerves**. The nerves terminate in the *olfactory bulb*, which is attached to the cerebral hemisphere by the *olfactory peduncle* (Fig. 18–3=3). The bulb and peduncle are hollow, containing an *olfactory ventricle* filled with cerebrospinal fluid.

Seven histologic layers comprise the wall of the **olfactory bulb** (*bulbus olfactorius*). From superficial to deep, they are: (1) an olfactory nerves layer; (2) a layer of glomeruli (multiple olfactory axons synapse with an individual mitral cell within a glomerulus); (3) an external plexiform layer; (4) a mitral cell layer (conical neuron cell bodies aligned in a row); (5) a thin internal plexiform layer; (6) a granule cell layer (granule cells are inhibitory interneurons); and (7) a periventricular layer, composed of axons leaving or entering the bulb (Berman and Jones, 1982). Mitral cell axons joining olfactory tracts constitute olfactory bulb output.

Axons from the **vomeronasal organ** accompany those from the olfactory mucosa through the cribriform plate. They terminate in the accessory olfactory bulb, embedded in the dorsomedial surface of the olfactory bulb. The **accessory olfactory bulb** (*bulbus olfactorius*

accessorius) is small, but it has a layered structure similar to that of the olfactory bulb. The accessory bulb has reciprocal connections with the amygdala. The vomeronasal organ detects pheromones that influence sexual behavior.

The **olfactory peduncle** (*pedunculus olfactorius*) extends from the olfactory bulb to the level of the *olfactory tubercle* (see Fig. 18–35). It is separated from the frontal lobe as medial and lateral rhinal sulci that meet dorsal to the peduncle. The olfactory peduncle contains an olfactory ventricle surrounded by three olfactory tracts and a three-layered paleocortex designated rostral olfactory nucleus.

The **lateral olfactory tract** (*tractus olfactorius lateralis*) conveys mitral axons destined for the rostral olfactory nucleus, olfactory tubercle, nucleus of the lateral olfactory tract, amygdala, and cortices of the lateral olfactory gyrus and piriform lobe. The **medial olfactory tract** (*tractus olfactorius medialis*) conveys axons to the septal region, including septal nuclei and the paraterminal gyrus. The **intermediate olfactory tract** (*tractus olfactorius intermedius*) channels axons through the rostral commissure to the contralateral olfactory bulb, connecting to the rostral limb of the commissure. The tract contains axons that are afferent and efferent per ipsilateral olfactory bulb.

The **olfactory tubercle** (*tuberculum olfactorium*) is a ventral bulge region located caudal to the olfactory peduncle and rostral to the diagonal gyrus (Figs. 18–28=35; Fig. 18–30). It is separated from the lateral olfactory tract by an *endorhinal sulcus.* The tubercle consists of a three-layered cortex that sends axons to the hypothalamus via the medial forebrain bundle. (Note: The terms *rostral perforated substance* (olfactory tubercle and the diagonal gyrus areas) and *olfactory trigone* are inappropriate for macrosomatic animals such as the dog (Nomina Anatomica Veterinaria 2005).

The **diagonal gyrus** (*gyrus diagonalis*) is between the olfactory tubercle and the optic chiasm and tract. It is continuous with the paraterminal gyrus of the septum (Fig. 18–30). The two gyri contain the *diagonal lamella* (*lamella diagonalis*; diagonal band of Broca). Axons of the lamella join the **medial forebrain bundle** (*fasciculus medialis telencephali*) to convey information from olfactory-related nuclei to the hypothalamus. Also deep to the diagonal gyrus, the **basal nucleus** (of Meynert) contains large cholinergic neurons that project broadly to cerebral cortex to enhance cortical activity via neuromodulation.

The **piriform lobe** (*lobus piriformis*) is concerned with conscious olfaction. It receives mitral axons from the olfactory bulb via the *lateral olfactory tract*. The piriform lobe consists of a flat rostral part demarcated from the swollen caudal part by a fossa (*fossa lateralis cerebri*) (Figs. 18–28=35; Fig. 18–30). The rostral part is bounded by the olfactory tubercle. It includes the **lateral olfactory gyrus** (*gyrus olfactorius lateralis*), which is prepiriform paleocortex.

The swollen caudal part of the piriform lobe bulges due to the underlying amygdala, hippocampus and lateral ventricle. The bulge is covered by different types of cortex. The rostral third of the piriform swelling features prepiriform paleocortex laterally and cortical nuclei of the amygdala medially. The caudal two thirds is coated by ***entorhinal cortex***, identifiable histologically by cell clusters in layer two of approximately six layers (Woznicka, et al. 2006). Entorhinal cortex blends medially with subicular and hippocampal archicortex with which it reciprocally communicates (Fig 18-37). The pirifom lobe is continued caudally by the **parahippocampal gyrus** (*gyrus parahippocampalis*), which is also covered by entorhinal cortex. The clustered neurons comprising layer two of entrorhinal cortex send their axons to the adjacent, attached hippocampus.

The **amygdala** (amygdaloid body), which is named for its almond shape, is located

within the piriform lobe. The amygdaloid complex contains about a dozen nuclei, including six major ones arranged in three groups (Fig. 18–21). A basolateral group (*nucleus basalis* and *nucleus lateralis*) receives sensory input. A cortical group (*nucleus corticalis* and *nucleus tractus olfactorii lateralis*) and the ventral tip of the hippocampus occupy the rostromedial surface of the caudal part of the piriform lobe. A centromedial group (*nucleus centralis* and *nucleus medialis*) contains output neurons. (Berman and Jones, 1982; …).

The amygdala assigns emotional reactions, particularly fear-related ones, to sensory information. It is major component of the limbic system. The amygdala receives axonal input from the lateral olfactory tract, the hippocampus, the rostral hypothalamus and, via the external capsule, areas of neocortex. Axonal output from the amygdala goes to the piriform cortex, hippocampal formation, dorsomedial thalamic nucleus, nucleus accumbens, and hypothalamus. Also, the amygdala has direct projections to the midbrain and pontomedullary reticular formation. The ***stria terminalis*** is a slender tract that connects the amygdala to the rostral hypothalamus and septal region (Fig. 18–35=29). A *nucleus of the stria terminalis* is associated with the rostral end of the stria.

THE SEPTUM. The **septal region** is located anterior to the rostral commissure and ventral to the genu and rostrum of the corpus callosum. A thin, variable, septum pellucidum (*septum telencephali pellucidum*) connects the thick cellular septum (*septum telencephali cellulare*) to the corpus callosum and continues caudally to fill the space between the corpus callosum and fornix. The septal region forms a medial wall of the lateral ventricle (Fig. 18–29). The cellular septum is a potent reward site of the Limbic System.

The **paraterminal gyrus** (*gyrus paraterminalis*) marks the medial surface of the septal wall and **septal nuclei** *(nuclei septi)* are content within the wall (Fig. 18–30). The nuclei receive

axonal input from the medial olfactory tract. They have reciprocal connections with the amygdala (via the stria terminalis), hippocampus (via the fornix), hypothalamus (via the medial forebrain bundle) and the habenula (via the stria habenularis).

The **rostral commissure** (*commissura rostralis*) traverses the lamina terminalis. Its axons connect the right and left rhinencephalon (Fig. 18-26). The **rostral part** (*pars rostralis*) of the commissure courses anteriorly along the ventral edge of the internal capsule and enters the olfactory peduncle, becoming **intermediate olfactory tract** (*tractus olfactorius intermedius*). The axons reciprocally connect olfactory bulbs and rostral olfactory nuclei of each side; they terminate on granule cells of the olfactory bulb. Axons of the **caudal part** (*pars caudalis*) of the rostral commissure join the external capsule. They reciprocally connect the amygdala and piriform lobe bilaterally.

HIPPOCAMPAL FORMATION. The hippocampal formation (hippocampus) is a principal component of the Limbic System. It is necessary for long-term memory formation (though not long-term memory recall). It is essential for spatial memory (a dog recalling how it got where it is and how to return whence it came).

Phylogenetically and during embryonic development, three parts of the hippocampus can be identified. The *pars precommissuralis*, located rostral to the corpus callosum, blends with the parterminal gyrus and is not otherwise evident in the mature brain. The *pars supracommissuralis* persists as thin gray band around the corpus callosum, forming: *gyrus geniculi* (ventral to the rostrum), *supracallosal gyrus* (around the genu), and ***indusium griseum*** (along the dorsal surface of the corpus callosum, within the callosal sulcus). The *pars retrocommissuralis* becomes the prominent archicortex complex referred to as hippocampal formation (Fig. 18–38=37).

The term **hippocampus** is subject to varying interpretations, but typically it is a synonym

for **hippocampal formation**. The **hippocampal formation** consists of the ***dentate gyrus***, ***hippocampus proper***, and ***subiculum***. These are sequential regions joined together as infolded cortex, connected to and tucked deep to the piriform lobe and parahippocampal gyrus (Fig 18-37).

The **dentate gyrus** (*gyrus dentatus*) is three-layered archicortex (molecular, granular cells, and polymorph cells) embedded into the concavity of the hippocampus proper. **The hippocampus proper** (*pes hippocampi, cornu ammonis*) is a gyrus folded concave medially. It is archicortex composed of three major layers: (1) molecular, (2) double pyramidal cells, and (3) polymorph cell layer. The gyrus is divisible into four zones (CA1 at the subiculum to CA4 at the dentate gyrus) (Fig 18-37).

The **subiculum** is composed of variable layers. It is a major source of hippocampal output to the adjacent entorhinal cortex of the piriform lobe and parahippocampal gyrus. A transitional gyrus designated *prosubiculum* is situated between the hippocampus proper and the subiculum. The terms *presubiculum* and *parasubiculum* refer to transitional regions between the subiculum and entorhinal cortex.

Grossly, the hippocampal formation makes a rostrally concave semicircle that forms the medial wall of the temporal horn of the lateral ventricle (Fig. 18–38=37). The ventral tip of the hippocampus, *hippocampal tuberculum* (*tuberculum hippocampi*), is located beside the amygdala deep to the rostromedial surface of the caudal part of the piriform lobe. Dorsally, a prominent *tubercle of the dentate gyrus* is evident where the hippocampal formation ends ventral to the splenium of the corpus callosum (Fig. 18–30). The term *gyrus fasciolaris* refers to a continuity between the dentate tubercle and indusium griseum encircling the splenium.

The hippocampal formation has reciprocal connections with entorhinal cortex of the

piriform lobe and parahippocampal gyrus with which it is continuous. The hippocampal formation also sends axons to the septum and diencephalon via the fornix. Input to the hippocampal formation includes axons from the septum, amygdala, thalamus, brain stem, and contralateral hippocampus, plus neuromodulatory input from various sources (serotonin, norepinephrine, dopamine and acetycholine).

Axons to the fornix arise from double pyramidal cells of the hippocampus proper. They join the **alveus** *(alveus hippocampi),* a surface layer of axons deep to the ependyma of the lateral ventricle. The axons continue, as the **fimbria** *(fimbria hippocampi)*, which forms a ledge along the lateral surface of the hippocampal formation (Fig. 18–21). At the margin of the fimbria, axons turn rostrally becoming the **crus of the fornix** *(crus fornicis)*. The **body of the fornix** *(corpus fornicis)* is formed by merger of the two crura along the midline. Axons of the fornix body continue rostrally. They turn ventrally at the rostral commissure, dividing into a precommissural projection to the septum and rostral hypothalamus and a postcommissural **column of the fornix** *(columna fornicis)* that goes to rostral thalamic nuclei and mamillary nuclei, some axons continue into the midbrain.

A **ventral commissure of the fornix** (*commissura fornicis [hippocampi] ventralis*) is present in the vicinity of the rostral commissure. A **dorsal commissure of the fornix** (*commissura fornicis [hippocampi] dorsalis*) is between the two crura ventral to the splenium of the corpus callosum.

THE LIMBIC SYSTEM. The term *limbic system* is applied to a collection of brain structures involved with affective (emotional) behavior and memory (Fig. 18-39). Emotional drive ensures that dogs will exert sufficient effort to preserve themselves and their species. Thus, self-defense, escape, hunting food, courtship, mating, territory defense and offspring protection

are all emotionally driven. Emotion involves autonomic responses and greatly impacts memory and learning.

Emotional drive was a survival requirement early in phylogenetic development, when olfaction was the chief sensory modality; thus, much of the rhinencephalon is included in the limbic system. Stimulation or ablation of various limbic system components evokes responses such as docility, apparent pleasure, hyper-sexuality, irritability, aggression, and rage. A major function of the cerebral neocortex is to keep the limbic system under cognitive control.

Interconnected telencephalic structures bordering the rostral end of the brain stem give the limbic system its name (limbic = border). The border is comprised of two telencephalic rings, separated by the corpus callosum. The outer circle consists of the *piriform lobe*, *parahippocampal gyrus*, *cingulate gyrus*, and *septal region* (Fig. 18-39). The inner ring includes the *amygdala*, *hippocampus*, and *nucleus accumbens*. The limbic system also includes components of the diencephalon: *habenula*, *hypothalamus* (particularly preoptic and mamillary components), and parts of the *thalamus* (rostral, dorsomedial, lateral dorsal, paraventricular, and intralaminar nuclei) (Fig. 18–40=24). Related midbrain structures include *interpeduncular* and *tegmental nuclei*.

Structures belong to the limbic system by virtue of their connections with one another. Major limbic highways include *cingulum* within the cingulate gyrus and the *fornix* which projects hippocampal output to the septum and diencephalon. The *stria terminalis* links the amygdala with the rostral hypothalamus and septal region. The *stria habenularis* connects the septal region to the habenula (Fig. 18-39).

Neocortex surrounding the corpus callosum is part of the limbic system. The **cingulate gyrus**, a transitional isocortex, connects to neocortical association areas, rostral nuclei of the

thalamus, and the parahippocampal gyrus. The **septal region** projects to adjacent cortex, to the hippocampus, and to the habenula. The **parahippocampal gyrus** *(gyrus parahippocampalis)* extends from the piriform lobe to the cingulate gyrus. Like the piriform lobe, it is coated by entorhinal cortex and has reciprocal connections with the hippocampal formation which it conceals. (A short branch of the parahippocampal gyrus, the *callosal gyrus***,** is situated ventral to the splenium of the corpus callosum and caudomedial to the tubercle of the dentate gyrus (Fig. 18–30).

CEREBRAL NEOCORTEX. The term neocortex refers to surface gray matter covering the dorsal portion of cerebral hemisphere that is not rhinencephalon. Neocortex is composed of six layers, named from superficial to deep: **molecular** (*stratum moleculare*), **outer granular** (*stratum granulare externum*), **outer pyramidal** (*stratum pyramidale externum*), **inner granular** (*stratum granulare internum*), **inner pyramidal** (*stratum pyramidale internum*), and **multiform layer** (*stratum multiforme*) (Fig. 18–41). The molecular layer has relatively few cell bodies. The outer pyramidal neurons are smaller than those in the inner pyramidal layer. Both thickness of the six individual layers and the total depth of the cortex vary across different cortical regions.

Functionally, the cortex is organized into vertical columns (about 0.4 mm in diameter), such that all neurons within a column respond to the same specific feature of a particular stimulus. Thalamocortical projections from thalamic nuclei terminate in the internal granular layer, conveying the specific information pertinent to the cortical column. Nonspecific thalamocortical projections from intralaminar thalamic nuclei terminate in superficial cortical layers and function to alert cortical column neurons. Within a cortical column, granule cells serve as excitatory interneurons. Outer pyramidal neurons project axons to adjacent cortex. Inner

pyramidal neurons project to distant locations. Multiform layer neurons project to the thalamus (Fig. 18–41).

WHITE MATTER RELATED TO NEOCORTEX. Cerebral white matter consists of commissural, projection, or association axons. Relative to the neocortex, axons comprising white matter are either corticopedal or corticofugal. Commissural axons are corticofugal from one hemisphere and corticopedal to the other hemisphere. The largest commissure in the brain is the ***corpus callosum***, which links corresponding neocortical regions of the two hemispheres, enabling the cerebrum to function coherently as a single cognitive center.

Projection axons travel outside the cerebrum or run from the neocortex to basal nuclei. Corticopedal projection axons typically arise from the thalamus, except for widely distributed axons from neuromodulation cell bodies located in the brain stem or rhinencephalon. Corticopedal axons from the thalamus run in the internal capsule. From lateral and medial geniculate nuclei, respectively, **optic** and **acoustic radiations** (*radiatio optica et acustica*) join the caudal limb of the internal capsule. While corticofugal projection axons to the thalamus arise from the multiform layer, all other corticofugal axons originate from pyramidal neurons. Projection axons destined for basal nuclei, brain stem or spinal cord, enter the external or internal capsules (Fig. 18-24).

The **internal capsule** (*capsula interna*) is compressed between basal nuclei and thalamus. It exhibits a medially convex angle caudal to the head of the caudate nucleus. The angular region is termed the **genu of the internal capsule** *(genu capsulae internae),* and regions rostral and caudal to the genu are called **rostral crus** *(crus rostrale capsulae internae)* and **caudal crus** *(crus caudale capsuae internae)***,** respectively. The **external capsule** (*capsula externa*), located between the putamen and claustum, is composed of projection axons to basal

nuclei and axons from the caudal limb of the rostral commissure. An **extreme capsule** (*capsula extrema*) is present between the claustum and adjacent insular cortex (Fig. 18–29).

Association axons are corticofugal from one cortical region and cortipedal to another region of cortex within the same hemisphere (Fig. 18–33=33; Fig. 18–34=34). Association axons may connect adjacent gyri, **arcuate fibers** (*fibrae arcuatae cerebri*), or travel to distant regions, e.g., the **superior longitudinal fasciculus** (*fasciculus longitudinalis superior*) from the occipital pole to the frontal pole; the **inferior longitudinal fasciculus** (*fasciculus longitudinalis inferior*) from the occipital pole to the ventral temporal region; and the **uncinate fasciculus** (*fasciculus uncinatus*) from the ventral temporal region to the ventral frontal region. The ***cingulum*** is a band of association axons that run deep to the cingulate gyrus, connecting the paraterminal gyrus of the septum to the parahippocampal gyrus in the temporal lobe. The ***subcallosal fasciculus***, which is distinct in the roof of the lateral ventricle, has connections similar to the cingulum but it includes axons to the caudate nucleus.

FUNCTIONAL REGIONS OF NEOCORTEX. Neocortical regions vary in horizontal layer thicknesses and axonal connections according to their functional role (sensory, association, motor). Axonal connections between neocortical regions are typically reciprocal. Regional connections are made by direct exchange of axonal projections and also via cortico-thalamo-cortical circuits. The circuits involve basal nuclei in the case of motor functions.

Neocortical regions that are designated *primary sensory areas* are the first cortical regions to receive afferent input for a particular sensory modality (Fig. 18–42). The primary cortical areas are surrounded by zones of *association cortex*, where increasingly complex levels of significance are extracted from the sensation. Ultimate zones of sensory association cortex amalgamate multimodal perception and memory into an ongoing world view. Neocortex of the

frontal pole operates as an executive association cortex, deciding behavioral responses and initiating directive cascades to the premotor cortex for movement selection and the motor area for movement execution. Association areas constitute about 20 per cent of the canine neocortex (versus 85 per cent of the human neocortex) (King, 1987).

The primary **somatosensory area** is located beside the coronal and ansate sulci (Fig. 18–42). The area receives tactile, kinesthetic, and nociceptive axonal projections from ventral caudal thalamic nuclei via the internal capsule. It is somatotopically organized with head representation facing rostrally. Cortical area (number of cortical columns) is proportional to receptor density per region, thus lips and face occupy more cortical area than does the back. Somatosensory cortex is the source of pyramidal tract axons that regulate sensory pathway traffic, by altering synaptic transmission between primary afferent and projection neurons. An additional, smaller, somatotopic area is situated ventral to the primary area. It receives bilateral nociceptive input and is called *somatosensory area II*.

A **gustatory (taste) area** is adjacent to the tongue and pharynx area of the somatosensory cortex. The **insula gyrus** (*gyri insulae*), buried deep to the pseudosylvian fissure, receives sensory information originating from viscera. (The olfactory sensory area is in the piriform lobe of the rhinencephalon).

The primary **visual area** is surrounds the caudal half of the marginal gyrus (Fig. 18–42). The visual area receives axonal input from the lateral geniculate nucleus. Geniculate projections comprise the *optic radiation* (*radiatio optica*) of the internal capsule. The visual area is arranged retinotopically. The area centralis (visual streak) of the retina, where cones are concentrated, occupies an expanded proportion of the visual area compared to other retinal regions where rods dominate. The two components of visual information (cone-generated detailed vision and rod-

generated movement/size detection) reach the same visual area; but, the two components are dispersed to separate zones of visual association cortex.

The primary **auditory area** of the dog is centered around the middle ectosylvian gyrus, which receives tonotopic input from the ventral portion of the medial geniculate nucleus (Kowalska, 2000). The caudal ectosylvian and sylvian gyri receive non-tonotopic input. Axons from the medial geniculate nucleus arrive via the *acoustic radiation* (*radiatio acustica*) of the internal capsule. Dorsal and rostral regions of the sylvian gyrus are auditory association cortex. A primary **vestibular area** is rostral to the auditory area.

Prefrontal association cortex occupies the frontal pole. It directs goal-oriented behavior, sending projections to premotor cortex for movement selection. The prefrontal cortex processes emotional status and cognitive perception as a prelude to deciding, planning, and temporally organizing behavior directed toward achieving goals. Attention to goal-oriented behavior involves short-term working memory and suppression of distracting influences, including inappropriate emotional behavior.

Prefontal cortex is identified by corticopedal projections from the dorsomedial thalamic nucleus. The cortex has broad connections to association and premotor neocortex; additionally, it sends axons to the caudate nucleus, cerebellum, and hypothalamus. The medial portion of the prefrontal cortex has strong limbic connections; the lateral portion has strong somatic (premotor) connections.

The **premotor cortex** is located between the prefrontal cortex and the motor cortex. It receives projections from the former and projects to the latter. Premotor cortex is active particularly during complex movement selection and while learning new movements. Also, patterns of sequential rapid movements are encoded in premotor regions. Premotor cortex drives

the motor cortex via circuits involving basal and thalamic nuclei. Premotor projection axons join the pyramidal tract and synapse on pontine nuclei that project to the cerebellum.

The premotor cortex is actually a collection of related cortical regions including a frontal eye field and supplemental motor area. The *frontal eye field* is involved in visual attention and visually tracking objects of interest. The **supplementary motor area** extends onto the medial surface of the hemisphere and features a separate somatotopic arrangement of the entire body. The area is active when movements are being contemplated or observed, prior to movement execution. The supplemental cortex receives projections from prefrontal cortex and projects to motor cortex.

The **motor cortex** occupies the postcruciate gyrus; head representation is positioned laterally (Breazile and Thompson, 1967; Buxton and Goodman, 1967). The cortex is somatotopically organized with respect to joint movement, i.e., individual projection neurons activate multiple muscles producing a particular joint movement. The degree of excitation of cortical projection neurons is related to movement force/amplitude. The motor cortex contributes the majority of the pyramidal tract corticospinal/corticonuclear axons. It is also the main driver of movement involving extrapyramidal tracts, via projections to the red nucleus and nuclei that give rise to pontine and medullary reticulospinal tracts (Fig. 18–43).

The motor cortex itself can execute movements that are simple, automatic, or habitual in response to trigger stimuli, e.g., from somatosensory cortical input. In the case of movements that are complex or being learned, the motor cortex is driven by the premotor cortex. In either situation, the motor cortex is activated via circuits involving basal and thalamic nuclei, including cerebellar-thalamic circuit involvement.

BASAL NUCLEI. Anatomically, the term **basal nuclei** refers to non-cortical gray

matter of the cerebral hemisphere. (*Note:* The term "basal ganglia" is a commonly used but anatomically improper synonym for basal nuclei.) Telencephalic basal nuclei include: accumbens, caudate, putamen, pallidum (globus pallidus), endopeduncular, claustrum, and amygdala (Fig. 18-44). The amygdala assigns emotional context to sensory information; it is a major component of the limbic system. The function of the claustrum is unknown. The remaining basal nuclei operate within movement control circuits involving the cerebral cortex, thalamus, and cerebellum. In this context, the term "basal nuclei" is often expanded to include nuclei found in the diencephalon (subthalamic nucleus) and mesencephalon (substantia nigra).

Historical ways of grouping basal nuclei, e.g., *corpus striatum* (all telencephalic nuclei), *neostriatum* (caudate & putamen), *lentiform nucleus* (putamen & pallidum) are not functionally useful. Stripes of gray matter that intersect the internal capsule give rise to the term "striatum". **Striatum**, including accumbens, caudate and putamen nuclei, is a useful grouping in the context of movement control.

Telencephalic basal nuclei, which contain inhibitory GABAergic neurons, participate in circuits responsible for movement selection and execution. The overall role of basal nuclei in these circuits is selective inhibition of unwanted movement and release of desired movement, avoiding what otherwise would be a massive uncontrolled motor output (Brooks, 1986). Pending cortical input, basal nuclei selectively suppress thalamocortical circuits while the cerebellum selectively excites thalamocortical circuits. Thus, when motivated by limbic drive and decided upon by prefrontal cortex, voluntary movements are then selected and executed via circuits involving basal nuclei (cerebellar circuits monitor on-going movement progress) (Fig. 18–43).

Individual basal nuclei have input/output roles within movement control circuits (Fig. 18-45). The three basal nuclei of the striatum receive cortical input. Limbic impact is funneled to the

accumbens nucleus. The *caudate nucleus* is the particular target of association cortex. Control of movement execution is directed to the *putamen*. These striate nuclei project axons to the *globus pallidus* and *endopeduncular nucleus*, both of which contain spontaneously active inhibitory projection neurons. The endopeduncular nucleus provides final output to the thalamus. A *direct path* from input basal nuclei to the endopeduncular nucleus facilitates (disinhibits) desired movement. An *indirect path* suppresses unwanted movement by inhibiting the globus pallidus. Another route for movement suppression is provided by cortical control of the subthalamic nucleus. Net facilitation of movement results from neuromodulation of direct and indirect paths via dopamine released by substantia nigra compacta. (The substantia nigra reticulata tonically inhibits the rostral colliculus and saccadic eye movements.)

The **caudate nucleus** (*nucleus caudatus*) is bounded medially by the lateral ventricle and laterally by the internal capsule (Fig. 18–29). The rostral enlargement of the nucleus is the head (*caput nuclei caudati*). Caudal to the head, the body (*corpus nuclei caudati*) tapers into a tail (*cauda nuclei caudati*) which loops caudal to the internal capsule and terminates near the amygdala (Fig. 18-44). The caudate nucleus receives projections from the prefrontal and premotor cortical regions. It is active particularly during complex movement selection and learning.

The **nucleus accumbens** (*nucleus accumbens*) can be found ventral to the head of the caudate nucleus, interposed between the caudate nucleus and septal region (Fig. 18-44). The accumbens nucleus receives projections from medial prefrontal and limbic (cingulate; parahippocampal) cortex, as well as amygdala, insula cortex, and piriform entorhinal cortex. Accumbens projections go to the hypothalamus and habenula in addition to other basal nuclei.

The **putamen** is situated between internal and external capsules. It is linked to the head

of the caudate nucleus by strands of gray matter that penetrate the internal capsule (Fig. 18–29). The putamen receives projections from sensory and motor areas of neocortex. It is active during simple movements, regulating movement amplitude and force.

The **globus pallidus** or **pallidum** (*pallidum* (*globus pallidus*)) is located medial to the putamen and lateroventral to the internal capsule. The nucleus has a reticulated appearance because many white matter bundles penetrate it (Fig. 18-26). A **lateral medullary lamina** *(lamnia medullaris lateralis)* is located between the globus pallidus and the putamen and a **medial medullary lamina** *(lamina medullaris medialis)* separates globus pallidus from **endopeduncular nucleus** (*nucleus endopeduncularis*) (Fig. 18-24). The globus pallidus inhibits the endopeduncular nucleus, alleviating movement suppression that the endopeduncular nucleus imposes on thalamocortical circuits. Both nuclei are tonically acitive and controlled by other basal nuclei. (*Note:* The endopeduncular nucleus of the carnivore corresponds to the internal/medial globus pallidus division of the primate.)

The **claustrum** forms a broad plate between the extreme capsule and insular cortex laterally the external capsule medially (Fig. 18-26). The function of the claustrum is not understood, but it has broad connections with wide areas of cerebral cortex, including the visual system (Berman and Jones, 1982). The ventral part of the claustrum, which merges with insular cortex, may be related to the limbic system.

The **amygdala** (amygdaloid body) is a rhinencephalic basal nucleus located within the piriform lobe. It is a major component of the limbic system, responsible for implementing emotional reactions. It has reciprocal projections with the prefrontal cortex, but most of its connections are with the limbic components. (*It was described in detail in the* RHINENCEPHALON *section.*)

THE CEREBELLUM

The cerebellum coordinates posture and movement by regulating muscle tone and joint action. The cerebellum detects errors in on-going movement and sends corrective excitatory output to upper motor neurons in the brainstem and thalamocortical circuits that drive voluntary movement. The cerebellar cortex of the flocculonodular lobe corrects vestibular reflex errors. Beyond movement, the cerebellum is crucial for sensorimotor timing, including visual guidance of movement; also, the cerebellum is necessary for judging the distance rate of change of an approaching object/wall. Finally, cerebellar involvement in cognition has been reported, particularly in primates (Salman, 2010).

The cerebellum is the dorsal component of the metencephalon (Fig. 18–46). The entire cerebellum can be partitioned into a median **vermis** and bilateral **cerebellar hemispheres** (*hemispherium cerebelli*). The cerebellum can be further subdivided into lobes and lobules separated by fissures (Table 18–2; Larsell, 1970). The cerebellar surface features narrow ridges (*folia cerebelli*) separated by grooves (*sulci cerebelli*). Each ridge is called a ***folium***, each groove is a ***sulcus.***

A *uvulonodular fissure* (*fissura uvulonodularis*) divides the cerebellum into a small **flocculonodular lobe** (*lobus flocculonodularis*) and a **cerebellar body** (*corpus cerebelli*). The body is divided by the **primary fissure** (*fissura prima*) into a **rostral lobe** (*lobus rostralis*) and a **caudal lobe** (*lobus caudalis*) (Fig. 18–47). These three lobes are phylogenetically and functionally distinct.

The **flocculonodular lobe** (archicerebellum; vestibulocerebellum) functions like a vestibular nucleus (nystagmus and wide-base stance can result when it is damaged). The **rostral lobe** (paleocerebellum; spinocerebellum) has connections with the spinal cord and regulates

posture and gait (opisthotonus and ataxia can result when it is damaged). The **caudal lobe** (neocerebellum; cerebrocerebellum) connects to the forebrain and impacts voluntary movement, including pre-movement preparation (dysmetria is one consequence of caudal lobe damage).

The major histological components of the cerebellum are cortex, white matter and nuclei. The **cerebellar cortex** (*cortex cerebelli*) is surface gray matter. The cortex features large inhibitory Purkinje (piriform) neurons. Their axons are the sole output from the cerebellar cortex. The axons terminate in cerebellar nuclei, or in vestibular nuclei in the case of flocculonodular cortex.

On a median section through the cerebellum, white matter has the appearance of tree branches and is called the **arbor vitae**. The arbor is composed of a **lamina** (*lamina albae*) within each folium and a center mass (*corpus medullare*) referred to as **cerebellar medulla**.

Axons within cerebellar white matter can be categorized as afferent or efferent relative to the cerebellum and as corticopedal or corticofugal relative to the cerebellar cortex. Corticofugal axons are from Purkinje cells. They are inhibitory and terminate in vestibular or cerebellar nuclei. Axons arising from cerebellar nuclei are excitatory. They exit the cerebellum as efferent axons in cerebellar peduncles.

Afferent axons enter the cerebellum through cerebellar peduncles. They are excitatory. All afferent axons send collateral branches to cerebellar nuclei before terminating in the cerebellar cortex. There are two kinds of corticpedal afferent axons based on their terminal endings in the cortex. *Climbing fiber* afferents come from the olivary nucleus, which pre-processes proprioceptor and motor center information. *Mossy endings* are found on all other cerebellar afferents (both proprioception and upper motor neuron input).

CEREBELLAR NUCLEI. Bilaterally, three **cerebellar nuclei** are embedded deeply

within cerebellar white matter. From medial to lateral, they are: **fastigial nucleus** (*nucleus fastigii*), **interpositus nucleus** (*nucleus interpositus cerebelli*), and **lateral (dentate) nucleus** (*nucleus lateralis cerebelli*) (Fig. 18–46). Except for Purkinje axons that are directed to vestibular nuclei, all efferent axons leaving the cerebellum originate from cerebellar nuclei. All cerebellar afferent axons are excitatory and send excitatory collateral branches to cerebellar nuclei before terminating in the cerebellar cortex. Cerebellar nuclei receive inhibitory input from Purkinje axons of the cortex. Thus the cerebellar cortex modulates excitatory output from cerebellar nuclei.

Based on direct axonal projections from cerebellar cortex to the nearest cerebellar nucleus, the cerebellum can be functionally partitioned into three bilateral longitudinal zones: The **vermis zone**, located most medially, projects to the fastigial nucleus. This zone activates vestibulospinal and reticulospinal tracts and regulates muscle tone in connection with posture and locomotion. The **paravermis zone**, located immediately lateral to the vermis, projects to the interpositus nucleus, which regulates joints of limbs via the rubrospinal tract. The **lateral** or **hemispheric zone** projects to the lateral (dentate) nucleus which projects to the ventral lateral thalamic nucleus to impact motor cortex excitation.

CEREBELLAR PEDUNCLES. The cerebellum is attached bilaterally to the brain stem by three cerebellar peduncles that convey afferent and efferent cerebellar axons (Fig. 18–48=41). The **caudal cerebellar peduncle** (*pedunculus cerebellaris caudalis*) contains both afferent and efferent axons. It connects the cerebellum with the pons, medulla oblongata and spinal cord (Fig. 18–49). The caudal peduncle may be regarded as having two components: a *restiform body* (*corpus restiforme*) and a *juxtarestiform body* (*corpus juxtarestiforme*). The latter refers to the medial part of the peduncle that contains cerebellar efferent axons to reticular

formation nuclei, reciprocal connections with vestibular nuclei, and afferent axons from the vestibular nerve. The remaining restiform body conveys cerebellar afferent axons from the brainstem and spinal cord.

The contralateral olivary nucleus sends olivocerebellar climbing axons to the entire cerebellar cortex through the caudal cerebellar peduncle. Spinal proprioceptive and tactile information destined for vermal and paravermal cerebellar zones reaches the caudal peduncle via the dorsal spinocerebellar tract (caudal half of body) and lateral cuneate nucleus (neck and thoracic limb). Via the caudal peduncle, vermal and paravermal zones receive descending tract information from brainstem nuclei (lateral reticular nucleus, paramedian reticular nucleus, and pontine tegmental reticular nucleus). The nucleus of the solitary tract sends visceral axonal input to the vermis via the caudal peduncle.

The **middle cerebellar peduncle** (*pedunculus cerebellaris medius*) is entirely afferent to the cerebellum (Fig. 18–49). The middle peduncle, also called brachium pontis, is formed by projections to lateral and paravermal cerebellar zones from cell bodies in contralateral pontine nuclei. The axons travel along the ventral surface of the pons as transverse pontine fibers before becoming the middle cerebellar peduncle. The pontine nuclei receive information from the cerebral cortex via axons that travel through the internal capsule, crus cerebri, and corticopontine tract within the ventral pons. The pontine nuclei also receive axonal input from rostral and caudal colliculi.

The **rostral cerebellar peduncle** (*pedunculus cerebellaris rostralis*) is composed of efferent axons from interpositus and lateral (dentate) nuclei, plus some afferent axons (rubrocerebellar and spinocerebellar). The efferent axons decussate in the caudal midbrain and terminate in contralateral brain stem nuclei (Fig. 18–49). The interpositus nucleus sends axons to

the magnocellular part of the red nucleus to modulate activity of the rubrospinal tract. Both interpositus and lateral nuclei project to thalamic nuclei (ventral rostral, ventral lateral, and centrum medianum). The interpositus nucleus innervates thalamic neurons that project to the motor cortex. The lateral nucleus innervates thalamic neurons that project to premotor and supplemental motor areas.

Neuronal cell bodies of the lateral cerebellar nucleus become excited prior to the onset of a movement, whereas interpositus and fastigial neurons become excited during movement execution. The lateral nucleus sends axons to the oculomotor nucleus, to parvicellular neurons of the red nucleus that project to the thalamus, and to the olivary nucleus and reticular nuclei that project to the cerebellum.

The rostral cerebellar peduncle also conveys afferent axons from two spinal tracts. The ventral spinocerebellar tract arises from spinal projection neurons that receive synaptic input similar to that of spinal motor neurons. The axons that decussate in the spinal cord and then decussate again within the cerebellum. The ventral spinocerebellar tract is concerned with the caudal half of the body. Comparable axonal input from the thoracic limb and neck is conveyed ipsilaterally in the rostral spinocerebellar tract which runs with the ventral spinocerebellar tract but contributes axons to both caudal and rostral cerebellar peduncles.

THE CEREBELLAR CORTEX. The cerebellar cortex is composed of three layers: a superficial, cell-sparse, **molecular layer** (*stratum moleculare*), a deep **granule cell layer** (*stratum granulosum*), and an intermediate layer (*stratum neuronorum piriformium*) of **Purkinje** (*piriform neuron*) **cells** (Fig. 18–50).

Purkinje (piriform) neuronal cell bodies align in a row at the interface of the superficial and deep cortical layers. Purkinje neurons are inhibitory, as are basket-cell neurons located deep

in the molecular layer and the Golgi neurons found within the granule cell layer. Granule neurons are the only excitatory neurons in the cerebellar cortex.

Purkinje neurons have broad, flattened dendritic trees that extend into the molecular layer, oriented with the broad dendritic surface perpendicular to the longitudinal axis of the folium. Axons of Purkinje neurons, the only output from the cerebellar cortex, terminate in cerebellar nuclei (or vestibular nuclei in the case of the flocculonodular lobe).

Granule neurons send axons into the molecular layer. The axons bifurcate and course longitudinally in the folium, synapsing on dendritic trees of numerous Purkinje neurons. Granule neurons also excite basket-cell neurons that project transversely in a folium and inhibit laterally positioned Purkinje neurons. Thus, granule neurons excite a longitudinal band of Purkinje neurons, and, via basket cells, they inhibit Purkinje neurons positioned bilateral to the band. Purkinje neuronal excitability is translated into inhibition at the level of cerebellar nuclei where Purkinje axons terminate.

Afferent axons to the cerebellar cortex are categorized as **mossy fibers** or **climbing fibers**, based on terminal branch morphology (Fig. 18–50). Climbing axons come from the olivary nucleus. Each axon intensely activates one Purkinje neuron by climbing along its dendritic tree and forming numerous synapses. All other afferent axons to the cerebellar cortex terminate as mossy fibers. Mossy endings terminate within glomerular synaptic complexes, exciting a number of granule cell dendrites. All afferent axons send excitatory collateral branches to cerebellar nuclei before proceeding to the cortex.

To serve its regulatory function, the cerebellum compares axonal input from motor command sites with proprioceptive and tactile information generated by ongoing movements. Cerebellar nuclei project excitatory drive to motor command sites. The cerebellar cortex

selectively inhibits ongoing excitatory drive from cerebellar nuclei, via Purkinje axon projections to the nuclei.

The olivary nucleus and the cerebellum are closely related and damage to either structure produces similar deficits of coordination (Brooks, 1986; Murphy and O'Leary, 1971). The olivary nucleus receives and processes motor command and proprioceptive axonal input. Climbing fiber axonal output from the olivary nucleus activates selective microzones within the cerebellar cortex.

BRAIN ATLAS

Appended are 10 plates that represent a sampling of sections through a canine brain (Fig. 18–51=42).

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