The brain of the common vampire bat, *Desmodus rotundus murinus* (Wagner, 1840): a cytoarchitectural atlas

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(With 27 figures)

Abstract

The vampire bat, *Desmodus rotundus*, is exceptionally agile and stealthy in nature. Feeding at night on cattle blood, it is a known scourge carrying rabies. It is endowed with a very high neocortical volume among bats, acute olfactory capabilities and an accessory olfactory system. These characteristics have resulted into an impressive number of neuroanatomical investigations except a long due atlas on its brain. This study presents a cytoarchitectural atlas of the brain of the common vampire, *Desmodus rotundus murinus*, in the frontal plane, serially between the olfactory bulb and the medulla oblongata. Twenty six selected sections are presented, each separated by about 300 to 560 microns. The atlas figures show lugol fast blue-cresyl echt violet stained hemisections with their matching half in a labeled line drawing. About 595 discrete brain structures (some repeating) have been identified. This study is likely to provide the accurate localization of nuclear groups, whole structures, fiber tracts, and interconnections to facilitate future neuroanatomical and neurophysiological investigations on the vampire brain.

Keywords: bats, brain, cytoarchitectural atlas, *Desmodus rotundus*, vampire.

O cérebro do morcego vampiro comum, *Desmodus rotundus murinus* (Wagner, 1840): um atlas citoarquitetural

Resumo

O morcego vampiro, *Desmodus rotundus*, é excepcionalmente ágil e furtivo. Alimentando-se à noite do sangue de gado, é um conhecido flagelo portador da raiva. Entre os morcegos, apresenta um alto volume neocortical, capacidades olfatórias agudas e um sistema ofatório suplementar. Estas características têm suscitado um número impressionante de estudos neuroanatômicos, no entanto, não foi produzido ainda um atlas do cérebro desta espécie. O presente estudo apresenta, assim, um atlas citoarquitetural do cérebro do vampiro comum, *Desmodus rotundus murinus*, no plano frontal, serialmente entre o bulbo ofatório e a medula oblongata. Vinte e seis seções selecionadas são aqui apresentadas, cada uma separada por em torno de 300 a 560 mícrones. As figuras do atlas mostram hemisseções manchadas com lugol violeta de cresilo, com a sua respectiva metade apresentada numa figura rotulada. Em torno de 595 estruturas cerebrais discretas (algumas repetidas) foram identificadas. Este estudo proverá a localização precisa de grupos nucleares, estruturas inteiras, tratos de fibras, e interconexões para facilitar futuras investigações neuroanatômicas e neurofisiológicas realizadas no cérebro do morcego vampiro.

Palavras-chave: morcegos, cérebro, atlas citoarquitetural, *Desmodus rotundus*, vampiro.

1. Introduction

Of the three species of vampires (*Desmodus, Diaemus*, and *Diphylla*), *Desmodus* is the most common and best known as a pest and a scourge. *Desmodus* is unique among bats in having the largest neocortical volume (size index 1024) amongst the nearly 276 species of bats investigated (Baron et al., 1996a; b, c). For this characteristic alone *Desmodus* is considered one of the most evolved bats studied thus far. Monographic works on chiropteran brain anatomy are those of Schneider (1957; 1966), Mann (1963), Henson (1970), and McDaniel (1976). An unparalleled, three-volume, encyclopedic work on the neurobiology of Chiroptera authored by Georg Baron, Heinz Stephan and Heiko Frahm appeared in 1996. While this work is priceless for data on brains of bats, and includes brain atlases of a megabat (*Rousettus*) and a microbat (*Myotis*), there have been no systematic studies on the vampire brain. Several other chiropteran brain atlases have also been available in the literature (Table 1).

For the Latin American countries, *Desmodus* carries a special threat. It is called 'thief of the night', and causes substantial loss of cattle from transmitted rabies (Greenhall et al., 1983). Its importance is further enhanced in the newly discovered use of the clot-buster, plasminogen activator (desmoteplase or DSPA) in its saliva (Hawkey, 1966) in prevention of strokes in the human (Fauber, 2003). It is not an overstated conclusion that knowledge of the brain cytoarchitectonics on this species is essential to have.

The association of the vampire behavioral complexity with its voluminous neocortex has been established. (Baron et al., 1996a; b; c). These features make *Desmodus* an ideal bat species for neuroanatomical and neurophysiological research. This study was, therefore, undertaken to analyze the serial brain anatomy of the common vampire bat.

2. Materials and Methods

2.1. Specimens

Adult *Desmodus rotundus* were captured live from a wild colony in Veracruz, Mexico through the courtesy of the late Professor William Wimsatt, and William Lopez-Forment. Five females and two males were transported to the author's laboratory in Louisville and remained in good health in captivity for several years.

2.2. Brain preparation

Bats were deeply anesthetized with ether and intracardiacally perfused first with saline in nitrite solution with the right atrium punctured. Perfusion was then continued using one of the three solutions: Bouin's, 4% glutaraldehyde, or 10% buffered formalin. The skin and muscles were dissected away from the cranium and the neck. The head was severed at the neck and kept immersed in the fixative for several hours, after which the calvarium and the dorsal half of the upper cervical vertebrae were chipped away. The exposed brain and the spinal cord were further left in the fixative for several more hours. The olfactory nerves were transected and the frontal lobes were gently lifted, gradually severing other cranial nerves. The hypophysis was gently pushed out of the sella turcica. When the entire brain (Figure 1) was thus freed, it was kept in the fixative for 24-48 hours, washed, and processed in graded ethyl alcohol. Paraffin embedding as well as cellosolve (ethylene-glycol-monoethyl ether) procedures were followed for the individual brains.

Table 1. A partial list of atlases and monographs on the brains of bats.

Species (Family)	Reference	Notes
1. *Rousettus aegyptiacus* (PTEROPODIDAE)	Schneider, 1966	Frontal, sagittal, and horizontal series; Weigert's hematoxylin-eosin; Heidenhain's hematoxylin
2. *Rousettus amplexicaudatus* (PTEROPODIDAE)	Baron et al., 1996	Frontal series; Gallocyanin
3. *Pteropus giganteus* (PTEROPODIDAE)	Igrashi and Kamiya, 1972	Six frontal sections
4. *Dobsonia praedatrix* (PTEROPODIDAE)	Bhatnagar et al., 1990	One sagittal section
5. *Desmodus rotundus* (PHYLLOSTOMIDAE)	Bhatnagar, this study	Lugol-fast blue-cresyl echt violet
6. *Pteronotus parnellii* (MORMOOPIDAE)	Henson, 1970	Line drawings of 14 frontal sections
7. *Tonatia bidens* (PHYLLOSTOMIDAE)	McDaniel, 1976	Photos of 18 coronal sections
8. *Tadarida mexicana* (MOLOSSIDAE)	Humphrey, 1936	Line drawings of the telencephalic region in 16 figures
9. *Myotis montivagus* (VESPERTILIONIDAE)	Baron et al., 1996	Frontal series, Gallocyanin
10. *Miniopterus schreibersii* (VESPERTILIONIDAE)	Igrashi and Kamiya, 1972	Six frontal sections
11. *Rhinolophus ferrumequinum, Pipistrellus abramus, Plecotus auritus* (RHINOLOPHIDAE, VESPERTILIONIDAE)	Tamura, 1950	Reticular formation of the entire brainstem in cross sections

Other monographs on bat brains: Schneider, 1957; two species of megachiroptera and 22 species of microchiroptera, Brauer and Schober, 1970, 1976; sixty-five species of phyllostomids, McDaniel, 1976.

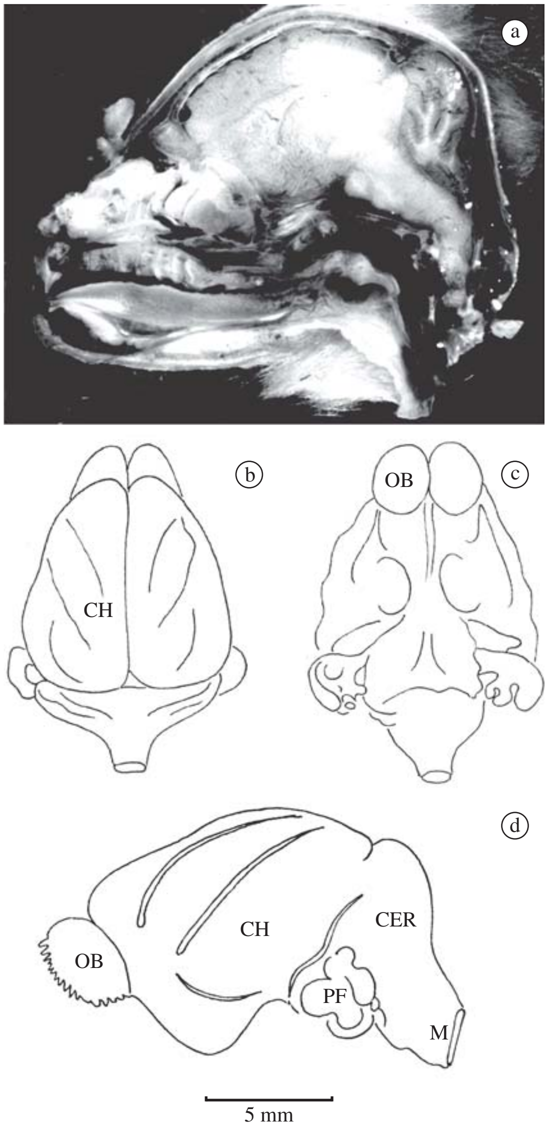

Figure 1. a) Hemisected head of a female *Desmodus rotundus* showing the brain in its major subdivisions. Compare with Figure 1d. Figures 1b, c and d) respectively are the dorsal, ventral and lateral views of the brain. CER, cerebellum; CH, cerebral hemisphere; M, medulla oblongata; OB, olfactory bulb; PF, paraflocculus.

For the cellosolve infiltration, the brain was processed through four changes of cellosolve, leaving it overnight in the last change. Three changes of one hour duration each in benzene, followed by three one-hour changes in paraffin were made under vacuum at 58 °C. The infiltrated brain was then embedded in paraffin. Serial frontal (coronal) sections were cut at 20 µm thickness, arranged on albumen-coated slides which were kept at 58 °C in an oven for drying. Staining was achieved with lugol fast blue overnight, differentiated in 70% alcohol, rinsed, and counterstained with cresyl echt violet for 5-7 minutes, cleared in xylene and mounted in permount.

Another 10 µm thick serial section series of the decalcified heads of several specimens, perfused with Bouin's solution, was prepared. These were stained with the one-step Gomori trichrome procedure (Bhatnagar and Kallen, 1974; Bhatnagar, 1980). A partly incomplete, 20 µm thick, stained serial series made from a female *Desmodus rotundus murinus* brain was received from the late Professor William A. Wimsatt, Cornell University, Ithaca, New York.

2.3. Brain analysis

Using a macrophotography apparatus, selected sections, primarily from the lugol fast blue-cresyl echt violet series, beginning with the olfactory bulb and ending with the medulla oblongata, were photographed with gaps of about 300-560 µm between sections. A total of 710 sections, each 20 µm thick, was prepared. Even though over 100 sections were photographed, studied and labeled, 26 sections were finally selected for this atlas, representing the entire brain, without unduly repeating. In this process of selecting representative sections, a few structures may be found missing. These were purposely left out to conserve space.

Desmodus brain cytoarchitecture was studied in comparison with the brain anatomy of the human (Villiger-Ludwig-Rasmussen, 1951), rat (Paxinos and Watson, 1997), muskrat (Panneton and Watson, 1991), cat, hamster, guinea pig, and other bat species (Table 1). Structures were localized and identified on a camera lucida drawing, an exact match control of the right half of the photographed section (Atlas Figures 2-27).

3. Results and Discussion

The primary objective of this investigation was to prepare an atlas of the brain of the vampire, *Desmodus rotundus* and identify the structures, such as the nuclear groups, ascending and descending fiber tracts, cranial nerve nuclei, cortical regions, and brainstem components. This species, being so commonly available and so unique in its behavioral characteristics, has long deserved detailed cytoarchitectural studies of its brain. *Desmodus* has the largest neocortical volume compared to 276 species of bats (Table 2; see Baron et al., 1996a; b; c). Most early studies on the vampire brain anatomy are on *Desmodus rotundus* (see Mann, 1960, 1963). Plenty of data are provided in the three-volume work "Comparative Neurobiology in Chiroptera" by Baron et al. (1996a; b; c). The superior olivary complex was investigated by Kuwabara and Bhatnagar (1999). They also reported that the lateral lemniscus is columnar and similar as in other echolocating bats (Kuwabara and Bhatnagar, 2000). Data on the three species of vampire brains were reviewed in detail by Bhatnagar (1988a) Ultrastructural observations on the pineal gland of *Desmodus* were also reported (Bhatnagar, 1988b). The accessory olfactory bulb in *Desmodus*, though short in height, extends nearly to the full diameter of the main olfactory bulb (Cooper and Bhatnagar, 1976), an ob-

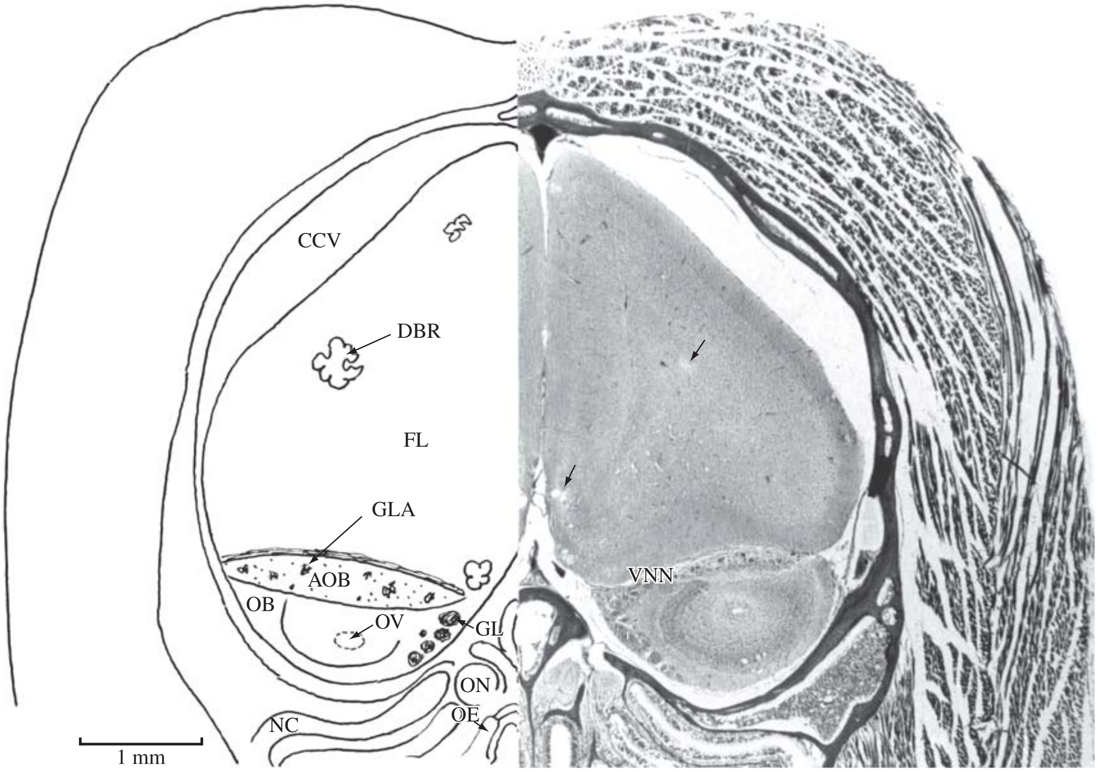

Figure 2. This anterior-most section is from the caudal olfactory bulb region. It is from a wild caught *Desmodus rotundus* held captive in our laboratory. This bat's entire brain showed 'holes' or degenerated regions as depicted here (arrows). Refer to the text. AOB, accessory olfactory bulb; CCV, cranial cavity; DBR, degenerated brain region; FL, frontal lobe; GL, glomerular layer of the main olfactory bulb; GLA, glomeruli of the accessory olfactory bulb; NC, nasal cavity; OB, main olfactory bulb; OE, olfactory epithelium; ON, olfactory nerve; OV, olfactory ventricle; VNN, vomeronasal nerve. Section No. 65, De1-201; Gomori one-step trichrome, 10 µm.

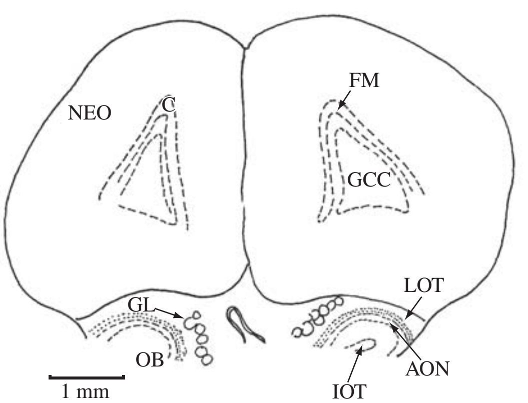

Figure 3. AON, anterior olfactory nucleus; C, cingulum; FM, forceps minor of the corpus callosum; GCC, genu of the corpus callosum; GL, glomerular layer of the main olfactory bulb; IOT, intermediate olfactory tract; LOT, lateral olfactory tract; NEO, neocortex; OB, olfactory bulb. Section No. 70.

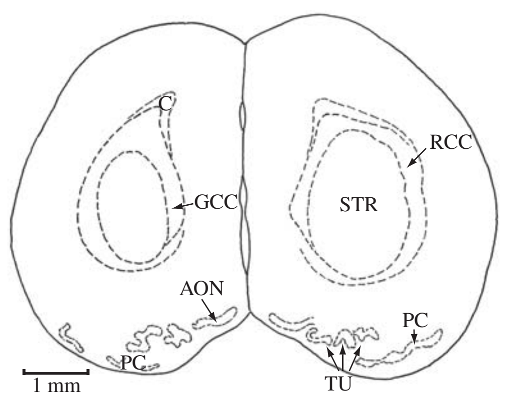

Figure 4. AON, anterior olfactory nucleus; C, cingulum; GCC, genu of the corpus callosum; PC, piriform (olfactory) cortex; RCC, radiation of the corpus callosum; STR, striatum (caudate-putamen). TU, olfactory tubercle. Section No. 75.

Note for Figures 3-27: A cytoarchitectural serial series of the brain of *Desmodus rotundus murinus*, female. Lugol fast blue – cresyl echt violet stain, 20 µm. Sections are presented in an antero-posterior direction, beginning with the olfactory bulb and ending in the medulla oblongata. The neocortex in most line drawings has been omitted. Figure legends indicate section number, slide-row-section and the relative position of the section in microns beginning postero-anteriorly (medulla oblongata – olfactory bulb) where known. Scale bars primarily apply to the photo panels.

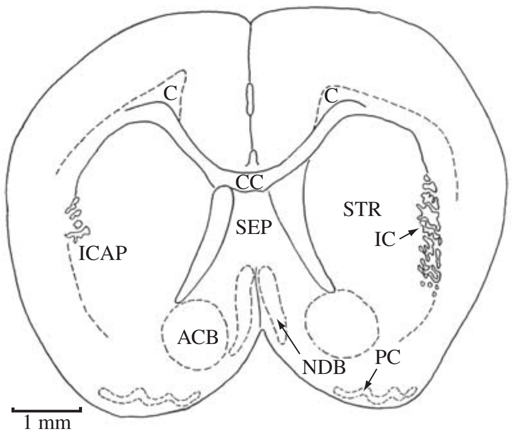

Figure 5. ACB, accumbens nucleus; C, cingulum; CC, corpus callosum; ICAP, internal capsule; NDB, nucleus of diagonal band (tract); PC, piriform (olfactory) cortex; SEP, septal nucleus; STR, striatum (caudate-putamen). Section No. 81.

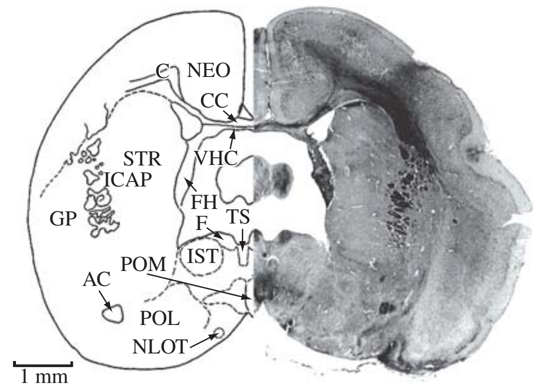

Figure 7. AC, anterior commissure; C, cingulum; CC, corpus callosum; F, fornix; FH, fimbria of the hippocampus; GP, globus pallidus; ICAP, internal capsule; IST, interstitial nucleus of stria terminalis; NEO, neocortex; NLOT, nucleus of the lateral olfactory tract; POL, lateral preoptic nucleus; POM, medial preoptic nucleus; STR, striatum; TS, triangular nucleus of septum; VHC, ventral hippocampal commissure. Section No. 105, 96-5, 10880 µm.

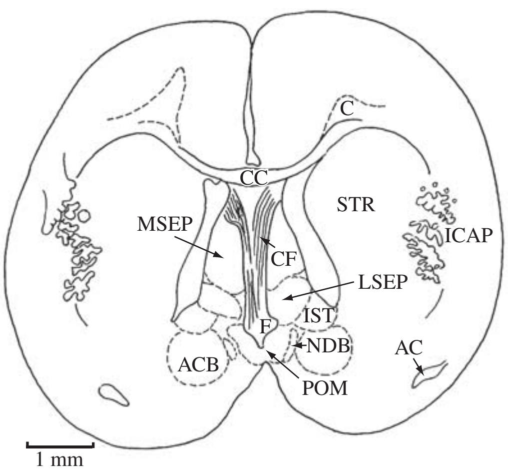

Figure 6. AC, anterior commissure; ACB, accumbens nucleus; C, cingulum; CC, corpus callosum; CF, column of fornix; F, fornix; ICAP, internal capsule; IST, interstitial nucleus of stria terminalis; LSEP, lateral septal nucleus; MSEP, medial septal nucleus; NDB, nucleus of diagonal band (tract); POM, medial preoptic nucleus; STR, striatum (caudate-putamen). Section No. 89, 99-4, 11180 µm.

servation that has not been made in other mammalian olfactory bulbs, including those of bats. There is an olfactory ventricle. In one of the brains, prepared from a wild caught *Desmodus* (see Figure 2), isolated telencephalic regions were devoid of brain tissue, as though it had been punched out. It would be interesting to investigate if this strange morphological finding bears any relationship to the rabies virus carrying characteristics of the vampire.

The *Desmodus* brain is short, lissencephalic (smooth; sulci lacking on the outer surface), with high hemispheres (Figure 2), and a rostral sulcus. Parafloculus is unexposed. The pons is large, and the pyramidal tracts are huge until they cross. Accurately detailed and painstakingly measured volumes on the vampire brains (*Desmodus rotundus*, and including another vampire species, *Diphylla ecaudata*) are provided in Baron et al. (1996a; b; c). These are summarized in Table 3. For the sake of space, those specifically not included in Table 3 are the volumes of subdivisions and parts of medulla oblongata, mesencephalic components, cerebellar nuclei, and lateral geniculate body. For the data on these structures and others, the reader is directed to Baron et al. (1996a; b; c).

Even though major senses (vision, hearing, echolocation and olfaction) are well developed in the vampire, it is not practical for the bat to use phyllostomid type of sonar for locating its prey. Statements have been made in the literature that vampires use olfaction to a greater extent in feeding (Mann, 1963). If greater sizes or volumes are related to greater sense of acuity, then the size of the olfactory and the vomeronasal organs are indicative of an olfactory sense acuter than in most bat species. Even by cursory examination, of the three vampires, *Diaemus* appears to have larger volumes dedicated to the olfactory and the vomeronasal (accessory) systems than *Desmodus. Diphylla* appears to occupy the last position amongst vampires in this regard.

Mann (1963) has described ten rhinencephalic circuits using *Desmodus* as an example. They are summarized as follows: for detection and discrimination of odors, reflex motor responses to olfactory stimuli with or without the intervention of lower pallidal sectors, high level reflex motor responses through nigropallidial pathways (the development of these circuits depends upon the development of the anterior olfactory nucleus). Extrapyramidal functions, olfactory tubercle, pale-

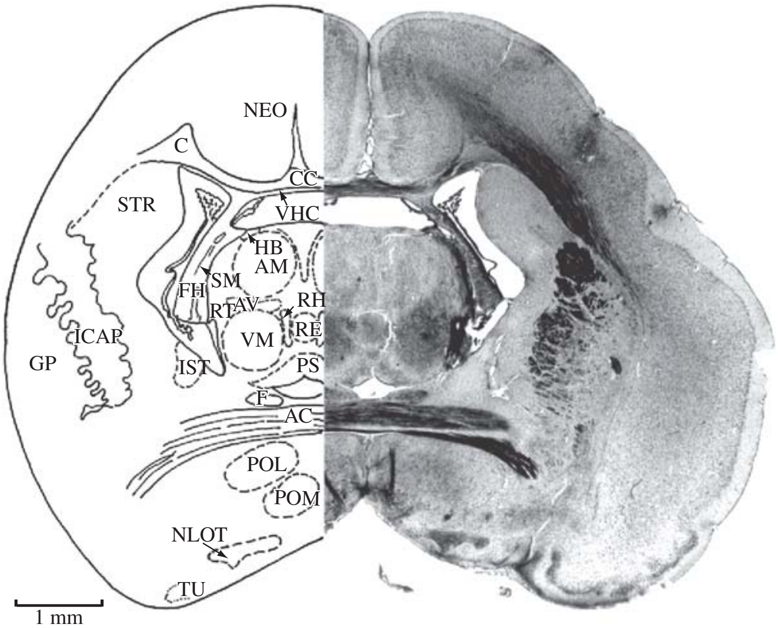

Figure 8. AC, anterior commissure; AM, anteromedial thalamic nucleus; AV, anteroventral thalamic nucleus; C, cingulum; CC, corpus callosum; F, fornix; FH, fimbria of hippocampus; GP, globus pallidus; HB, habenular nucleus; ICAP, internal capsule; IST, interstitial nucleus of stria terminalis; NEO, neocortex; NLOT, nucleus of the lateral olfactory tract; POL, lateral preoptic nucleus; POM, medial preoptic nucleus; PS, periventricular stellatocellular nucleus; RE, reuniens thalamic nucleus; RH, rhomboid thalamic nucleus; RT, reticular thalamic nucleus; SM, striamedullaris of the thalamus; STR, striatum; TU, olfactory tubercle; VHC, ventral hippocampal commissure; VM, ventromedial nucleus of the thalamus. Section No. 118, 93-3, 10540 µm.

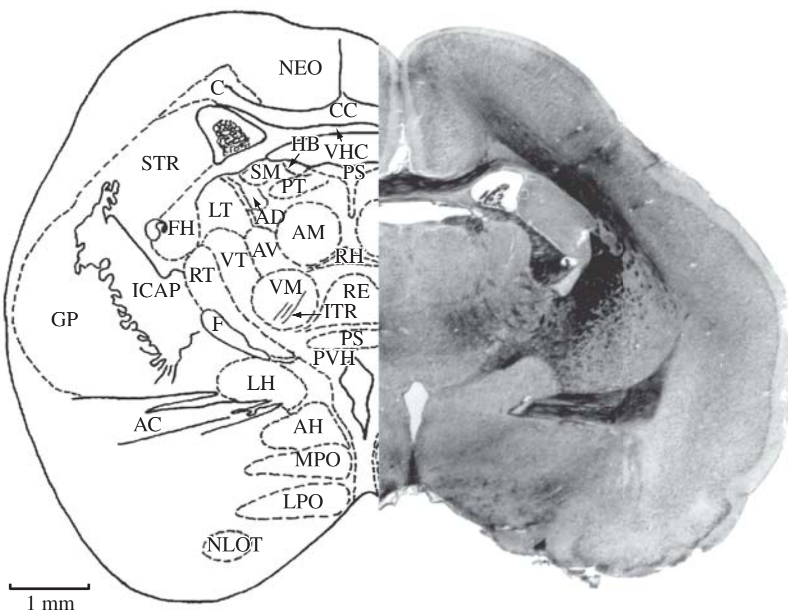

Figure 9. AC, anterior commissure; AD, anterodorsal thalamic nucleus; AH, anterior nucleus of hypothalamus; AM, anteromedial thalamic nucleus; AV, anteroventral thalamic nucleus; C, cingulum; CC, corpus callosum; F, fornix; FH, fimbria of hippocampus; GP, globus pallidus; HB, habenular nucleus; ICAP, internal capsule; ITR, inferior thalamic radiation; LH, lateral nucleus of hypothalamus; LPO, lateral preoptic nucleus; LT, lateral thalamic nucleus; MPO, medial preoptic nucleus; NEO, neocortex; NLOT, nucleus of the lateral olfactory tract; PS, periventricular stellatocellular nucleus; PT, paratenial thalamic nucleus; PVH, periventricular nucleus of the hypothalamus; RE, reuniens thalamic nucleus; RH, rhomboid thalamic nucleus; RT, reticular thalamic nucleus; SM, stria medullaris of the thalamus; STR, striatum; VHC, ventral hippocampal commissure; VM, ventromedial nucleus of the thalamus; VT, ventral nucleus of the thalamus. Section No. 133, 90-3, 10240 µm.

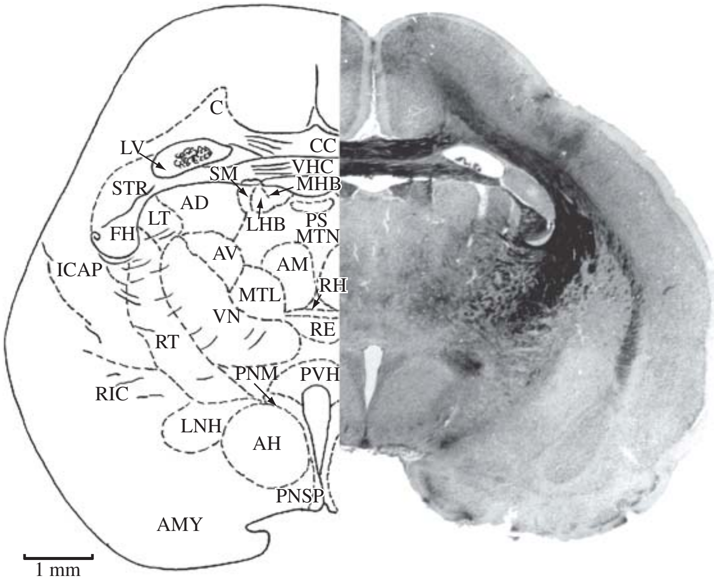

Figure 10. AD, anterodorsal thalamic nucleus; AH, anterior nucleus of hypothalamus; AM, anteromedial nucleus of thalamus; AMY, amygdala; AV, anteroventral thalamic nucleus; C, cingulum; CC, corpus callosum; FH, fimbria of hippocampus; ICAP, internal capsule; LHB, lateral nucleus of habenula; LNH, lateral nucleus of hypothalamus; LT, lateral thalamic nucleus; LV, lateral ventricle; MHB, medial nucleus of habenula; MTL, median nucleus of thalamus, lateral portion; MTN, median thalamic nucleus; PNM, paraventricular nucleus, magnocellular part; PNSP, paraventricular nucleus, parvicellular part; PS, periventricular stellatocellular part; PVH, periventricular nucleus of hypothalamus; RE, reuniens thalamic nucleus; RH, rhomboid thalamic nucleus; RIC, retrolenticular internal capsule; RT, reticular thalamic nucleus; SM, stria medullaris of thalamus; STR, striatum; VHC, ventral hippocampal commissure; VN, ventral nucleus of thalamus. Section No. 151, 86-1, 9880 μm.

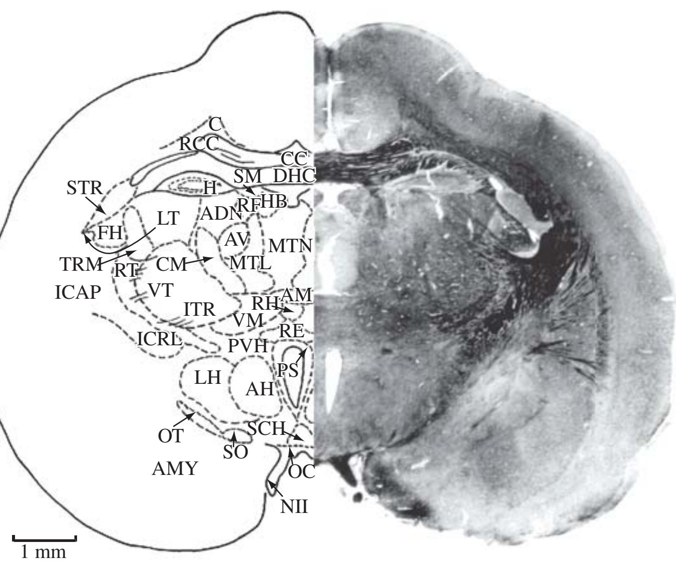

Figure 11. AD, anterodorsal thalamic nucleus; AH, anterior nucleus of hypothalamus; AM, anterior medial thalamic nucleus; AMY, amygdala; AV, anterior ventral thalamic nucleus; C, cingulum; CC, corpus callosum; CM, centromedian thalamic nucleus; DHC, dorsal hippocampal commissure; FH, fimbria of hippocampus; H, hippocampus; HB, habenular nucleus; ICAP, internal capsule; ICRL, retrolenticular internal capsule; ITR, inferior thalamic radiation; LH, lateral nucleus of the hypothalamus; LT, lateral thalamic nucleus; MTL, median nucleus of thalamus, lateral portion; MTN, median nucleus of thalamus; N II, optic nerve; OC optic chiasm; OT, optic tract; PS, periventricular stellatocellular nucleus; PVH, periventricular nucleus of hypothalamus; RCC, radiation of corpus callosum; RE, reunions thalamic nucleus; RF, retroflex fasciculus; RH, rhomboid thalamic nucleus; RT, reticular thalamic nucleus; SCH, suprachiasmatic nucleus; SM, stria medullaris of thalamus; SO, supraoptic nucleus; STR, striatum; TRM, median thalamic radiation; VM, ventromedial nucleus of thalamus; VT, ventral nucleus of thalamus. Section No. 175, 82-5, 9580 μm.

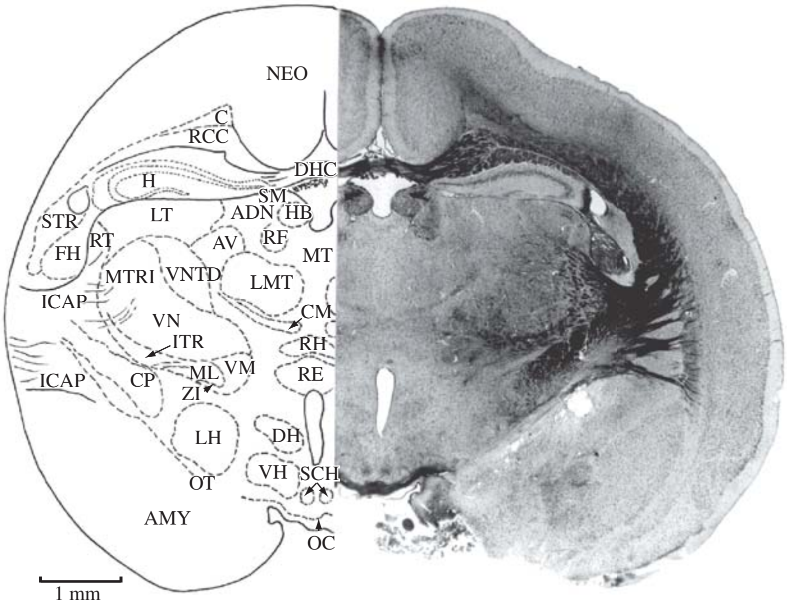

Figure 12. AD, anterodorsal thalamic nucleus; AMY, amygdala; AV, anteroventral nucleus of thalamus; C, cingulum; CM, centromedian thalamic nucleus; CP, cerebral peduncle; DH, dorsal nucleus of hypothalamus; DHC, dorsal hippocampal commissure; FH, fimbria of hippocampus; H, hippocampus; HB, habenular nucleus; ICAP, internal capsule; ITR, inferior thalamic radiation; LH, lateral nucleus of the hypothalamus; LMT, lateral medial nucleus of thalamus; LT, lateral thalamic nucleus; ML, medial lemniscus; MT, median nucleus of thalamus; MTRI, intermediate thalamic radiation; NEO, neocortex; OC, optic chiasm; OT, optic tract; RE, reuniens thalamic nucleus; RCC, radiation of corpus callosum; RF, retroflex fasciculus; RH, rhomboid thalamic nucleus; RT, reticular thalamic nucleus; SCH, suprachiasmatic nucleus; SM, stria medullaris of thalamus; STR, striatum (caudate-putamen) nucleus; VH, ventral nucleus of the hypothalamus; VM, ventromedian nucleus of thalamus; VN, ventral nucleus of thalamus; VNTD, ventral nucleus of thalamus, dorsal portion; ZI, zona inserta. Section No. 194, 79-5, 9220 µm.

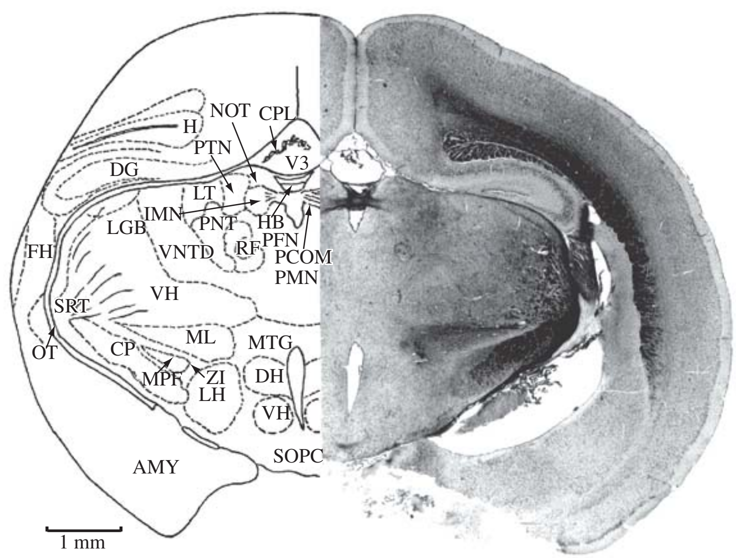

Figure 13. AMY, amygdala; CP, cerebral peduncle; CPL, choroid plexus; DG, dentate gyrus; DH, dorsal nucleus of hypothalamus; FH, fimbria of hippocampus; H, hippocampus; HB, habenular nucleus; IMN, interstitial magnocellular nucleus of posterior commissure; LGB, lateral geniculate body; LH, lateral nucleus of hypothalamus; LT, lateral nucleus of thalamus; ML, medial lemniscus; MPF, medial prosencephalic fasciculus; MTG, mammillotegmental tract; NOT, nucleus of optic tract; OT, optic tract; PCOM, posterior commissure; PFN, parafascicular nucleus; PMN, posteromedian nucleus of thalamus; PNT, posterior nucleus of thalamus; PTN, pretectal nucleus; RF, retroflex fasciculus; SOPC, supraoptic commissure; SRT, superior radiation of thalamus; VH, ventral nucleus of hypothalamus; V 3, third ventricle; VNTD, ventral nucleus of thalamus, dorsal portion; ZI, zona incerta. Section No. 205, 76-5, 8980 µm.

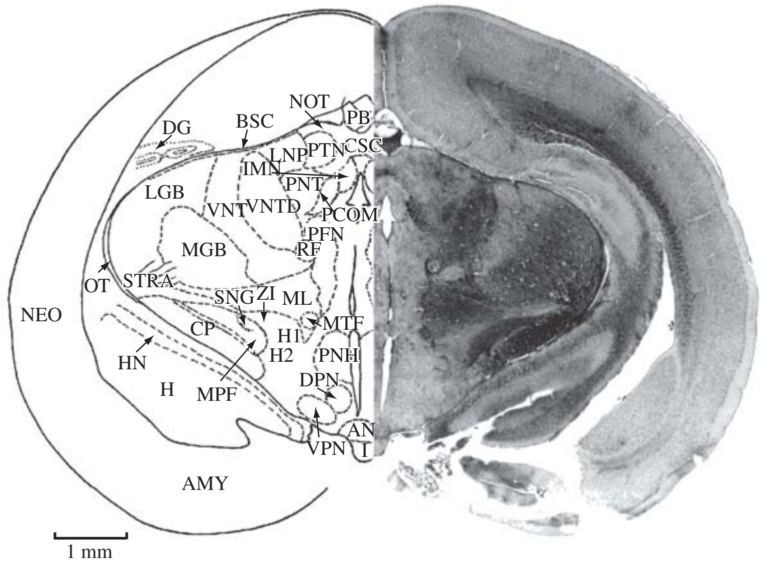

Figure 14. AMY, amygdala; AN, arcuate nucleus; BSC, brachium of superior colliculus; CP, cerebral peduncle; CSC, commissure of superior colliculus; DG, dentate gyrus; DPN, dorsal premammillary nucleus; H, hippocampus; HN, hippocampal nucleus; H1, H2, Forel's fields; I, infundibulum; IMN, interstitial magnocellular nucleus of posterior commissure; LGB, lateral geniculate body; LNP, lateral nucleus of thalamus (posterior portion); MGB, medial geniculate body; ML, medial lemniscus; MPF, medial prosencephalic nucleus; MTF, mamillotegmental fasciculus; NEO, neocortex; NOT, nucleus of optic tract; OT, optic tract; PB, pineal body (epiphysis); PCOM, posterior commissure; PFN, parafascicular nucleus; PNH, posterior nucleus of hypothalamus; PNT, posterior nucleus of thalamus; PTN, pretectal nucleus; RF, retroflex fasciculus; SNG, substantia nigra; STRA, superior thalamic radiation; VNT, ventral nucleus of thalamus; VNTD, ventral nucleus of thalamus, dorsal portion; VPN, ventral premamillary nucleus; ZI, zona incerta. Section No. 225, 72-5, 8560 µm.

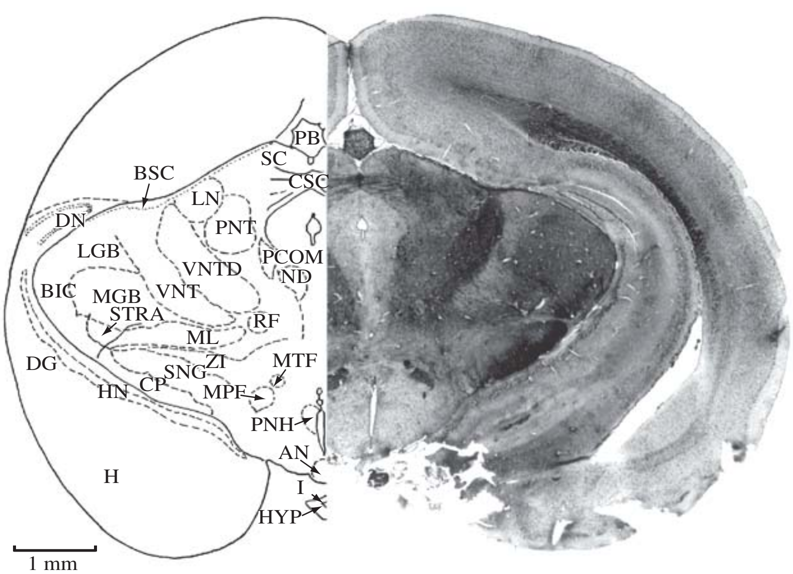

Figure 15. AN, arcuate nucleus; BIC, brachium of inferior colliculus; BSC, brachium of superior colliculus; CP, cerebral peduncle; CSC, commissure of superior colliculus; DG, dentate gyrus; DN, dentate nucleus; H, hippocampus; HN, hippocampal nucleus; HYP, hypophysis; I, infundibulum; LGB, lateral geniculate body; LN, lateral nucleus of thalamus (posterior part); MGB, medial geniculate body; ML, medial lemniscus; MPF, medial prosencephalic fasiculus; MTF, mamillotegmental fasciculus; ND, nucleus of Darkschewitsch; PB, pineal body (epiphysis); PCOM, posterior commissure; PNH, posterior nucleus of hypothalamus; PNT, posterior nucleus of thalamus; RF, retroflex fasciculus; SC, superior colliculus; SNG, substantia nigra; STRA, superior thalamic radiation; VNT, ventral nucleus of thalamus; VNTD, ventral nucleus of thalamus (dorsal portion); ZI, zona incerta. Section No. 240, 69-1-5, 8260 µm.

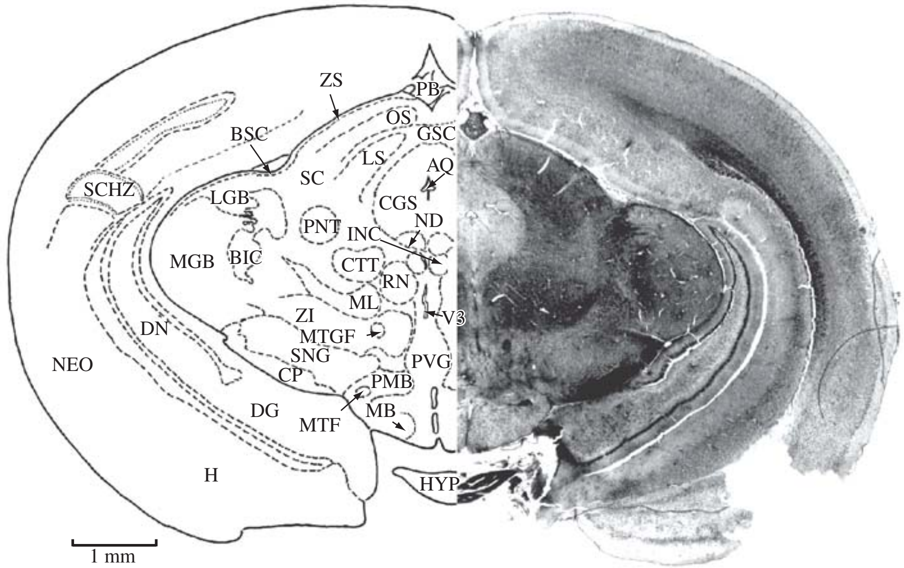

Figure 16. AQ, aqueduct, cerebral; BIC, brachium of inferior colliculus; BSC, brachium of superior colliculus; CGS, central gray substance; CP, cerebral peduncle; CSC, commissure of superior colliculus; CTT, central tegmental tract; DG, dentate gyrus; DN, dentate nucleus; H, hippocampus; HYP, hypophysis; INC, interstitial nucleus of Cajal; LGB, lateral geniculate body; LS, leminiscal stratum; MB, mamillary body; MGB, medial geniculate body; ML, medial lemniscus; MTGF, mamillotegmental fasciculus; MTF, mamillothalamic fasciculus; ND, nucleus of Darkschewitsch (one of the accessory oculomotor nuclei); NEO, neocortex; OS, optic stratum; PB, pineal body; PMB, peduncle of mamillary body; PNT, posterior nucleus of thalamus; PVG, periventricular gray; RN, red nucleus; SC, superior colliculus; SCHZ, schizocortex; SNG, substantia nigra; ZI, zona incerta; ZS, zonal stratum; V 3, third ventricle. Section No. 251, 66-1, 7980 µm.

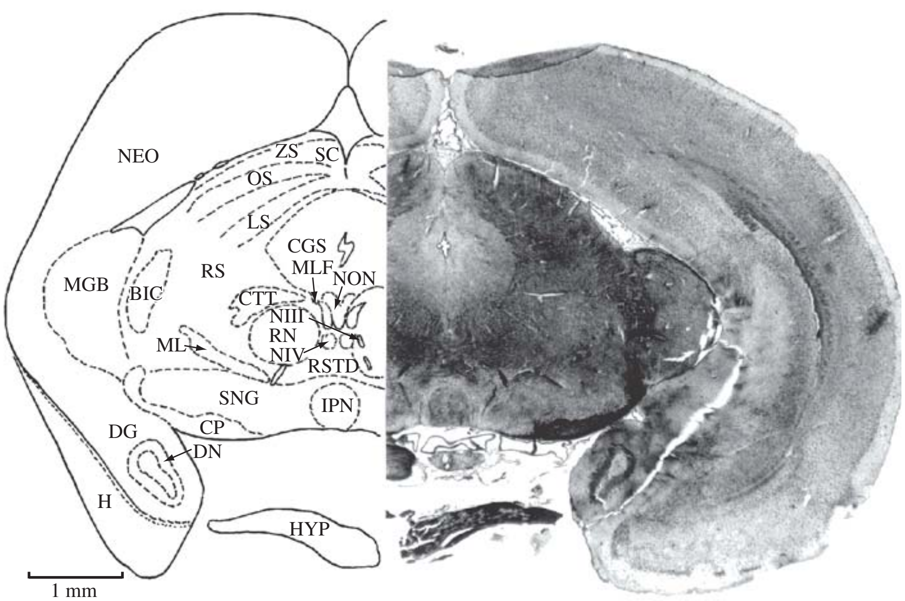

Figure 17. BIC, brachium of inferior colliculus; CGS, central gray substance; CP, cerebral peduncle; CTT, central tegmental tract; DG, dentate gyrus; DN, dentate nucleus; H, hippocampus; HYP, hypophysis; IPN, interpeduncular nucleus; LS, lemniscal stratum; MGB, medial geniculate body; ML, medial lemniscus; MLF, medial longitudinal fasciculus; NEO, neocortex; NON, oculomotor nucleus; N III, oculomotor nerve; OS, optic stratum; RN, red nucleus; RS, reticular substance; RSTD, rubrospinal tract, decussation; SC, superior colliculus; SNG, substantia nigra; ZS, zonal stratum; N IV, trochlear nucleus. Section No. 274, 62-4, 7560 µm.

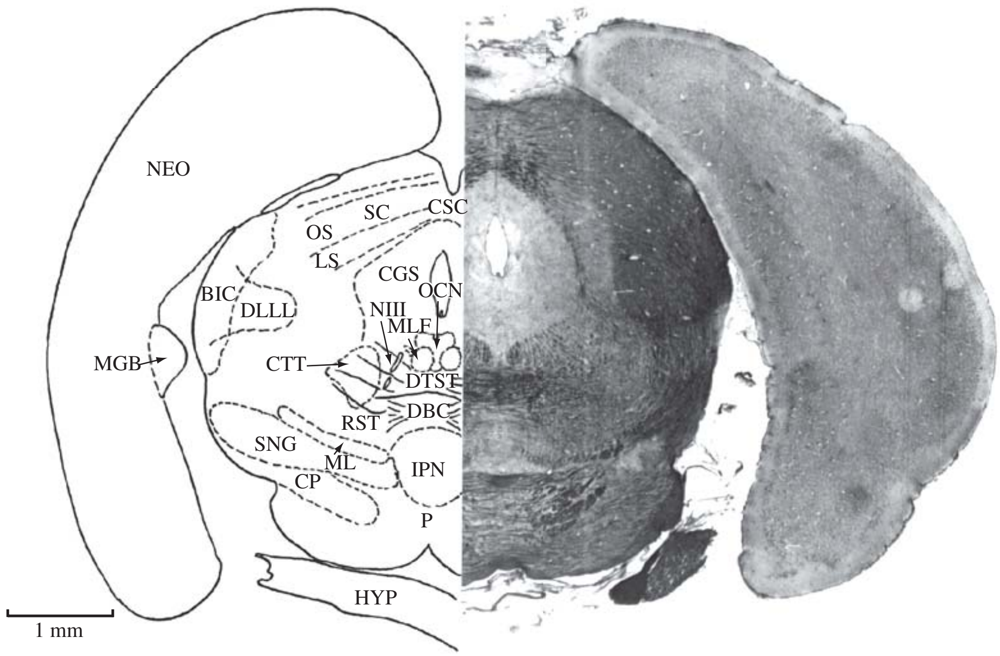

Figure 18. BIC, brachium of inferior colliculus; CGS, central gray substance; CP, cerebral peduncle; CSC, commissure of superior colliculus; CTT, central tegmental tract; DBC, decussation of middle cerebral peduncle; DLLL, dorsal loop of lateral lemniscus; DTST, decussation of tectospinal tract; HYP, hypophysis; IPN, interpeduncular nucleus; LS, lemniscal stratum; MGB, medial geniculate body; ML, medial lemniscus; MLF, medial longitudinal fasciculus; NEO, neocortex; N III, oculomotor nerve; OCN, oculomotor nucleus; OS, optic stratum; P, pons; RST, rubrospinal tract; SC, superior colliculus; SNG, substantia nigra. Section No. 295, 58-1-5, 7380 µm.

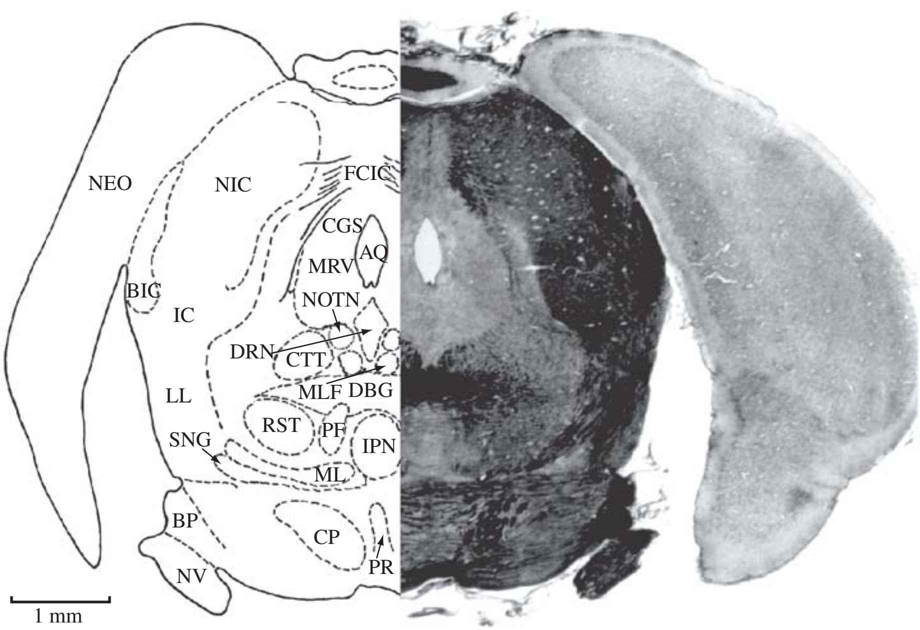

Figure 19. AQ, aqueduct, cerebral; BIC, brachium of inferior colliculus; BP, brachium pontis; CGS, central gray substance; CP, cerebral peduncle; CTT, central tegmental tract; DBC, decussation of brachium of middle cerebral peduncle; DRN, dorsal raphe nucleus; FCIC, fibers of commissure of inferior colliculus; IC, inferior colliculus; IPN, interpeduncular nucleus; LL, lateral lemniscus; ML, medial lemniscus; MLF, medial longitudinal fasciculus; MRV, mesencephalic root of trigeminal nerve; NEO, neocortex; NIC, nucleus of inferior colliculus; NOTN, nucleus of origin of trochlear nerve; NV, trigeminal nerve; PF, predorsal fasciculus; PR, pontine raphe; RST, rubrospinal tract; SNG, substantia nigra. Section No. 319, 53-4, 7040 µm.

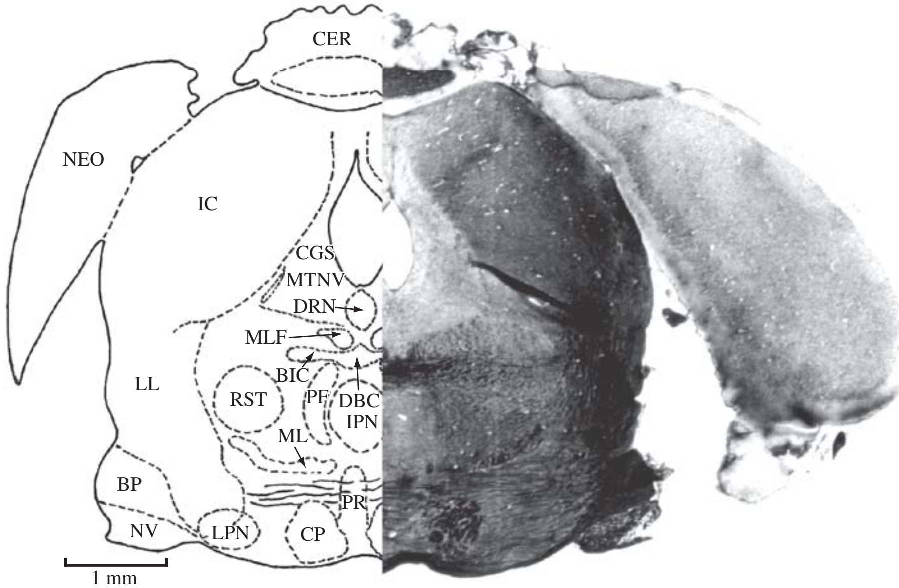

Figure 20. BIC, brachium of inferior colliculus; BP, brachium of middle cerebral peduncle; CER, cerebellum; CGS, central gray substance; CP, cerebral peduncle; DBC, decussation of brachium of inferior colliculus; DRN, dorsal raphe nuclei; IC, inferior colliculus; IPN, interpeduncular nucleus; LL, lateral lemniscus; LPN, lateral pontine nuclei; ML, medial lemniscus; MLF, medial longitudinal fasciculus; MTNV, mesencephalic tract of trigeminal nerve; NEO, neocortex; NV, trigeminal nerve; PF, predorsal fasciculus; PR, pontine raphe and nuclei; RST, rubrospinal tract. Section No. 329, 51-1-4, 6640 µm.

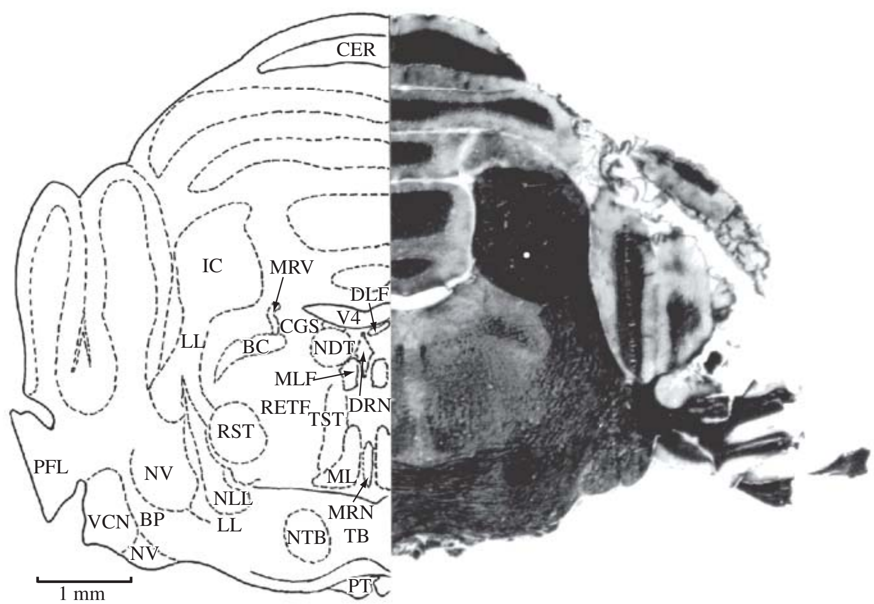

Figure 21. BIC, brachium of inferior colliculus; BP, brachium pontis; CER, cerebellum; CGS, central gray substance; DLF, dorsal longitudinal fasciculus; DRN, dorsal raphe nucleus; IC, inferior colliculus; LL, lateral lemniscus; ML, medial lemniscus; MLF, medial longitudinal fasciculus; MRN, median raphe nucleus; MRV, mesencephalic root of trigeminal nerve; NDT, dorsal tegmental nuclei; NLL, nucleus of lateral lemniscus; NTB, nucleus of trapezoid body; NV, nerve trigeminal; PFL, paraflocculus; PT, pyramidal tract (corticospinal), anterior; RETF, reticular formation; RST, rubrospinal tract; TB, trapezoid body; TST, tectospinal tract; VCN, ventral cochlear nucleus; V 4, fourth ventricle. Section No. 360, 44-1-5, 6060 µm.

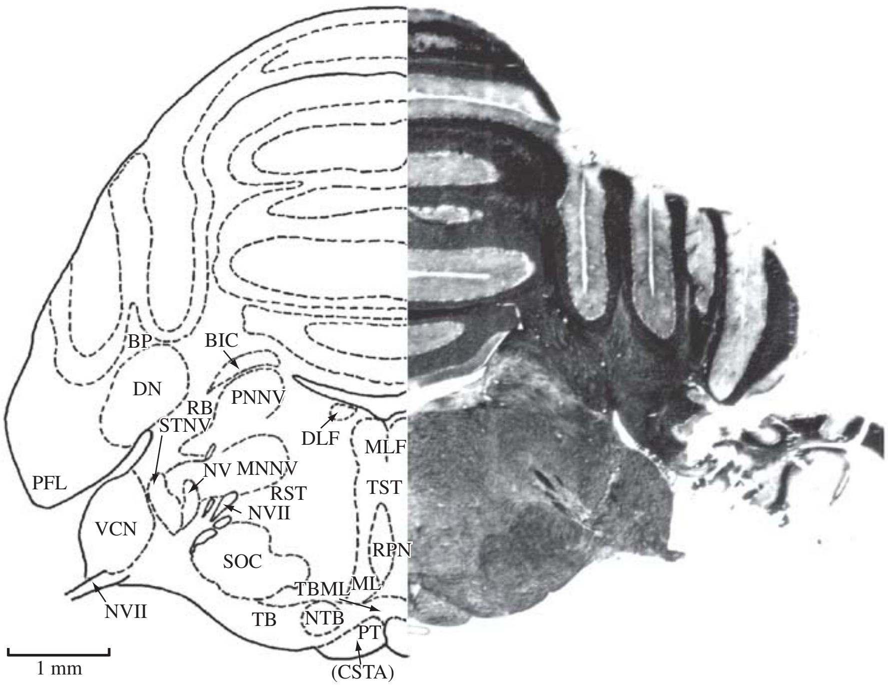

Figure 22. BIC, brachium of inferior colliculus; BP, brachium pontis; DLF, dorsal longitudinal fasciculus (mesencephalic); DN, dentate nucleus; ML, medial lemniscus; MLF, medial longitudinal fasciculus; MNNV, motor nucleus of trigeminal nerve; NTB, nucleus of trapezoid body; NV, trigeminal nerve; N VII, facial nerve; PFL, paraflocculus; PNNV, principal nucleus of trigeminal nerve; PT, pyramidal tract (corticospinal), anterior; RB, restiform body; RPN, raphe nucleus; RST, rubrospinal tract; SOC, superior olivary nucleus (complex); STNV, spinal tract of trigeminal nerve; TB, trapezoid body; TBML, trapezoid body and medial lemniscus; TST, tectospinal tract; VCN, ventral cochlear nucleus. Section No. 402, 35-1-2, 5360 µm.

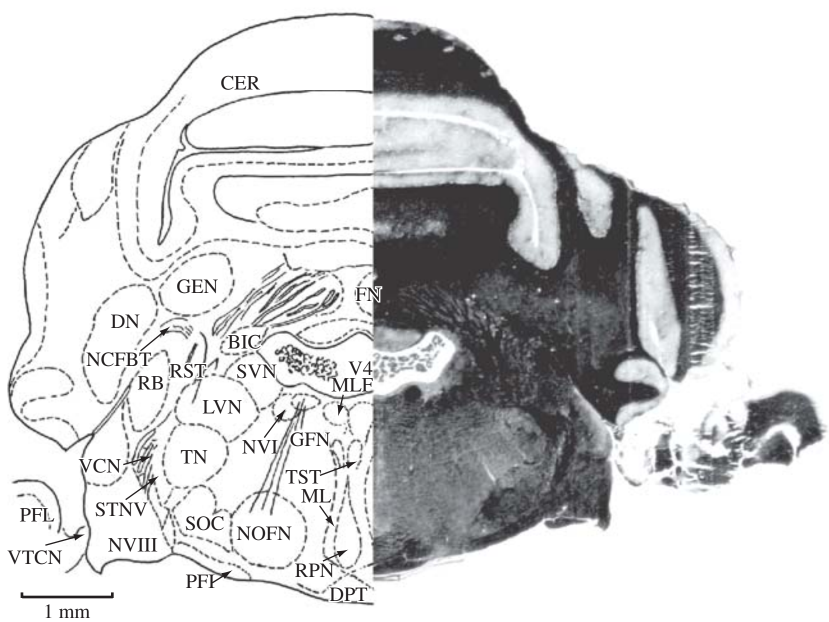

Figure 23. BIC, brachium of inferior colliculus; CER, cerebellum; DN, dentate nucleus; DPT, decussation of pyramidal tract; FN, fastigial nucleus; GEN, globiform-emboliform nuclei; GFN, genu of facial nerve; LVN, lateral vestibular nucleus; ML, medial lemniscus; MLF, medial longitudinal fasciculus; NCFBT, nucleocerebellar and fastigiobulbar tract; N VI, abducens nucleus; NOFN, nucleus of origin of facial nerve; PFL, paraflocculus; PFI, pontine fibers; RB, restiform body; RPN, raphe nuclei (median); RST, rubrospinal tract; N VIII, vestibulocochlear nerve; SOC, superior olivary nucleus; STNV, spinal tract of trigeminal nerve; SVN, superior vestibular nucleus; TN, trigeminal nucleus; TST, tectospinal tract; VCN, ventral cochlear nucleus; VTCN, ventral terminal cochlear nucleus; V 4, fourth ventricle; Section No. 429, 30-1-4, 4860 µm.

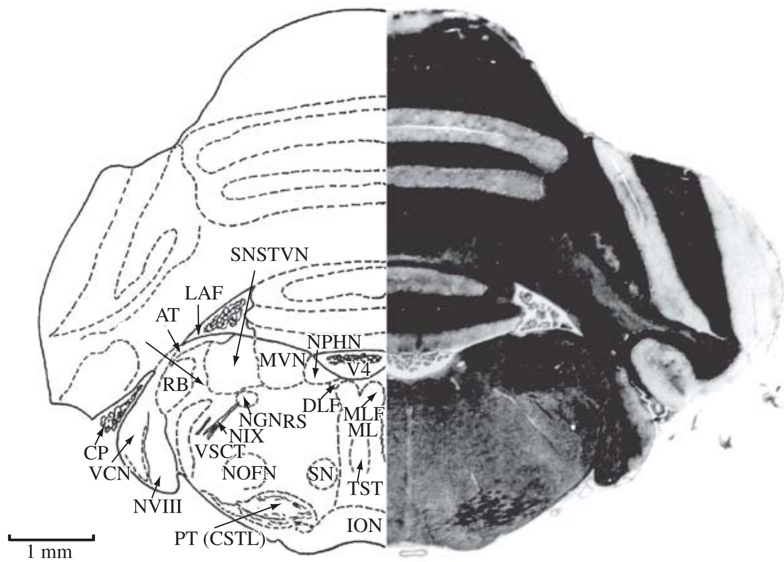

Figure 24. AT, acoustic tuberculum; CP, choroid plexus; DLF, dorsal longitudinal fasciculus; ION, inferior olivary nucleus; LAF, lateral aperture, fourth ventricle; ML, medial lemniscus; MLF, medial longitudinal fasciculus; MVN, medial vestibular nucleus; NGN, nucleus of glossopharyngeal nerve; NOFN, nucleus of origin of facial nerve; NPHN, nucleus prepositus of hypoglossal nerve; N IX, glossopharyngeal nerve; PT (CSTL), pyramidal (corticospinal tract); RB, restiform body; RS, reticular substance; SN, salivatory nucleus; SNSTVN, spinal nucleus and spinal tract of vestibular nerve; STNV, spinal tract of trigeminal nerve; TST, tectospinal tract; VCN, ventral (anterior) cochlear nucleus; N VIII, vestibulocochlear nerve; VSCT, ventral spinocerebellar tract; V 4, fourth ventricle. Section No. 464, 25-2-4, 4300 µm.

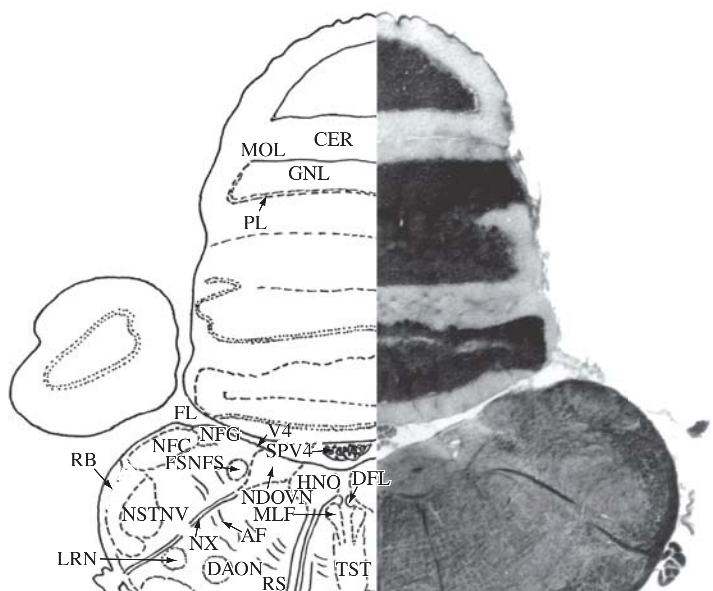

Figure 25. CER, cerebellum; CPV4, choroid plexus, fourth ventricle; DAON, dorsal accessory olivary nucleus; DLF, dorsal longitudinal fasciculus; FL, foramen of Luschka; FSNFS, fasciculus solitarius and nucleus of fasciculus solitarius; GNL, granular layer; HNO, hypoglossal nucleus of origin; IAF, internal arcuate fibers; ION, inferior olivary nucleus; LRN, lateral reticular nuclei; MLF, medial longitudinal fasciculus; MOL, molecular layer; NDOVN, nucleus of dorsal origin of vague nerve; NFC, nucleus of fasciculus cuneatus; NFG, nucleus of fasciculus gracilis; N X, vagus nerve; N XII, hypoglossal nerve; NSTNV, nucleus of spinal tract of trigeminal nerve; PL, Purkinje layer; PT (CSTL) pyramidal (corticospinal) tract; RB, restiform body; RS, reticular substance; STNV, spinal tract of trigeminal nerve; TST, tectospinal tract; VCST, ventral corticospinal tract; VSCT, ventral spinocerebellar tract; V 4, fourth ventricle. Section No. 513, 20-2-3, 3320 µm.

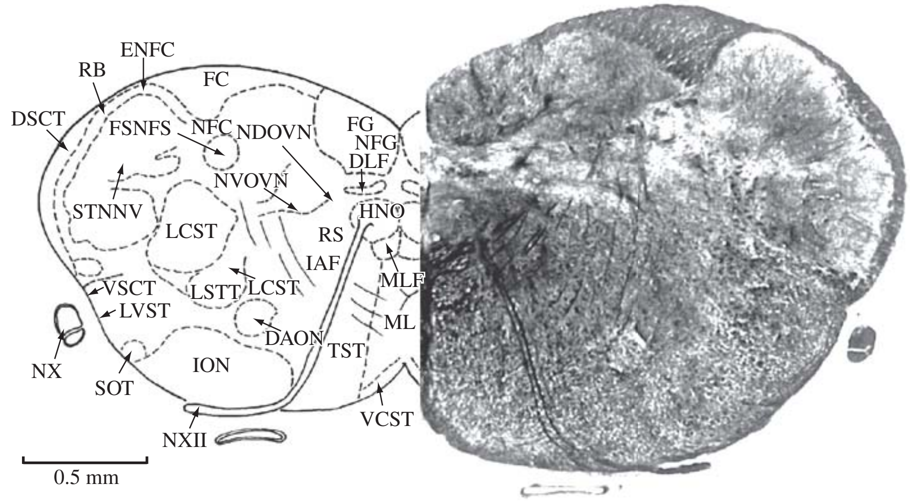

Figure 26. DAON, dorsal (posterior) accessory olivary nucleus; DLF, dorsal longitudinal fasciculus; DSCT, dorsal (posterior) spinocerebellar tract; ENFC, external nucleus of fasciculus cuneatus; FC, fasciculus cuneatus; FG, fasciculus gracilis; FSNFS, fasciculus solitarius and nucleus of fasciculus solitarius; HNO, hypoglossal nucleus of origin; IAF, internal arcuate fibers; ION, caudal inferior olivary nucleus; LCST, lateral corticospinal tract; LSTT, lateral spinothalamic tract; LVST, lateral vestibulospinal tract; ML, medial lemniscus; MLF, medial longitudinal fasciculus; NDOVN, nucleus of dorsal origin of vagus nerve; NFC, nucleus of fasciculus cuneatus; NFG, nucleus of fasciculus gracilis; NVOVN, nucleus of ventral origin of vagus nerve; N X, vagus nerve; N XII, hypoglossal nerve; RB, restiform body (inferior cerebellar peduncle); RS, reticular substance; SOT, spinoolivary tract (end point); STNNV, spinal tract and nucleus of trigeminal nerve; TST, tectospinal tract; VCST, ventral corticospinal tract; VSCT, ventral spinocerebellar tract. Section No. 565, 15-2-5, 1900 µm.

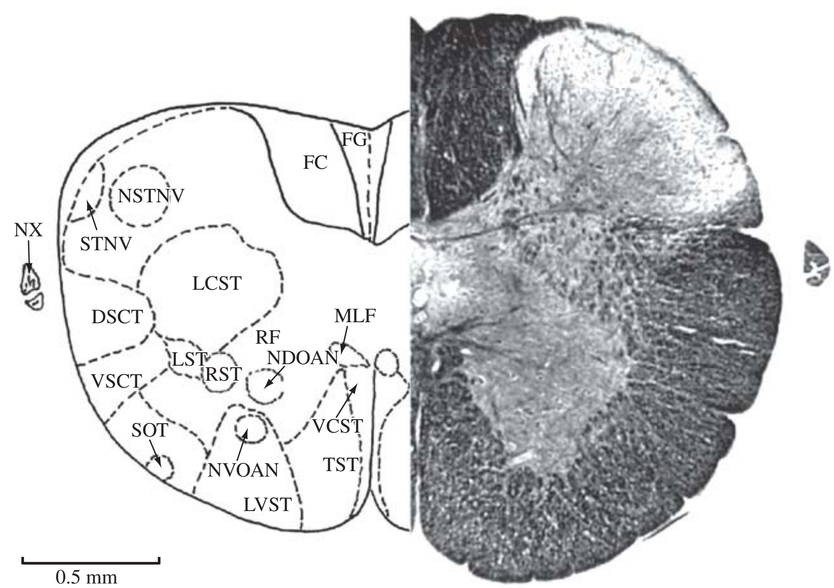

Figure 27. DSCT, dorsal spinocerebellar tract; FC, fasciculus cuneatus; FG, fasciculus gracilis; LCST, lateral (pyramidal) corticospinal tract; LST, lateral spinothalamic tract; LVST, lateral vestibulospinal tract; MLF, medial longitudinal fasciculus; NDOAN, nucleus of dorsal origin of accessory nerve; NSTNV, nucleus of spinal tract of trigeminal nerve; NVOAN, nucleus of ventral origin of accessory nerve; RF, reticular formation; RST, rubrospinal tract; SOT, spinoolivary tract; STNV, spinal tract of trigeminal nerve; TST, tectospinal tract; VCST, ventral corticospinal tract; VSCT, ventral spinocerebellar tract. Section No. 675, 4-2-10, 760 µm.

Table 2. Average percentages and range for the five main regions of the brain of 47 megachiropteran and 225 microchiropteran species including the Desmodontidae. Data on *Desmodus* and *Diphylla* have been calculated and shown separately. The values for human brain are provided for comparison. (After Baron et al., 1996a, p. 89).

	Megachiroptera % (Range)	**Microchiroptera % (Range)**	***Desmodus* (%)**	***Diphylla* (%)**	**Human (%)**
Medulla oblongata	7.1 (5.3-8.9)	13.1 (7.8-19.7)	8.5	8.3	0.8
Cerebellum	13.5 (11.5-16)	19.5 (15.3-28.9)	17.6	17.4	11.0
Mesencephalon	5.4 (4.2-6.9)	9.8 (5.5-14.6)	6.2	7.0	0.6
Diencephalon	8.6 (7.9-9.4)	8.0 (6.7-10.6)	7.9	8.4	2.7
Telencephalon	65.3 (60.1-70.2)	49.6 (37.7-63.4)	59.8	58.9	85.0

Table 3. Neurobiological data on *Desmodus rotundus* (from Baron et al., 1996a; b; c).

Brain length	16.80 mm
Standard brain volume	964 mm^3
Net brain volume	944 mm^3
Brain weight	999 mg
Body weight	36.3 g
Volumes of brain parts, mm^3	
Telecephalon	564.8
Neocortex	312.5
main olf bulb	33.0
acc. olf bulb	0.355
Diencephalon	74.9
Mesencephalon	58.3
Cerebellum	166.4
Medulla oblongata	80.0

opallium and the synaptic cascades of its sectors, cortical involvement of instinctive action patterns and responses based on neocortical associations are the remaining circuitary. The pursuit of the main and the accessory olfactory systems in *Desmodus* is likely to provide the neuroanatomical explanation of its behavioral complexities.

For neurological information on *Desmodus*, the reader is directed to Greenhall et al. (1983, species account), Mann (1960, neurobiology), Escobar et al. (1968, inferior olivary nucleus), Yamamoto et al. (1955, abducens nucleus, pyramidal tract and the vestibular nucleus), Palacios Prü and Briceno (1972, glial cell and neuronal dendrite ultrastructural relationship in the olfactory bulb), and Palacios Prü (1970, ultrastructure of mossy fibers).

The cytoarchitectural organization of the *Desmodus* brain deserves to be compared in parallel with that of other vampire species, bats of other families (especially megachiroptera), and some other representative mammals. When nuclear groups, fiber tracts, and their interconnections are thus compared and contrasted, the neuroanatomical basis of behavior in the vampire is more likely to become apparent. This atlas has been presented with exactly that future goal in mind.

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