An Atlas of the Brain of the Gilthead Seabream (*Sparus aurata*)

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INTRODUCTION

As for any class of vertebrates, the development of neuroendocrinology in fish has been tightly dependent on anatomo-functional studies aiming at identifying brain regions potentially implicated in neuroendocrine regulation of pituitary functions and at tracing the neuronal systems participating in those regulations. For a given species, such studies require the availability of an atlas of the brain of that particular species or one that is closely related. The best example of this requirement is illustrated by the tremendous impact that the atlas of the goldfish brain (Peter and Gill, 1975) had on fish neuroendocrinology. Fishes, representing the largest group of vertebrates with over 25,000 species, 58 orders and 468 families (Nelson, 1984), have a long evolutionary history and exhibit a wide diversity. Although the overall pattern of organization of the brain is similar in all fish, there is considerable variation in the topology of many brain regions from one species to another and the amplitude of this variation increases with the evolutionary distance separating these species. Thus, complete brain atlases for the electric fish, *Apteronotus leptorhynchus* (Gymnotiform; Maler et al., 1991), the swordtail fish, *Xiphophorus helleri* (Cyprinodontiform; Anken and Rahmann, 1994), and the zebrafish, *Danio rerio* (Cypriniform; Wullimann et al., 1996), as well as a number of partial brain atlases have already been published on the goldfish, *Carassius auratus* (Cypriniform; Peter and Gill, 1975), the killifish, *Fundulus heteroclitus* (Cyprinodontiform; Peter et al., 1975), and two salmonids, the rainbow trout, *Oncorhynchus mykiss* (Billard and Peter, 1982) and the Atlantic salmon, *Salmo salar* (Peter et al., 1991). A comparative approach to the central nervous system of the vertebrates, including fishes, has also been published recently by Nieuwenhuys et al. (1997).

Perciforms, with 154 families and over 7000 species (37% of the teleosts, according to Nelson, 1984) represent the largest group of teleosts and include many species of commercial interest. Surprisingly, little attention has been focused on this order. Thus, major cell groups comprising the telencephalon have only been reported in the green sunfish, *Lepomis cyanellus* (Northcutt and Davis, 1983) and the Siamese fighting fish, *Betta splendens* (Marino-Neto and Sabbatini, 1988). A detailed neuroanatomical study of the diencephalon and pretectum of cichlid fish *Haplochromis burtoni*, has also been carried out (Fernald and Shelton, 1985) and a number of partial studies have been focused on diverse diencephalic areas in perciform species (Wullimann, 1988; Northcutt and Wullimann, 1988; Wullimann and Northcutt, 1988, 1989; Striedter and Northcutt, 1989). Fortunately, critical improvements in understanding the perciform brain organization have been achieved more recently (Wullimann and Meyer, 1990; Northcutt and Butler, 1991; Butler et al., 1991; Lannoo and Eastman, 1995; Anken and Rahmann, 1995). However, further descriptions on the cytoarchitectonic organization and patterns of connectivity of the perciform brain seem to be necessary for comparative purposes. The gilthead seabream (*Sparus aurata*; Sparidae, Figure 1) is a characteristic hermaphroditic teleost of the South Atlantic and Mediterranean coasts, and represents one of the most important species for aquaculture in these regions. We present here a complete atlas for the brain of the gilthead seabream, a species which also represents an interesting model for research and has recently been the focus of physiological and endocrine studies (Powell et al., 1994; Zohar et al., 1995; Gothilf et al., 1996, 1997).

A. Arias
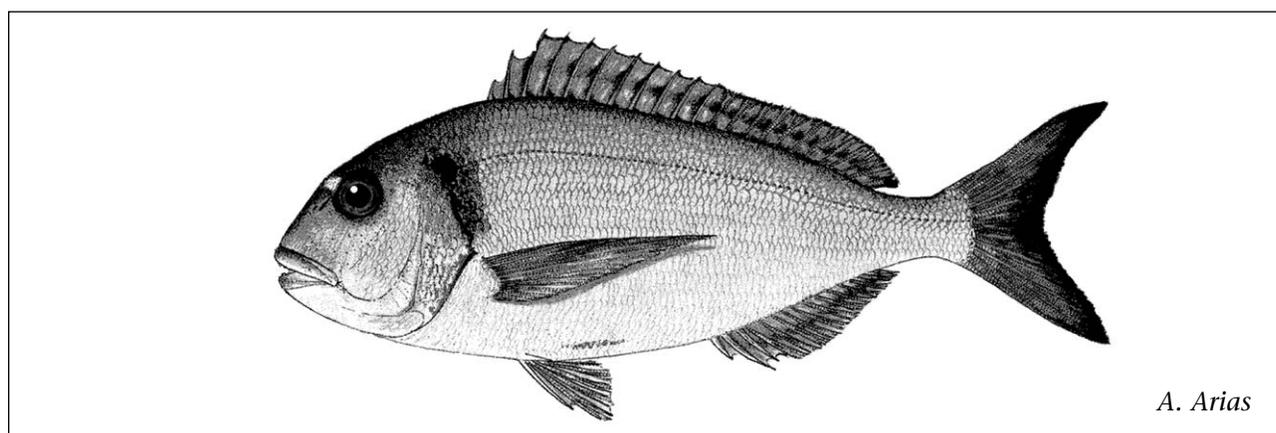
Figure 1. The Gilthead Seabream, Sparus aurata.

METHODOLOGICAL CONSIDERATIONS

Adult male and female gilthead seabream, *Sparus aurata*, ranging in body length from 30 to 40 cm (2-3 years old) were purchased from a local fishery (C.I.C.E.M. El Toruño, Puerto de Santa María, Cadiz, Spain). The animals were anesthetized with phenoxyethanol and perfused through the aortic bulb with 0.9% saline solution followed by Bouin's fixative. The brains were removed and postfixed in sublimated Bouin-Hollande's fixative for 72 h before they were embedded in paraffin and cut transversely and sagittally at 7 μm on a rotary microtome. For transverse sectioning, brains were oriented in order to obtain sections perpendicular to the mid-sagittal and horizontal planes. Brain sections were stained with paraldehyde fuchsin, Groat's hematoxylin-picroindigocarmin or 1% cresyl violet (Gabe, 1968), analyzed on a Leitz photomicroscope and photographed using panchromatic Agfapan APX 25 Films (AGFA). Size, shape, density, staining and pattern of distribution of perikaryon, as well as the spatial discontinuity of cell masses were used as major criteria to identify different cell groups. For descriptive purposes, we have subdivided the cells into four categories: small (5-10 μm), medium-sized (11-20 μm), large (21-40 μm) and very large (more than 40 μm). The boundaries of cell masses and fiber tracts were drawn on photographs of the brain sectioned most symmetrically and copied onto transparent paper. Serial drawings were digitized using an HP 4L scanner (Hewlett Packard) and processed on a IBM-compatible personal computer with the help of the Aldus PhotoStyler 2.0 program. The first section through the posterior commissure was chosen as the transverse zero point. Distances from the zero point are expressed in μm and atlas drawings anterior or posterior to the zero point are indicated as + or –, respectively. Average distance between drawings was 210 μm, but sometimes this distance was reduced or slightly increased. Scale bar numbers on the plates represent millimeters and the minor divisions correspond to 100 μm. No compensation was made for possible shrinkage of the tissue during the fixation and embedding processes. The levels of orientative transverse sections are indicated in Figure 2.

BRAIN SUBDIVISIONS AND NOMENCLATURE

As in other actinopterygian fishes, the brain of gilthead seabream has been divided in five main parts: telencephalon, diencephalon, mesencephalon, cerebellum and rhombencephalon
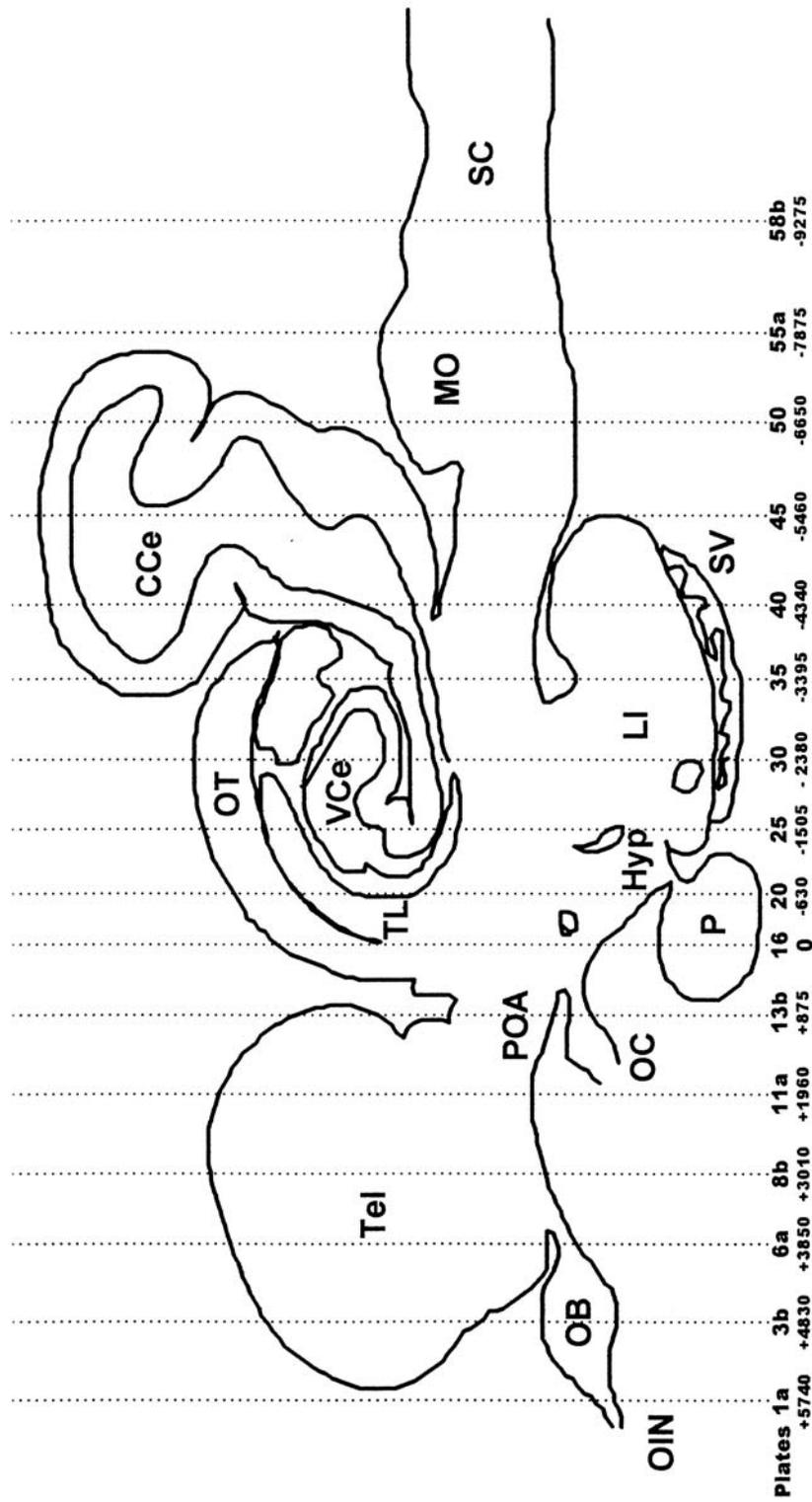
Figure 2. Sagittal section of the brain of the gilthead seabream, Sparus aurata, *showing the levels of orientative transverse sections. The number of the corresponding plates and the distances in μm from the zero point are indicated. + and – represent rostral and caudal sections to the zero point, respectively. For abbreviations, see the illustration key, pages 49-53.*

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(Nieuwenhuys, 1982). In turn, these parts can be subdivided into different areas, zones and nuclei (Table I). The telencephalon consists of olfactory bulbs located rostroventrally to paired cerebral hemispheres, in which dorsal and ventral areas can be discerned (Northcutt and Davis, 1983). The diencephalon represents one of the most complex regions in the brain. Our analysis of the diencephalon in gilthead seabream presented the same subdivisions found by Braford and Northcutt (1983) and Butler and Northcutt (1993): preoptic area, hypothalamus, thalamus (posterior tuberculum, ventral and dorsal thalamus), epithalamus, synencephalon, pretectum and the accessory optic nuclei. The mesencephalon can be divided into a bilobular dorsal tectum and a ventral tegmentum, which continues caudally into the rhombencephalon (Nieuwenhuys, 1982). The cerebellum comprises three main subdivisions: a valvula cerebelli, a corpus cerebelli and a lobus vestibulolateralis (Finger, 1983a). Finally, the rhombencephalon represents the most caudal part of the brain. As in other teleosts, a reticular formation, an area octavolateralis, as well as somatomotor and visceromotor nuclei can be found in the rhombencephalon of gilthead seabream (Nieuwenhuys, 1982; Wullimann and Northcutt, 1988). Dorsal, ventral and lateral views of the gilthead seabream brain are presented in Figure 3.

Often, interspecific differences and different degrees of brain complexity prevent the development of a consistent nomenclature suitable for all teleost. This is also true for the brain of the gilthead seabream, in which some areas are hypertrophied or exhibit more subdivisions than expected. However, in order to avoid more confusion in the literature, we have tried, when possible, to adopt in this atlas the most accepted nomenclatures for every brain area. For the telencephalon our nomenclature follows the cytoarchitectonic description of Northcutt and Braford (1980) and Northcutt and Davis (1983). For most of the diencephalon, the nomenclature developed by Braford and Northcutt (1983) was generally used, with additional elaborations by Wullimann and Meyer (1990). However, for the preoptic area and hypothalamus the cytoarchitectonic scheme of Peter and Gill (1975) and Peter et al. (1975) was adopted, with some modifications according to Braford and Northcutt (1983) and Wullimann and Northcutt (1988, 1989). We have used the description of Northcutt (1983) and Wullimann and Northcutt (1988) for the mesencephalon. For the cerebellum, the neuroanatomical nomenclature follows the revision of Finger (1983a) and studies of Wullimann and Northcutt (1988, 1989) in *Lepomis cyanellus* and *Carassius auratus*. Finally, the terminology used here for the rhombencephalon is primarily adopted from McCormick (1982), Nieuwenhuys and Pouwels (1983) and Prasada Rao et al. (1987).

Dorsal view

Ventral view
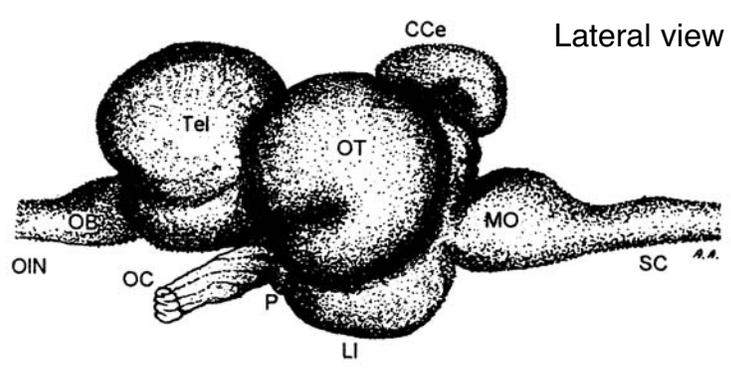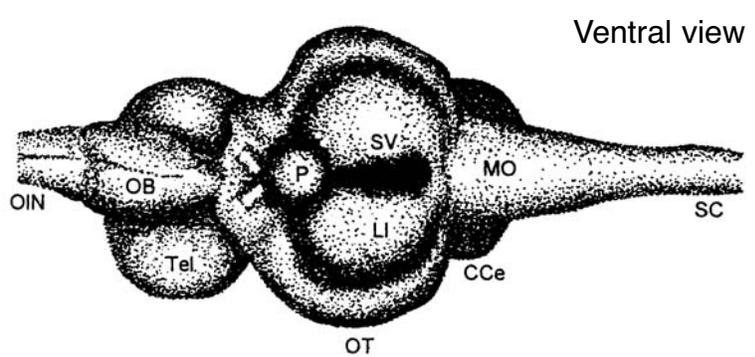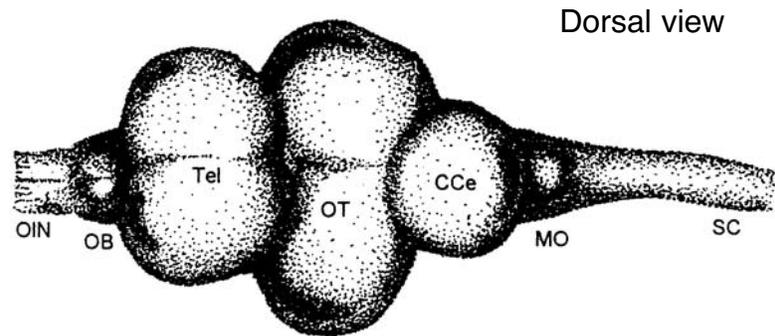
Lateral view

Figure 3. Drawings of the gilthead seabream brain in dorsal, ventral and lateral views. For abbreviations, see the illustration key, pages 49-53.

Table I. Brain Subdivisions and Nomenclature for Cell Masses in *Sparus aurata.*

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1. TELENCEPHALON

1.1. OLFACTORY BULBS (OB)
Olfactory nerve fibers (OlN): + 5740 to + 4830. Plates 1a-3b
Glomerular layer (GL): + 5740 to + 4200. Plates 1a-5a
External cellular layer (ECL): + 5740 to + 4200. Plates 1a-5a
Secondary olfactory fibers (SOF): + 5530 to + 4200. Plates 1b-5a
Internal cellular layer (ICL): + 5530 to + 4200. Plates 1b-5a
Terminal nerve ganglion cells (TNgc): + 4375 to + 4060. Plates 4b-5b

1.2. CEREBRAL HEMISPHERES
Area dorsalis
pars medialis (Dm)
 subdivision 1 (Dm1): + 4620 to + 3745. Plates 4a-6b
 subdivision 2 (Dm2): + 5250 to + 1295. Plates 2b-12b
 subdivision 3 (Dm3): + 5530 to + 1085. Plates 1b-13a
 subdivision 4 (Dm4): + 5250 to + 1085. Plates 2b-13a
pars centralis (Dc)
 subdivision 1 (Dc1): + 4830 to + 3325. Plates 3b-7b
 subdivision 2 (Dc2): + 3570 to + 1295. Plates 7a-12b
pars dorsalis (Dd): + 4200 to + 3010. Plates 5a-8b
pars lateralis (Dl)
 dorsal (Dld): + 5040 to + 1085. Plates 3a-13a
 ventral (Dlv)
  subdivision 1 (Dlv1): + 4830 to + 3010. Plates 3b-8b
  subdivision 2 (Dlv2): + 4620 to + 2135. Plates 4a-10b
  subdivision 3 (Dlv3): + 4375 to + 3850. Plates 4b-6a
 posterior (Dlp): + 2765 to + 1505. Plates 9a-12a
pars posterioris (Dp): + 1960 to + 875. Plates 11a-13b
nucleus taenia (NT): + 2765 to + 1960. Plates 9a-11a
Area ventralis
pars dorsalis (Vd): + 3850 to + 3010. Plates 6a-8b
pars ventralis (Vv): + 3325 to + 2555. Plates 7b-9b
pars lateralis (Vl): + 3325 to + 2555. Plates 7b-9b
pars supracommissuralis (Vs): + 3325 to + 1960. Plates 7b-11a
pars centralis (Vc): + 2555 to + 1960. Plates 9b-11a
pars postcommissuralis (Vp): + 2380 to + 1295. Plates 10a-12b
pars intermedia (Vi): + 1715 to +1295. Plates 11b-12b
nucleus entopeduncularis (NE): + 1715 to + 1085. Plates 11b-13a
lateral septal organ (LSO): + 3325 to + 2555. Plates 7b-9b

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2. DIENCEPHALON

2.1. PREOPTIC AREA
Nucleus preopticus parvocellularis (NPO)
pars anteroventralis (NPOav): + 2135 to + 1295. Plates 10b-12b
pars parvocellularis (NPOpc): + 2135 to + 1295. Plates 10b-12b
Nucleus preopticus magnocellularis (PM)

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pars parvocellularis (PMpc): + 1715 to + 1505. Plates 11b-12a
pars magnocellularis (PMmc): + 1505 to + 875. Plates 12a-13b
pars gigantocellularis (PMgc): + 1505 to – 420. Plates 12a-18
Nucleus anterioris periventricularis (NAPv): + 1505 to + 245. Plates 12a-15
Nucleus suprachiasmaticus (NSC): + 875 to + 245. Plates 13b-15
Nucleus posterioris periventricularis (NPPv): 0 to – 630. Plates 16-20

2.2. HYPOTHALAMUS
Medial tuberal zone
nucleus lateralis tuberis (NLT)
pars lateralis (NLTl): + 245 to – 210. Plates 15-17
pars ventralis (NLTv): + 245 to – 840. Plates 15-22
pars dorsalis (NLTd): 0 to – 735. Plates 16-21
pars medialis (NLTm): 0 to – 840. Plates 16-22
pars inferioris (NLTi): – 1050 to – 1295. Plates 23-24
nucleus anterior tuberis (NAT): 0 to – 840. Plates 16-22
nucleus recessus lateralis
pars ventralis (NRLv): – 630 to – 840. Plates 20-22
pars dorsalis (NRLd): – 840. Plate 22
nucleus recessus posterioris (NRP): – 735 to – 1295. Plates 21-24
nucleus saccus vasculosus (NSV): – 840 to – 1505. Plates 22-25
Lateral or inferior zone
nucleus diffusus lobi inferioris (NDLI): – 210 to 5460. Plates 17-45
pars lateralis (NDLIl): – 1295 to – 4830. Plates 24-42
pars medialis (NDLIm): – 1295 to – 4830. Plates 24-42
pars caudalis (NDLIc): – 3185 to – 5460. Plates 34-45
nucleus recessus lateralis
pars lateralis (NRLl): – 840 to – 5005. Plates 22-43
nucleus centralis lobi inferioris (NCLI): – 1295 to – 4165. Plates 24-39
nucleus medialis lobi inferioris (NMLI): – 1505 to – 1785. Plates 25-27

2.3. THALAMUS
2.3.1. Posterior tuberculum
2.3.1.1. periventricular nuclei
periventricular nucleus of the posterior tuberculum (TPp): – 490 to -1295. Plates 19-24
paraventricular organ (PVO): – 630 to – 840. Plates 20-22
nucleus of the paraventricular organ (nPVO): – 735 to – 1050. Plates 21-23
nucleus posterior tuberis (NPT): – 840 to – 1050. Plates 22-23
2.3.1.2. migrated nuclei
nucleus glomerulosus
pars anterioris (NGa): – 210 to – 1295. Plates 17-24
pars posterioris (NGp): – 1295 to – 2590. Plates 24-31
preglomerular nuclear complex
nucleus preglomerulosus anterioris (NPGa): + 455 to – 210. Plates 14b-17
nucleus preglomerulosus lateralis (NPGl): 0 to – 630. Plates 16-20
nucleus gustatorius tertius (NGT): – 210 to – 1050. Plates 17-23
nucleus preglomerulosus medialis (NPGm): – 420 to – 1995. Plates 18-28

2. DIENCEPHALON, *continued*

    caudomedial nuclei
        nucleus preglomerulosus commissuralis (NPGc): – 1295 to – 2800. Plates 24-32
        corpus mammillare (CM): – 1505 to – 2590. Plates 25-31
    outlying nuclei
        nucleus of the torus lateralis (TLa): – 420 to – 1785. Plates 18-27
        nucleus posterior thalami (PT): – 1295 to – 1505. Plates 24-25
        nucleus lateralis thalami (LT): – 1715 to – 2975. Plates 26-33
        nucleus of the tractus pretectoisthmicus (nTPI): – 1715 to – 1785. Plates 26-27
        nucleus periglomerulosus dorsalis (pgd): – 1715 to – 1995. Plates 26-28
        nucleus of the fasciculus retroflexus (nFR): – 1785 to – 1995. Plates 27-28

2.3.2. Ventral thalamus
    nucleus eminentia thalami (nTE): + 1085 to + 630. Plates 13a-14a
    nucleus ventromedialis thalami (VM): + 455 to – 490. Plates 14b-19
    nucleus ventrolateralis thalami (VL): + 455 to 0. Plates 14b-16
    nucleus intermedius thalami (I): 0 to – 420. Plates 16-18

2.3.3. Dorsal thalamus
    nucleus anterior thalami (A): + 245 to – 490. Plates 15-19
    nucleus centralis posterior thalami (CP): 0 to – 1050. Plates 16-23
    nucleus dorsalis posterior thalami (DP): – 210 to – 840. Plates 17-22

2.4. EPITHALAMUS
Nucleus habenularis
    pars ventralis (NHv): + 630 to + 245. Plates 14a-15
    pars dorsalis (NHd): + 455 to + 245. Plates 14b-15

2.5. SYNENCEPHALON
Nucleus pretectalis periventricularis
    pars dorsalis (PPd): – 210 to – 840. Plates 17-22
    pars ventralis (PPv): – 210 to – 1505. Plates 17-25
Nucleus paracommissuralis (NP): 0 to – 735. Plates 16-21
Nucleus of the medial longitudinal fasciculus (nMLF): – 1050 to – 2380. Plates 23-30
Subcommissural organ (SCO): 0 to – 735. Plates 16-21

2.6. PRETECTUM
Nucleus pretectalis superficialis
    pars parvocellularis (PSp): + 875 to + 245. Plates 13b-15
    pars intermedius (PSi): + 245 to 0. Plates 15-16
    pars magnocellularis (PSm): 0 to – 490. Plates 16-19
Nucleus pretectalis centralis (NPC): + 245 to – 1505. Plates 15-25
Nucleus corticalis (NC): + 245 to – 840. Plates 15-22
Nucleus pretectalis accessorius (AP): – 210 to – 490. Plates 17-19
Nucleus pretectalis lateralis (LP): – 735 to – 1715. Plates 21-26

2.7. ACCESSORY OPTIC NUCLEI
Dorsal accessory optic nucleus (DAO): + 245 to – 630. Plates 15-20
Ventral accessory optic nucleus (VAO): – 420 to – 490. Plates 18-19

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3. MESENCEPHALON

3.1. TECTUM MESENCEPHALI

    3.1.1. Optic tectum (OT): + 630 to – 5005. Plates 14a-43

        superficial white and grey zone (SWGZ): + 455 to – 4620. Plates 14b-41

        central zone (CZ): + 455 to – 4620. Plates 14b-41

        deep white zone (DWZ): 0 to – 4620. Plates 16-41

        periventricular grey zone (PGZ): + 455 to – 4620. Plates 14b-41

    3.1.2. Torus longitudinalis (TL): – 210 to – 2590. Plates 17-31

3.2. TEGMENTUM MESENCEPHALI

    3.2.1. Medial zone

        nucleus nervi oculomotorius (nIII): – 2380 to – 3185. Plates 30-34

        nucleus ruber (NR): – 2380 to – 2800. Plates 30-32

        nucleus of Edinger-Westphal (EW): – 2590. Plate 31

        nucleus nervi trochlearis (nIV): – 3185 to – 3745. Plates 34-37

        nucleus gustatorius secundarius (NGS): – 3745 to – 4830. Plates 37-42

    3.2.2. Central zone

        nucleus perilemniscularis

            pars medialis (PLm): – 2170 to – 2975. Plates 29-33

            pars lateralis (PLl): – 3185 to – 4165. Plates 34-39

        nucleus tegmentalis dorsalis (DT): – 2380 to – 3185. Plates 30-34

        nucleus tegmentalis ventralis (VT): – 2380 to – 2975. Plates 30-33

        nucleus lateralis valvulae (NLV)

            pars anterioris (NLVa): – 2800 to – 3745. Plates 32-37

            pars centralis (NLVc): – 2975 to – 3955. Plates 33-38

            pars posterioris (NLVp): – 3395 to – 4620. Plates 35-41

                ventral (NLVpv): – 4165 to – 4620. Plates 39-41

        nucleus ithsmi (NI): – 3395 to – 4340. Plates 35-40

        nucleus of the locus coeruleus (LC): – 4165 to – 4620. Plates 39-41

    3.2.3. Lateral zone

        Torus semicircularis (TS)

            pars centralis (TSc): – 1505 to – 4340. Plates 25-40

            pars ventralis (TSv): – 1785 to – 4340. Plates 27-40

            pars intermedius (TSi): – 1785 to – 3955. Plates 27-38

            pars lateralis (TSl): – 1995 to – 3570. Plates 28-36

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4. CEREBELLUM

4.1. VALVULA CEREBELLI (VCe): – 210 to – 4340. Plates 17-40

    Molecular layer (M): – 210 to – 4165. Plates 17-39

    Granular layer (G): – 210 to – 4340. Plates 17-40

4.2. CORPUS CEREBELLI (CCe): – 3185 to – 7595. Plates 34-54

    Molecular layer (M): – 3185 to – 7595. Plates 34-54

    Granular layer (G): – 3395 to – 7595. Plates 34-54

4.3. LOBUS VESTIBULOLATERALIS (LV)

    Eminentia granularis (EG): – 5005 to – 6440. Plates 43-49

4. CEREBELLUM, *continued*

Caudal lobe
 periventricular granular cell mass (PG): – 4830 to – 6650. Plates 42-50
 molecular layer (M): – 4620 to – 6895. Plates 41-51
 granular layer (G): – 4340 to – 6440. Plates 40-49

5. RHOMBENCEPHALON

5.1. RETICULAR FORMATION
Median zone
 nucleus raphes superior (SR): – 3955 to – 6195. Plates 38-48
 nucleus raphes inferior (IR): – 6650 to – 9275. Plates 50-58b
Medial zone
 nucleus reticularis superioris (RS): – 2975 to – 5250. Plates 33-44
 nucleus reticularis medius (RM): – 5460 to – 6650. Plates 45-50
 nucleus reticularis inferioris (RI): – 6895 to – 9065. Plates 51-58a
Lateral zone
 nucleus reticularis lateralis (RL): – 8190 to – 8645. Plates 55b-57a

5.2. AREA OCTAVOLATERALIS
Crista cerebellaris (CC): – 6650 to – 8855. Plates 50-57b
Octaval nerve nuclei
 nucleus octavus anterioris (AON): – 5250 to – 5950. Plates 44-47
 nucleus octavus descendens (DON): – 6195 to – 8645. Plates 48-57a
 nucleus magnocellularis (MAG): – 6195 to – 6650. Plates 48-50
 nucleus tangentialis (T): – 6440 to – 7385. Plates 49-53
 nucleus octavus posterioris (PO): – 8190 to – 9275. Plates 55b-58b
Lateral line nerve nuclei
 nucleus octavolateralis medialis (MON): – 5460 to – 8435. Plates 45-56b
 nucleus caudalis (C): – 8645 to – 9275. Plates 57a-58b

5.3. SOMATOMOTOR NUCLEI
Nucleus nervi abducentis
 pars rostralis (nVIr): – 5950 to – 6195. Plates 47-48
 pars caudalis (nVIc): – 6440 to – 6650. Plates 49-50

5.4. VISCEROMOTOR NUCLEI
Nucleus motorius nervi trigemini (Vm): – 4830 to – 5460. Plates 42-45
Nucleus motorius nervi facialis (VIIm): – 6650 to – 7140. Plates 50-52
Nucleus motorius nervi glossopharyngei (IXm): – 7385. Plate 53
Nucleus motorius nervi vagi (Xm): – 7875 to – 9275. Plates 55a-58b

5.5. OTHER NUCLEI
Nucleus interpeduncularis (IP): – 3185 to – 4165. Plates 34-39
Cells of Mauthner (Mc): – 5705. Plate 46
Vagal lobe (VLo): – 7595 to – 9275. Plates 54-58b
Nucleus of the commissure of Wallenberg (NCW): – 7595 to – 7875. Plates 54-55a
Inferior olive (IO): – 8190 to – 8855. Plates 55b-57b

1. TELENCEPHALON

1.1. OLFACTORY BULBS

The olfactory bulbs of the seabream are small and sessile (Figure 3). They are located ventral to the telencephalic hemispheres and appear attached to these hemispheres caudally. As in other ray-finned fish, they exhibit concentric cell layers in the following order from the periphery to the center: glomerular layer, external cellular layer, secondary olfactory fibers and internal cellular layer (Plates 1-5). A dense population of catecholaminergic cells is observed in the internal cell layer of gilthead seabream (Muñoz-Cueto et al., 1997). Rostrally, a layer of olfactory nerve fibers is found in the ventromedial and lateral aspects of the olfactory lobes. Just rostral to the junction of olfactory bulbs with the ventral telencephalon lies a group of very large cell bodies scattered along the ventromedial surface of the olfactory bulbs (Plates 4b-5b). These neurons correspond to the ganglion cells of the terminal nerve and have been recognized to synthesize salmon gonadotrophin releasing hormone in the gilthead seabream (Gothilf et al., 1996).

Efferent projections of the olfactory bulbs have been determined in different fish species (Finger, 1975; Bass, 1981a; Von Bartheld et al., 1984; Prasada Rao and Finger, 1984; Levine and Dethier, 1985; Rooney et al., 1989; Sas et al., 1993; Riedel and Krug, 1997). Fascicles of the medial and lateral olfactory tracts project to different nuclei of the ventral (Vv, Vd, Vs, Vp, Vc, Vi) and dorsal telencephalon (Dlv, nT, Dlp, Dp), as well as to the diencephalic habenula, preoptic region (parvocellular and magnocellular areas) and caudal hypothalamus. The analysis of olfactory bulb afferents in teleosts reveals the existence of bulbopetal cells in the contralateral olfactory bulb, the transitional zone between the olfactory bulb and the telencephalon, some nuclei of the ventral (Vv, Vd, Vs, Vi) and dorsal (Dlv, Dm, Dc, nT, Dlp, Dp) telencephalon, the caudal hypothalamus, and some mesencephalic and isthmal nuclei as the nucleus raphe or the locus coeruleus (Bass, 1981b; Von Bartheld et al., 1984; Prasada Rao and Finger, 1984; Levine and Dethier, 1985; Rooney et al., 1989; Sas et al., 1993).

1.2. TELENCEPHALIC HEMISPHERES

The telencephalic hemispheres consist of dorsal (area dorsalis) and ventral (area ventralis) components, which have been generally homologized to the pallium and subpallium of other vertebrates, respectively (Nieuwenhuys, 1963; Braford, 1995; Northcutt, 1995; Nieuwenhuys et al., 1997). In the present study, it was found that the organization of the telencephalic hemispheres of the seabream resembles that described in *Lepomis cyanellus* by Northcutt and Davis, (1983) and thus, the corresponding nomenclature has primarily been used.

The area dorsalis of the gilthead seabream is hypertrophied and occupies the majority of the telencephalic hemispheres. In fact, only pallial nuclei are observed in the rostral telencephalon (Plates 1-5). According to Northcutt and Braford (1980), the dorsal telencephalon of the gilthead seabream has been further divided into medial (Dm), central (Dc), dorsal (Dd), lateral (Dl) and posterior (Dp) components (Plates 1a-13b), some of which had to be further subdivided due to a clear increase in complexity when compared, for example, to the brains of the goldfish (Peter and Gill, 1975) or trout (Billard and Peter, 1982). As in *Lepomis* (Northcutt and Davis, 1983) and *Astyanax hubbsi* (Riedel, 1997), the medial zone (Dm) of gilthead seabream was subdivided in Dm1, Dm2,

Dm3 and Dm4, representing the two last regions, and especially Dm3, the most developed components. However, a single Dm zone was considered in *Ictalurus punctatus* (Bass, 1981a, b), two subdivisions were observed in *Sebastiscus marmortus* (Murakami et al., 1983) and *Barbus meridionalis* (Diez et al., 1987) and three subdivisions of Dm were described in *Betta splendens* (Marino-Neto and Sabbatini, 1988). The central zone (Dc) is constituted by scattered medium-sized and large cells, organized in two nuclei, a rostral Dc1 (Plates 3b-7b) and a caudal Dc2 (Plates 7a-12b). Rostral and caudal subdivisions of Dc were also considered in *Channa striatus* (Singh, 1969). Four subdivisions of Dc were described in two perciforms, *Lepomis cyanellus* (Northcutt and Davis, 1983) and *Betta splendens* (Marino-Neto and Sabbatini, 1988). In a recent revision, Braford (1995) considered that the central zone of the area dorsalis should be better considered as migrated cells of the periventricular telencephalic nuclei. In this study, we have maintained the old nomenclature given the difficulty to ascribe definitively these cell groups to one or another nucleus. However, it seems that our Dc1 represents a central cell mass of the lateroventral zone of the area dorsalis (Dlv) and our Dc2 may represent a migrated cell population of the Dm3. The Dd of gilthead seabream is composed of large and intensely stained packed cells associated to the lateral sulcus (Plates 5a-8b). This nucleus is larger in *Lepisosteus*, *Lepomis* (Northcutt and Davis, 1983) and the blind cave fish, *Astyanax*, (Riedel, 1997) than in gilthead seabream. The lateral zone of the area dorsalis (Dl) has been subdivided into dorsal (Dld, Plates 3a-13a), ventral (Dlv, Plates 3b-10b) and posterior (Dlp, Plates 9a-12a) components. In *Sebastiscus marmoratus*, histochemical localization of zinc and studies of the regional fiber connections revealed a subdivision of the area dorsalis pars lateralis into a dorsal and a ventral zone (Yamane et al., 1996). Similarly, in some perciforms, such as *Lepomis cyanellus* (Northcutt and Davis, 1983) or *Betta splendens* (Marino-Neto and Sabbatini, 1988) and in the gymnotiform *Apteronotus* (Maler et al., 1991), several subdivisions could be recognized in the medial, the central and the lateral divisions of the area dorsalis. However, in the gilthead seabream such subdivisions are also extended to the ventral part of the lateral zone of the area dorsalis telencephali (Dlv). Dlv1 is located laterally and limited by a lateral and a ventrolateral sulcus of the telencephalon (Plates 3b-8b). This subdivision is composed of small round and ovoid cells that are arranged caudally in vertical columns. Dlv2 appears more ventrally and is composed of slightly larger and more intensely stained cells (Plates 4a-10b). Dlv3 represents the most medial subdivision of Dlv and is separated from Dlv2 by a distinct space devoid of cells (Plates 4b-6a). A nucleus taenia (NT) is also recognized in the caudal telencephalon, lateral to the ventromedial sulcus (sulcus externus) from which the membranous roof arises (Plates 9a-11a). This nucleus is composed of small and medium-sized cells, that appear intensely stained and arranged in layers parallel to the surface of the brain.

Although the subdivisions of the area dorsalis of gilthead seabream seems well correlated with those observed in the perciform *Lepomis* (Northcutt and Davis, 1983), the anatomical localization of those nuclei and the gross anatomy of the telencephalon is quite different in both species. In fact, the hypertrophy of Dm3 determines that other nuclei, such as Dm2, Dd or Dc1, adopt an almost 90°-rotated position compared to that described in *Lepomis*. Also, two prominent sulcus are observed in the medial and lateral regions of the telencephalon of gilthead seabream, which seems to represent the sulcus limitans and the sulcus ypsiliformis, respectively. We have considered that the cell mass located dorsally to the lateral sulcus corresponds to the Dld because its cells appear rostrally arranged in columns perpendicular to the ependymal surface, as in other teleosts (Northcutt and Davis, 1983). However, there is also the possibility that this cell population represents a part of the hypertrophied Dm3 or an undescribed dorsomedial subdivision. If this is true,

Dld might be located ventrally to the lateral sulcus and correlate with our Dlv1. Further immuno-cytochemical and fiber connectivity analysis could contribute to the clarification of this question, although the differential connections of Dld and Dlv have not yet been established in teleosts (Northcutt, 1995).

A review of the known connections and topology of the major zones of the area dorsalis in ray-finned fishes and a comparison with tetrapods is presented by Braford (1995). This author established tentative homologies between the Dm and the pallial amygdala, the Dp and the primary olfactory cortex, and the Dl and non-olfactory and non-limbic pallial areas.

The organization of the area ventralis of the telencephalon in gilthead seabream is similar to that described previously in ray-finned fishes (Northcutt and Braford, 1980; Nieuwenhuys and Meek, 1990). It consists of eight cell masses: dorsal (Vd), ventral (Vv), lateral (Vl), central (Vc), supracommissural (Vs), postcommissural (Vp), intermediate (Vi) and entopeduncular (NE) nuclei. Vd appears rostrally (Plates 6a-8b), dorsal to the caudal olfactory bulbs and ventral to the Dm. Slightly ventrocaudal to it starts Vv, which extends from the caudal end of the olfactory bulbs (Plate 7b) to the anterior commissure (Plate 9b). Some tyrosine-hydroxylase positive cells are observed in both Vv and Vd of gilthead seabream (Muñoz-Cueto et al., 1997). Further caudal, Vd migrates laterally, leaves its periventricular position and is progressively replaced by a supracommissural subdivision (Vs, Plates 7b-11a) and then by a postcommissural division (Vp, Plates 10a-12b). Vl contains a few small and poorly stained neurons associated with the sulcus externus and surrounded by nerve fibers of the olfactory bulbs and the forebrain bundles (Plates 7b-9b). Vc represents a migrated nucleus starting at the level of the anterior commissure (Plates 9b). This nucleus is composed of larger and more intensely stained cells, surrounded by the fibers of the lateral forebrain bundle (Plates 10b, 11a). In the caudal aspect, this nucleus lies lateral to the anterior preoptic area. In *Sparus aurata,* as in *Lepomis* and other teleost (Nieuwenhuys, 1963; Northcutt and Davis, 1983), an intermediate nucleus (Vi) can be recognized in the caudal region of the ventral telencephalon (Plates 11b-12b). Vi is a periventricular nucleus that appears ventrally to the Vp and is replaced caudally by the nucleus eminentia thalami. Caudally to the Vc, tightly associated with fibers of the lateral forebrain bundle (LFB) appears the nucleus entopeduncularis (NE). This nucleus starts lateral to the preoptic area (Plate 11b) and ends just rostral to the thalamic region (Plate 13a). As in *Lepomis* and *Salmo* (Northcutt and Davis, 1983), only a single small-celled nucleus can be distinguished in *Sparus aurata*.

Based on topography and immunocytochemistry, as well as on afferent and efferent connections, presumptive homologies have been established between the subpallial nuclei of ray-finned fishes and other gnathostomes (Northcutt, 1995). Thus, Vv has been homologized to the lateral septal nucleus, although homology with the nucleus accumbens and other basal nuclei are also possible (Reiner and Northcutt, 1992; Northcutt, 1995). In gilthead seabream, a structure which resembles the lateral septal organ (LSO) described in other vertebrates (Baylé et al., 1974; Kuenzel and Masson, 1988) can be recognized in the ventral telencephalon (Plates 7b-9b). This organ is composed of columnar, densely packed and darkly stained cells which appear in a periventricular position. Interestingly, the putative LSO of gilthead seabream is associated with the Vv, which may support the consideration of Vv of ray-finned fishes as a septal nucleus (Reiner and Northcutt, 1992; Northcutt, 1995). In turn, possible homologies between the Vd and the corpus striatum, the Vl and the medial septal nucleus and olfactory tubercle, the Vs and the bed nucleus of the stria terminalis, and the Vp and the basal amigdala of other gnathostomes have been also reported (Northcutt, 1995).

2. DIENCEPHALON

The diencephalon represents one of the most complex regions in the brain of teleosts. In our analysis of the diencephalon in the gilthead seabream, we recognized the same subdivisions described by Braford and Northcutt (1983) and Butler and Northcutt (1993): preoptic area, hypothalamus, thalamus (posterior tuberculum, ventral thalamus, and dorsal thalamus), epithalamus, synencephalon, pretectum and accessory optic nuclei.

2.1. PREOPTIC AREA

The preoptic area surrounds the preoptic recess of the third ventricle. It is limited rostrally by the anterior commissure, caudally by the ventral thalamus in its dorsal extent and ventrally by the optic chiasm and the hypothalamus. As in all teleosts, cell masses in the preoptic area are mainly located in periventricular position, whereas the lateral parts principally contain fiber tracts including the lateral forebrain bundle (LFB).

Cell masses in the anterior preoptic area have been divided into nucleus preopticus parvocellularis pars anteroventralis (NPOav) and nucleus preopticus parvocellularis pars parvicellularis (NPOpc), ventrolateral and lateral to the third ventricle, respectively (Plates 10b-12b). More caudally, NPOpc is displaced laterally from its periventricular position by the magnocellular nuclei of the preoptic area while NPOav remains in a position ventral and ventrolateral to the preoptic recess. In gilthead seabream, some cells in the NPOpc have been described as expressing the seabream form of GnRH (Gothilf et al., 1996). Both NPOpc and NPOav described in *Sparus aurata* represent the nucleus preopticus parvocellularis anterioris described in *Carassius auratus* (Braford and Northcutt, 1983), *Haplochromis burtoni* (Fernald and Shelton, 1985) and *Ictalurus punctatus* (Striedter, 1990a). In rainbow trout, such subdivision has a functional correlation and was introduced to differentiate the area in the ventral wall of the preoptic recess containing dopaminergic neurons from the neighboring territories notably lacking those neurons (Linard et al., 1996; Kah et al., 1997). Similarly, in gilthead seabream, NPOav can be clearly differentiated of nearest nuclei as a region containing tyrosine hydroxylase-positive neurons (Muñoz-Cueto et al., 1997).

More caudally, the nucleus preopticus magnocellularis (corresponding to the aldehyde fuchsine positive neurons) has been subdivided, according to Braford and Northcutt (1983), into the pars parvocellularis (PMpc), magnocellularis (PMmc) and gigantocellularis (PMgc). Such subdivisions were also described in another perciform, *Haplochromis burtoni* (Fernald and Shelton, 1985). PMpc appears rostroventrally (Plates 11b-12a) and is composed of cells slightly larger and more darkly stained than those of the NPOpc. PMmc is located dorsocaudally (Plates 12a-13b) and exhibits larger cells in relation to PMpc. PMgc represents the most dorsal subdivision (Plates 12a-18) and corresponds to the largest cell group described in the preoptic area by Charlton (1932) and Braford and Northcutt (1983). In *Sparus aurata*, one to eight very large and intensely stained neurons/section are observed. At least in some teleost species, the size of the magnocellular preoptic nucleus varies seasonally (Gómez-Segade and Anadon, 1986).

Another population of small cells appears ventral to NPOpc and the nucleus preopticus magnocellularis. According to Peter and Gill (1975) this population has been termed nucleus anterioris periventricularis (NAPv, Plates 12a-15). Rostrally, NAPv is composed primarily by round and ovoid cells arranged in dense clusters or laminae bordering the preoptic recess. This nucleus exhibits numerous TH-positive cells in the gilthead seabream (Muñoz-Cueto et al., 1997). Caudally, the

number of cells and laminae in NAPv decreases and this nucleus is replaced by the nucleus posterioris periventricularis (NPPv) that lies ventral to the PMgc and ventral thalamus, and dorsal to the nucleus lateralis tuberis of the hypothalamus (Plates 16-20). Cells in NPPv are larger and more scattered than in NAPv and exhibit typical ovoid, fusiform or pyramidal shapes. Both NAPv and NPPV described in our study were considered together as the nucleus preopticus parvocellularis posterioris in *Carassius auratus* (Braford and Northcutt, 1983), *Haplochromis burtoni* (Fernald and Shelton, 1985) and *Ictalurus punctatus* (Striedter, 1990a). However, subdivisions into NAPv and NPPv were also considered in neuroanatomical studies performed in the diencephalon of *Fundulus heteroclitus* (Peter et al., 1975), *Salmo gairdneri* (Billard and Peter, 1982), *Salmo salar* (Peter et al., 1991) and *Apteronotus leptorhynchus* (Maler et al., 1991). In *Sparus aurata*, the NAPv has been reported to exhibit numerous tyrosine hydroxylase-positive cells (Muñoz-Cueto et al., 1997), whereas NPPv contains neuropeptide Y-immunoreactive neurons (Muñoz-Cueto, unpublished). Ventral to the NAPv and along the dorsal part of the supraoptic (SOCo) and minor (MCo) commissures, a separate population of cells constitutes the nucleus suprachiasmaticus (NSC, Plates 13b-15). As in other species, this nucleus contains tyrosine hydroxylase-positive cells in gilthead seabream (Muñoz-Cueto et al., 1997). In teleosts, NSC receives retinal projections (Braford and Northcutt, 1983) and seems to project to the telencephalon (Striedter, 1990b) and the inferior lobe (Wullimann and Northcutt, 1990; Northcutt, 1995).

In teleost, the preoptic area represents a source of hypophysial (Johnston and Maler, 1992; Anglade et al., 1993) and spinal cord (Prasada Rao et al., 1993) afferents and seems to receive retinal, tectal and cerebellar inputs (Striedter, 1990b; Northcutt, 1995).

2.2. HYPOTHALAMUS

The hypothalamus of *Sparus aurata* is delineated rostrally by the chiasmatic ridge, dorsorostrally by the caudal preoptic area, dorsocaudally by the posterior tuberculum and ventrally by the pituitary and the saccus vasculosus. The hypothalamus can be divided in two main zones: a medial tuberal zone and a paired and lobular lateral (or inferior) zone. The medial tuberal zone contains nuclei that surround the third ventricle. From rostral to caudal, it consists of the nucleus lateralis tuberis, the nucleus anterior tuberis, the nucleus recessus posterioris and the nucleus saccus vasculosus. The medial subdivisions of the nucleus recessus lateralis (i.e., the nucleus recessus lateralis pars ventralis and the nucleus recessus lateralis pars dorsalis) are also considered to be included in this zone. The large bilobular inferior lobes of the hypothalamus are penetrated by lateral extensions of the third ventricle, the lateral recess, that extends very caudally. This zone comprises the nucleus diffusus lobi inferioris, the lateral subdivision of the nucleus recessus lateralis, the nucleus centralis lobi inferioris and the nucleus medialis lobi inferioris.

The nucleus lateralis tuberis (NLT) can be subdivided in five regions. The nucleus lateralis tuberis pars lateralis (NLTl) consists of large and darkly stained cells that lie ventral to the horizontal commissure and along the rostroventral protrusion of the third ventricle (Plates 15-17). Caudally, NLTl migrates laterally to the ventrolateral surface of the hypothalamus. A similar nucleus, termed lateral tuberal nucleus, was previously described in a perciform, *Haplochromis burtoni* (Fernald and Shelton, 1985). The rostral NLTl was included within the nucleus lateralis tuberis pars anterioris of Peter and Gill (1975) and corresponds to the nucleus ventralis tuberis of Sheldon (1912). The caudal aspect of our NLTl was named nucleus lateralis tuberis pars lateralis by Peter and Gill (1975) and nucleus lateralis tuberis by Sheldon (1912). The nucleus lateralis tuberis pars ven-

tralis (NLTv) begins rostrally as a column of medium-sized cells slightly separated from the ventricular surface (Plate 15). Caudally the NLTv lies close to the ependyma and is composed of a cell layer two to eight cells thick, which is slightly thicker ventrally than dorsally (Plates 16-22). This nucleus was termed ventral hypothalamus in other teleosts, including perciforms (Braford and Northcutt, 1983; Fernald and Shelton, 1985; Northcutt and Wullimann, 1988; Striedter, 1990a; Butler and Northcutt, 1993), and seems to represent both the nucleus lateralis tuberis pars anterioris and pars posterioris of Peter and Gill (1975). The nucleus lateralis tuberis pars dorsalis (NLTd) appears in a periventricular position, medial to the horizontal commissure, ventral to the caudal preoptic area and the rostral posterior tuberculum and dorsal to the NLTv (Plates 16-21). This nucleus consists of cells somewhat larger than in NLTv, arranged in a column of two to three cells thick and slightly separated from the ependyma. This nucleus was included in the nucleus anterior tuberis of Peter and Gill (1975) and is referred to as the dorsal hypothalamus in the description of Braford and Northcutt (1983). The nucleus lateralis tuberis pars medialis (NLTm) lies just caudal to the rostral aspect of the NLTl and ventral to the nucleus anterior tuberis (NAT) and consists of small and scattered cells that extend dorsolaterally from the NLTv (Plates 16-22). Caudally, NLTm is replaced by the nucleus lateralis tuberis pars inferioris (NLTi), which lies between the recessus lateralis and the recessus posterioris (Plates 23, 24). The transition between NLTm and NLTi is clearly identified in gilthead seabream because the cells in NLTi become more densely packed and darkly stained than in NLTm. Also, NLTi exhibits TH-positive cells, whereas NLTm does not (Muñoz-Cueto et al., 1997). NLTm and NLTi described in our atlas were considered as lateral hypothalamic nucleus and caudal periventricular hypothalamus, respectively, in *Carassius auratus* (Braford and Northcutt, 1983), *Haplochromis burtoni* (Fernald and Shelton, 1985) and *Ictalurus punctatus* (Striedter, 1990a). The NLT has been known for a long time to be a major hypophysiotropic area (Fryer and Maler, 1981) and cells labeled retrogradely were found in the NLT of goldfish after DiI pituitary implantations (Anglade et al., 1993).

The nucleus anterior tuberis (NAT) is a migrating group of loosely scattered small and medium-sized cells. This nucleus begins slightly ventrocaudal to the nucleus suprachiasmaticus (Plate 16) and medial to the horizontal commissure (HCo). Caudally, it lies ventromedial to the HCo and lateral to the dorsal and ventral subdivisions of the NLT (Plates 17-22). In catfish, an hypertrophied NAT is reciprocally connected with the torus semicircularis and the telencephalon (Finger, 1980; Striedter, 1990b; Striedter, 1991). In cyprinids, characins and gymnotoids, the NAT also has reciprocal connections with the lateral preglomerular nucleus, but the projections from the NAT to the lateral preglomerular nucleus seem to be absent in catfish (Striedter, 1992).

The nucleus recessus lateralis (NRL) represents a collection of small intensely stained and packed cells that lies along the lateral reccess of the third ventricle. In the midline, two distinct cell populations are observed in association with the most rostral evaginations of the lateral recess. As they are in discontinuity and appear associated with NLTv and NLTd, we named them nucleus recessus lateralis pars ventralis (NRLv, Plates 20-22) and nucleus recessus lateralis pars dorsalis (NRLd, Plate 22), respectively. In the gilthead seabream, both NRLd and NRLv contain serotonin-immunoreactive cells, which join around the rostro-medial aspect of the lateral recess, just at the level where it appears separated from the midline (Munoz-Cueto, unpublished results). NRLd is closely associated to the ventral portion of the paraventricular organ (PVO), which in gilthead seabream also exhibits serotonin-positive cells (Munoz-Cueto, personal observations). This fact might suggest a common embryonic origin for NRLd, NRLv, and PVO cells. Maler et al. (1991), in their brain atlas of *Apteronotus lepthorynchus* recognized medial and inferior subdivisions of the NRL

that seem to correlate anatomically with our NRLd and NRLv, respectively. These subdivisions were considered by Braford and Northcutt (1983) and Striedter (1990a) as PVO and lateral hypothalamic nuclei, respectively. The migrated cells of the nucleus recessus lateralis pars lateralis will be considered later.

In the caudal part of the ventral hypothalamus, the ventricle gives rise to the posterior recess, which displays small laterally directed diverticula. This recess is bordered by small and tightly packed cells which constitute the nucleus recessus posterioris (NRP, Plates 21-24). A similar nucleus was observed in the caudal hypothalamus of *Carassius auratus* (Peter and Gill, 1975), *Fundulus heteroclitus* (Peter et al., 1975), *Salmo gairdneri* (Billard and Peter, 1982), *Salmo salar* (Peter et al., 1991) and *Apteronotus leptorhynchus* (Maler et al., 1991).

A nucleus saccus vasculosus (NSV), as described by Peter and Gill (1975), can be seen in the caudal hypothalamus of gilthead seabream (Plates 22-25). The NSV starts at the rostral pole of the saccus vasculosus, which appears at the caudal end of the pituitary. Rostrally, this nucleus begins as a column of small and intensely stained cells located in the roof of the caudal third ventricle (Plates 22, 23). As the posterior tuberculum develops, the NSV migrates ventrally and adopts a ring shape around the most caudal aspect of the ventricle (Plates 24, 25). The caudal zone of the periventricular hypothalamus considered by Braford and Northcutt (1983) and Striedter (1990a) includes both NRP and NSV described in this atlas.

The lateral or inferior lobes are primarily occupied by the nucleus diffusus lobi inferioris (NDLI), that consists of loosely distributed small and medium-sized cells (Plates 17-45). The largest cells are found at the periphery of the nucleus, near the surface of the brain. Caudally, the lateral recess separates two distinct areas in this nucleus: a pars lateralis (NDLIl), occupying the majority of the inferior lobe and a pars medialis (NDLIm), which contains more scattered cells (Plates 24-42). Even more caudally, when the connection between the inferior lobes and the rest of the brain disappears, a zone almost devoid of cells can be observed in the dorsal inferior lobes (Plates 34-45). This region represents our nucleus diffusus lobi inferioris pars caudalis (NDLIc), composed of very small cells lying dorsal to the nucleus centralis of the lobi inferioris (NCLI). This latter nucleus begins as a population of medium-sized cells located ventrolateral to the nucleus glomerulosus (Plates 24-30). Caudally, as the nucleus glomerulosus disappears, the NCLI migrates medially and exhibits larger cells interspersed with fibers of the tractus glomerulolobaris (Plates 31-39).

The lateral subdivision of the nucleus recessus lateralis (NRLl) lies around the laterocaudal extensions of the third ventricle into the inferior lobes, corresponding to the caudal lateral recesses (Plates 22-43). This nucleus, which reaches very caudal levels in gilthead seabream, was also considered in *Apteronotus* (Maler et al., 1991) and corresponds to the nucleus ventricularis of Demski et al. (1975), being included in the dorsal hypothalamus by Braford and Northcutt (1983).

Finally, a nucleus that has not been described previously is observed in the inferior lobes of gilthead seabream. Given its anatomical position, we named it nucleus medialis lobi inferioris (NMLI). This nucleus consists of medium-sized darkly stained cells located ventrally to the nucleus glomerulosus, between the corpus mammillare and the dorsal tip of the lateral recess (Plates 25-27). The cells of the NMLI resemble in appearance those of the central nucleus of the inferior lobe, but this cell mass could also represent a migrated nucleus of the posterior tuberculum. In fact, a nucleus subglomerulosus has been described in a similar position in the posterior tuberculum of *Carassius* and other ray-finned fishes, but its presence in advanced teleosts has never been reported (Braford and Northcutt, 1983).

2.3. THALAMUS

The thalamus lies dorsal and dorsolateral to the preoptic area and the hypothalamus, ventral to the habenula and the periventricular pretectum, medial to the lateral pretectum and the lateral expansions of the optic tectum and rostral to the tegmentum of the mesencephalon. According to Braford and Northcutt (1983), three major regions can be distinguished in the thalamus: the posterior tuberculum, the ventral thalamus and the dorsal thalamus.

2.3.1. Posterior Tuberculum

The posterior tuberculum of the thalamus seems to be greatly variable between teleosts and its comparison with any region of the diencephalon in other vertebrates remains unclear. As in other cytoarchitectonical studies performed in teleosts (Braford and Northcutt, 1983; Fernald and Shelton, 1985; Striedter, 1990a) we considered periventricular nuclei and migrated nuclei in the posterior tuberculum.

2.3.1.1. Periventricular Nuclei. In the periventricular region four nuclei can be identified: the periventricular nucleus of the posterior tuberculum, the paraventricular organ, the nucleus of the paraventricular organ and the nucleus posterior tuberis. The periventricular nucleus of the posterior tuberculum (TPp) appears at the caudal pole of the nucleus ventromedialis thalami and lies ventral to the dorsal thalamus (Plates 19-24). Small and darkly stained cells can be observed near the ventricular surface while medium-sized paler cells are scattered more laterally.

When the nucleus ventromedialis thalami disappears, a band of small, darkly stained and densely packed cells emerges in a periventricular position (Plates 20-22). This cell group constitutes the paraventricular organ (PVO), which is excised at the level where both hemispheres fuse medially (Plate 22). Some medium-sized to large cells can be found laterally to the PVO (Plates 21-23). These scattered cells seem to represent the nucleus of the paraventricular organ (nPVO) described by Braford and Northcutt (1983) and Striedter (1990a). However, this nucleus is less evident in *Sparus aurata* than in *Carassius auratus* or *Ictalurus punctatus*.

The nucleus posterior tuberis (NPT) lies in the midline, caudal to the point of fusion of hemispheres, ventral to the PVO, dorsal to the roof of the ventricular recess and rostral to the nucleus preglomerulosus commissuralis (Plates 22, 23). This nucleus consists of medium-sized and large cells which are separated from the periventricular cells of the NSV by a bundle of fibers projecting to the saccus vasculosus. Some of these large neurons have been identified as immunoreactive against tyrosine hydroxylase antibodies (Muñoz-Cueto et al., 1997).

2.3.1.2. Migrated Nuclei. The migrated region of the posterior tuberculum represents a complex area of the diencephalon constituted by migrated nuclei located rostrally in a ventrolateral position, and medially in more caudal aspects. According to the criteria of Braford and Northcutt (1983) we have considered in the migrated region the nucleus glomerulosus, the preglomerular nuclear complex, the caudomedial nuclei and the outlying nuclei. However, given the homology suggested between the nucleus glomerulosus of paracanthopterygians and acanthopterygians and the posterior pretectal nucleus of non-neoteleost (Wullimann and Meyer, 1990; Butler et al., 1991; Wullimann et al., 1991) the nucleus glomerulosus should be included probably in the pretectal area.

The Nucleus Glomerulosus. The nucleus glomerulosus of gilthead seabream consists of a rostral subdivision, the pars anterioris (NGa), and a caudal subdivision, the pars posterioris (NGp). NGa begins in the lateral pretectal area just caudal to the pars intermedius of the nucleus pretectalis superficialis (Plate 17). NGa consists of small cells, glomeruli and fibers. Further caudal, NGa is located dorsal to the NPGm and moves ventromedially to fuse with the dorsorostral pole of the NGp (Plates 18-24). NGp represents a larger round-shaped nucleus, that dominates the caudal diencephalon of gilthead seabream (Plates 24-31). This nucleus emerges in the position occupied by the NPGm and displaces it medially. Caudally, HCo appears associated to the dorsal pole of the nucleus and fibers of the tractus glomerulolobaris surround it. NGp consists of an external layer of medium-sized and large cells that surround abundant glomeruli intermingled with fibers, small and some large cells. The organization of the nucleus glomerulosus of gilthead seabream can be considered as type II, or the incompletely laminated type, according to the criteria of Ito and Kishida (1975). The presence of a distinct nucleus glomerulosus has been recognized in paracanthopterygians and acanthopterygians (Northcutt and Wullimann, 1988) and anterior and posterior zones of the nucleus glomerulosus have been described in other percomorphs (Wullimann and Meyer, 1990; Butler et al. 1991). The nucleus glomerulosus receives afferent projections from visually related pretectal nuclei, the nucleus corticalis and the pars intermedius of the nucleus pretectalis superficialis and sends efferent projections to the nucleus diffusus lobi inferioris (Sakamoto and Ito, 1982; Northcutt and Wullimann, 1988; Butler et al., 1991). Both the nucleus pretectalis superficialis pars intermedius and the nucleus glomerulosus of acantopterygians seem to be homologous to the posterior pretectal nucleus of non-neoteleosts (Wullimann and Meyer, 1990; Butler et al., 1991).

The Preglomerular Nuclear Complex. The preglomerular nuclear complex consists of cells masses that appear rostrally to the nucleus glomerulosus: the nucleus preglomerulosus anterioris, the nucleus preglomerulosus lateralis, the nucleus gustatorius tertius and the nucleus preglomerulosus medialis. The nucleus preglomerulosus anterioris (NPGa) starts in a ventromedial position, ventral to the LFB and just caudal to the optic chiasma (Plate 14b). Caudally, the cells of this nucleus migrate dorsolaterally and adopt a median position between the LFB and the ventral optic tract (Plates 15-17). NPGa consists of small and medium-sized cells, round to fusiform in shape. Ventral to the caudal pole of the NPGa, a collection of small, round and packed cells which constitute the nucleus preglomerulosus lateralis (NPGl, Plates 16-20) appears. Slightly caudal, the nucleus gustatorius tertius (NGT) begins dorsal to the NPGl (Plate 17). This nucleus lies rostrally in a lateroventral position in relation to the NPGm (Plates 17-20). Caudally, NGT is lateral to NPGm (Plates 21-23). The cells of the NGT are distributed between the fibers of the LFB and more caudally, this nucleus appears surrounded by a layer, one to two cells thick, of small and darkly stained neurons. The limits between the NGT and the NPGm are difficult to delineate but the cells in the NPGm are slightly more packed and move medially (Plates 18-23). Even more caudal, the small and round darkly stained cells of NPGm lie medial to the NGp and fuse caudally with the nucleus preglomerulosus commissuralis, which appears just in the midline (Plates 24-28).

The organization of the preglomerular nuclear complex in *Sparus aurata* is very similar to that described in another perciform, *Haplochromis burtoni* (Fernald and Shelton, 1985). However, homology among preglomerular nuclei across teleosts having or lacking a true nucleus glomerulosus is not always clear. NPGa observed in this study can be correlated with the nucleus anterioris hypothalami of Peter and Gill (1975), the nucleus preglomerulosus anterior of Braford and

Northcutt (1983) and the nucleus periglomerular rostral of Maler et al. (1991). Our NPGl could correspond to the lateral preglomerular nucleus of cyprinids and other ostariophysan teleosts (Braford and Northcutt, 1983; Striedter, 1992). A preglomerular subdivision involved in gustation and named nucleus gustatorius tertius was first described in *Lepomis cyanellus* (Wullimann, 1988). This author proposed that the term nucleus glomerulosus should be restricted to the visually related nucleus and that the nucleus named nucleus 'glomerulosus' in cyprinids (Braford and Northcutt, 1983) should be termed nucleus gustatorius tertius. NPGm described in gilthead seabream seems to correlate with the medial preglomerular complex of Braford and Northcutt (1983), as well as the caudal aspect of nucleus preglomerulosus pars lateralis of Peter and Gill (1975). In *Lepomis* and *Carassius*, the existence of afferent and efferent connections between the preglomerular nuclear complex and the telencephalon as well as reciprocally directed connections between the preglomerular nuclei and the optic tectum have been described (Northcutt and Wullimann, 1988; Braford, 1995). A role of the preglomerular nuclear complex in the relay of gustatory, acoustic, electrosensory and mechanosensory lateral line information could be inferred by its patterns of connections (Striedter, 1991; Northcutt, 1995; Wullimann, 1998).

Caudomedial Nuclei. The caudomedial region of the migrated posterior tuberculum lies in the midline and consists of two nuclei, the nucleus preglomerulosus commissuralis and the corpus mammillare. The nucleus preglomerulosus commissuralis (NPGc) begins dorsal to the caudal pole of the NPT and is fused across the midline (Plate 24), contrary to that described in *Carassius auratus*, where NPGc represents a bilateral nucleus (Peter and Gill, 1975; Braford and Northcutt, 1983). In gilthead seabream, the NPGc consists of small and medium-sized intensely stained cells which lie rostrally ventral to the TPp and the nucleus of the medial longitudinal fasciculus (nMLF, Plates 24-29) and caudally ventral to the nucleus nervi oculomotorius (nIII, Plates 30-32). Rostrally, an elongated NPGc is surrounded by a distinct three-to-six-cell-thick layer of small neurons. Caudally, when NPGm fuses with NPGc, this layer becomes less evident and cells in the inner nucleus appear interspersed with fibers. A similar nucleus has also been described in *Haplochromis burtoni* (Fernald and Shelton, 1985). In many reports on olfactory bulb connections, a similar cell mass to our NPGc has been reported to receive secondary olfactory projections, not only in goldfish (Levine and Dethier, 1985), but also in perciforms or closely related species (Murakami et al., 1983; Prasada Rao and Finger, 1984; Rooney et al., 1992; Wulliman, personal communication). However, they all named this secondary olfactory area nucleus of the posterior tuberculum (NPT). Thus, our NPGc might include the NPGc of goldfish in its lateral aspect (Braford and Northcutt, 1983), but in its major medial aspect, could represent the NPT described by other authors.

The corpus mammillare (CM) is a paired structure that starts slightly caudal and ventral to the NPGc (Plates 25-32). The CM is composed of small, densely packed and intensely stained cells which are concentrated in the periphery or around the fibers entering the nucleus. Caudally, the cells are found mainly in the medial and dorsal aspects of the CM, whereas the lateral zone appears almost devoid of cells. The localization and the appearance of CM is similar in gilthead seabream to those described for other teleosts (Braford and Northcutt, 1983; Fernald and Shelton, 1985; Striedter, 1990a).

Outlying Nuclei. The outlying nuclei include some cell masses located around the preglomerular nuclear complex and the nucleus glomerulosus. They correspond to the nucleus of the torus lateralis, the nucleus posterior thalami, and the nucleus lateralis thalami observed in other teleosts

(Braford and Northcutt, 1983; Fernald and Shelton, 1985). Three small nuclei that, to our knowledge, have not been described previously were also considered as outlying nuclei of the migrated posterior tuberculum. We named them as nucleus periglomerulosus dorsalis, nucleus of the tractus pretectoisthmicus and nucleus of the fasciculus retroflexus.

The nucleus of the torus lateralis (TLa) starts much more rostral than the other outlying nuclei of the migrated posterior tuberculum and lies rostrally lateral to the preglomerular complex, and caudally, lateral to the NGp (Plates 18-27). This nucleus adopts a dorsal position in relation to the NDLI of the hypothalamus, which is separated from the former by a lateral sulcus of the inferior lobe. The cells of the TLa are slightly smaller but very similar in appearance and organization to those of NDLI. In this way, we agree with Striedter (1990a), who reported a possible hypothalamic derivation of this nucleus in teleosts.

The nucleus posterior thalami (PT) begins caudal to the NGT, just at the level where the NGa and NGp fuse (Plates 24-25). This nucleus adopts a lateral position in relation to the NGp and is composed of small and medium-sized cells interspersed with nerve fibers.

The nucleus lateralis thalami (LT) starts around the fibers of the tractus pretectoisthmicus and the tractus mesencephalocerebellaris anterior and lies dorsal to the NGp. It consists of medium-sized to large scattered cells that caudally are seen in a more ventral position (Plates 26-33). Very large cells are also observed in the most caudal aspect of the nucleus. In the percomorph, *Lepomis cyanellus*, the lateral thalamic nucleus occupies a similar position and contains large cells that receive pretectal inputs and project to the optic tectum (Striedter and Northcutt, 1989).

Three small nuclei were found around the nucleus glomerulosus of *Sparus aurata*. Ventrolateral to the rostral pole of the nucleus of the medial longitudinal fasciculus and dorsomedial to the nucleus glomerulosus, begins a small round-shaped nucleus, named nucleus periglomerulosus dorsalis (pgd). Fifteen to sixty small packed cells by section can be seen intermingled with nerve fibers in this nucleus (Plates 26-28). In catfish, the presence of a supraglomerular nucleus has also been described dorsal to the nucleus glomerulosus (Striedter, 1990a). However, a homology between both nuclei seems improbable, because the nucleus periglomerulosus of gilthead seabream contains small packed cells whereas the supraglomerular nucleus of catfish exhibits very large and loosely scattered cells. Dorsolaterally to the NGp, just at the level where the fibers of the horizontal commissure exit at its dorsal pole, a collection of very small cells appears concentrated ventrally to the tractus pretectoisthmicus. We named this nucleus, consisting of twenty to forty cells by section (Plates 26, 27), as the nucleus of the tractus pretectoisthmicus (nTPI). Slightly caudal, a conspicuous nucleus lies around the fasciculus retroflexus. This nucleus, named nucleus of the fasciculus retroflexus (nFR), is composed of three to nine medium-sized round and fusiform cells by section (Plates 27, 28). Whether or not these nuclei belong to the migrated posterior tuberculum or represent other thalamic or synencephalic structures remains to be elucidated.

2.3.2. Ventral Thalamus

The ventral thalamus is bordered rostroventrally by the dorsal preoptic area, dorsally by the habenula and the dorsal thalamus, and caudally by the periventricular posterior tuberculum. This region of the thalamus has been described as a retinorecipient area in *Lepomis cyanellus* (Northcutt and Butler, 1991) and *Haplochromis burtoni* (Presson et al., 1985). Four nuclei can be identified in the ventral thalamus of gilthead seabream: nucleus eminentia thalami, nucleus ventromedialis thalami, nucleus ventrolateralis thalami and nucleus intermedius thalami.

The nucleus eminentia thalami (nTE) represents the most rostral nucleus of the ventral thalamus. The nTE begins just caudal to the intermediate nucleus of the area ventralis telencephali (Vi) and consists of small cells that lie in apposition to the ependyma and extend ventrolaterally (Plate 13a). More caudally, when the habenula becomes evident, the nTE appears as a layer of intensely stained and densely packed neurons, two to five cells thick, bordering the ventricular surface, which is replaced later by the nucleus ventromedialis thalami (Plate 14b). The nTE could be recognized in *Carassius auratus* (Braford and Northcutt, 1983) or *Haplochromis burtoni* (Fernald and Shelton, 1985) but was not described in other species as *Ictalurus punctatus* (Striedter, 1990a) or *Pantodon buchholzi* (Butler and Saidel, 1991). Recent data of Puelles and Rubenstein (1993) suggests that the nTE has its origin in the prosomere 4, not in the prosomere 3 which represents the ventral thalamic prosomere. It has been suggested that the thalamic eminence may be involved in higher order olfactory circuits (Northcutt, 1995).

The main component of the ventral thalamus is the nucleus ventromedialis thalami (VM), bordered rostroventrally by the preoptic area and caudally by the periventricular posterior tuberculum. Rostrally, VM is seen as a periventricular column of compact small and medium-sized cells ventral to the habenula (Plates 14b-15). Slightly caudal, the laminae of cells extends ventrolaterally away from the ventricle and the thickness of the column diminishes (Plates 16, 17). The cells in VM become more loosely arranged and, more caudally, they concentrate again near the ventricle before being replaced by the cells of the periventricular posterior tuberculum (Plates 18, 19). These cells constituted a continuous nucleus in gilthead seabream, as has also been described in *Carassius auratus* (Braford and Northcutt, 1983), *Haplochromis burtoni* (Fernald and Shelton, 1985) and *Lepomis cyanellus* (Northcutt and Butler, 1991), whereas distinct rostral and caudal parts were identified in the channel catfish (Striedter, 1990a) and the freshwater butterfly fish (Butler and Saidel, 1991). Tectal and cerebellar projections have been described to enter the VM in longnose gar and channel catfish (Northcutt and Butler, 1980; Striedter, 1990b) but the existence of direct retinal input to the VM remains unclear (Northcutt, 1995). Efferents from the VM to the telencephalon (Murakami et al., 1986b), optic tectum (Striedter, 1990b) and spinal cord (Prasada Rao et al., 1993) have already been described in ray-finned fishes. In gilthead seabream, as in other teleosts, most VM cells represent tyrosine-hydroxylase positive cells and an intense TH-positive fiber tract exits from this nucleus (Muñoz-Cueto et al., 1997).

The nucleus ventrolateralis thalami (VL) is located ventrolateral to the habenula and lateral to VM (Plates 14b-16). Its cells are slightly larger and more scattered than in VM and appear interspersed with nerve branchs. In other fish species, it has been shown that this neuropil is composed of retinofugal and tectal terminals as well as dendrites of ventromedial thalamic cells (Northcutt and Wullimann, 1988; Striedter, 1990b). The VL also is the target of cerebellar projections in catfishes (Striedter, 1990b) and a source of afferent projections to the optic tectum and the corpus cerebelli in ray-finned fishes (Striedter, 1990b; Northcutt, 1995). Whereas in *Haplochromis burtoni*, VL is replaced caudally by the central thalamic nucleus, a cell mass of the ventral thalamus that contains retinal efferents (Fernald and Shelton, 1985; Presson et al., 1985) such a nucleus is not recognized in our material.

The nucleus intermedius thalami (I) of gilthead seabream begins at the same level as the posterior commissure (Plates 16-18). This nucleus is located dorsolateral to the rostral VM and ventrolateral to the dorsal thalamus. It consists of small cells interspersed with fibers lying at the ventral border of the cell plate of the nucleus anterior thalami. This nucleus has been described in a similar position in *Lepomis* and other teleosts and it has been shown as a primary retinofugal ter-

minal field (Braford and Northcutt, 1983; Northcutt and Butler, 1991). In *Ictalurus*, this nucleus sends efferent projections to the optic tectum (Striedter, 1990b).

2.3.3. Dorsal Thalamus

The dorsal thalamus is bordered dorsally by the habenula and the periventricular pretectum, ventrorostrally by the ventral thalamus, ventrocaudally by the posterior tuberculum and caudally by the nucleus of the medial longitudinal fasciculus (nFLM). We have recognized three cell masses in the dorsal thalamus of gilthead seabream: nucleus anterior thalami, nucleus centralis posterior thalami and nucleus dorsalis posterior thalami.

The nucleus anterior thalami represents the most rostral nucleus of the dorsal thalamus. It begins ventrally to the caudal habenula and dorsally to the VM (Plate 15). Caudally, the nucleus anterior leaves its periventricular position and appears surrounded ventrally by the cells of the nucleus centralis posterior and dorsally by the nucleus dorsalis posterior (Plates 17-19). The nucleus anterior consists of small rounded cells, relatively packed in the rostral pole of the nucleus. Slightly caudal, these cells are arranged in two columns and the nucleus becomes U-shaped. Further caudal, a single laminae of cells having a dorsomedial top and a ventrolateral bottom is observed. At the caudal end, the nucleus anterior is replaced ventrally by the nucleus centralis posterior and dorsally by the nucleus dorsalis posterior. In other teleosts, the nucleus anterior thalami has been described as a target for retinal and tectal inputs (Braford and Northcutt, 1983; Northcutt and Butler, 1991; Butler and Saidel, 1991) and a source of fibers reaching the optic tectum (Northcutt and Wullimann, 1988; Striedter, 1990b) and the telencephalon (Echteler and Saidel, 1981; Braford, 1995).

The nucleus centralis posterior thalami (CP) lies ventral to the nucleus anterior and the nucleus dorsalis posterior, and dorsal to the nucleus ventromedialis and the periventricular nucleus of the posterior tuberculum. Its cells are small and medium-sized and remain restricted in a periventricular position rostrally (Plates 16-18). Further caudal, the cells of the CP appear arranged on a lamina and extend ventrolaterally from a ventricular sulcus, occupying the place of the nucleus anterior and the nucleus intermedius (Plates 19-23). These cells are mixed with nerve fibers and a gradient from smaller to larger cells can be observed when progressing from the periventricular to the lateral aspects of the nucleus. This nucleus seems to be involved in auditory and mechanosensory circuits that implicate the torus semicircularis, the dorsal thalamus and the telencephalon (Northcutt, 1995; Wullimann, 1998). However, in ostariophysian teleosts the CP does not receive ascending mechanosensory lateral line inputs (Echteler, 1984; Finger and Tong, 1984).

The nucleus dorsalis posterior thalami (DP) begins ventral to the fasciculus retroflexus (Plate 17). This nucleus contains small and medium-sized cells, loosely distributed ventrally to the periventricular pretectum and dorsally to the nucleus anterior. Caudally, its cells replace the cells of the nucleus anterior, extend ventrolaterally and appear more concentrated. However, the DP does not appear to form a lamina as pronounced as in the CP (Plates 18-22). This characteristic organization of CP and DP has also been described in other teleosts (Braford and Northcutt, 1983; Striedter, 1990a; Butler and Northcutt, 1993). Northcutt (1995) and Wullimann (1998) referred to the possible role of DP in visual circuitry as a relay nucleus between the optic tectum and the telencephalon. In fact, the optic tectum projects to the DP (Northcutt and Butler, 1980) and the latter sends its projections to the optic tectum (Striedter, 1990b) and the telencephalon (Echteler and Saidel, 1981; Northcutt, 1995).

2.4. EPITHALAMUS

The epithalamus is composed of the habenula and the habenular commissure. The habenula is a paired finger-shaped structure that appears in the dorsal pole of the rostral diencephalon and is bordered rostroventrally by the ventral thalamus and caudoventrally by the dorsal thalamus (Plates 14a-15). In gilthead seabream, the habenula lacks an evident asymmetry, as has been found in other teleosts (Braford and Northcutt, 1983; Striedter, 1990a). Two subdivisions could be distinguished in the nucleus habenularis, the pars ventralis (NHv) and the pars dorsalis (NHd). NHv consists of small and densely packed cells arranged in periventricular laminae six to twenty cell thick (Plates 14a-15), whereas NHd is composed of slightly larger cells concentrated near the ventricle, but which also extend laterally (Plates 14b-15).

2.5. SYNENCEPHALON

The synencephalon is considered as a transitional area between the diencephalon proper and the mesencephalon, representing the pretectal prosomere (P1) in the neuromeric model of Puelles and Rubenstein (1993). According to Braford and Northcutt (1983), the synencephalon represents a zone adjacent to the posterior commissure that lies, at the rostral position, dorsal to the dorsal thalamus, and caudally, dorsal to the posterior tuberculum. This region includes the pars ventralis and the pars dorsalis of the nucleus pretectalis periventricularis and the nucleus of the medial longitudinal fasciculus. As in other teleosts (Wullimann and Northcutt, 1988), a nucleus paracommissuralis is also recognized in the synencephalon of gilthead seabream.

The nucleus pretectalis periventricularis pars ventralis (PPv) starts just caudal to the habenula, at the rostral pole of the posterior commissure, and remains ventromedial to the fasciculus retroflexus (Plates 17-23). This nucleus consists of small cells that appear more densely packed and intensely stained in the medial aspects of the nucleus. At the caudal end of the posterior commissure, the cells of the PPv are larger and migrate laterally appearing slightly scattered near the dorsal ependymal ridge (Plates 24, 25). The nucleus pretectalis periventricularis pars dorsalis (PPd) has a dorsolateral position with respect to the fasciculus retroflexus, and lies ventral to the nucleus paracommissuralis, its cells being more loosely distributed (Plates 17-22). In gilthead seabream, PPv was identified as a TH-positive nucleus, and intensely immunostained fibers were observed exiting from the periventricular pretectum (Muñoz-Cueto et al., 1997). The PPd especially, but also the PPv, have been described as main sites of the termination of medial optic tract fibers (Northcutt and Wullimann, 1988; Northcutt and Butler, 1991; Butler and Saidel, 1991). In *Carassius* and *Lepomis* the PPd gives rise to fibers that reach the optic tectum and the cerebellum, and ascending cerebellar efferent fibers contact this nucleus (Northcutt and Wullimann, 1988; Wullimann and Northcutt, 1988).

The nucleus paracommissuralis (NP) of gilthead seabream is located dorsal to the periventricular pretectal nuclei (Plates 16-21). This nucleus is composed of small and medium-sized cells, round to ovoid in shape, which present a laminar organization along the lateral expansions of the posterior commissure. The NP may correspond to the nucleus mesencephalicus dorsalis of Finger (1978a) and has been found in silurids, characiforms and percomorphs. In cypriniforms, the NP is described as a simpler nucleus (Ito et al., 1982; Wullimann and Northcutt, 1988; Striedter, 1990a). In the green sunfish, the cells of the NP send afferent fibers to the corpus cerebelli (Wullimann and Northcutt, 1988).

The nucleus of the medial longitudinal fasciculus (nMLF) appears rostrally where the posterior commissure ends caudally (Plate 23). It is located dorsal to the caudal nuclei of the posterior tuberculum, and is replaced caudally by the nucleus nervi oculomotorius (Plates 24-30). The nMLF is easily recognized by its large and intensely stained neurons distributed along the ventricular wall and close to the midline. In gilthead seabream, these cells were identified as cGnRH-II mRNA-positive cells (Gothilf et al., 1996). As it has been described in lungfishes (Ronan and Northcutt, 1985) and other teleosts (Prasada Rao et al., 1987), lateral and medial groups of neurons can be observed in the nMLF of *Sparus aurata*. Generally, the smallest cells are found caudally, in the lateral aspect of the nucleus. In teleosts, the cells of the nMLF give rise to axons organized as the medial longitudinal fasciculus (MLF) and represent a source of descending spinal projections (Oka et al., 1986a; Prasada Rao et al., 1987).

Finally, as shown in other teleosts (Braford and Northcutt, 1983; Fernald and Shelton, 1985), a subcommissural organ is observed in the diencephalon of the gilthead seabream (Plates 16-21). This organ consists of small, densely packed and intensely stained cells that located in the roof of the ventricle and ventral to the posterior commissure.

2.6. PRETECTUM

The pretectum represents a lateral zone of the diencephalon composed by the nucleus pretectalis superficialis and its subdivisions (pars parvocellularis, pars intermedius and pars magnocellularis), the nucleus pretectalis centralis, nucleus corticalis and nucleus pretectalis accessorius. An undescribed cell mass, that we have named nucleus pretectalis lateralis (LP), was also considered in the laterocaudal pretectal area of the gilthead seabream.

The nucleus pretectalis superficialis pars parvocellularis (PSp) represents the most rostral nucleus of the pretectum. This nucleus appears in the lateral surface of the brain, ventral to the rostral end of the optic tectum (Plate 13b-15). As in other teleosts (Braford and Northcutt, 1983; Fernald and Shelton, 1985; Striedter and Northcutt, 1989; Butler and Northcutt, 1993), PSp in gilthead seabream is composed of a single laminae of small cells that surround folded bands of neuropil. In teleosts, the pars parvocellularis is a recipient of retinal, tectal and isthmal inputs (Presson et al., 1985; Northcutt and Wullimann, 1988; Striedter and Northcutt, 1989) and projects to the nucleus pretectalis superficialis pars intermedius, nucleus trochlearis and inferior raphe in *Lepomis* (Striedter and Northcutt, 1989). In *Hemichromis*, the cells and the neuropil of the PSp exhibit acetylcholinesterase reactivity (Wullimann and Meyer, 1990). PSp was named corpus geniculatum laterale by Nieuwenhuys and Bodenheimer (1966) but this nomenclature was abandoned by Braford and Northcutt (1983) since this nucleus does not project to the telencephalon.

The nucleus pretectalis superficialis pars intermedius (PSi) appears medial to the caudal end of the PSp and lies ventromedial to the nucleus pretectalis superficialis pars magnocellularis (PSm). In gilthead seabream, this nucleus has a glomerular aspect and contains small, medium-sized and large cells interspersed with neuropil (Plates 15, 16). These cells are mainly restricted to the dorsomedial region of the nucleus, whereas the ventrolateral area is richer in fibers. More caudally, PSi moves dorsomedially and disappears slightly rostral to the level where nucleus glomerulosus pars anterioris starts. The pars intermedius of the nucleus pretectalis superficialis has been identified in other acanthopterygians but seems to be characteristic of teleosts, and has not been recognized in non-neoteleosts (Sakamoto and Ito, 1982; Striedter and Northcutt, 1989; Butler et al., 1991). In *Lepomis* and *Hemichromis* (Wullimann and Meyer, 1990; Butler et al., 1991), PSi exhibits a similar

organization as in the gilthead seabream, but this nucleus was not described in another perco-morph, *Haplochromis burtoni* (Fernald and Shelton, 1985). In percomorphs, PSi receives bilateral inputs from the PSp and projects to the nucleus glomerulosus (Murakami et al., 1986a; Striedter and Northcutt, 1989).

The nucleus pretectalis superficialis pars magnocellularis (PSm) starts caudomedial to the PSp and is located ventral to the nucleus corticalis and dorsal to the ventral optic tract (Plates 16-19). It is composed of giant multipolar cells that are intensely stained and loosely scattered throughout its neuropil. PSm may correspond to the nucleus rotundus of Schnitzlein (1962) and the nucleus pretectalis of Ito et al., (1981). In teleosts, this nucleus shows acetylcholinesterase activity in both cells and the neuropil (Wullimann and Meyer, 1990). Although the PSm receives projections from the retina via the optic tectum in both cyprinids and percomorphs, this nucleus seems to be very different in cytoarchitecture and efferent connections between the two patterns (Striedter and Northcutt, 1989). In cyprinids, the cells of the PSm are smaller and project to the corpus mamil-lare and the nucleus lateralis valvulae (Northcutt and Braford, 1984). However, in *Lepomis* the cells are giant in size and project to the nucleus isthmi and the nucleus lateralis thalami (Striedter and Northcutt, 1989).

The nucleus pretectalis centralis (NPC) is a relatively diffuse nucleus that starts rostrally dor-somedial to the superficial nuclei of the pretectum (Plates 15, 16). Its cells are small and are loose-ly interspersed with nerve fibers. Further caudal, the cells of the NPC becomes slightly larger, stain more darkly and appear ventrolateral to the nuclei of the periventricular pretectum and dorsal to the pars anterioris of the nucleus glomerulosus (Plates 17-25). This nucleus may correspond to the P1 pretectal nucleus of Finger and Karten (1978) and the area pretectalis pars dorsalis of Vanegas and Ito (1983). The NPC is a primary retinofugal and tectal terminal field in teleosts (Presson et al., 1985; Northcutt and Wullimann, 1988; Northcutt and Butler, 1991) and projects to the lateral pre-glomerular nucleus in ostariophysan teleosts (Striedter, 1992). It has been also shown that the NPC of ray-finned fishes represents a source of tectopetal, corpopetal and valvulopetal projections (Wullimann and Northcutt, 1988, 1989; Striedter, 1990b; Northcutt, 1995).

The nucleus corticalis (NC) of gilthead seabream is composed of medium-sized and large cells embedded in the rostral pole of the optic tectum (Plate 15), that migrate slightly ventral when the tectum develops (Plates 16-22). Rostrally, just at the level where the ventral evagination of the optic tectum arises (Plates 17, 18), a ventral population of large fusiforms cells join the most dor-sal cell plate. Further caudal, this nucleus is located dorsal to the nucleus pretectalis superficialis, pars magnocellularis and lateral to the nucleus glomerulosus pars anterioris and the nucleus pre-tectalis accessorius. Although nucleus corticalis appears to be absent in *Lepisosteus osseus*, a mem-ber of the Ginglymodi (Northcutt and Butler, 1993a), the NC seems to be present in Halecomorphi (Butler and Northcutt, 1992) and has been identified in Teleostei (Butler et al., 1991). However, the identification of this nucleus in ostariophysians remains unclear (Springer and Gaffney, 1981; Sas and Maler, 1986; Northcutt and Wullimann, 1988; Striedter, 1990a) and in primitive teleosts, the cells of the NC does not form a discrete cell plate as in *Sparus aurata* and other percomorphs (Butler et al., 1991). When present, this nucleus can be identified by the presence of acetylcholinesterase activity (Wullimann and Meyer, 1990). The NC represents a target for direct retinal projections (Fernald, 1982; Northcutt and Butler, 1991, 1993b) and sends inputs to the posterior pretectal nucleus of primitive teleosts and to the nucleus glomerulosus of neoteleosts (Butler et al., 1991).

A nucleus pretectalis accessorius (AP) is evident in the lateral pretectal area of gilthead seabream. This nucleus is located medial to the nucleus corticalis, dorsolateral to the pars anteri-oris of the nucleus glomerulosus and dorsomedial to the caudal pole of the nucleus pretectalis

superficialis pars magnocellularis. The AP is composed of only a few small and medium-sized cells (Plates 17-19). The nucleus pretectalis accessorius was first described in *Osteoglossum*, *Carassius* and the percomorph *Hemichromis* (Wullimann and Meyer, 1990), and later recognized in other species of osteoglossomorphs, clupeomorphs, esocids, salmonids and acanthopterygians (Butler et al., 1991; Butler and Saidel, 1991; Butler and Northcutt, 1993).

Finally, a collection of small and medium-sized cells, ovoid, triangular and polygonal in shape, appearing between tectal fibers, are observed in the caudolateral pretectum of the gilthead seabream (Plates 21-26). We have named this cell mass as nucleus pretectalis lateralis (LP). This nucleus lies ventromedial to the caudal NC, and probably represents laterally migrated cells of the nucleus pretectalis centralis.

2.7. ACCESSORY OPTIC NUCLEI

Two accessory optic nuclei were found in the pretectum of gilthead seabream: the dorsal accessory optic nucleus and the ventral accessory optic nucleus. In both nuclei, the cells are interspersed between the fibers of the optic tracts. The dorsal accessory optic nucleus (DAO) is more rostral and appears dorsal to the caudal end of the nucleus preglomerulosus anterioris and ventromedial to the nuclei of the superficial pretectum (Plates 15-20). Its cells are medium-sized and fusiform although some larger and darkly stained cells can be observed, especially in the medial aspect of the nucleus. A well defined ventral accessory optic nucleus (VAO) starts further caudal and lies ventromedial to the DAO and dorsal to the nucleus preglomerulosus medialis (Plates 18, 19). The cells of the VAO are small and round to fusiform in shape. The fusiform cells exhibit their major axis orientated in a mediolateral direction, parallel with the nerve fibers running across the cell bodies. Similar accessory optic nuclei have been described in other teleosts (Northcutt and Wullimann, 1988; Striedter, 1990a; Butler and Northcutt, 1993). Fernald and Shelton (1985) described in the perciform *Haplochromis burtoni* two pretectal nuclei, the basal optic nucleus and the accessory optic nucleus, highly similar in appearance and position to our DAO and VAO, respectively. The DAO and the VAO have been described as recipients of retinofugal projections (Northcutt and Wullimann, 1988) and as the origin of corpopetal projections (Wullimann and Northcutt, 1988). Additionally, in *Lepomis* and *Carassius*, DAO projects to the valvula cerebelli (Wullimann and Northcutt, 1989).

3. MESENCEPHALON

The mesencephalon of the gilthead seabream consists of a dorsal tectum and a ventral tegmentum. The dorsal tectum evaginates into bilateral lobes bridged dorsally by the tectal commissure and is composed of the optic tectum and the torus longitudinalis. The tegmentum replaces the caudal diencephalon and synencephalon and is dorsally bordered by the valvula cerebelli, laterally by the optic tectum and ventrally by the inferior lobe of the hypothalamus.

3.1. TECTUM MESENCEPHALI

3.1.1. Optic Tectum

A prominent optic tectum can be recognized in the mesencephalon of gilthead seabream (Plates 14a-43). The optic tectum covers the thalamus and the synencephalon more rostrally, and the tegmentum more caudally. The valvula cerebelli is also surrounded by the optic lobes.

Rostrally, at the level where the superficial pretectal nuclei begin, the optic tectum of gilthead seabream expands ventrally (Plate 17) and a marked sulcus separates dorsal and ventral aspects in transverse sections (Plates 18-24), but caudally this sulcus disappears (Plate 25). A grossly visible sulcus has been also described in the tectum of clupeomorphs and some percomorph euteleosts (Collin, 1989; Butler, 1992).

As in most fishes, the optic tectum of gilthead seabream is laminated and four major zones are observed (Northcutt, 1983). Centripetally, they are the superficial white and gray zone (SWGZ), the central zone (CZ), the deep white zone (DWZ) and the periventricular gray zone (PGZ). The SWGZ represents the most external layer of the optic tectum and its ventral limit is found in a deep broad layer of nerve fibers. The thickness of this nerve fiber layer is higher in the dorsomedial and ventral optic tectum and is reduced in its lateral aspect. In other teleosts, this nerve fiber layer represents the main retinal terminal field (Northcutt, 1983; Vanegas and Ito, 1983; Presson et al., 1985; Northcutt and Butler, 1991; Butler and Saidel, 1991). More externally, a thin band of nerve fibers can be recognized in the SWGZ. This layer is also considered a retinofugal fascicle in other teleosts (Northcutt, 1983; Von Bartheld and Meyer, 1987). Two layers of neuropil are distinguished in the SWGZ: a superficial layer and an inner narrow layer separating both putative retino-tectal terminal layers. The most superficial layer in the tectum of teleosts is known as the marginal layer and it has been shown to contain some cells and unmyelinated fibers arising from the cells of the torus longitudinalis (Northcutt, 1983; Wullimann, 1994). The SWGZ of gilthead seabream contains few neurons, ovoid and pyramidal in shape. Generally, ovoid cells are smaller, but these pyramidal cells do not attain the large size described in other ray-finned fishes (Northcutt, 1983). Intense acetylcholinesterase activity has been observed in the superficial layers of the tectum in *Pantodon* (Butler and Saidel, 1991), *Osteoglossum*, *Hemichromis*, *Carassius* (Wullimann and Meyer, 1990) and *Lepisosteus* (Northcutt and Butler, 1993a). The SWGZ includes the stratum marginale, the stratum opticum and the stratum fibrosum et griseum superficiale of Vanegas and Ito (1983).

The central zone (CZ) of gilthead seabream exhibits three layers clearly distinguished in sagittal sections.The outer layer represents approximately one third to a half of the overall thickness of the CZ and is separated from the central layer by nerve fibers that become more evident close to the midline. This outer layer possesses a fibrous appearance and cell density is higher than in the central and deep layer. Rostrally, prior to and immediately after the appearance of the ventral evagination of the DWZ and PGZ, the central zone is thicker, especially at the level of the lateral tectal sulcus (Plates 18-25). However, caudally the thickness of the CZ is similar in dorsal, lateral and ventral aspects of the tectum. Cells in the CZ are generally small and medium-sized, although large and darkly stained somata are also observed, especially in the most external layer and in the proximity of the deep white zone (DWZ). In ray-finned fishes a retinofugal terminal field has been described in the central zone (Northcutt, 1983; Vanegas and Ito, 1983). The CZ of the optic tectum exhibits acetycholinesterase activity in both non-teleost and teleost fishes (Butler and Saidel, 1991; Wullimann and Meyer, 1990; Northcutt and Butler, 1993a).

The DWZ lies internal to the CZ and is principally composed of nerve fibers and some small and medium-sized cells intermixed with the fibers. In the rostral dorsomedial optic tectum, tangentially and radially oriented fibers of DWZ adopt a wheat spike-like pattern superficial to the PGZ. Butler (1992) considered this organization as an apomorphic feature of euteleosts. Some of these fibers constitute the tectal commissure and other seems to represent afferent retinal projections (Butler, 1992). Laterally and caudally, the fibers of DWZ are arranged in a discontinuous and circular disposition. The thickness of DWZ is greater rostrally and in the dorsal and ventral optic

tectum in relation to the lateral optic tectum, where sometimes the DWZ becomes less evident. A similar organization has been described in the DWZ of other euteleosts (Butler, 1992). In cyprinids and percomorphs, the existence of a deep retinotectal terminal lamina at the limit between DWZ and PGZ has also been described (Vanegas and Ito, 1983; Northcutt and Wullimann, 1988).

The periventricular gray zone (PGZ) is composed of a single external layer of densely packed and darkly stained small and medium-sized neurons, 10 to 20 cells thick, an internal fascicular layer which exhibits nerve fibers, small scattered cells and blood vessels and a periventricular ependymal layer. The thickness of the PGZ is higher in the lateral and ventral optic tectum in relation to the dorsal one. Rostromedially, the nerve fibers of the DWZ entering the tectal commissure can run between the cells of the external layer of the PGZ, becoming organized on horizontal laminae. Also rostrally, when the ventral expansion of the optic tectum starts, a separated ventral aspect of the PGZ can be observed in gilthead seabream (Plates 20-22). A similarly appearing subdivision of the PGZ has been named as the ventral part of the PGZ in *Clupea harengus* (Butler, 1992). However, in gilthead seabream the lateral aspect of the PGZ is joined by this ventral PGZ slightly caudal to its appearance (Plate 23) and becomes histologically indistinguishable from it, contrary to that described in *Clupea*. In transverse sections, it can be clearly observed how the circular fascicles of fibers of DWZ break the outer layer of cells of the PGZ dorsolaterally in the rostral tectum (Plates 22-31) and dorsomedially in the caudal tectum (Plates 32-39). Similar features have been described in *Lepomis*, where these circular fibers separate the lateroventral and the dorsal part of the periventricular gray zone and represent, as in other teleosts, the main tectal efferent pathway (Northcutt, 1983; Butler, 1992).

In teleosts, the optic tectum represents also a target area for non-retinal afferent fibers which originate in different telencephalic nuclei, the preoptic area, hypothalamus, dorsal and ventral thalamus, pretectal area, accessory optic system, posterior tuberculum, cerebellum, tegmentum of the mesencephalon and the optic tectum itself (Finger, 1983a; Northcutt, 1983; Vanegas and Ito, 1983; Northcutt and Wullimann, 1988; Striedter, 1990b). The SWGZ receives the inputs from the torus longitudinalis, telencephalon, nucleus isthmi and cerebellum (Northcutt, 1983; Vanegas and Ito, 1983; Striedter and Northcutt, 1989). The CZ is a terminal field of telencephalic and tectal afferents as well as of fibers of the nucleus isthmi, the torus semicircularis and octavolateralis efferents (Northcutt, 1983; Sakamoto et al., 1981; Vanegas and Ito, 1983; Striedter and Northcutt, 1989). The DWZ receives afferents from the tectum itself, cerebellum and torus semicircularis, which also projects to the PGZ (Northcutt, 1983; Vanegas and Ito, 1983). In ray-finned fishes, tectal efferents include ascending, intertectal and descending projections (Ebesson and Vanegas, 1976; Northcutt, 1983; Vanegas and Ito, 1983; Northcutt and Wullimann, 1988; Striedter, 1990b). Tectal ascending projections to the pretectal area, the dorsal thalamus, the ventral thalamus, the preglomerular complex and/or the periventricular posterior tuberculum have been described in ostariophysan (Grover and Sharma, 1979; Luiten, 1981; Northcutt and Wullimann, 1988; Striedter, 1990b) and percomorph species (Ebesson and Vanegas, 1976; Northcutt and Wullimann, 1988; Striedter and Northcutt, 1989). Intertectal connections seem to reach the ipsilateral torus longitudinalis as well as the deep white zone of the contralateral tectum (Northcutt, 1983; Vanegas and Ito, 1983). Finally, descending projections to the torus semicircularis, a rostral tegmental nucleus that seems to correspond to the nucleus lateralis valvulae, the nucleus isthmi, and the reticular formations of the rostral medulla have been observed in teleosteans, whereas tectospinal pathways are absent (Sakamoto et al. 1981; Northcutt, 1983; Vanegas and Ito, 1983; Striedter and Northcutt, 1989).

3.1.2. Torus Longitudinalis

The torus longitudinalis (TL) represents a paired midline structure of the dorsal mesencephalon that protrudes into the ventricle in close proximity to the valvula cerebelli. It starts slightly caudal to the rostral end of the posterior commissure (Plate 17) and dissappears at the caudal end of the nMLF (Plate 31). This organ is bordered dorsally by the nerve fibers of the tectal commissure and ventrally by those of the posterior commissure. Rostrally, the TL exhibits a lateral zone composed of small and tightly packed round cells and a medial zone composed of small cells more diffusely distributed and interspersed with tectal fibers. Some medium-sized cells are seen laterally in the medial zone, which is separated from the lateral zone by a region almost devoid of cells. Progressing caudally, the TL is fused ventrally and its cells become more densely packed, the cells in the lateral zone arranged in vertical columnae. Further caudal, bundles of fibers are observed in the dorsal aspect of the TL and medium-sized cells are distributed ventromedially to these fibers. The medial separation between the two lobes becomes more evident and finally, two heart-shaped lobes appear excised from the region of the posterior commissure (Plate 21). The cells of the caudal TL are arranged in layers oriented in parallel with the border of the structure, whereas the cells in the central TL appear less densely packed.

Unique to actinopterygians, the torus longitudinalis has been implicated in visual activity and eye movements (Northmore, 1984). Ito and Kishida (1978) reported that the valvula cerebelli projects to the TL but afferent or efferent connections between the TL and the valvula cerebelli have not been confirmed in other studies (Wullimann and Northcutt, 1989; Wullimann and Roth, 1994). On the other hand, the TL receives oculomotor inputs and is part of a sensory circuitry involving the tegmentum, the hypothalamus, the ventral thalamus and the pretectum (Wullimann, 1994). In this way, it has been proposed that the TL represents a main relay center in premotor circuitry descending from the telencephalon to the brainstem, more so than simply a part of an ascending cerebellotectal circuitry (Wullimann, 1994; Wullimann and Roth, 1994). In gilthead seabream, a connective, vascular and axonal link can be observed between the ventral torus longitudinalis and the granular layer of the rostromedial valvula cerebelli in a few transverse and sagittal sections (Muñoz-Cueto et al., 1998). It remains to be elucidated if these nerve fibers constitute a direct connection between the torus longitudinalis and the valvula cerebelli or represent fibers of passage that originate from other sources ascending to the torus longitudinalis through the valvula cerebelli.

3.2. TEGMENTUM MESENCEPHALI

The tegmentum of the mesencephalon is bordered rostrally by the caudal diencephalon and caudally by the rhombencephalon, and is placed ventromedial to the optic tectum and dorsal to the inferior lobes of the hypothalamus. The tegmentum of gilthead seabream is divisible into medial, central and lateral zones. The medial zone contains five cell masses: nucleus nervi oculomotorius (nIII), nucleus ruber (NR), nucleus of Edinger-Westphal (EW), nucleus nervi trochlearis (nIV), and nucleus gustatorius secundarius (NGS). Six nuclei are also observed in the central zone: nucleus perilemniscularis, in which a pars medialis (PLm) and pars lateralis (PLl) are distinguished, nucleus tegmentalis dorsalis (DT), nucleus tegmentalis ventralis (VT), nucleus lateralis valvulae, subdivided into pars anterioris (NLVa), pars centralis (NLVc), pars posterioris (NLVp) and pars posterioris ventral (NLVpv), nucleus ithsmi (NI) and nucleus of the locus coeruleus (LC). The lateral

zone is represented by the torus semicircularis and its subdivisions, the pars centralis (TSc), pars ventralis (TSv), pars dorsalis (TSd), and pars lateralis (TSl).

3.2.1. Medial Zone

The nIII is bordered rostrally by the nMLF (Plate 30) and is replaced caudally by the nIV (Plate 34). Both nuclei are located in the midline and contain large cells. The cells of the nIV start just ventral to a lateral expansion of the ventricle, medially to the caudal DT. Its cells are pyramidal, rounded and ovoid in shape and slightly smaller and paler in staining than those of the nIII. Caudally, the cells of the nIV become larger and more darkly stained and are placed dorsolaterally to the MLF (Plates 36, 37). Previous studies have shown that fibers arising from cells of the nIII innervated extraocular muscles as the rectus inferior, rectus superior, rectus internus and rectus obliquus inferior, whereas fibers innervating the rectus obliquus superior originated in the cells of the nIV (Luiten and Dijkstra De Vlieger, 1978). The nIII seems to receive afferents from the corpus cerebelli (Kidokoro, 1969; Finger, 1978b; Wullimann and Northcutt, 1988), the dorsal accessory optic nucleus (Finger and Karten, 1978) and the torus longitudinalis (Wullimann, 1994). A projection from the superficial pretectum to the nIV has also been described in percomorphs (Striedter and Northcutt, 1989).

The nucleus ruber (NR) lies close to the midline, ventrolateral to the MLF and the nIII (Plates 30-32). This small nucleus is composed of 2 to 10 medium-sized and large round and darkly stained cells by section. The NR reported in the present study is comparable to the red nucleus or nucleus ruber identified in *Raja* (Smeets and Timerick, 1981), lungfish (Ronan and Northcutt, 1985) and teleosts (Oka et al., 1986a; Prasada Rao et al., 1987). In other teleosts, this nucleus sends descending projections to the spinal cord (Oka et al., 1986a; Prasada Rao et al., 1987, 1993) and is a terminal field of crossed efferent axons of the corpus cerebelli (Finger, 1983a; Wullimann and Northcutt, 1988).

Just caudal to the posterior end of the nMLF, dorsolaterally to the rostral nIII and ventromedially to the DT, a small cell group with a rostro-caudal extent of 140 μm aproximately, is observed in the tegmentum mesencephali (Plate 31). The cells of this group are smaller and less intensely stained than the adjacent oculomotor neurons and seems to correspond to the Edinger-Westphal nucleus (EW) identified in other teleosts (Wathey, 1988; Wathey and Wullimann, 1988). This nucleus has been described as a source of afferents to the corpus cerebelli in sunfish and goldfish, but not in the kelp bass (Wullimann and Northcutt, 1988; Wathey and Wullimann, 1988).

At the caudal end of the nIV, lateral to the ventricle and dorsolateral to the rostral superior raphe lies the nucleus gustatorius secundarius (NGS) of gilthead seabream (Plates 37-42). This nucleus contains small and medium-sized darkly stained neurons interspersed with neuropil. Cells in the dorsal aspect of the nucleus are slightly smaller and less intensely stained than the caudomedial ones. In catfish, two subdivisions of the NGS are recognized: a rostrolateral zone that receives mostly vagal gustatory lobe inputs and a caudomedial zone that receives mostly facial lobe gustatory inputs (Finger and Kanwal, 1992). As in *Lepomis* (Wullimann, 1988), the NGS of gilthead seabream is relatively small compared to cyprinids (Morita et al., 1983) and silurids (Finger, 1983b). Afferent and efferent projections of NGS have been described in sunfish (Wullimann, 1988) and other teleosts (Finger, 1983b; Morita et al., 1983). Neurons projecting to the NGS are found in the viscerosensory column of the brainstem while terminal fields of NGS efferents have been described in a subdivision of the medial preglomerular complex, nucleus of the torus lateralis, nucleus lobob-

ulbaris, nucleus of the lateral thalamus, nucleus periventricularis recessus lateralis, and nucleus centralis and nucleus diffussus of the inferior lobe (Finger, 1983b; Morita et al., 1983; Wullimann, 1988; Lamb and Caprio, 1993a, b).

3.2.2. Central Zone

The nucleus perilemniscularis (PL) begins lateral to the caudal end of the nMLF and medial to the torus semicircularis (Plate 29) and is constituted by scattered cells located around the fibers of the fasciculus longitudinalis lateralis (FLL), the tractus mesencephalocerebellaris anterior and the tractus pretectoisthmicus. Two subdivisions are observed in this nucleus: a rostromedial nucleus (PLm) and a caudolateral nucleus (PLl). The PLm (Plates 29-33) is composed of fusiform and ovoid small and medium-sized cells. The cells of the PLl (Plates 34-39) lie more laterally, between the ventromedial aspect of the nucleus isthmi and the lateral aspect of the FLL and their appearance is similar to PLm cells, but cell density is slightly higher in PLl. Two subdivisions of PL were also recognized in *Apteronotus leptorhynchus* by Maler et al., (1991). In goldfish and sunfish, efferent axons of the PL innervate both the valvula and the corpus cerebelli (Wullimann and Northcutt, 1988, 1989). In goldfish, a nucleus adjacent to the lateral lemniscus, the nucleus of the lateral lemniscus, also sends descending projections to the spinal cord (Prasada Rao et al., 1993).

At the caudal end of the nMLF in the gilthead seabream, appears a nucleus that we have recognized as the putative nucleus tegmentalis dorsalis (DT) described by Wullimann and Northcutt (1988) in *Carassius* and *Lepomis*. This nucleus is composed of a lateromedially-oriented cell plate of small rounded and polygonal cells. The emergence of this nucleus, at the transitional zone among the ventral tegmentum and the valvula cerebelli (Plate 30), determines a discontinuity between the medial and lateral aspects of the ventricle in transverse sections. Caudally, when the nucleus lateralis valvulae begins, the DT migrates slightly medially and lies positioned just lateral to the medial edge of the ventricle (Plates 32-34). In teleosts, this nucleus has been considered a relay center of a telencephalo-cerebellar pathway because it projects to the valvula and the corpus cerebelli (Wullimann and Northcutt, 1988, 1989) and receives telencephalic efferent axons (Murakami et al., 1983; Wullimann and Northcutt, 1990; Wullimann and Meyer, 1993). A projection of the DT to the torus longitudinalis has also been described in *Pantodon* (Wullimann and Roth, 1994).

The nucleus tegmentalis ventralis (VT) is an inconspicuous nucleus composed of a few small round and ovoid cells that appear in the central zone of the tegmentum of gilthead seabream, ventral to the FLL and medial to the torus semicircularis (Plate 30). Caudally, the VT ends at the level where the running fibers of the tractus tectobulbaris become evident in the ventral aspect of the tegmentum and the inferior lobes excise from it (Plate 33). As in the DT, the VT is a source of efferent axons that innervate the valvula and the corpus cerebelli in *Carassius* and *Lepomis* (Wullimann and Northcutt, 1988, 1989), but this pathway has not been described in mormyrids (Meek et al., 1986a, b).

The nucleus lateralis valvulae of *Sparus aurata* has been subdivided into the pars anterioris (NLVa), pars centralis (NLVc), and pars posterioris (NLVp). In turn, a subdivision of NLVp was considered and named pars posterioris ventral (NLVpv). Such subdivisions seems to correlate with the different zones of the NLV described by Ito and Yoshimoto (1990) in the carp, although their rostral NLVa seems to represent our DT. The NLV first appears slightly caudal to the DT (Plate 32) and its more posterior subdivision disappears caudally to the posterior end of the nucleus isthmi and the torus semicircularis (Plate 41). Its cells are smaller than those of the DT and appear organized

in a cell plate thicker than in the DT and oriented in a dorsolateral to ventromedial direction. The NLVa is the most rostral subdivision of the nucleus (Plates 32-37) and starts close to the valvula cerebelli, lateral to the DT. The NLVa contains small cells and is the subdivision with the highest cell density. As NLVc becomes larger, the cells of the NLVa are displaced laterally, near the torus semicircularis. The NLVc lies between the DT and the NLVa and is easily recognized because its cell are less densely packed and organized between the fibers of the tractus mesencephalo-cerebellaris (Plates 33-38). Caudally, when the nucleus isthmi begins, the cells of the NLVc migrate laterally from a position medial to the nucleus isthmi (Plates 35, 36) to a position more dorsal to it (Plates 37, 38). The posterior subdivision of the NLV (NLVp) starts dorsomedial to the NLVc, lateral to the tractus mesencephalo-cerebellaris anterioris and ventral to the granular layer of the valvula cerebelli (Plate 35). Its cells are distinguished from the cells of the NLVc because they are less densely packed and paler in staining. When the cells of NLVc are displaced laterally, the NLVp replaces it and adopt a medial position in relation to the NI (Plates 37-39). More caudally, when the NGS starts, the NLVp migrates slightly lateral (Plate 40) and adopts a position dorsolateral to it before dissappearing (Plate 41). Given its cytoarchitecture, this caudal cell mass, which we currently consider to be a posterior subdivision of the NLV could really represent the secondary visceral nucleus described in other teleosts (Finger, 1983b; Finger and Kanwal, 1992). The elucidation of fiber connections of this cell mass in gilthead seabream should permit its precise consideration as a part of the NLV or as a visceral nucleus. Finally, a small collection of granular cells, slightly larger and less densely packed than those of the NLVp, appears ventral to the NI and ventrolateral to the NGS (Plates 39-41). Rostrally, these cells are almost continuous with the NLVp but caudally they are clearly separated, lying in a more ventral position. We have considered this cell mass as a ventral expansion of the NLVp and we have named it NLVpv. The existence of a cell subpopulation of the NLVp, adopting a similar position as seen in the NLVpv of gilthead seabream, has been described in the tegmentum of the carp (Ito and Yoshimoto, 1990).

In some teleosts, it has been reported that the NLV receives afferents from the nucleus pretectalis superficialis pars magnocellularis, nucleus ventromedialis thalami and inferior lobe (Northcutt and Braford, 1984; Ito et al., 1986; Ito and Yoshimoto, 1990) and projects to the inferior lobe, torus longitudinalis, valvula and corpus of the cerebellum (Finger, 1983a; Wullimann and Northcutt, 1988, 1989; Ito and Yoshimoto, 1990). In cyprinids, this nucleus seems to convey visual information to the cerebellum through a retino-tecto-pretecto-NLV-cerebellar pathway (Uchiyama et al., 1988; Ito and Yoshimoto, 1990), but connections between the superficial pretectum and the NLV are not present in percomorphs (Striedter and Northcutt, 1989).

At the rostral end of the nIV and ventral to the NLV, a round-shaped nucleus ithsmi (NI) arises as a collection of small and medium-sized cells interspersed between a profuse neuropil (Plates 35-40). Rostrally, the cells occupy the total surface of the nucleus in transverse sections. More caudally, the cells are concentrated in the ventromedial and the dorsolateral aspects, leaving the center of the NI almost devoid of cells and comprised principally of nerve fibers. Further caudal, the somata are restricted to the dorsolateral region, the central zone of the nucleus becomes more fibrous in appearance and bundles of axons are seen to enter at its ventromedial level (Plate 38). In percomorphs and cyprinids, some of these fibers represent thick afferent axons originating from the superficial pretectum (Ito et al., 1981; Striedter and Northcutt, 1989) and the lateral thalamic nucleus, respectively (King and Schmidt, 1993). Furthermore, in percomorphs the NI projects to the parvicellular and magnocellular subdivisions of the superficial pretectum (Striedter and Northcutt, 1989) and is reciprocally connected with the optic tectum in percomorphs (Sakamoto

et al., 1981; Williams et al., 1983; Striedter and Northcutt, 1989), cyprinids (King and Schmidt, 1993) and mormyrids (Wullimann and Northcutt, 1990), suggesting an important role of this nucleus in visual circuitry. A projection of the NI to the corpus and the valvula cerebelli has also been described in both percomorphs and cyprinids (Wullimann and Northcutt, 1988; 1989).

Ventral to the lateral expansion of the ventricle and among the fibers of the MLF and that of the FLL, we can see the medium-sized cells of the LC (Plates 39-41). This nucleus is bordered dorsolaterally by the cells of the nucleus gustatorius secundarius and ventrally by the cells of the nucleus reticularis superioris. The caudal limits of the LC coincide with the rostral end of the larger cells of the Vm. In gilthead seabream, TH-positive cells are observed in this nucleus (Muñoz-Cueto et al., 1997). The LC projects to the telencephalon (Northcutt, 1981; Ito et al., 1982; Wullimann and Northcutt, 1990), corpus cerebelli (Ito et al., 1982; Wullimann and Northcutt, 1988; Wullimann and Meyer, 1993), valvula cerebelli (Wullimann and Northcutt, 1989), optic tectum (Wullimann and Northcutt, 1990) and dorsal preglomerular nucleus (Wullimann and Roth, 1994).

3.2.3. Lateral Zone

The torus semicircularis (TS) in the gilthead seabream constitutes the dorsolateral region of the tegmentum and is less complex than in electric fish species as *Ictalurus* (Finger and Tong, 1984; Striedter, 1991) or *Apteronotus* (Maler et al., 1991). It is bordered laterally by the optic tectum, medially by the nucleus lateralis valvulae, dorsally by the mesencephalic ventricle and valvula cerebelli and ventrally by the tractus tectobulbaris, disappearing caudally at the same transverse level as the valvula cerebelli (Plates 25-40). The pars centralis (TSc) is composed of scattered small round and fusiform cells located laterodorsally to the fibers of the fasciculus longitudinalis lateralis. Fusiform cells are primarily arranged with their larger axis in a ventrolateral to dorsomedial orientation. The cells of the TSc are organized in slightly curved lateromedially oriented laminae, in parallel to the ependyma. At the caudal end, the cells become densely packed, especially near the ventricular surface. The pars ventralis (TSv) contains a few round and very small cells quite loosely distributed between the tectal fibers. Some medium-sized and more intensely stained cells are also seen, especially in the dorsal aspect. The pars intermedius (TSi) is composed of scattered cells appearing between the TSc, TSv and TSl, another subdivision of the TS that lies in the lateral torus and contains more densely packed neurons organized in laminae.

The subdivisions and boundaries of the different toral nuclei recognized in the lateral tegmentum of teleosts differ from one study to other (Finger and Tong, 1984; Maler et al., 1991; Striedter, 1991). In catfish, it has been demonstrated that there is a segregation of auditory-acoustic, electrosensory and mechanosensory lateral line modalities, which involves the medial, the lateral and the ventral aspects of the TS, respectively (Finger and Tong, 1984; Striedter, 1991). The multisynaptic pathways ascending from the lateral line and octaval nerves to the telencephalon through the TS, involves other relay nuclei as the electrosensory lateral line lobe, anterior and medial octavolateral nuclei, descending octaval nucleus, medial auditory nucleus, anterior tuberal nucleus, central posterior thalamic nucleus and lateral preglomerular complex (Finger and Tong, 1984; Striedter, 1991). Ascending pathways from the TS to the telencephalon have been described in other teleosts (Echteler, 1984; Murakami et al., 1986b, c; Wullimann and Northcutt, 1990) but the relay nuclei seems to vary between species (Striedter, 1991). Descending pathways from the TS have also been described in the ictalurid catfishes (Finger and Tong, 1984; Striedter, 1991).

4. CEREBELLUM

As in other actinopterygian fishes, three main parts are found in the cerebellum of the gilthead seabream: corpus cerebelli, valvula cerebelli and lobus vestibulolateralis (Nieuwenhuys, 1982; Finger, 1983a). The valvula cerebelli represents the most rostral subdivision and the lobus vestibulolateralis the most ventral and caudal one. In turn, the corpus cerebelli forms a dorsally protruding structure, which constitutes the remainder of the cerebellum.

4.1. VALVULA CEREBELLI

The valvula cerebelli (VCe) starts slightly caudal to the rostral end of the posterior commissure (Plate 17). Although the gilthead seabream is a nonelectrosensory teleost, the VCe is a well developed structure that fills almost completely the tectal ventricle (Plates 18-40). As in *Lepomis* (Wullimann and Northcutt, 1989), the VCe of the gilthead seabream is complexly folded and the lateral and medial aspects are apparently not distinguishable. When the torus longitudinalis displaces dorsally, the VCe expands medially and the left and right halves appear centrally joined (Plate 24). Two layers are clearly differentiated in the VCe, a granular layer and a molecular layer. In transverse sections, the granular layer is located superficially, although folded laminae of granular cells are also found internally in the VCe. This granular layer is composed of small round cells, densely packed and darkly stained. The molecular layer is located primarily in the internal portion of the VCe and is infiltrated by profuse interdigitations of the tectal ventricle covered by ependymal cells. The molecular layer contains small round, fusiform and triangular cells loosely interspersed within an abundant neuropil. A layer of Purkinje cells is interposed between the granular and molecular layers, although some Purkinje-like cells are also observed within the granular layer.

In mormyrids, the valvula cerebelli has been implicated in the electroreceptive capabilities because it receives afferents from the electrosensory portions of the torus semicircularis, as well as from other electrosensory-related nuclei (Finger et al., 1981). However, these connections are not present in nonelectrosensory cyprinids and percomorphs, where the valvula cerebelli receives afferent inputs from the pretectum, accessory optic system, tegmentum of the mesencephalon and rhombencephalic inferior olive (Wullimann and Northcutt, 1989). In addition, the LC and CCe represent a source of valvulopetal projections in *Lepomis,* but not in *Carassius,* and the contrary is true for the isthmic primary sensory trigeminal nucleus, nucleus pre-eminentialis and eminentia granularis (Wullimann and Northcutt, 1989). In teleosts in which medial and lateral aspects of the VCe are recognized, both subdivisions seem to differ in their efferent connections (Finger, 1983a). Thus, the medial VCe exhibits similar efferent pathways as found in the CCe, whereas almost all the fibers of the lateral VCe terminate massively in the nucleus lateralis valvulae.

4.2. CORPUS CEREBELLI

The corpus cerebelli (CCe) of the gilthead seabream arises at the level of the nIV (Plate 34). In rostral transverse sections, a dorsal pole that protrudes above the caudal optic tectum and a ventral pole which replaces the caudomedial VCe are observed (Plates 34-40). When progressing caudally, the optic tectum and the VCe disappear and the dorsal and ventral poles of the CCe join, making this caudal CCe continuous with the ventrally located lobus vestibulolateralis (Plates 41-54). Punkinje cells are recognized between the external molecular layer and the internal granular layer of the CCe, which are continous with both layers of the VCe and lobus vestibulolateralis.

In teleosts, anterior (diencephalocerebellar, pretectocerebellar and tegmentocerebellar) and posterior (reticulocerebellar, vestibulocerebellar and spinocerebellar) groups of nuclei have been described as a source of afferents to CCe (Finger, 1978a; Ito et al., 1982; Paul, 1982; Finger, 1983a; Meek et al., 1986a, b; Wullimann and Northcutt, 1988), although differences between groups and in the nomenclature sometimes make the interpretation rather confusing. Recently, the existence of, at least, three different patterns of corpopetal organization represented by cyprinids, percomorphs and mormyrids have been proposed (Wullimann and Northcutt, 1988). The corpofugal pathways in teleosts are represented by three main systems (Larsell, 1967; Paul, 1982; Finger, 1983a; Wullimann and Northcutt, 1988). The brachium conjuntivum contains fibers that terminate in the ventromedial and ventrolateral thalamus, periventricular pretectum, oculomotor nucleus, nucleus ruber, nucleus of the medial longitudinal fasciculus, torus semicircularis, optic tectum and superior and inferior reticular formations. Efferent fibers from the CCe run within the anterior mesencephalocerebellar tract and innervate both ipsilateral and contralateral torus longitudinalis, whereas posterior mesencephalocerebellar tract fibers terminate in the nucleus lateralis valvulae, octaval nuclei and inferior reticular formation (Finger, 1983a; Wullimann and Northcutt, 1988).

4.3. LOBUS VESTIBULOLATERALIS

As in other teleosts, the lobus vestibulolateralis (LV) of the gilthead seabream consists of paired eminentia granulares and a caudal lobe. The eminentia granularis (EG) is composed of small granule cells and some medium-size ovoid cells (Plates 43-49). In rostral transverse sections, the cells of the EG appear continuous with the other granule cells of the cerebellum (Plates 43-45), but two separated bulges can be observed further caudal in the lateral surface of the brain (Plates 46-49). Cell density is slightly higher in the dorsal aspect of the EG than in the ventral one. The caudal lobe surrounds the fourth ventricle and is composed of the periventricular granular cell masses (PG), a molecular layer above it and a layer of granule cells interconnected with the granular cell masses of the CCe and the EG. The PG is composed of small, compact and very darkly stained granule cells that appear concentrated in the dorsolateral border of the ventricle (Plates 42-50). At the caudal end of the EG, these cells expand dorsally, and horizontal columns of cells interconnecting bilateral cell groups are observed just at the level where the CCe excises from the LV (Plates 49-50). The molecular layer of the LV is continuous with the molecular layer of the dorsal CCe and with a caudal molecular layer overlying the rhombencephalic area octavolateralis, named crista cerebellaris (CC).

The LV has been described as a part of the cerebellum receiving fibers of the lateral line and eight nerves (Larsell, 1967; Paul, 1982; Meredith and Butler, 1983). In turn, the LV appears to give rise to efferent fibers that innervate the lateral line lobes, the vestibular nuclei and the reticular areas (Maler, 1974; Finger, 1983a).

5. RHOMBENCEPHALON

The rhombencephalon represents the most caudal part of the brain, and is bordered rostrally by the tegmentum of the mesencephalon, and caudally by the spinal cord. In order to facilitate our description, we have considered in the rhombencephalon of the gilthead seabream the following subdivisions: the reticular formation, area octavolateralis, somatomotor and visceromotor nuclei and remaining nuclei.

5.1. RETICULAR FORMATION

According to the criteria of Nieuwenhuys and Oey (1983), we have distinguished three longi-tudinal zones in the reticular formation: a median zone, a medial zone and a lateral zone.

Median Zone

The median zone comprises the cell groups situated in the rhombencephalic midline raphe area, including nucleus raphes superior (SR) and nucleus raphes inferior (IR). Just caudal to the nIV, the SR starts in the isthmic region between the ventricle and the MLF (Plate 38), and disappears caudally at the level of the nucleus nervi abducentis, pars rostralis (Plate 48). Its cells are rounded and ellipsoid in shape, but smaller than the nIV neurons. These cells exhibit a moderately stained granular cytoplasm and a large nucleus in which a nucleolus is usually evident. Rostrally, the cells are medium-sized and located dorsomedially to the MLF. More caudally, when the ventricle enlarges laterally, the cells of the SR become smaller and occupy a position more medial to the MLF, just in the midline. The IR is located in the most caudal part of the rhombencephalon, cau-dally to the SR, and is composed of small scattered and poorly stained cells (Plates 50-58b). Caudally, higher and intensely stained cells of the IR can be seen ventrally in the midline, with its main dendrite directed laterally in parallel to the ventral surface of the brain.

In the garfish, *Lepisosteus osseus*, both the SR and the IR contain serotoninergic neurons (Parent and Northcutt, 1982) and the IR projects to the tectum mesencephali (Northcutt, 1982), whereas corpopetal projections from IR have been described in *Lepomis* and *Carassius* (Wulllimann and Northcutt, 1988). The existence of projections from the SR to the telencephalon has been established in *Polypterus* (Northcutt, 1981) and *Gnathonemus petersii* (Wullimann and Northcutt, 1990). In addition, retrogradely-labeled neurons in the raphe nuclei were observed following HRP injections in the telencephalon (Ito et al., 1982), corpus cerebelli (Ito et al., 1982) and spinal cord (Prasada Rao et al., 1987; 1993) of different teleosts.

Medial Zone

The medial zone of the reticular formation is a continuous cell mass situated laterally to the median zone extending from the tegmentum mesencephali to the spinal cord. Its cells appear loosely scattered in the neuropil and vary considerably in size (small to large) and shape (round-ed, ovoid, pyramidal and multipolar). Although their limits are relatively difficult to assess, three nuclei were considered in this medial reticular formation, according with the criteria of Nieuwenhuys and Oey (1983): nucleus reticularis superioris (RS), nucleus reticularis medius (RM) and nucleus reticularis inferioris (RI). The RS starts rostrally in the ventral tegmentum, just at the level where the inferior lobes excise from the mesencephalon (Plate 33). This reticular nucleus lies lateral to the MLF and medial to the FLL, and is replaced caudally by the RM, at the posterior end of the nucleus motorius nervi trigemini (Plate 45). The cell density is greater and the neuropil is more profuse in the RM than in the RS, and some large and darkly stained neurons are seen, espe-cially in the dorsomedial aspect of the nucleus. Further caudal, at the level where the nucleus nervi abducentis pars caudalis ends, the RM is replaced by the RI (Plate 51). This nucleus contains cells slightly larger and stronger stained than in RM and forms a plate oriented in a dorsomedial to ven-trolateral direction. Even more caudally, the cells of the RI disappear and the giant spinal motor neurons occupy their place (Plate 58a).

In *Lepisosteus*, all subdivisions of the medial reticular formation project to the tectum mesen-cephali (Northcutt, 1982), but only the nucleus reticularis inferioris seems to receive tectal inputs (Northcutt and Buttler, 1980). Reciprocal connections have been described between the superior reticular formation and the optic tectum of *Gnathonemus petersii* (Wullimann and Northcutt, 1990), the inferior reticular formation and the corpus cerebelli of *Lepomis* and *Carassius* (Wulllimann and Northcutt, 1988), and between the reticular formation and the auditory region of the carp torus semicircularis (Echteler, 1984). In teleosts, the entire medial zone of the reticular formation also represents a source of descending spinal projections (Hlavacek et al., 1984; Oka et al., 1986a; Prasada Rao et al., 1987, 1993; Behrend and Donicht, 1990) as well as a target for ascend-ing spinal pathways (Murakami and Ito, 1985; Oka et al., 1986b). Finally, an eighth nerve projec-tion to the medial reticular formation is also present in *Amia* (McCormick, 1981) and *Astronotus* (Meredith and Butler, 1983).

Lateral Zone

In addition to the median and medial reticular formations, a lateral column of cells is present in the caudal rhombencephalon of the gilthead seabream, lateral to the RI and the commissure of Wallenberg (Plates 55b-57a). This cell mass, which we have named nucleus reticularis lateralis (RL), seems to correspond to the lateral reticular zone described in the reedfish (Nieuwenhuys and Oey, 1983), *Amia calva* (Heijdra and Nieuwenhuys, 1994), as well as in tetrapods (Cruce and Nieuwenhuys, 1974; Nikundiwe and Nieuwenhuys, 1983). This nucleus is composed of some small and medium-sized cells, rounded, ovoid and pyramidal in shape, located in the ventrolateral sur-face of the rhombencephalon between the incoming fibers of the IX and X nerves. In cyprini-formes and perciformes, the existence of a projection from the nucleus reticularis lateralis to the corpus cerebelli has been described (Murakami and Ito, 1985; Wullimann and Northcutt, 1988).

5.2. Area Octavolateralis

The area octavolateralis represents a brainstem zone implicated in the processing of auditory, vestibular and lateral line information (McCormick, 1982; Meredith and Butler, 1983; Finger and Tong, 1984). This area is covered dorsally by the crista cerebellaris (CC), which represents a caudal molecular layer in continuity with the molecular layer of the other cerebellar components (Plates 50-57b). In the CC, some small and poorly stained cells are seen loosely interspersed with fibers and neuropil.

As in other teleosts (McCormick, 1982, 1983), we have considered seven nuclei in the area octavolateralis: five octaval nerve nuclei — nucleus octavus anterioris (AON), nucleus magnocel-lularis (MAG), nucleus octavus descendens (DON), nucleus tangentialis (T), and nucleus octavus posterioris (PO); and two lateral line nuclei — nucleus octavolateralis medialis (MON) and nucle-us caudalis (C).

The AON represents the most rostral subdivision of the area octavolateralis (Plates 44-47). This nucleus is bordered ventrally by the nervus trigemini, dorsally by the eminentia granularis and medially by the MON. Small rounded cells of the AON are observed interspersed between the neu-ropil although some bigger and more intensely stained cells can also be observed, especially in the proximity of the nervus trigemini. At the level of entrance of the nervus octavus, the AON is replaced by two nuclei, the DON in a medial position and the MAG, slightly more ventrolateral (Plate 48). The DON is composed of round and small ellipsoid cells that lie dorsomedial to the

descending trigeminal tract (DTr). The cells of the MAG occupy a dorsolateral and lateral position with respect to the DTr (Plates 48-50). Two types of intensely stained cells are identified in this nucleus: fusiform medium-sized cells, with a very elongated perikaryon, and large ellipsoid cells. At the caudal end of the MAG, the DON cells expand laterally and occupy the position between the fibers of the DTr and the VIII nerve, and further caudally, these cells lie in the lateral edge of the brainstem (Plates 51-57a). A nucleus tangentialis (T) is also recognized in the ventrolateral surface of the gilthead seabream rhombencephalon (Plates 49-53). This nucleus, slightly medial to the fibers of the nervus octavus and ventral to the fibers of the DTr and the tractus gustatorius secundarius, exhibits one to eight medium-sized cells by hemisphere, round to ovoid in shape. Rostrally, these tangentialis cells are bordered dorsally by the MAG cells but caudally the DON cells constitute its dorsal limit. In the caudal brainstem, at the level where the crista cerebellaris and the MON terminate, a collection of small granular cells are observed in the dorsolateral rhombencephalon (Plates 55-58). These cells are loosely scattered ventrally, in the proximity of the DTr, but are arranged more compactly at the dorsal surface. These posterior cell masses seem to correspond, respectively, to the nucleus octavus posterioris (PO) and the nucleus caudalis (C) described in other teleosts (McCormick, 1982; Highstein et al., 1992).

The nucleus octavolateralis medialis (MON) starts slightly caudal to the rostral appearence of the AON, near the ventrolateral tip of the ventricle (Plate 45). It is bordered by the eminentia granularis dorsolaterally, by the periventricular granular cell mass of the caudal lobe dorsomedially, by the caudal cells of the Vm ventromedially and by the cells of the AON and the fibers of the DTr ventrolaterally. More caudally, at the posterior end of the EG, the cells of the MON expand laterally to the dorsolateral surface of the brainstem (Plate 49). Finally, when the caudal corpus cerebelli excises from the rhombencephalon, MON is covered dorsally by the crista cerebellaris. At this level, the ventromedial and ventrolateral borders of MON are the vagal lobe and the DON, respectively (Plates 50-56). This nucleus, constituted by small and medium-sized cells, is easily recognized in cresyl violet stained sections by the fibrous aspect of its profuse neuropil.

Both in teleost and non-teleost fishes, a generalized pattern of octavolateralis inputs has been described (McCormick,1982; 1983). According to this pattern, eighth nerve fibers terminate in the ventral part of the octavolateralis area (AON, DON, T and PO) and lateralis fibers end in the dorsal portion of the octavolateralis area (MON and C), with an overlap of both types of inputs only found in the MAG. However, a specialized pattern is present in mormyrids, in which the eighth nerve projects additionally to lateral line nuclei, similar to the MON and C, and auditory and vestibular centers seems to be separated within the octavolateral area (Bell and Russell, 1978; Bell, 1981). In catfishes, the electrosensory lateral line, the mechanosensory lateral line and the auditory/acoustic pathways are distinct. Thus, the AON and the DON are implicated in auditory connections whereas the MON is involved in mechanosensory lateral line connections, involving the relay in different subdivisions of the torus semicircularis (Finger and Tong, 1984). Octavolateral nuclei have also been described as a source of projections to the spinal cord (Hlavacek et al., 1984; Prasada Rao et al., 1993) and the corpus cerebelli (Ito et al., 1982; Wullimann and Northcutt, 1988).

5.3. SOMATOMOTOR NUCLEI

Somatomotor nuclei are represented by the nucleus nervi oculomotorius (nIII), nucleus nervi throclearis (nIV) and nucleus nervi abducentis (nVI). As nIII and nIV were already considered in the medial zone of the tegmentum mesencephali only the nVI will be described here. Two subdivisions constitute the nVI of the gilthead seabream: pars rostralis (nVIr) and pars caudalis (nVIc).

The nVIr begins in the ventral rhombencephalon, ventrocaudal to the Mauthner cells and ventrolateral to the nucleus reticularis medius (Plate 47). Its pyramidal and ovoid cells are medium-sized and smaller than in the other somatomotor nuclei. A discontinuity of 150-200 μm, aproximately, is observed between the cells of the nVIr and the nVIc, which appears laterally to the commissure of Wallenberg (Plates 49, 50). Two nVI subnuclei have also been defined in the goldfish (Sterling, 1977) and the carp (Luiten and Djikstra De Vlieger, 1978) which innervate an extraocular muscle, the rectus externus.

5.4. VISCEROMOTOR NUCLEI

Four visceromotor nuclei are distinguished in the rhombencephalon of the gilthead seabream. These nuclei represent the efferent centers of cranial nerves V, VII, IX and X and are, from rostral to caudal, the nucleus motorius nervi trigemini (Vm), nucleus motorius nervi facialis (VIIm), nucleus motorius nervi glossopharyngei (IXm) and nucleus motorius nervi vagi (Xm).

The Vm starts near the ventricle (Plate 42), caudally to the locus coeruleus, and disappears slightly rostral to the Mauthner cells (Plate 45). This nucleus is composed of medium-sized and large cells that lie lateral to the MLF and dorsal to the nucleus reticularis superioris. Further caudal, the cells of the Vm leave its periventricular localization and adopt a more ventral position lateral to the medial reticular formation.

At the posterior end of the nVIc, the VIIm appears lateral to the MLF, between the ventricle and the cells of the medial zone of the reticular formation (Plate 50). This nucleus contains medium-sized and large intensely stained cells with a granular cytoplasm. These cells are primarily round to ellipsoid in shape although some fusiform cells are observed. As in *Amia* (Heijdra and Nieuwenhuys, 1994), the VIIm of the gilthead seabream can be clearly distinguished from the IXm.

The VIIm is replaced caudally by the IXm (Plate 53) and the Xm (Plate 55a). The former is a more conspicuous nucleus that has a rostrocaudal extent of 250-300 μm and appears in discontinuity with the Xm cells. Rostrally, the cells of the Xm are organized in a column which extends laterally from the MLF (Plates 55a-56a). These cells are mainly ovoid and fusiform in shape, with the major axis oriented in a dorsomedial to ventrolateral direction. Caudally, the cells of the Xm adopt a more dorsal position and are bordered dorsally by the vagal lobe and ventrally by the nucleus reticularis inferioris (Plates 56b-58b).

5.5. OTHER NUCLEI

Finally, the remaining nuclei of the rhombencephalon will be considered in this section. They are, from rostral to caudal, the nucleus interpeduncularis (IP), cells of Mauthner (Mc), cells of the vagal lobe (VLo), nucleus of the commissure of Wallenberg (NCW) and inferior olive (IO).

The IP is an unpaired cell mass that starts in the midline, just at the level where the inferior lobes excise from the tegmentum (Plate 34). The IP, which lies ventral to the nIV rostrally (Plates 35-37) and to the superior raphe caudally (Plates 38, 39), is composed of very small round and poorly stained neurons. This nucleus is the target of axons from the fasciculus retroflexus in *Erpetoichthys calabaricus* (Nieuwenhuys, 1983).

The giant cells of Mauthner (Mc) appear lateral to the MLF, dorsal to the nucleus reticularis superioris, and slightly caudal to the Vm (Plate 46). In gilthead seabream, the cell bodies of Mc have a rostro-caudal extent of 140-160 μm, representing, as in other teleost, the largest neurons of

the brain. These Mc send descending projections to the spinal cord in teleosts (Oka et al., 1986a; Prasada Rao et al., 1987, 1993; Behrend and Donicht, 1990).

In the caudal brainstem, the cells of the vagal lobe (VLo) occupy the space between the ventricle and the fibers of the DTr, the TGS and the DMON (Plates 54-58b). At the rostral level, these small cells are bordered dorsally by the cells of the MON and the crista cerebellaris, but caudally, the cells of the VLo continue to the dorsal edge of the brainstem. Some tyrosine-hydroxylase positive cells are observed in the VLo of the gilthead seabream (Muñoz-Cueto et al., 1997).

In the ventrocaudal rhombencephalon of the gilthead seabream, a collection of a few small cells are observed lateral to the commissure of Wallenberg. According to the nomenclature used in other teleosts (Wullimann and Northcutt, 1988), we have named this nucleus as the nucleus of the commissure of Wallenberg (Plates 54-55a).

Finally, small cells appear distributed along the ventral surface of the caudal rhombencephalon, between the midline cells of the inferior raphe and the fibers of the commissure of Wallenberg. These cells represent the nucleus of the inferior olive (Plates 55b-57b), which is present in all actinopterygians (Nieuwenhuys and Pouwels, 1983). In teleosts, it has been observed that the IO projects to the VCe (Wullimann and Northcutt, 1989; Ito and Yoshimoto, 1990) and the CCe (Finger, 1978a; Ito et al., 1982; Wullimann and Northcutt, 1988; Ito and Yoshimoto, 1990).

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ILLUSTRATIONS

ILLUSTRATION KEY

A: nucleus anterior thalami
AC: anterior cerebellar tract
ACo: anterior commissura
ALL: anterior lateral line nerve
AON: nucleus octavus anterioris
AP: nucleus pretectalis accessorius
BC: brachium conjunctivum
C: nucleus caudalis
CC: crista cerebellaris
CCe: corpus cerebelli
CM: corpus mammillare
CP: nucleus centralis posterior thalami
CW: commissure of Wallenberg
CZ: central zone of the optic tectum
DAO: dorsal accesory optic nucleus
Dc: area dorsalis telencephali, pars centralis
Dc1: area dorsalis telencephali, pars centralis, subdivision 1
Dc2: area dorsalis telencephali, pars centralis subdivision 2
Dd: area dorsalis telencephali, pars dorsalis
Dl: area dorsalis telencephali, pars lateralis
Dld: area dorsalis telencephali, pars lateralis dorsal
Dlp: area dorsalis telencephali, pars lateralis posterior
Dlv: area dorsalis telencephali, pars lateralis ventral
Dlv1: area dorsalis telencephali, pars lateralis ventral, subdivision 1
Dlv2: area dorsalis telencephali, pars lateralis ventral, subdivision 2
Dlv3: area dorsalis telencephali, pars lateralis ventral, subdivision 3
Dm: area dorsalis telencephali, pars medialis
Dm1: area dorsalis telencephali, pars medialis, subdivision 1
Dm2: area dorsalis telencephali, pars medialis, subdivision 2
Dm3: area dorsalis telencephali, pars medialis, subdivision 3
Dm4: area dorsalis telencephali, pars medialis, subdivision 4
DMON: decussation of the octavolateralis area
DON: nucleus octavus descendens
DOT: dorsal optic tract
Dp: area dorsalis telencephali, pars posterioris
DP: nucleus dorsalis posterior thalami
DT: nucleus tegmentalis dorsalis
DTr: descending trigeminal tract
DWZ: deep white zone of the optic tectum
ECL: external cellular layer of olfactory bulbs
EG: eminentia granularis
EW. nucleus of Edinger-Westphal

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FLL: fasciculus longitudinalis lateralis

FR: fasciculus retroflexus

G: granular layer of the cerebellum

GL: glomerular layer of olfactory bulbs

HaCo: habenular commissure

HCo: horizontal commissure

Hyp: hypothalamus

I: nucleus intermedius thalami

ICL: internal cellular layer of olfactory bulbs

III: nervus oculomotorius

IO: inferior olive

IP: nucleus interpeduncularis

IR: nucleus raphes inferior

IX: nervus glossopharyngeus

IXm: nucleus motorius nervi glossopharyngei

LC: nucleus of the locus coeruleus

LFB: lateral forebrain bundle

LI: lobi inferioris

LP: nucleus pretectalis lateralis

LSO: lateral septal organ

LT: nucleus lateralis thalami

LV: lobus vestibulolateralis

M: molecular layer of the cerebellum

MAG: nucleus magnocellularis

MaOT: marginal optic tract

Mc: cells of Mauthner

MCo: minor commissure

MFB: medial forebrain bundle

MLF: fasciculus longitudinalis medialis

MO: medulla oblongata

MON: nucleus octavolateralis medialis

NAPv: nucleus anterioris periventricularis

NAT: nucleus anterior tuberis

NC: nucleus corticalis

NCLI: nucleus centralis lobi inferioris

NCW: nucleus of the commissure of Wallenberg

NDLI: nucleus diffusus lobi inferioris

NDLIc: nucleus diffusus lobi inferioris, pars caudalis

NDLIl: nucleus diffusus lobi inferioris, pars lateralis

NDLIm: nucleus diffusus lobi inferioris, pars medialis

NE: nucleus entopeduncularis

nFR: nucleus of the fasciculus retroflexus

NGa: nucleus glomerulosus, pars anterioris

NGp: nucleus glomerulosus, pars posterioris

NGS: nucleus gustatorius secundarius

NGT: nucleus gustatorius tertius
NHd: nucleus habenularis, pars dorsalis
NHv: nucleus habenularis pars ventralis
NI: nucleus isthmi
nIII: nucleus nervi oculomotorius
nIV: nucleus nervi trochlearis
NLT: nucleus lateralis tuberis
NLTd: nucleus lateralis tuberis, pars dorsalis
NLTi: nucleus lateralis tuberis, pars inferioris
NLTl: nucleus lateralis tuberis, pars lateralis
NLTm: nucleus lateralis tuberis, pars medialis
NLTv: nucleus lateralis tuberis, pars ventralis
NLV: nucleus lateralis valvulae
NLVa: nucleus lateralis valvulae, pars anterioris
NLVc: nucleus lateralis valvulae, pars centralis
NLVp: nucleus lateralis valvulae, pars posterioris
NLVpv: nucleus lateralis valvulae, pars posterioris ventral
nMLF: nucleus of the medial longitudinal fasciculus
NMLI: nucleus medialis lobi inferioris
NP: nucleus paracommissuralis
NPC: nucleus pretectalis centralis
NPGa: nucleus preglomerulosus anterioris
NPGc: nucleus preglomerulosus commissuralis
NPGl: nucleus preglomerulosus lateralis
NPGm: nucleus preglomerulosus medialis
NPO: nucleus preopticus parvocellularis
NPOav: nucleus preopticus parvocellularis, pars anteroventralis
NPOpc: nucleus preopticus parvocellularis, pars parvocellularis
NPPv: nucleus posterioris periventricularis
NPT: nucleus posterior tuberis
nPVO: nucleus of the paraventricular organ
NR: nucleus ruber
NRLd: nucleus recessus lateralis, pars dorsalis
NRLv: nucleus recessus lateralis, pars ventralis
NRLl nucleus recessus lateralis, pars lateralis
NRP: nucleus recessus posterioris
NSC: nucleus suprachiasmaticus
NSV: nucleus saccus vasculosus
NT: nucleus taenia
nTE: nucleus eminentia thalami
nTPI: nucleus of the tractus pretectoisthmicus
nVIc: nucleus nervi abducentis, pars caudalis
nVIr: nucleus nervi abducentis, pars rostralis
OB: olfactory bulb
OC: optic chiasm

OlN: olfactory nerve
OT: optic tectum
OVLT: organum vasculosum laminae terminalis
P: pituitary
PCo: posterior commissure
PG: periventricular granular cell mass of the caudal lobe
pgd: nucleus periglomerulosus dorsalis
PGZ: periventricular gray zone of the optic tectum
PLm: nucleus perilemniscularis, pars medialis
PLl: nucleus perilemniscularis, pars lateralis
PLL: posterior lateral line nerve
PM: nucleus preopticus magnocellularis
PMgc: nucleus preopticus magnocellularis, pars gigantocellularis
PMmc: nucleus preopticus magnocellularis, pars magnocellularis
PMpc: nucleus preopticus magnocellularis, pars parvocellularis
PO: nucleus octavus posterioris
POA: preoptic area
PPd: nucleus pretectalis periventricularis, pars dorsalis
PPv: nucleus pretectalis periventricularis, pars ventralis
PSi: nucleus pretectalis superficialis, pars intermedius
PSm: nucleus pretectalis superficialis, pars magnocellularis
PSp: nucleus pretectalis superficialis, pars parvocellularis
PT: nucleus posterior thalami
PVO: paraventricular organ
RI: nucleus reticularis inferioris
RL: nucleus reticularis lateralis
RM: nucleus reticularis medius
RS: nucleus reticularis superioris
S: sensory root of the nervus facialis
SC: spinal cord
SCO: subcommissural organ
SOCo: supraoptic commissure
SOF: secondary olfactory fiber layer of olfactory bulbs
SR: nucleus raphes superior
SV: saccus vasculosus
SWGZ: superficial white and gray zone of the optic tectum
T: nucleus tangentialis
TCo: tectal commissure
Tel: telencephalon
TGL: tractus glomerulolobaris
TGS: tractus gustatorius secundarius
TL: torus longitudinalis
TLa: nucleus of the torus lateralis
TMCa: tractus mesencephalocerebellaris anterior
TMCp: tractus mesencephalocerebellaris posterior

TN: terminal nerve

TNgc: terminal nerve ganglion cells

TPI: tractus pretectoisthmicus

TPp: periventricular nucleus of the posterior tuberculum

TS: torus semicircularis

TSc: torus semicircularis, pars centralis

TSi: torus semicircularis, pars intermedius

TSl: torus semicircularis, pars lateralis

TSv: torus semicircularis, pars ventralis

TTB: tractus tectobulbaris

V: nervus trigeminus

VAO: ventral accessory optic nucleus

Vc: area ventralis telencephali, pars centralis

VCe: valvula cerebelli

Vd: area ventralis telencephali, pars dorsalis

Vi: area ventralis telencephali, pars intermedia

VII: nervus facialis

VIII: nervus octavus

VIIm: nucleus motorius nervi facialis

Vl: area ventralis telencephali, pars lateralis

VL: nucleus ventrolateralis thalami

VLo: vagal lobe

Vm: nucleus motorius nervi trigemini

VM: nucleus ventromedialis thalami

VOT: ventral optic tract

Vp: area ventralis telencephali, pars postcommissuralis

Vs: area ventralis telencephali, pars supracommissuralis

VT: nucleus tegmentalis ventralis

Vv: area ventralis telencephali, pars ventralis

X: nervus vagus

Xm: nucleus motorius nervi vagi

+5740

a

+5530

b

Plate 1

Plate 2

Plate 3

Plate 4

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Plate 5

Plate 6

a

+3570

Dm3
Dld
Dm4
Dc2
Dm2
Dd
Vd
Dc1
Dlv1
OB
Dlv2

b

+3325

Dm3
Dld
Dm4
Vs
Dm2
Dc2
Dd
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Dc1
Dlv1
Vv
Vl
LSO
Dlv2

Plate 7

60

a

+3115

b

+3010
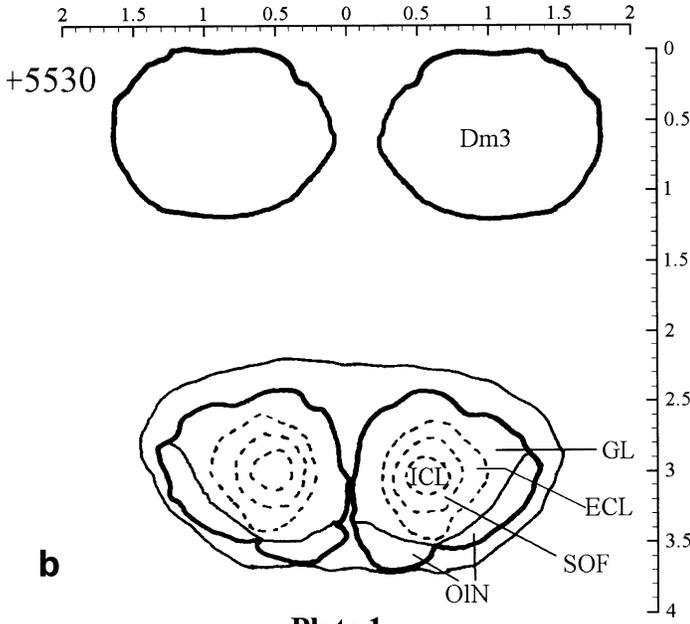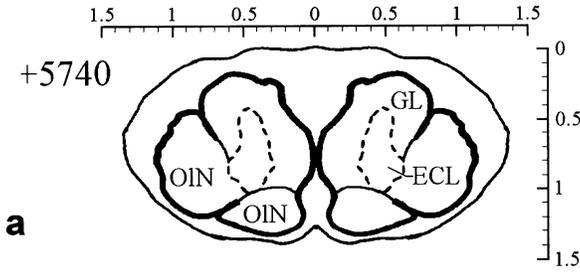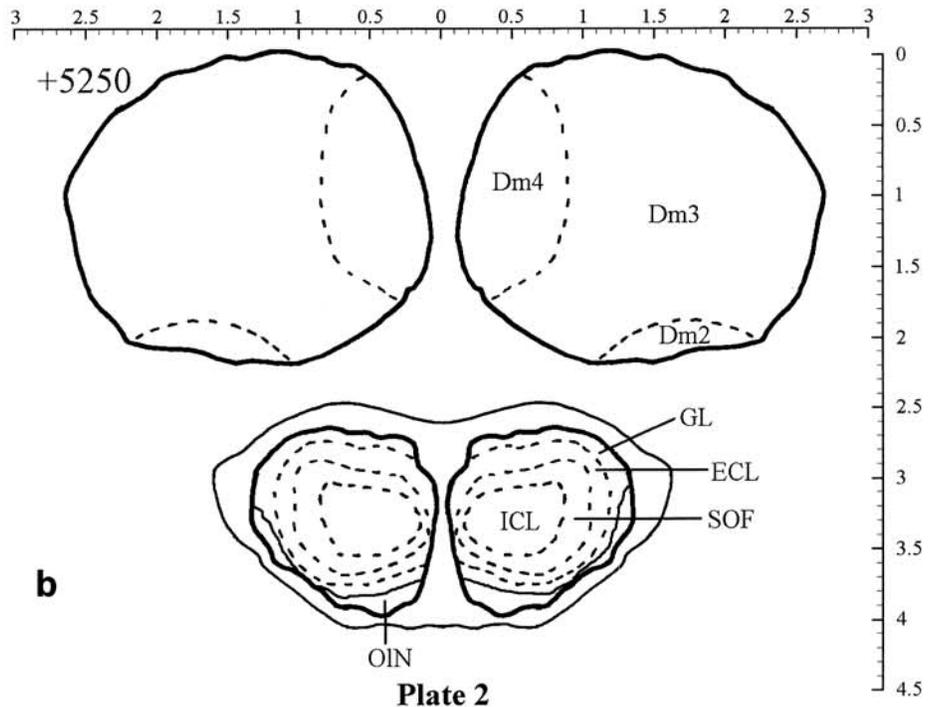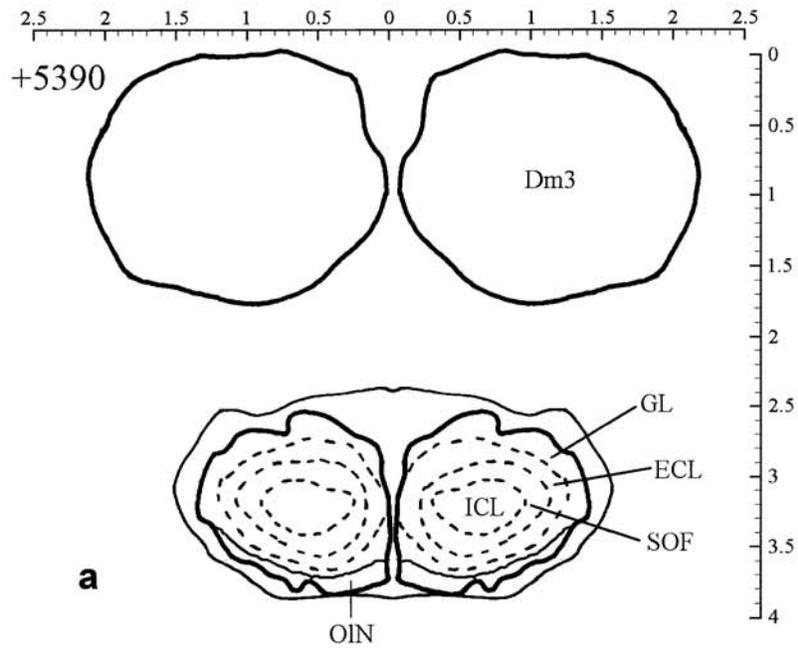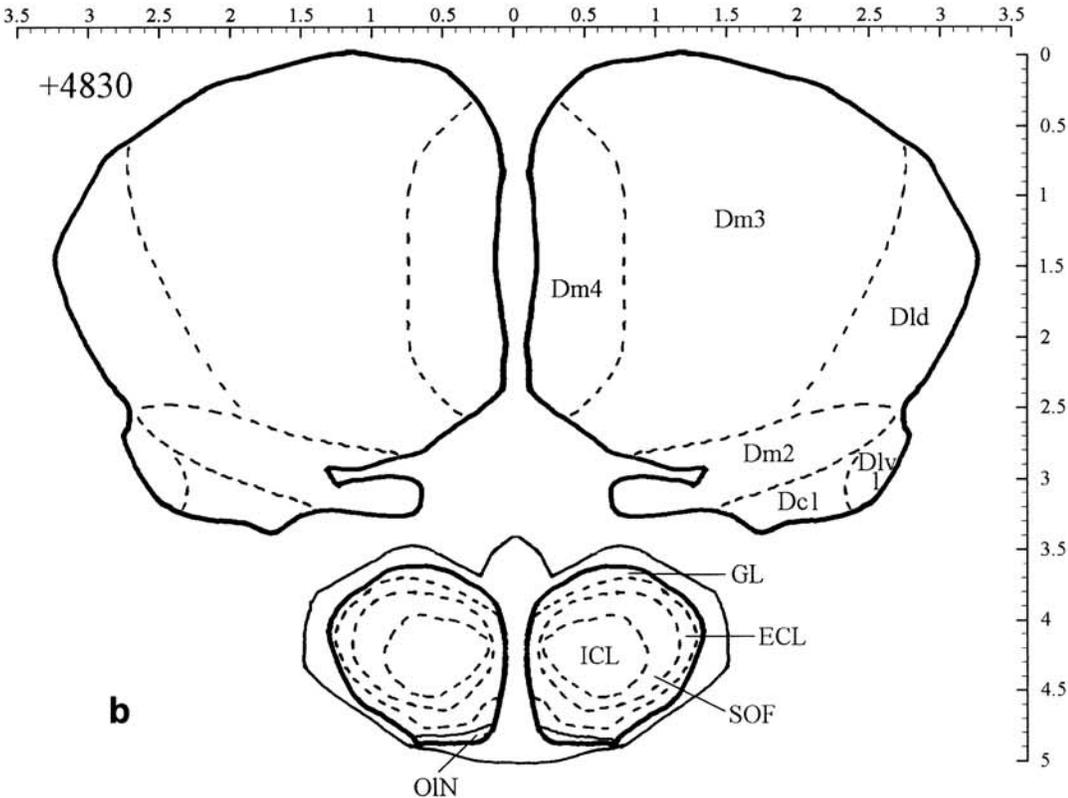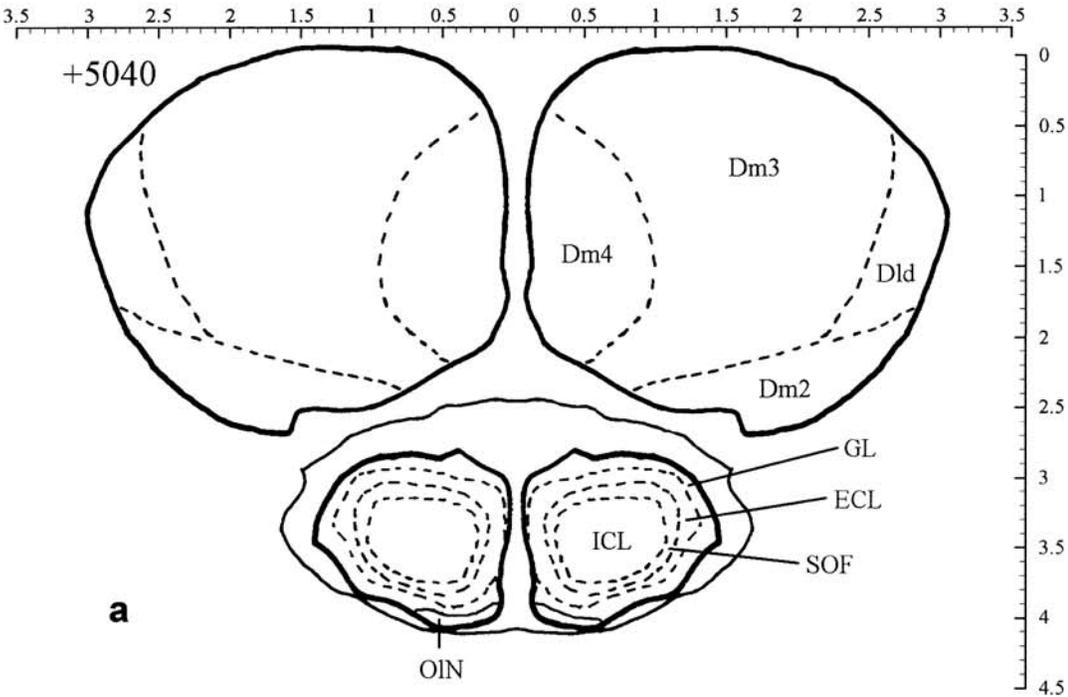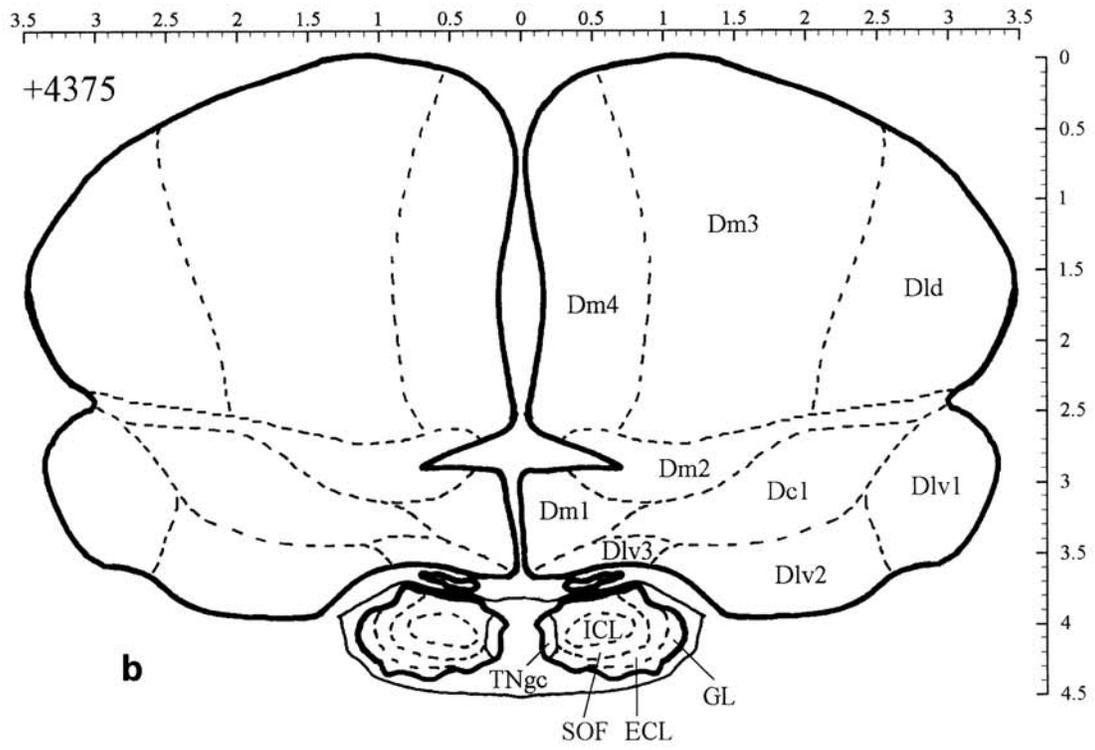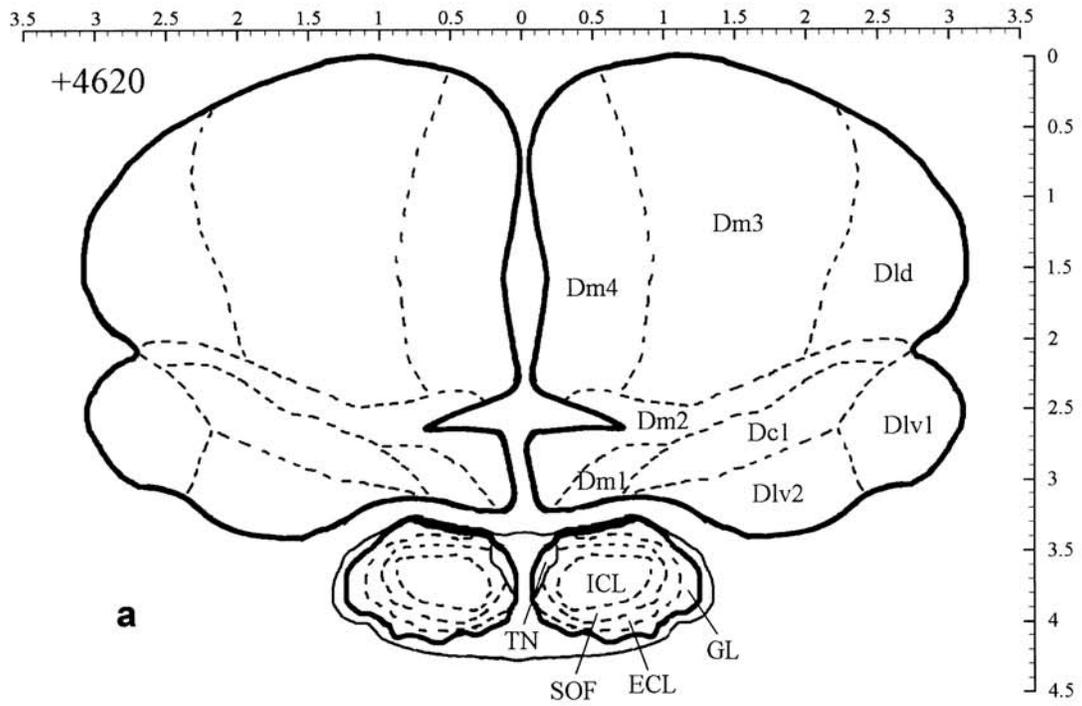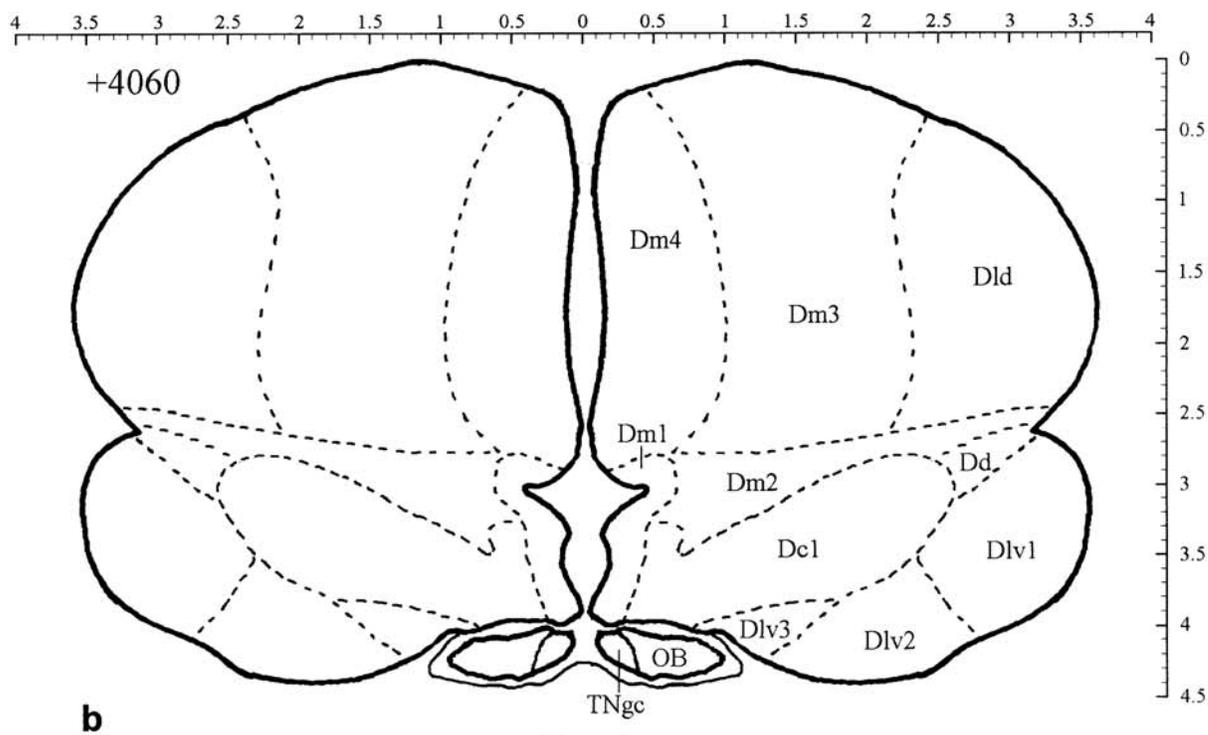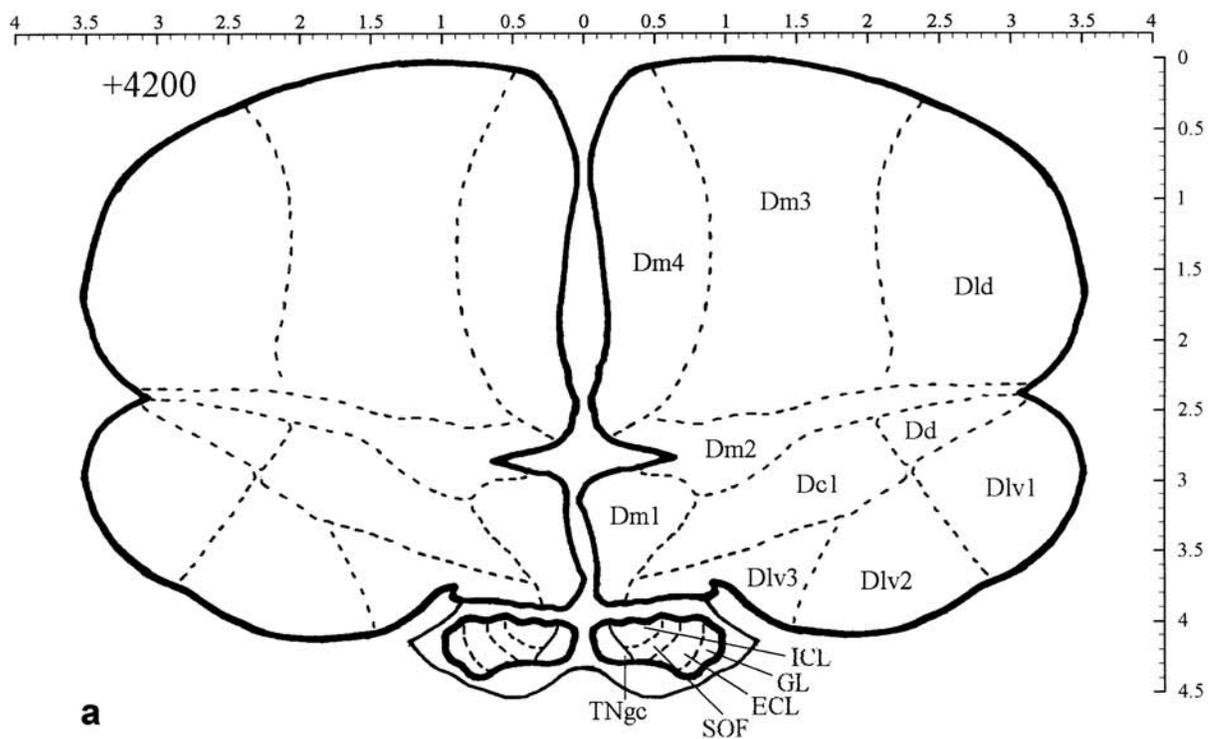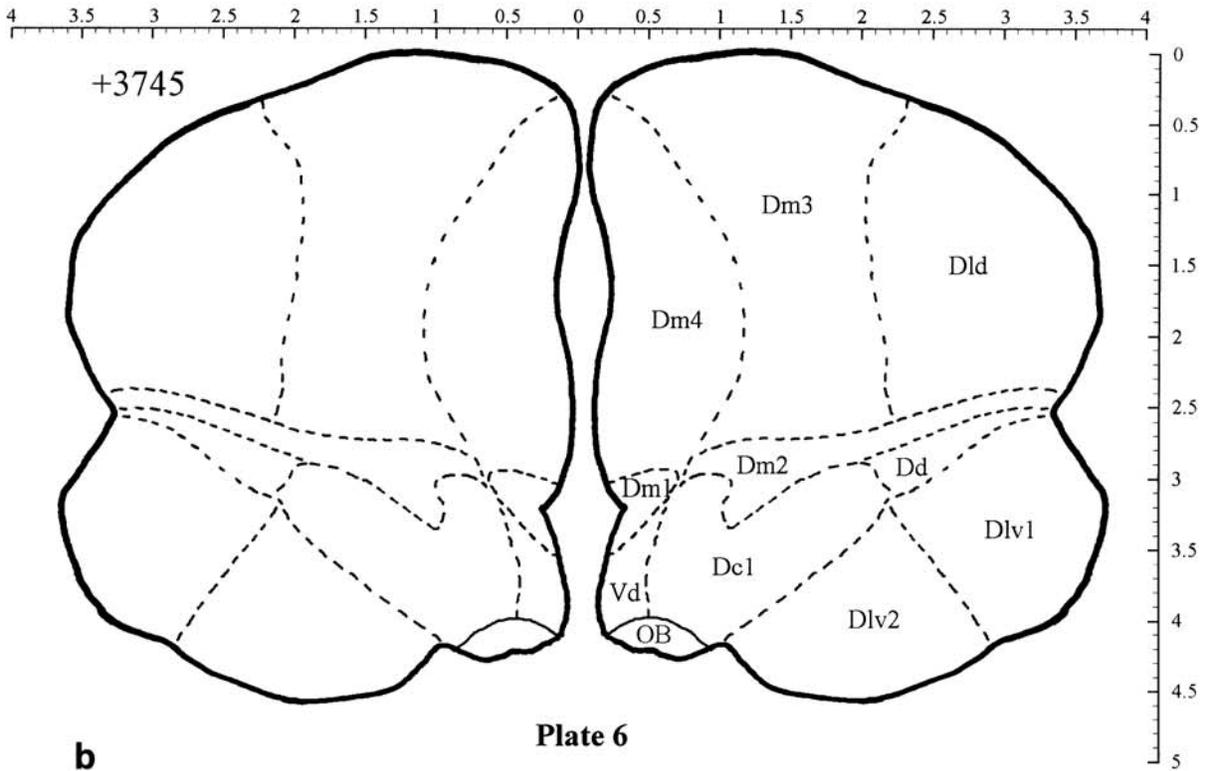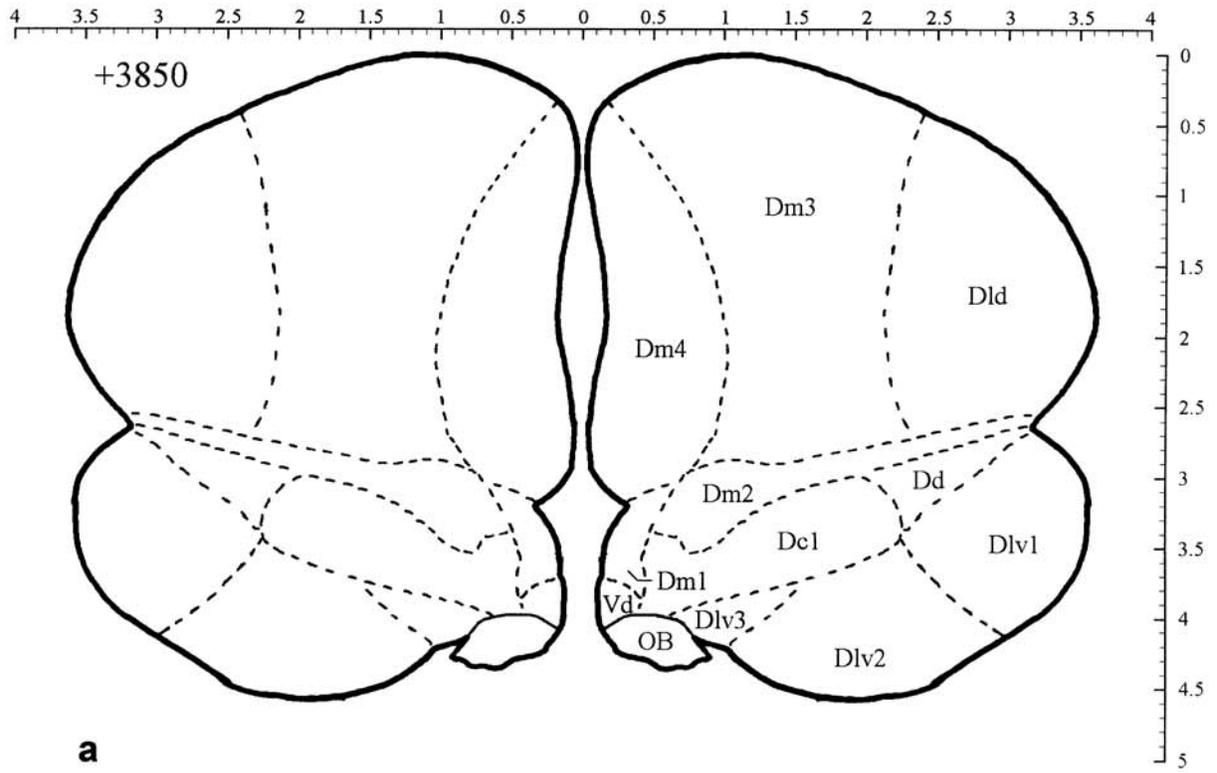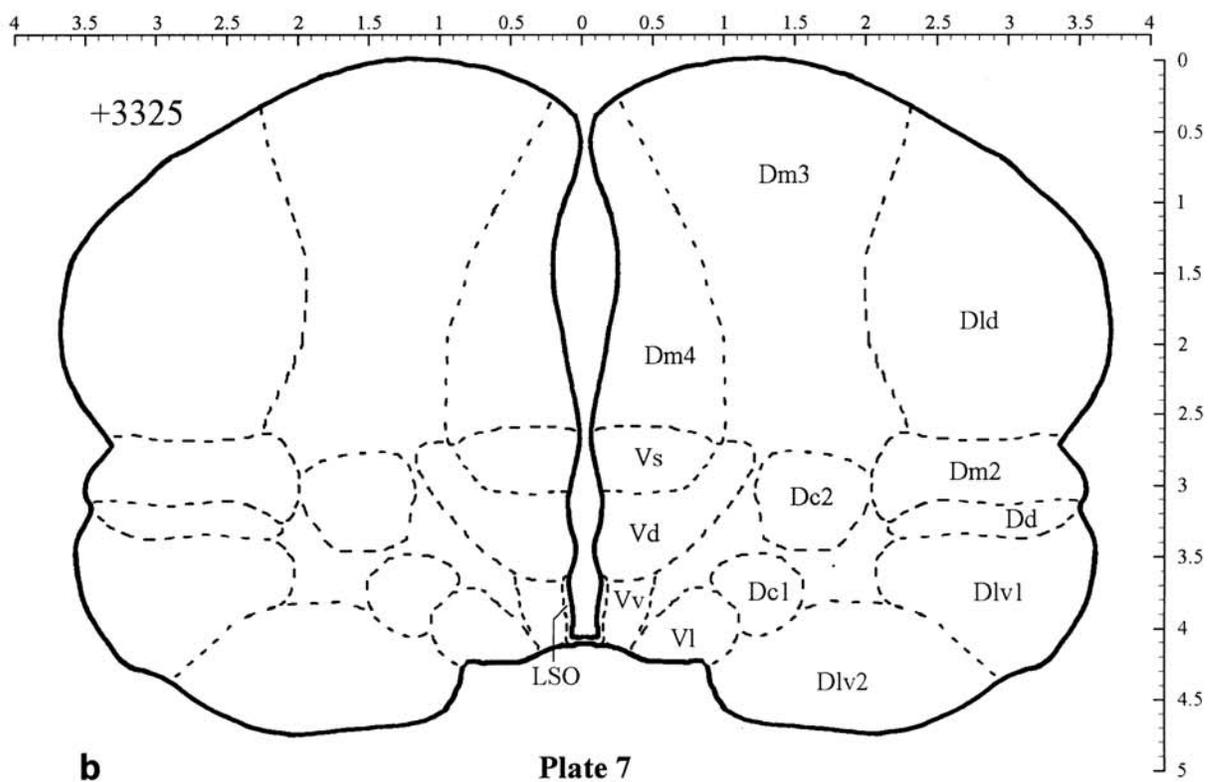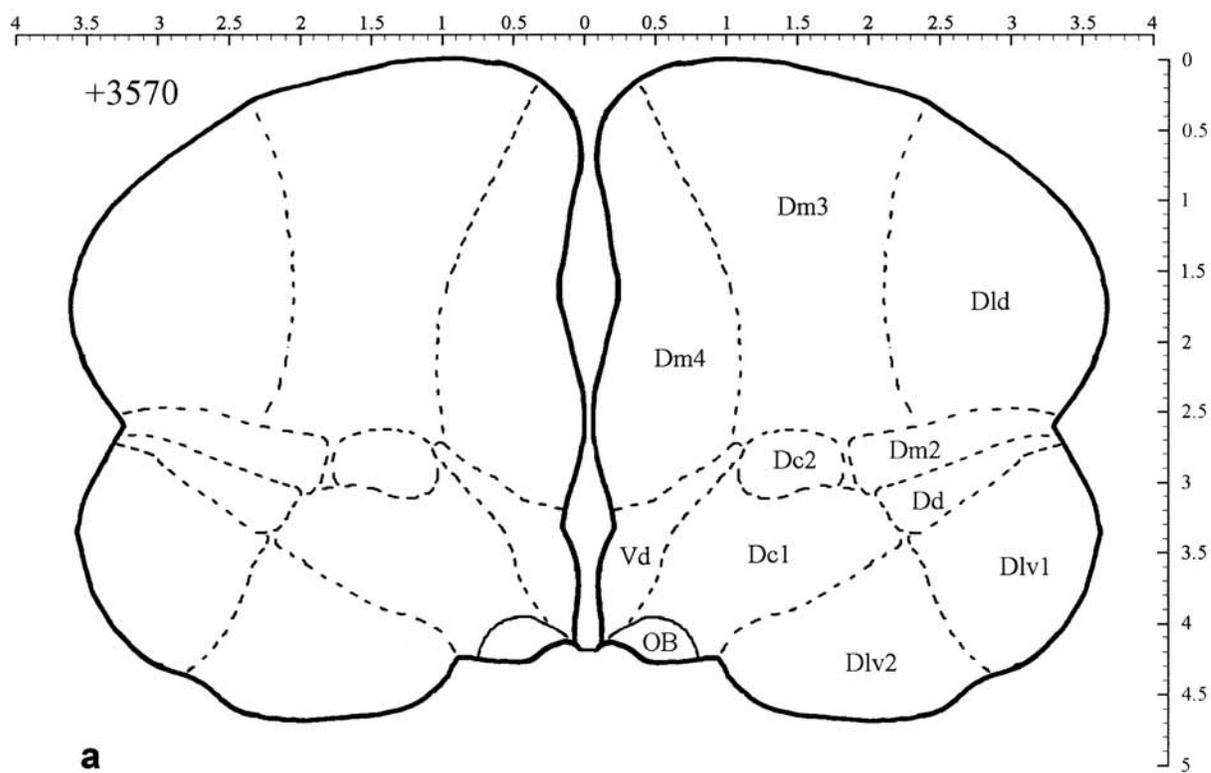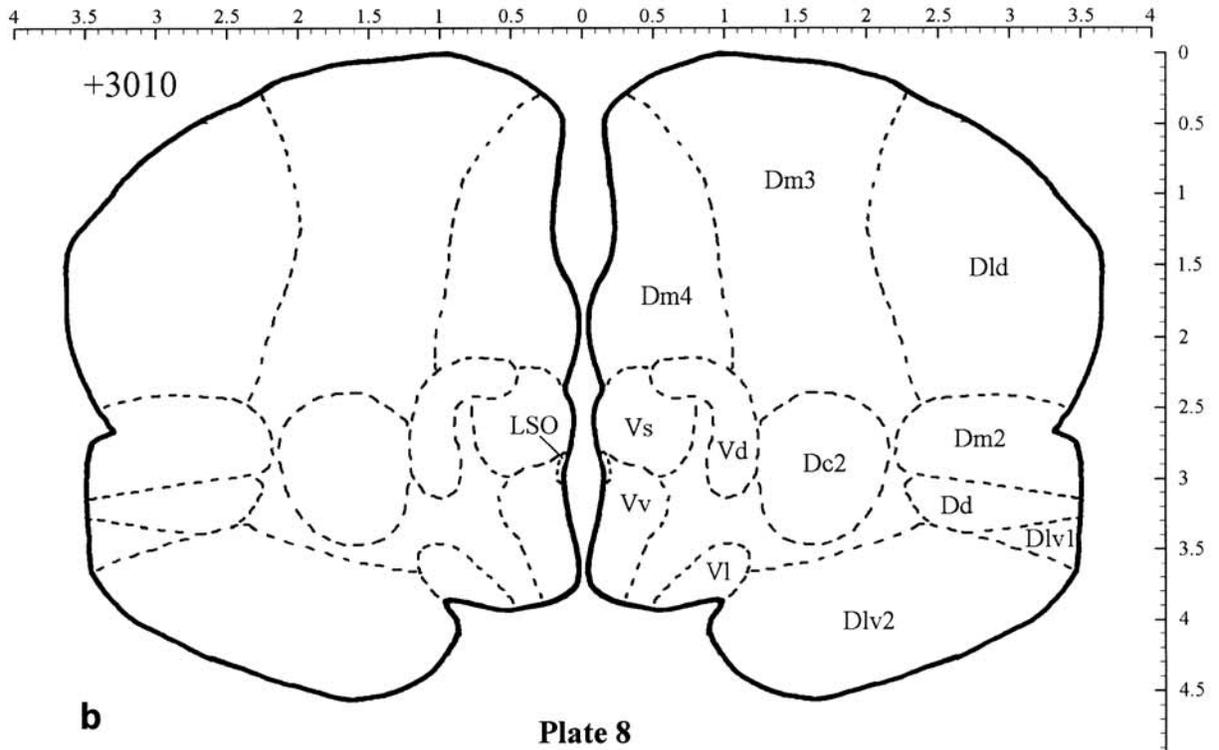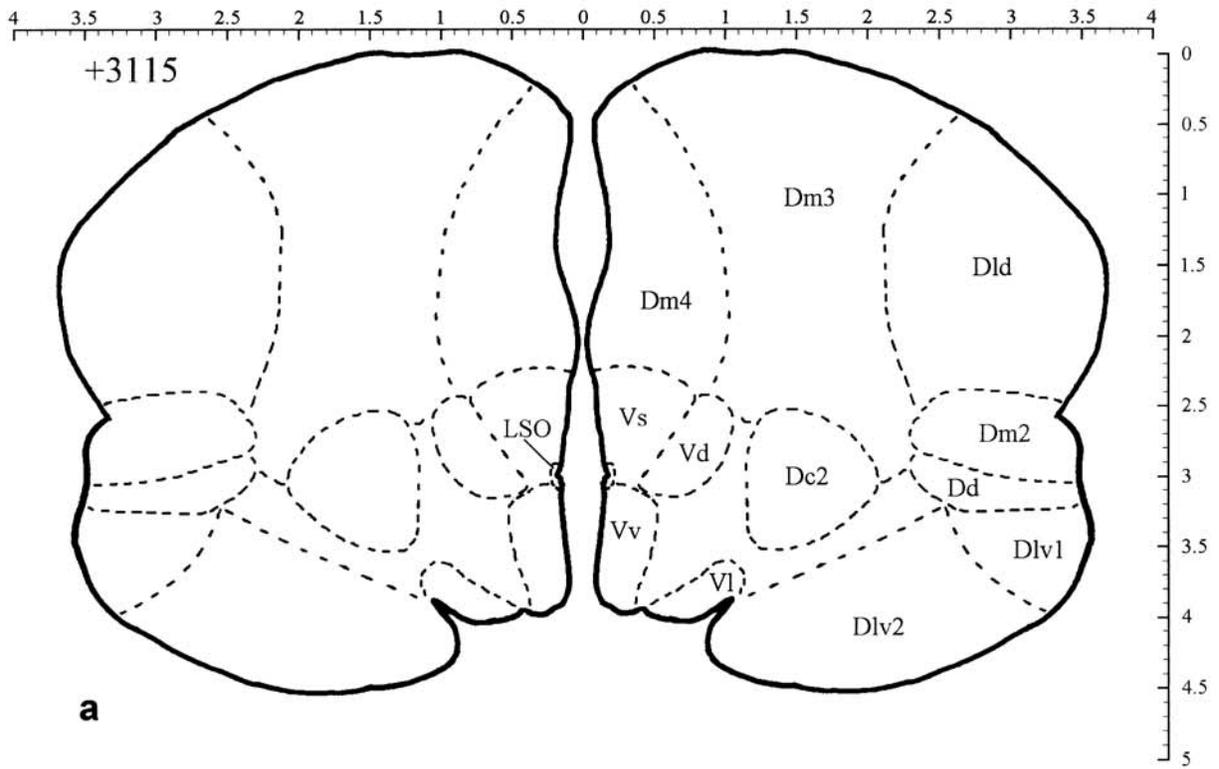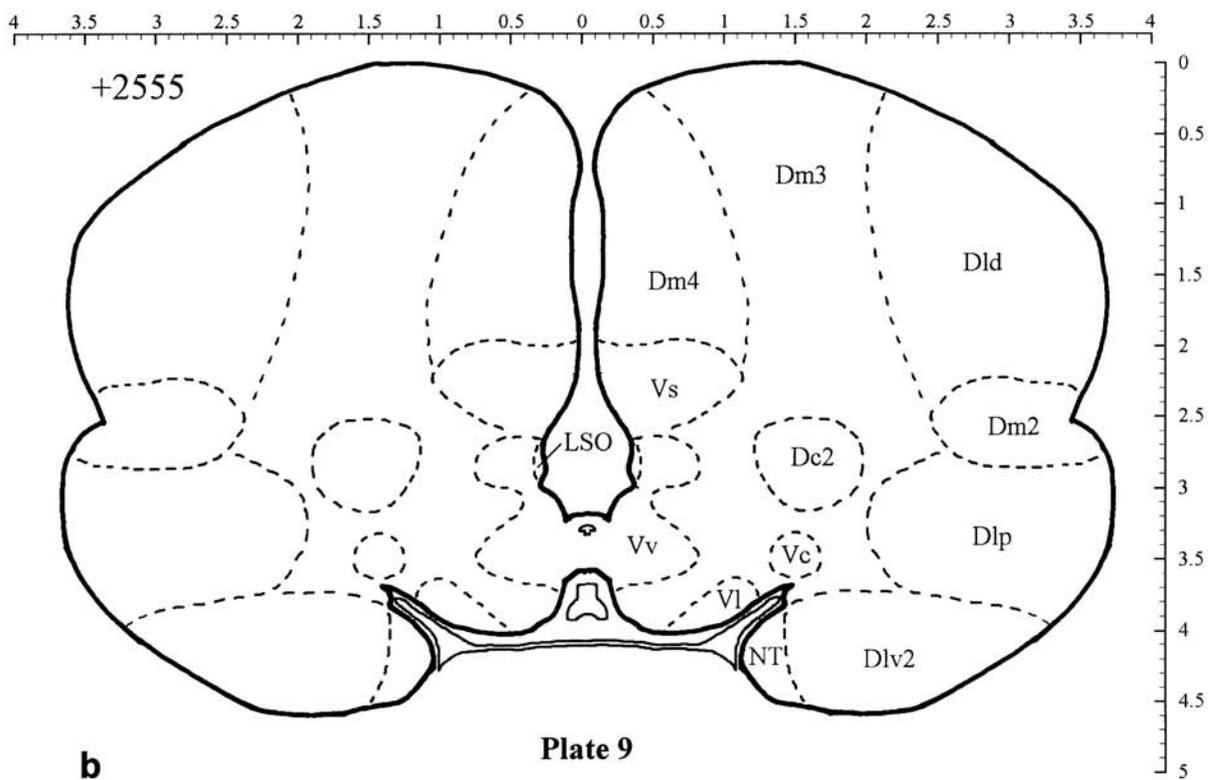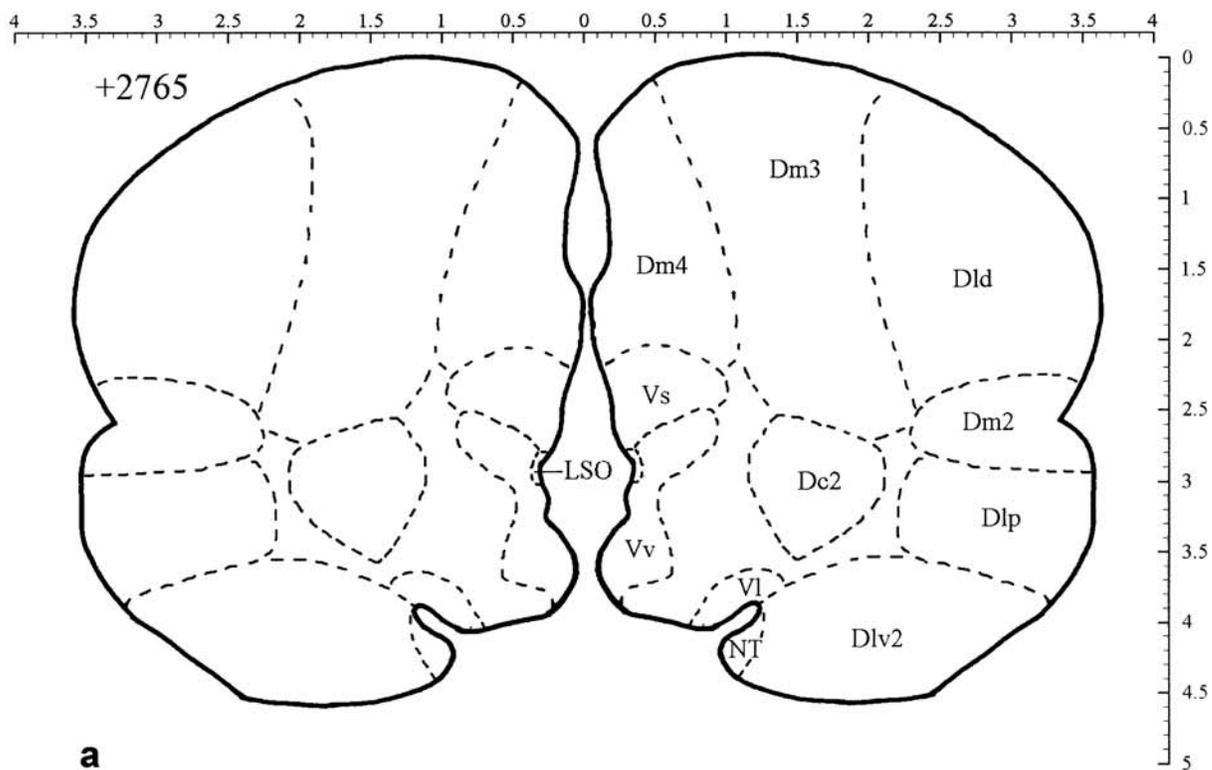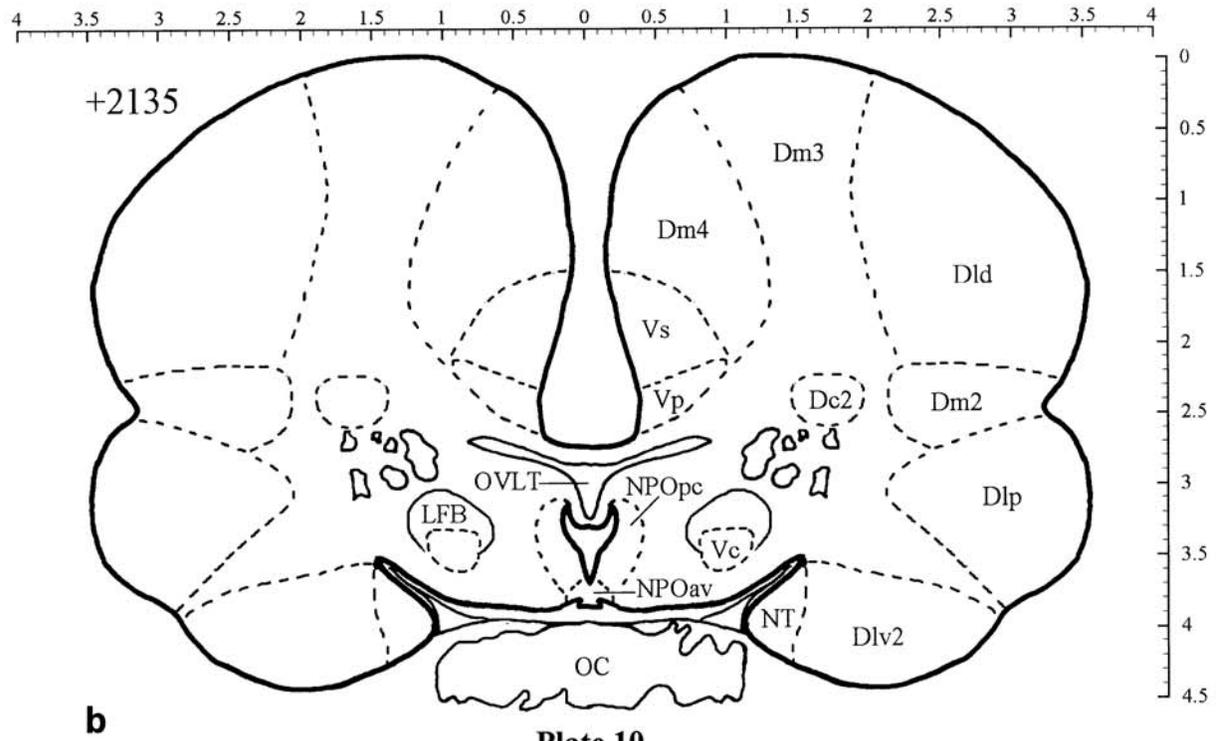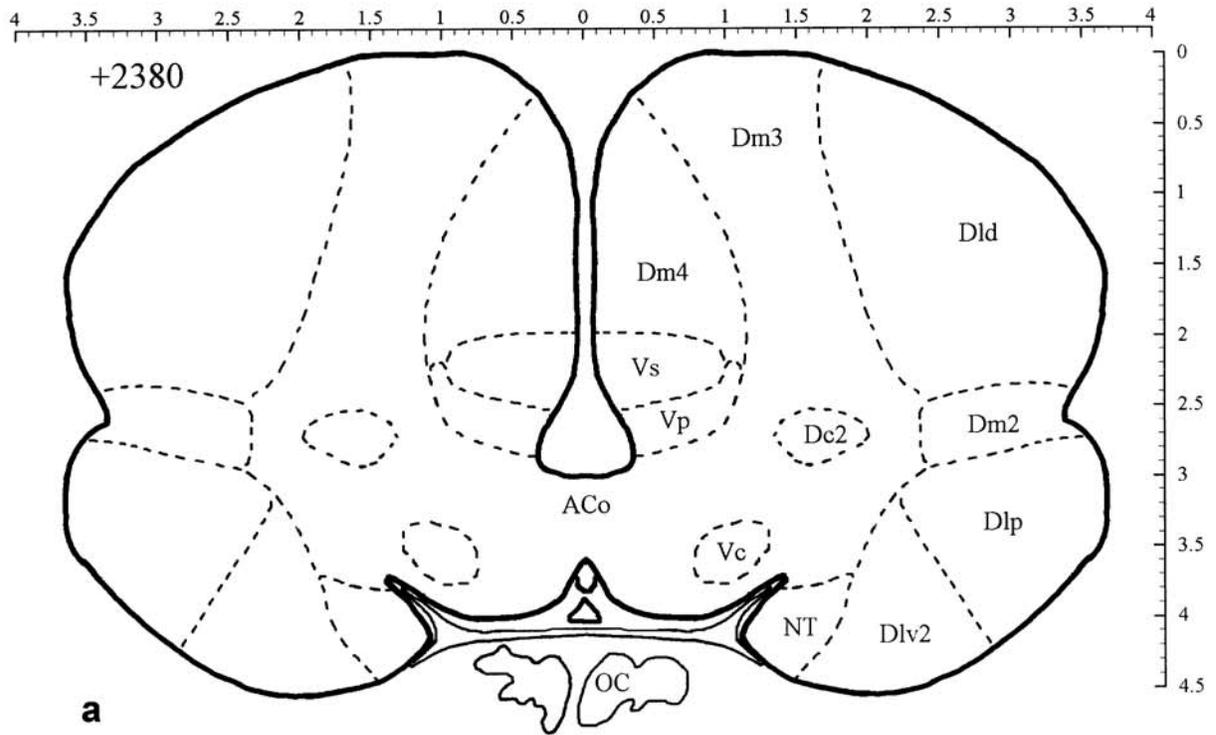
Plate 8

Plate 9

Plate 10

Plate 11

Plate 12

a +1085

b +875
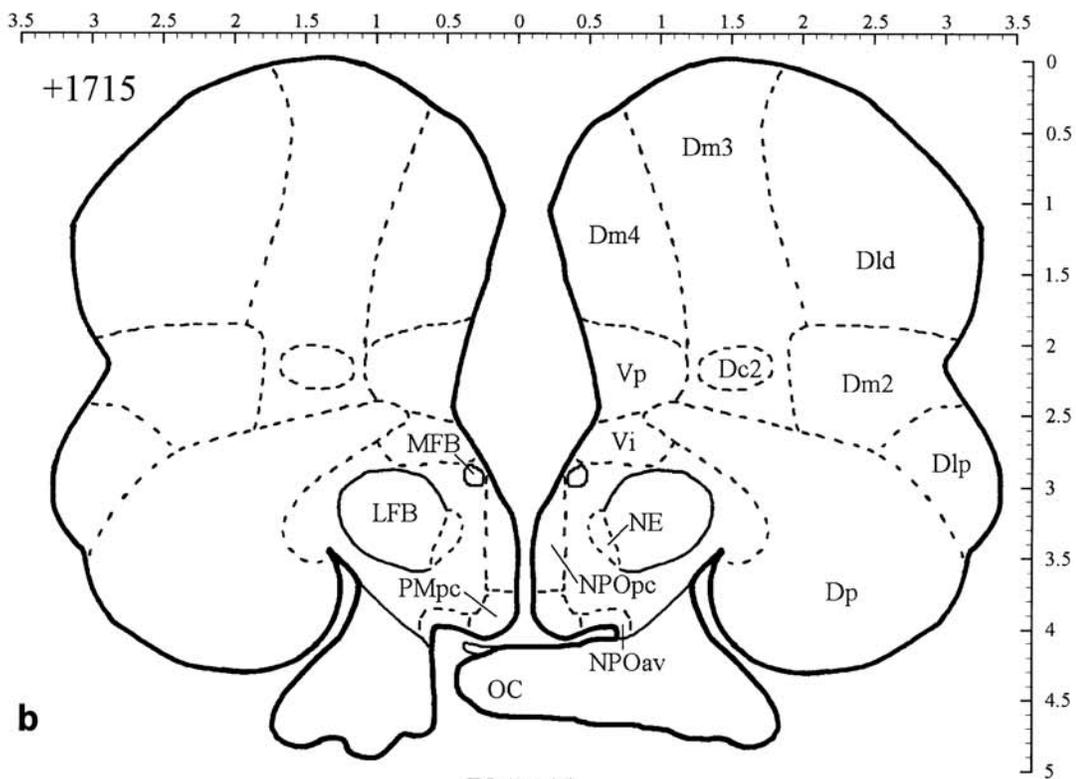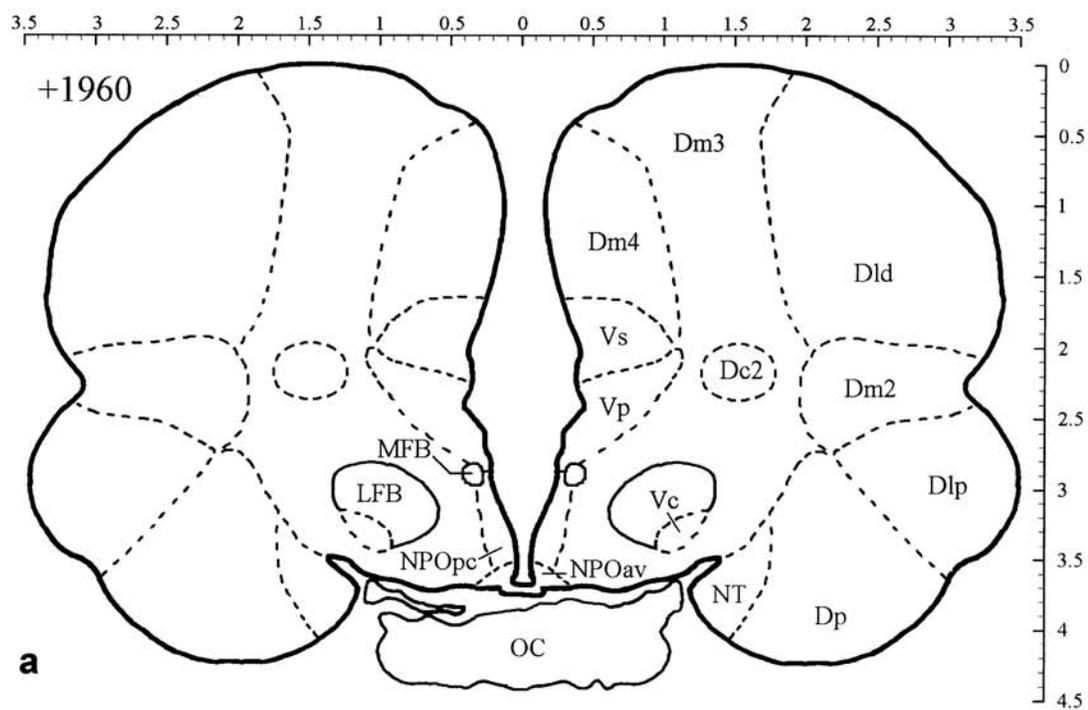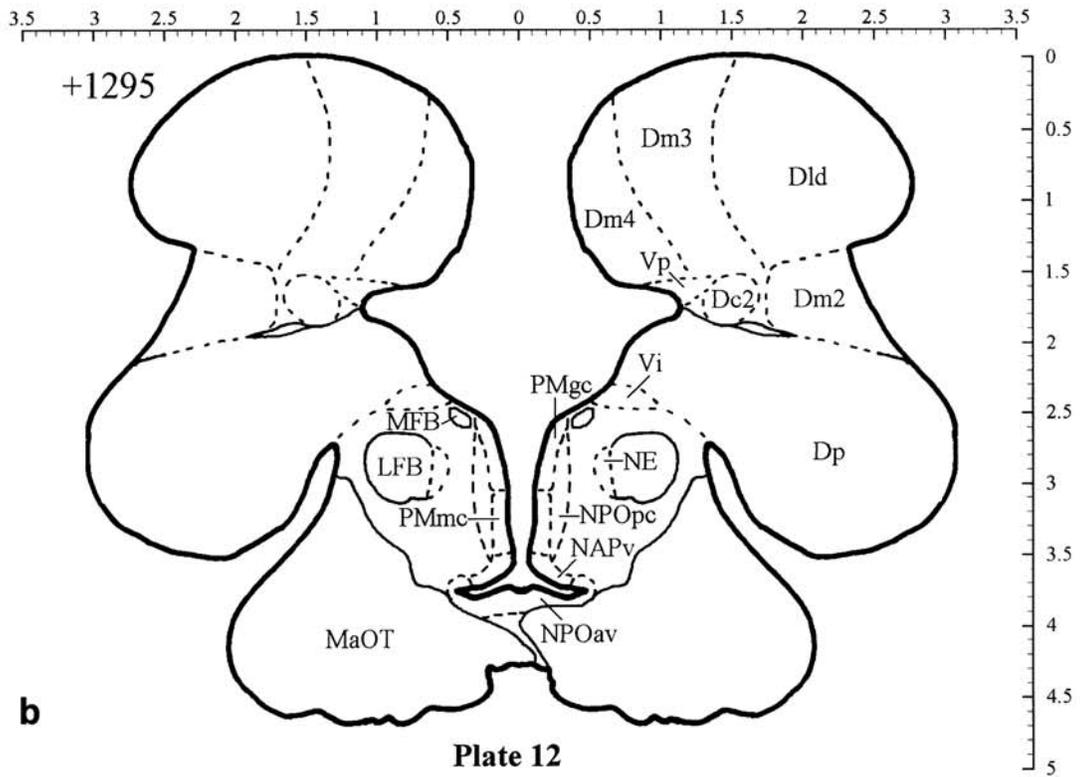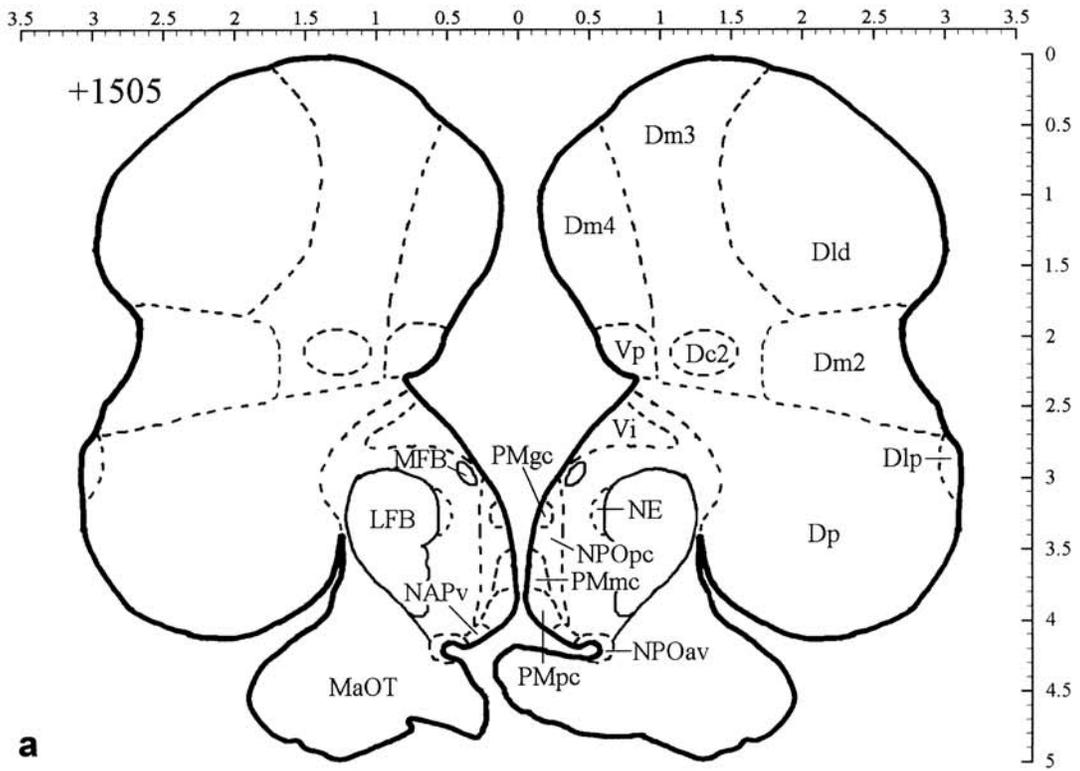
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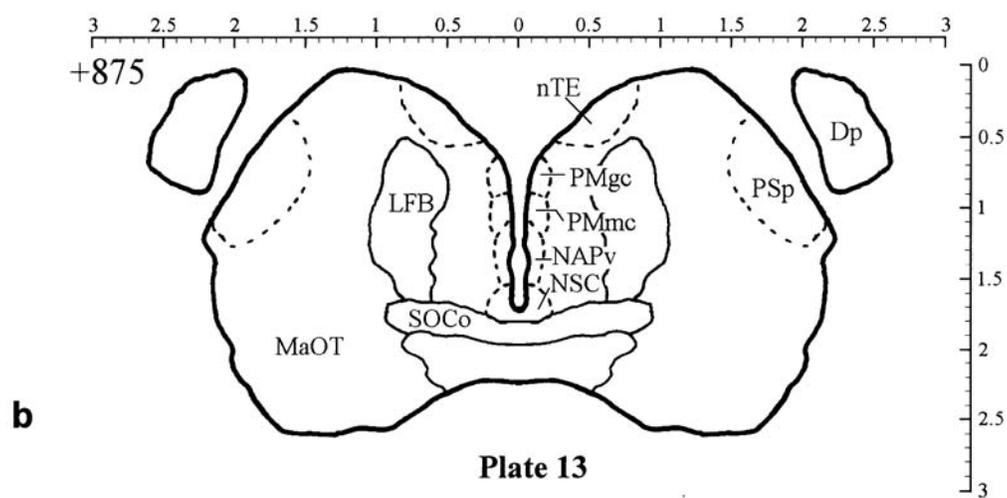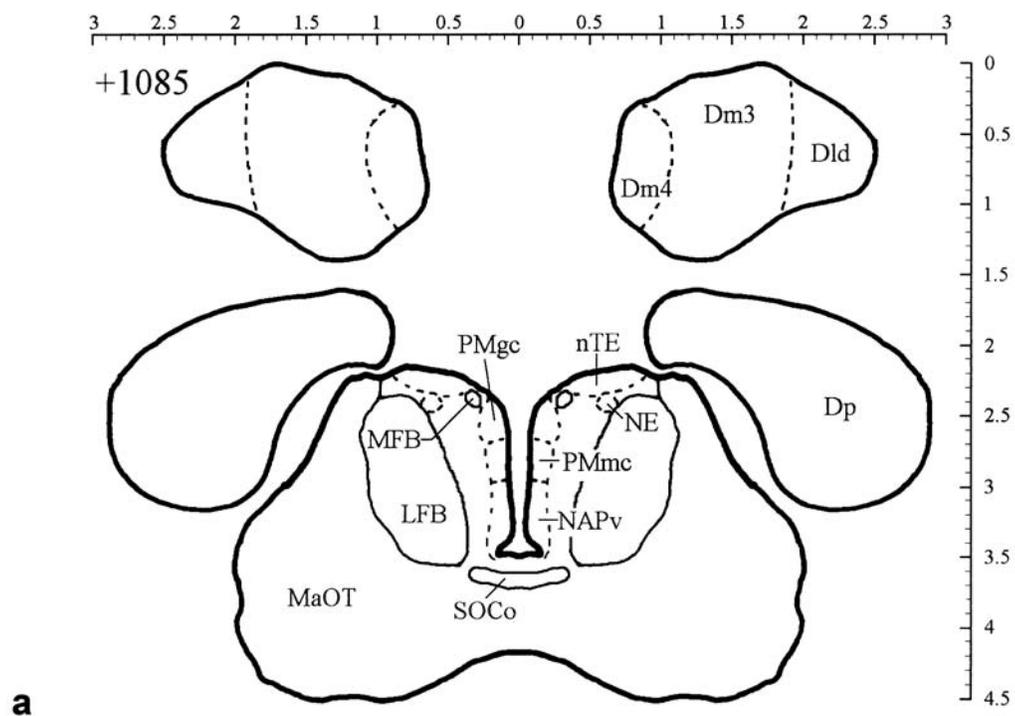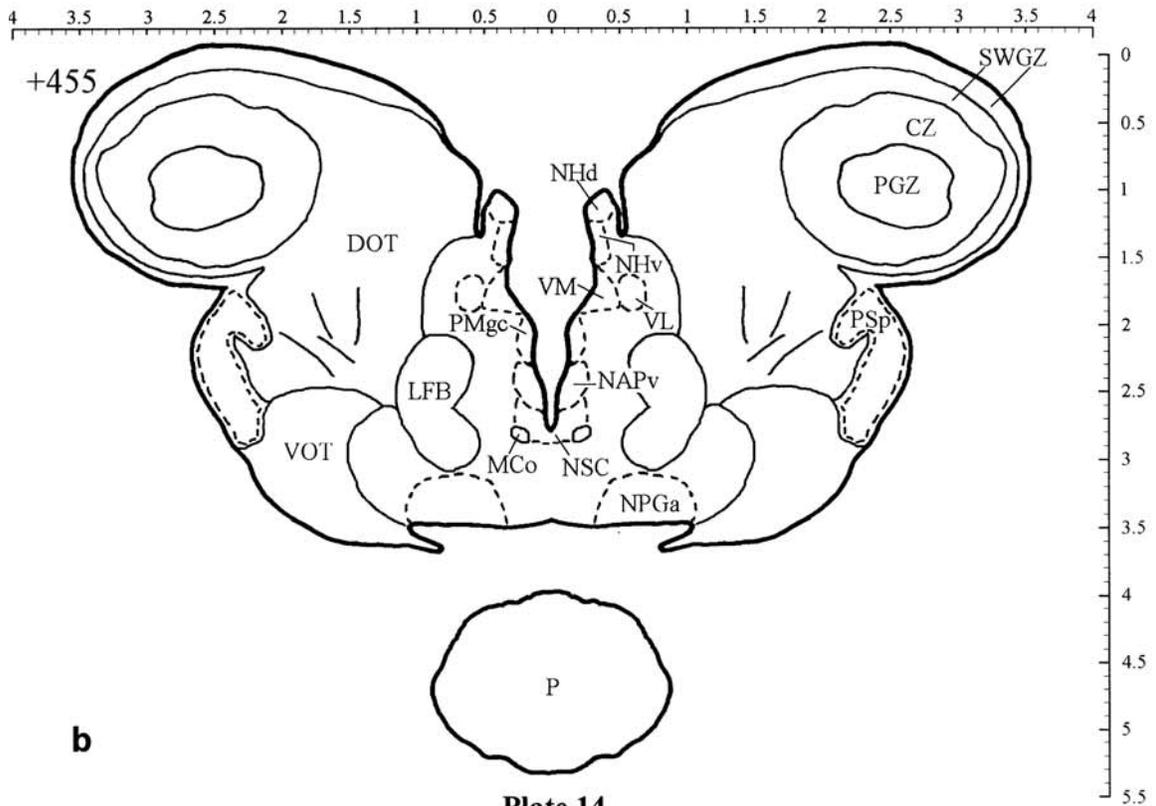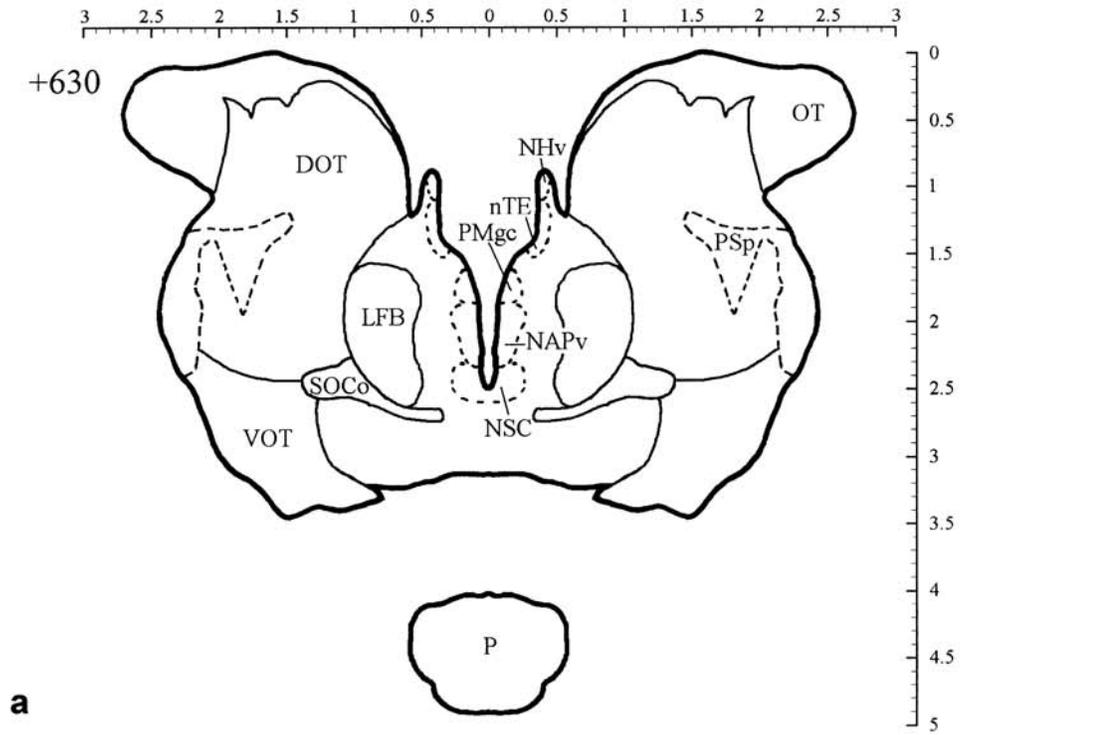
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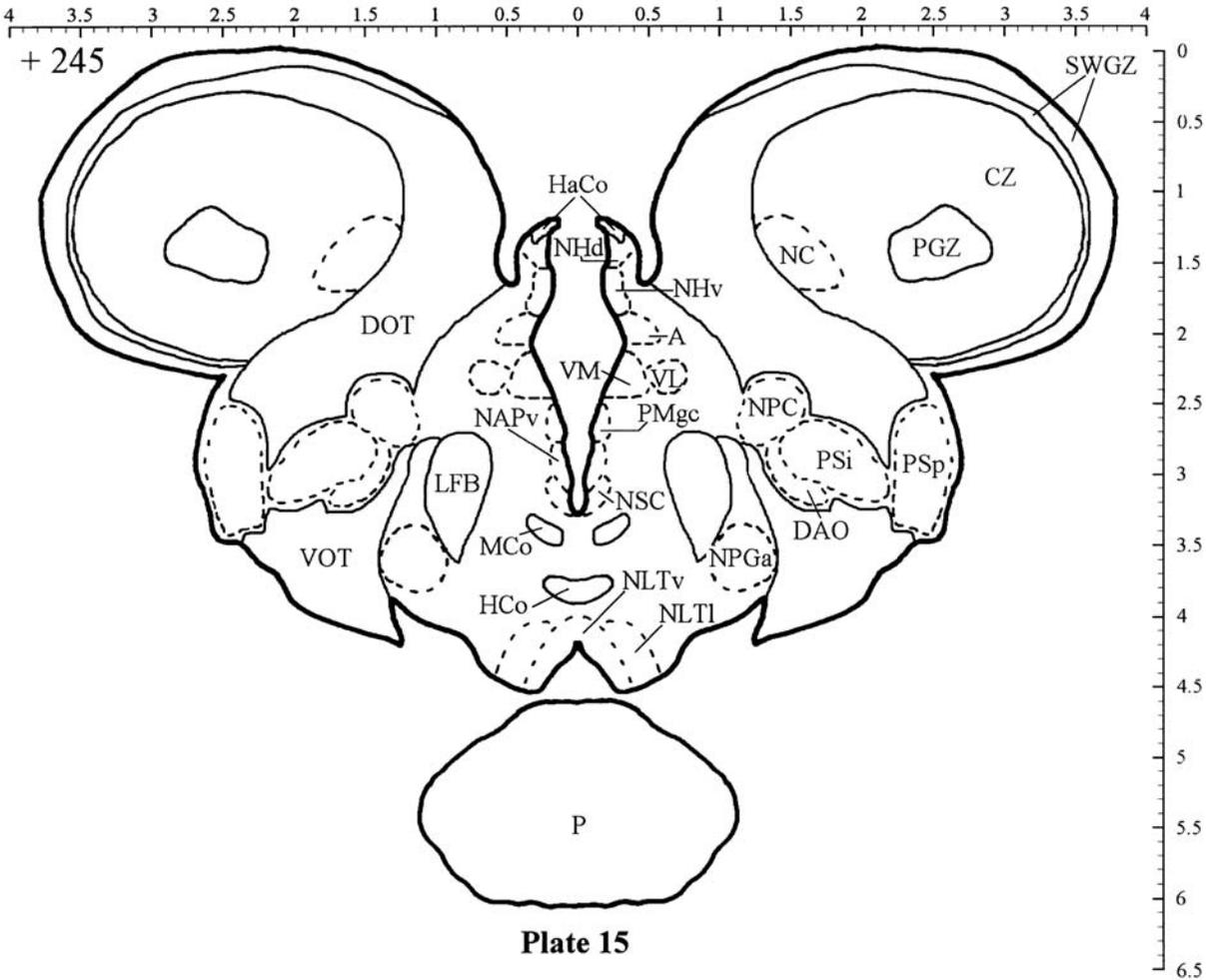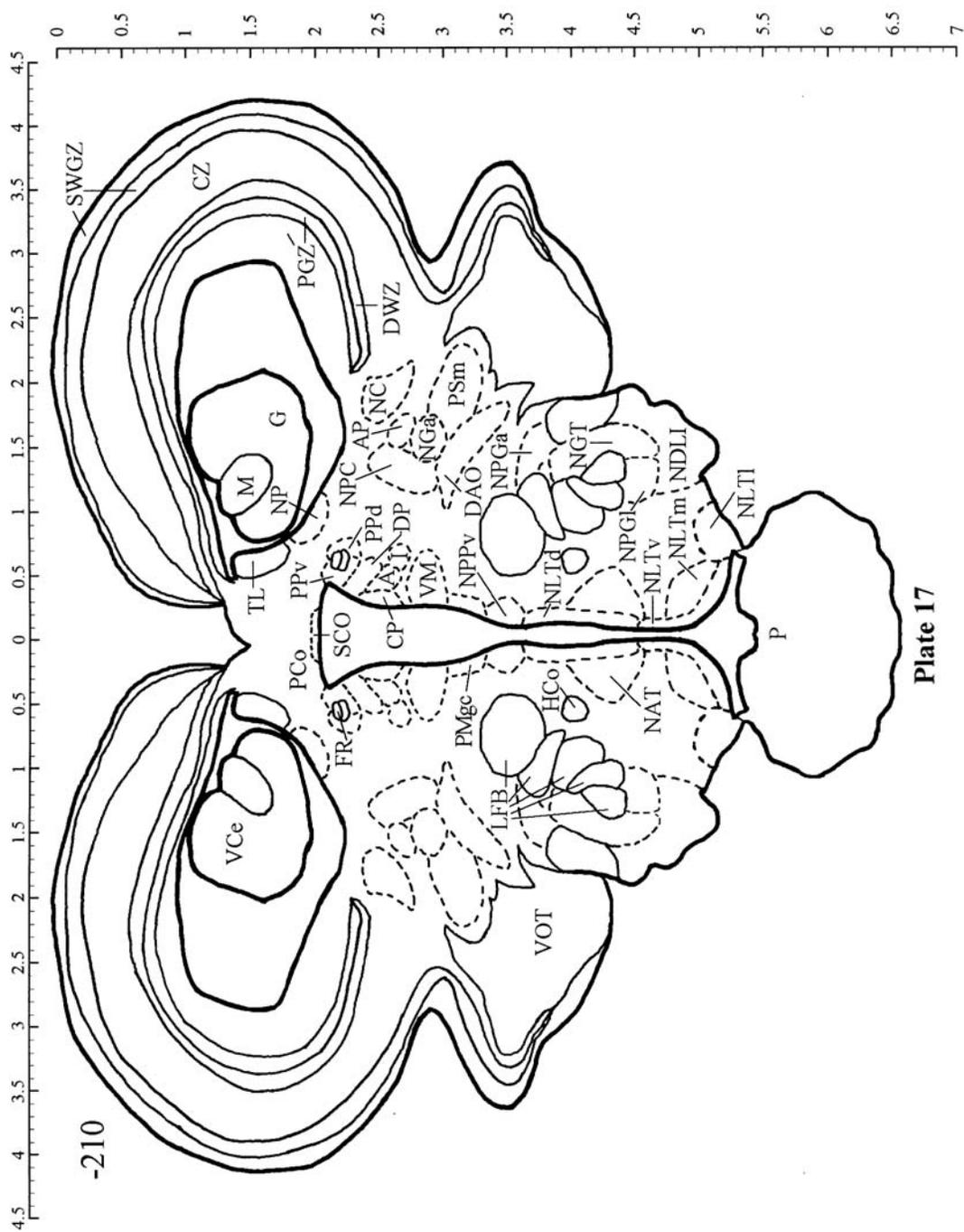
Plate 15

Plate 16

Plate 17

Plate 18

Plate 19
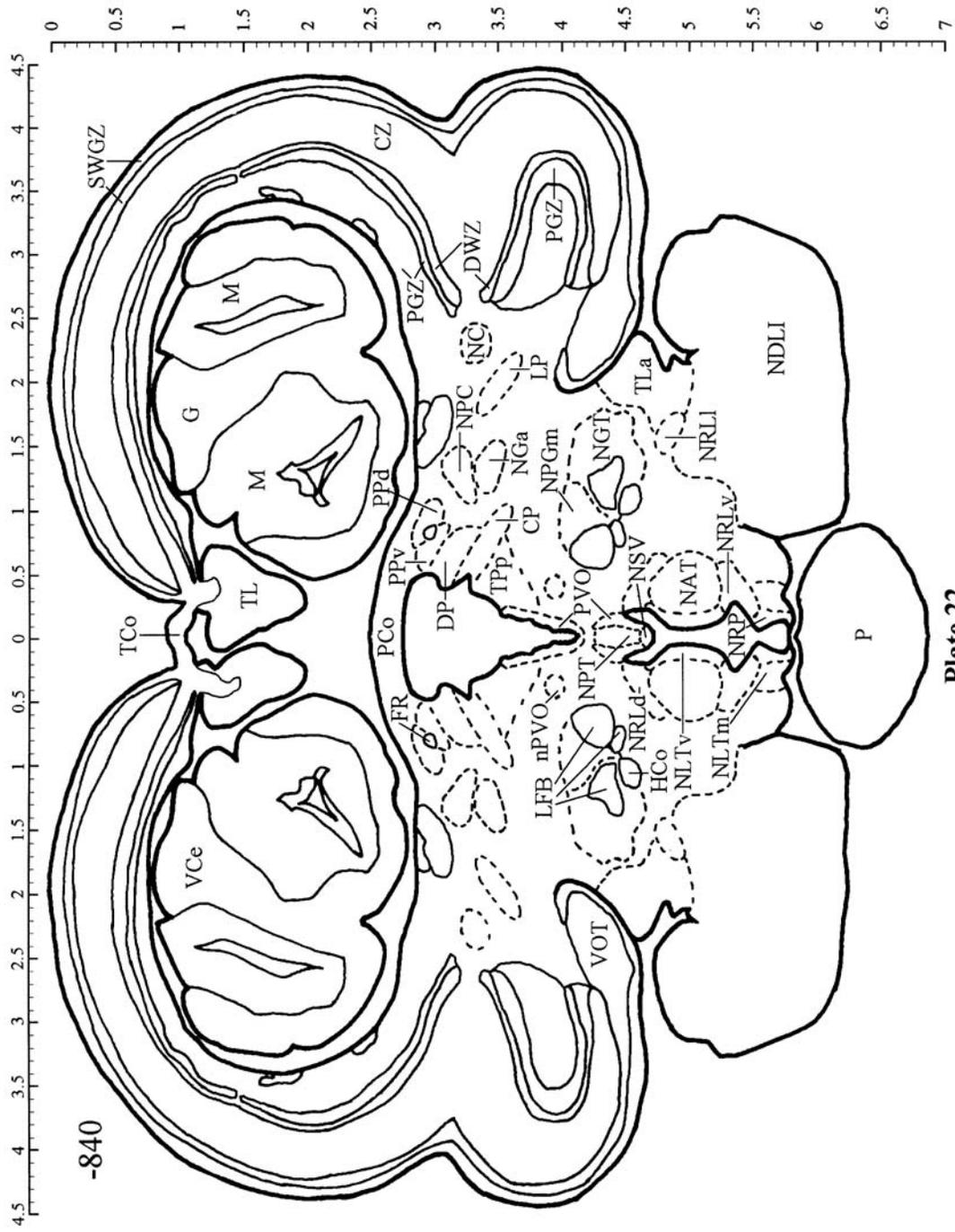
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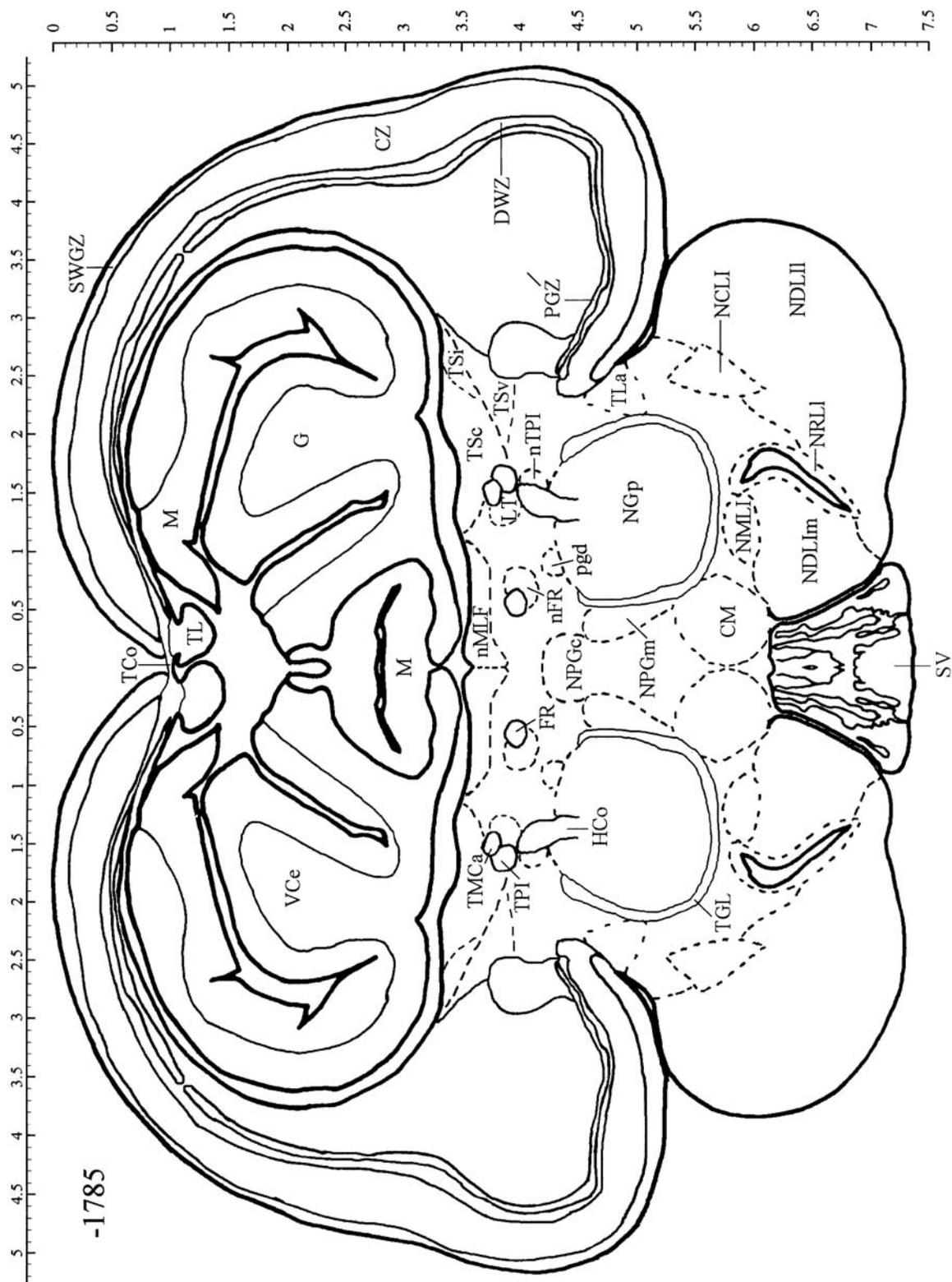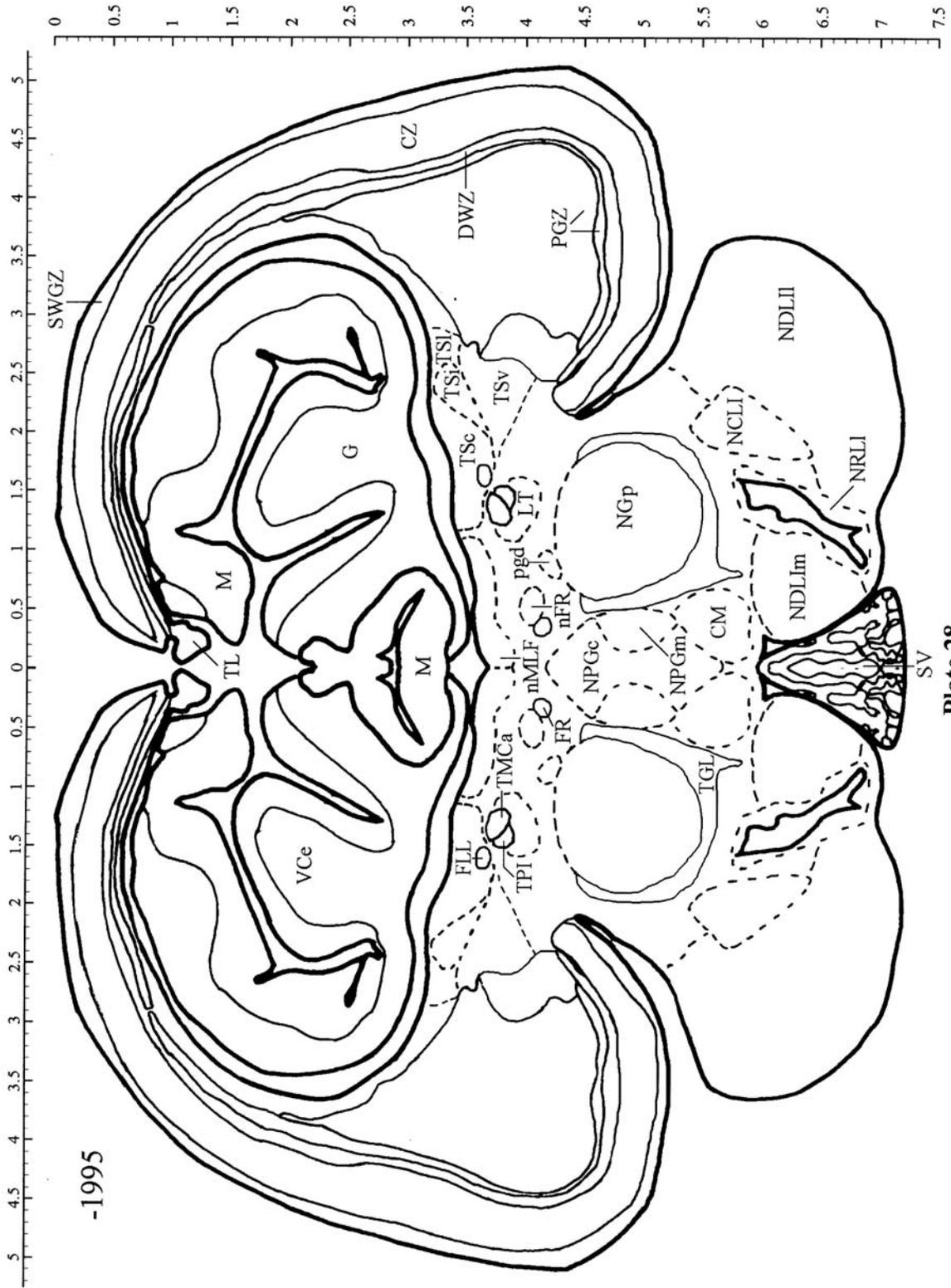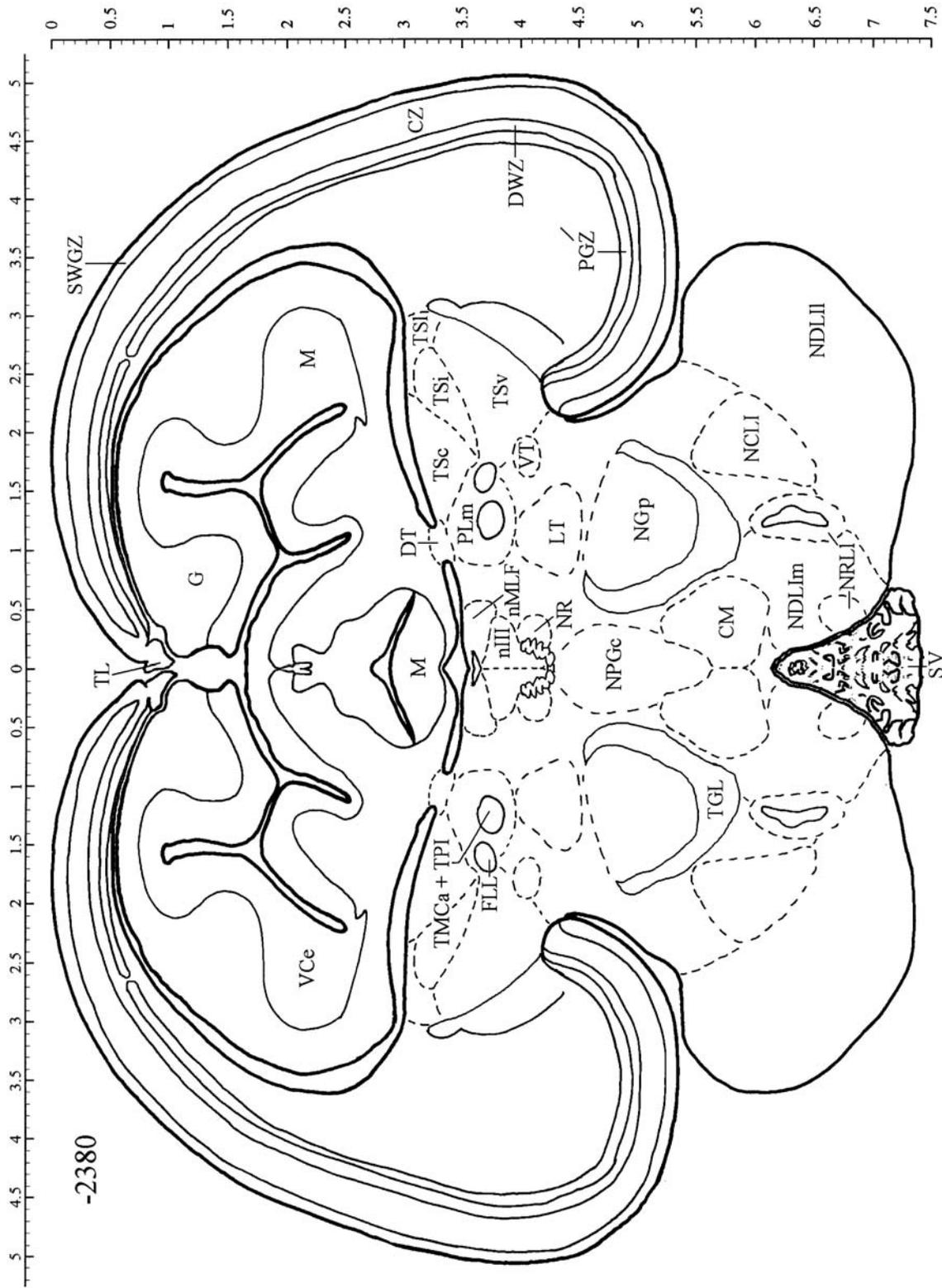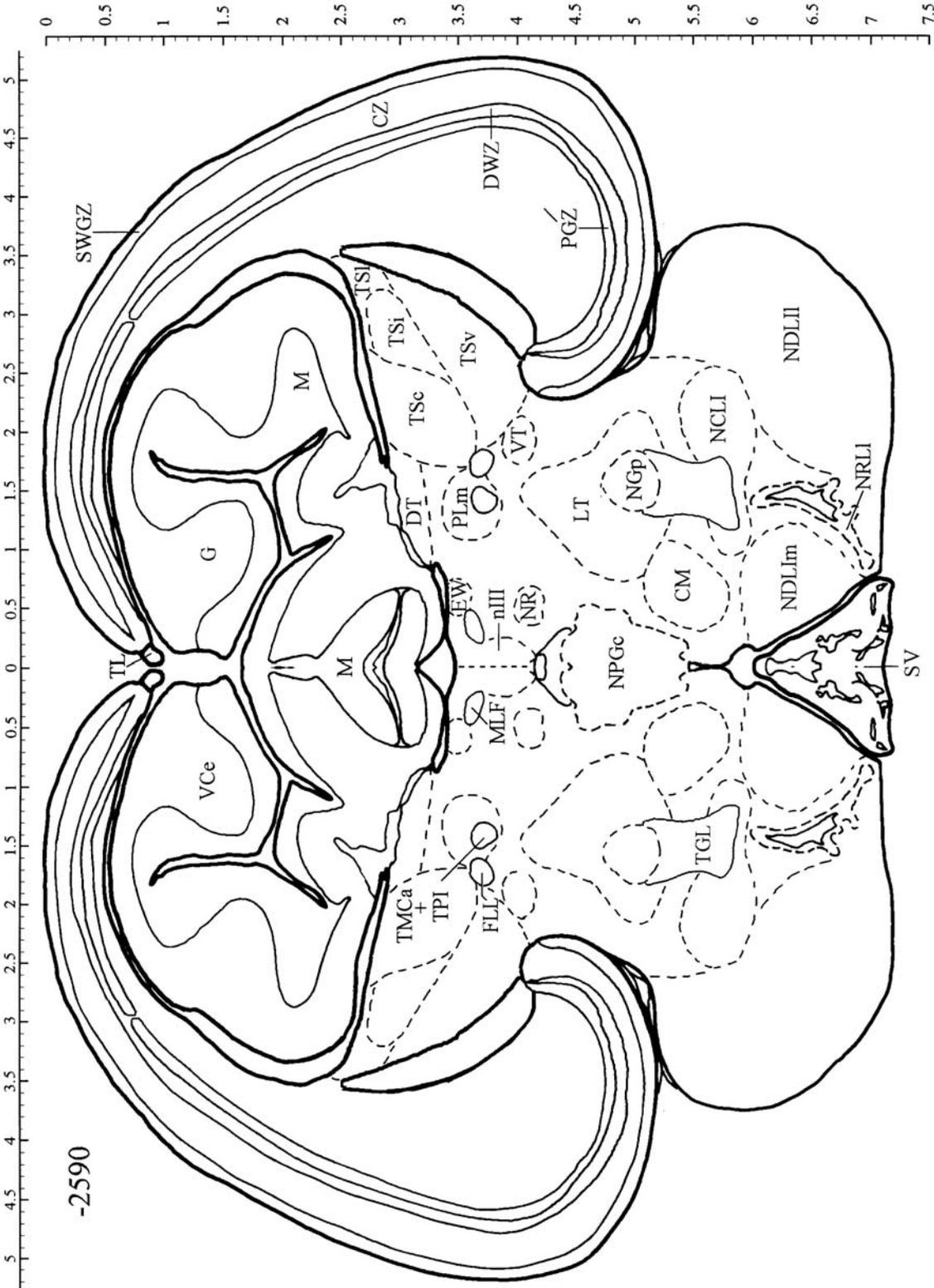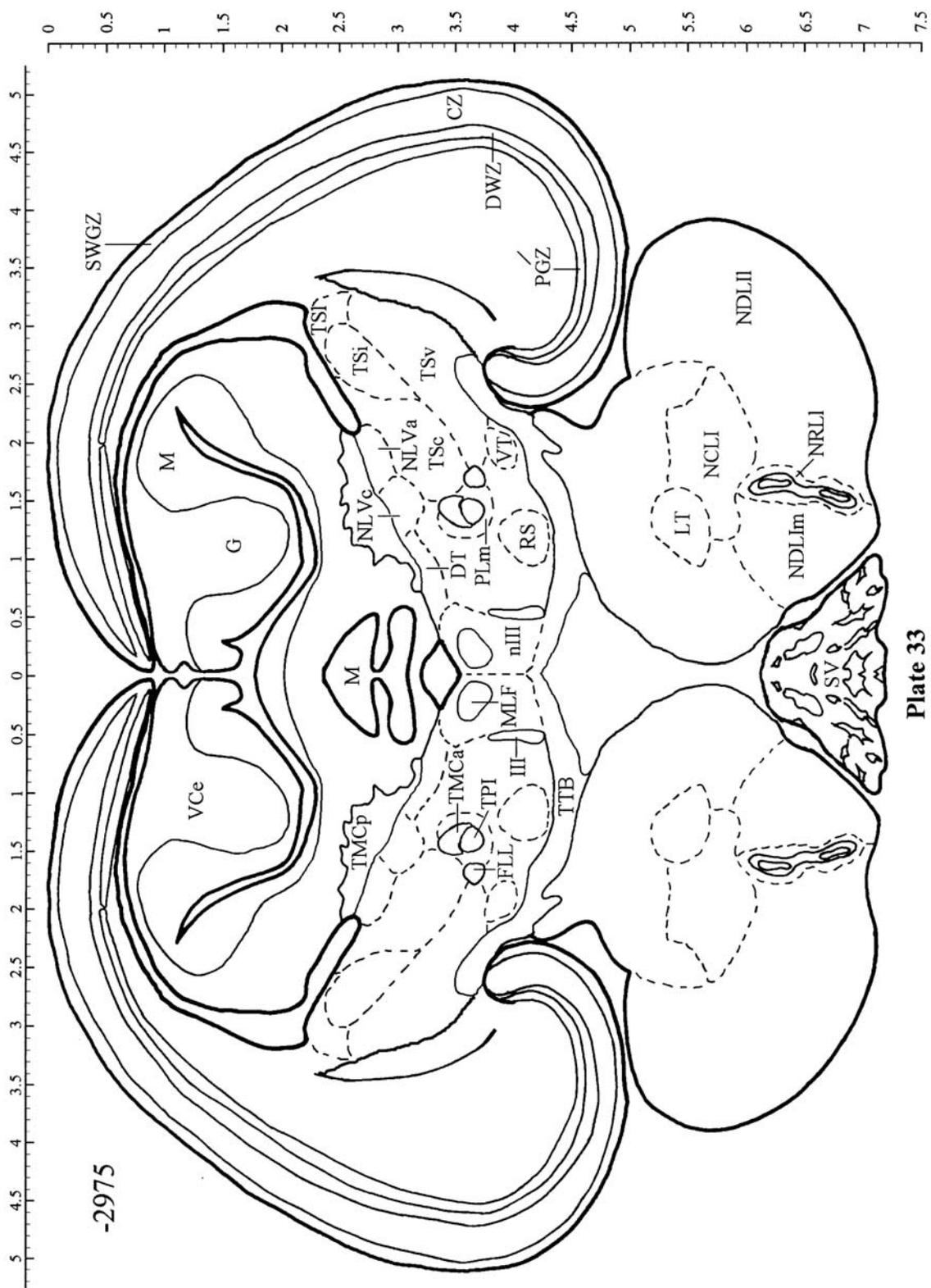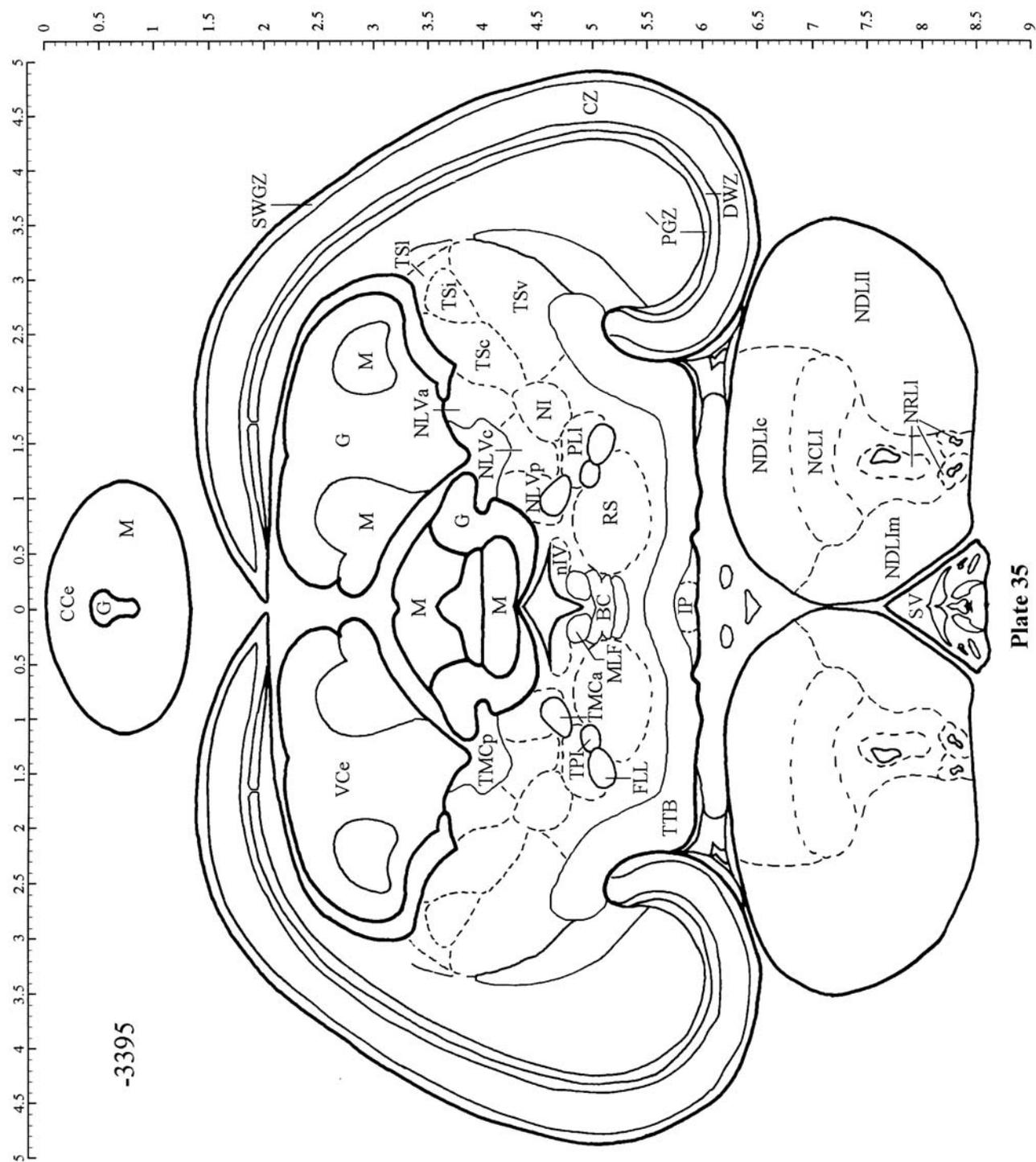
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Plate 21

Plate 22

Plate 23

-1050

Plate 24

-1295

Plate 25

-1505

-1715

Plate 26

Plate 27

-1785

Plate 28

-1995

-2170

Plate 29

Plate 30

-2380

Plate 31

-2590

Plate 32

-2800

Plate 33

-3185

Plate 34

Plate 35

-3395

Plate 36

-3570

Plate 37

-3745

Plate 38

-3955

-4165

Plate 39

-4340

Plate 40

-4620

Plate 41

-4830

Plate 42

Plate 43

-5250

M

CCe

G

AC

G

M

EG

PG

AON

Vm

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MLF

RS

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NDLIc

SV

Plate 44

Plate 45

Plate 46

Plate 47

-6195

CCe

G

M

G

PG

EG

MON

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MAG

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SR

nVIr

Plate 48

Plate 49

Plate 50

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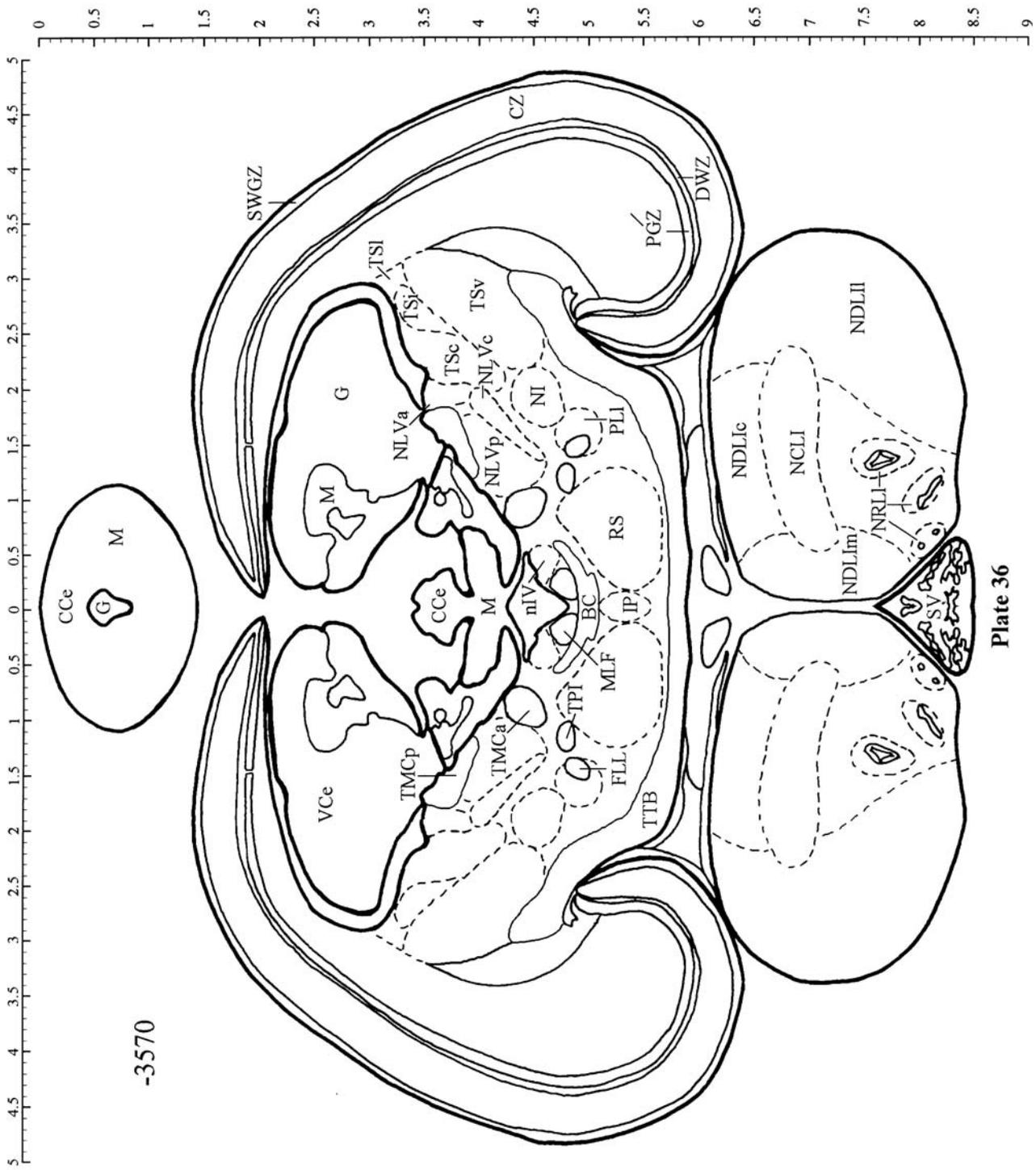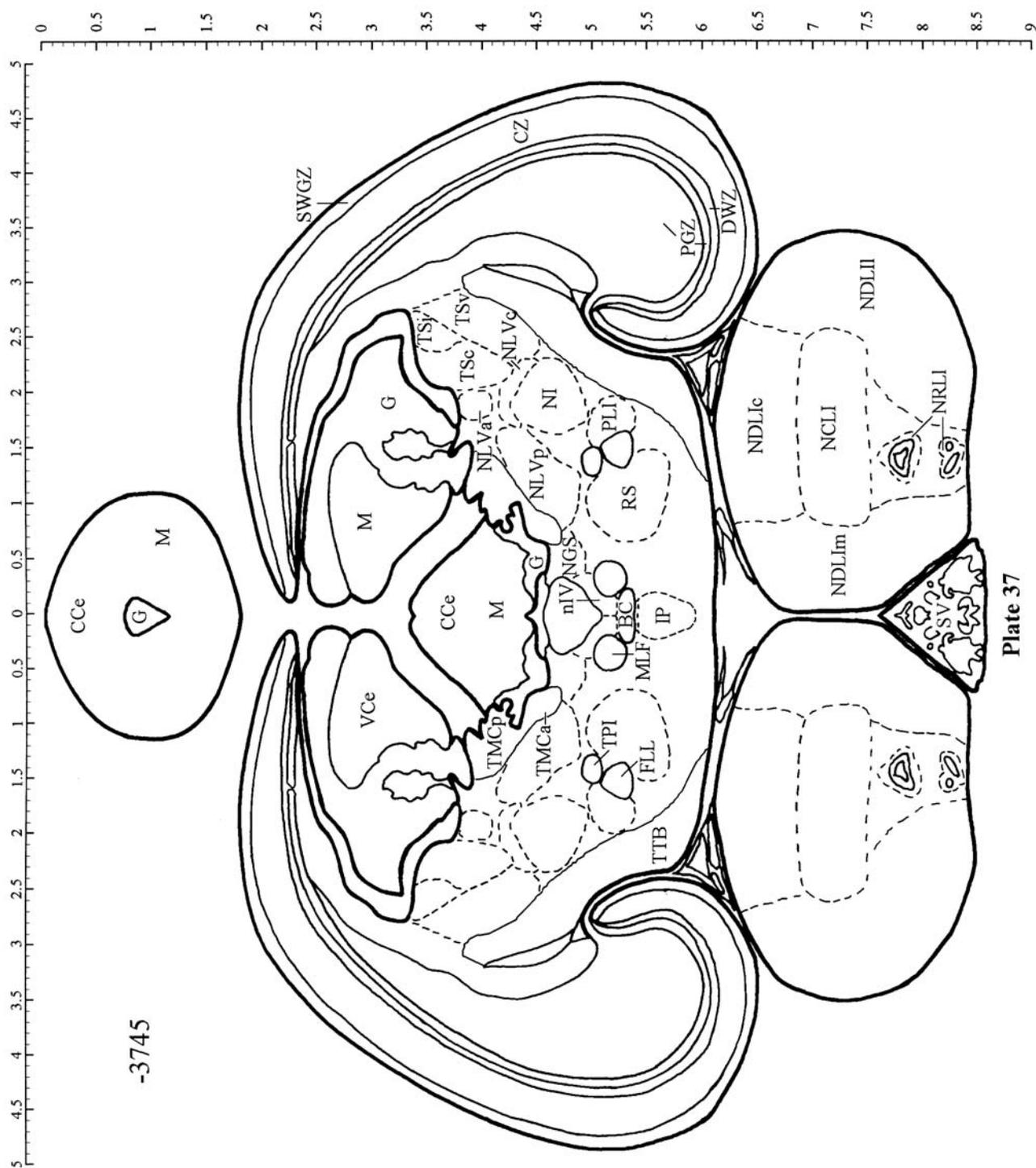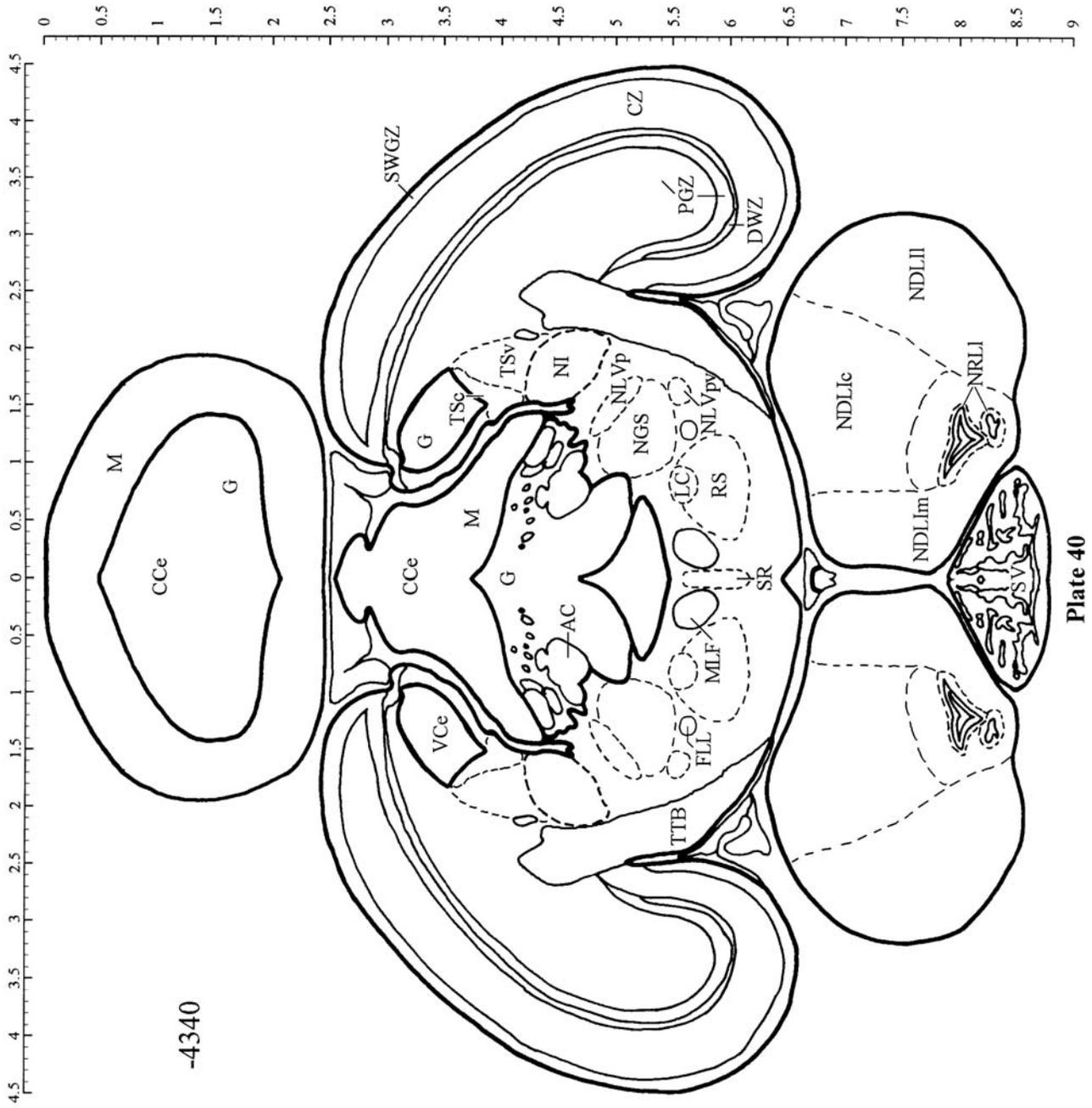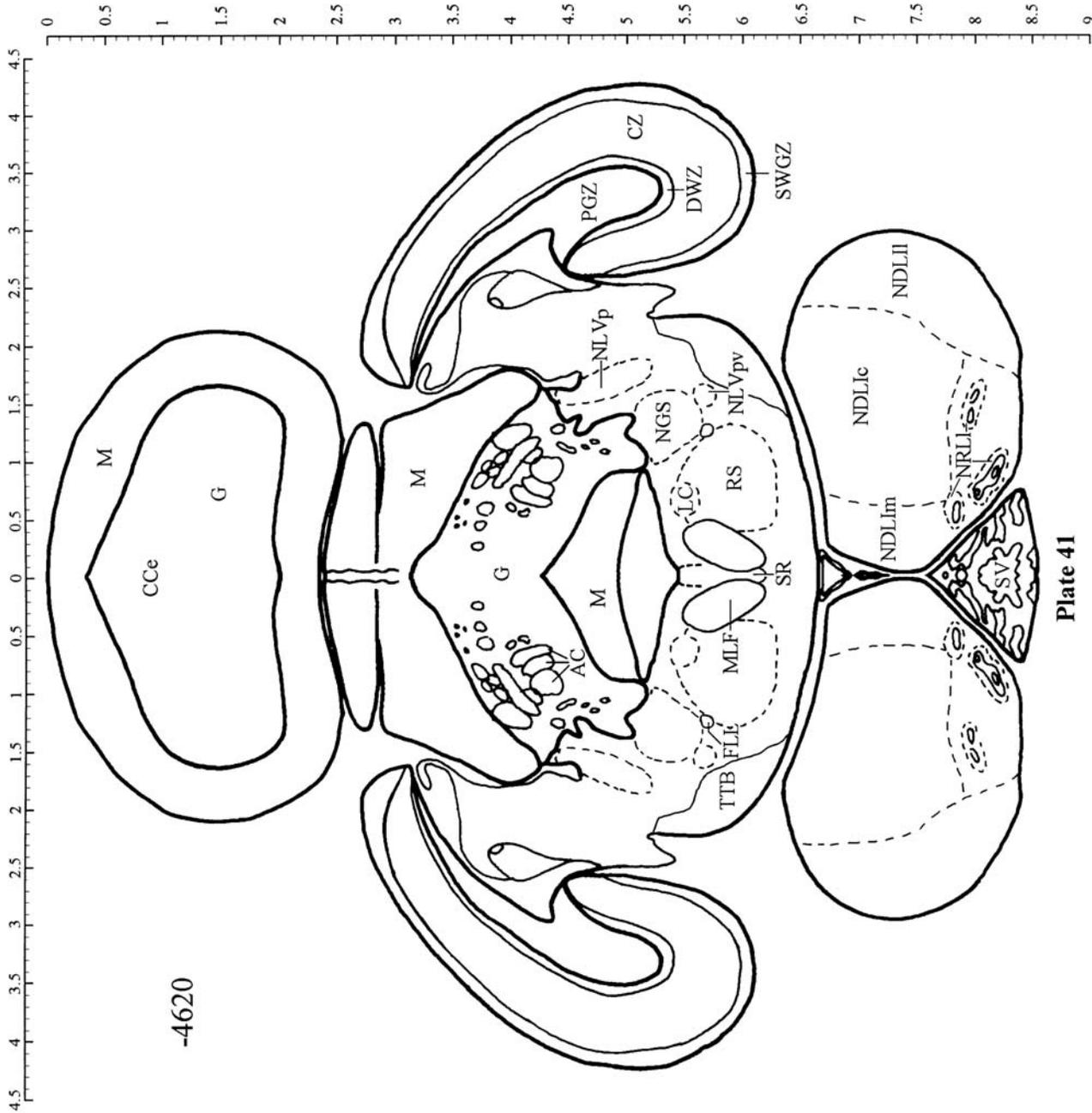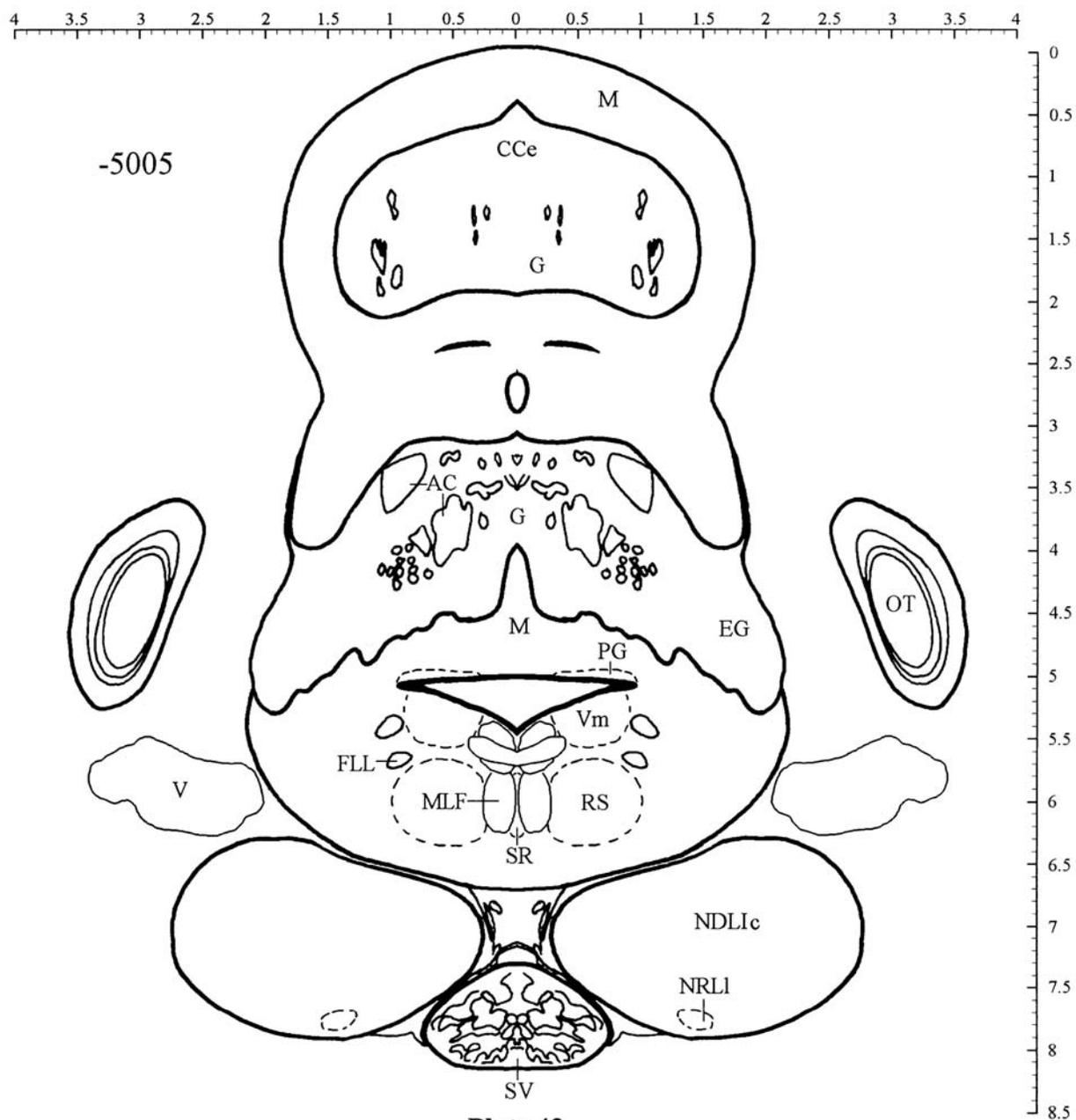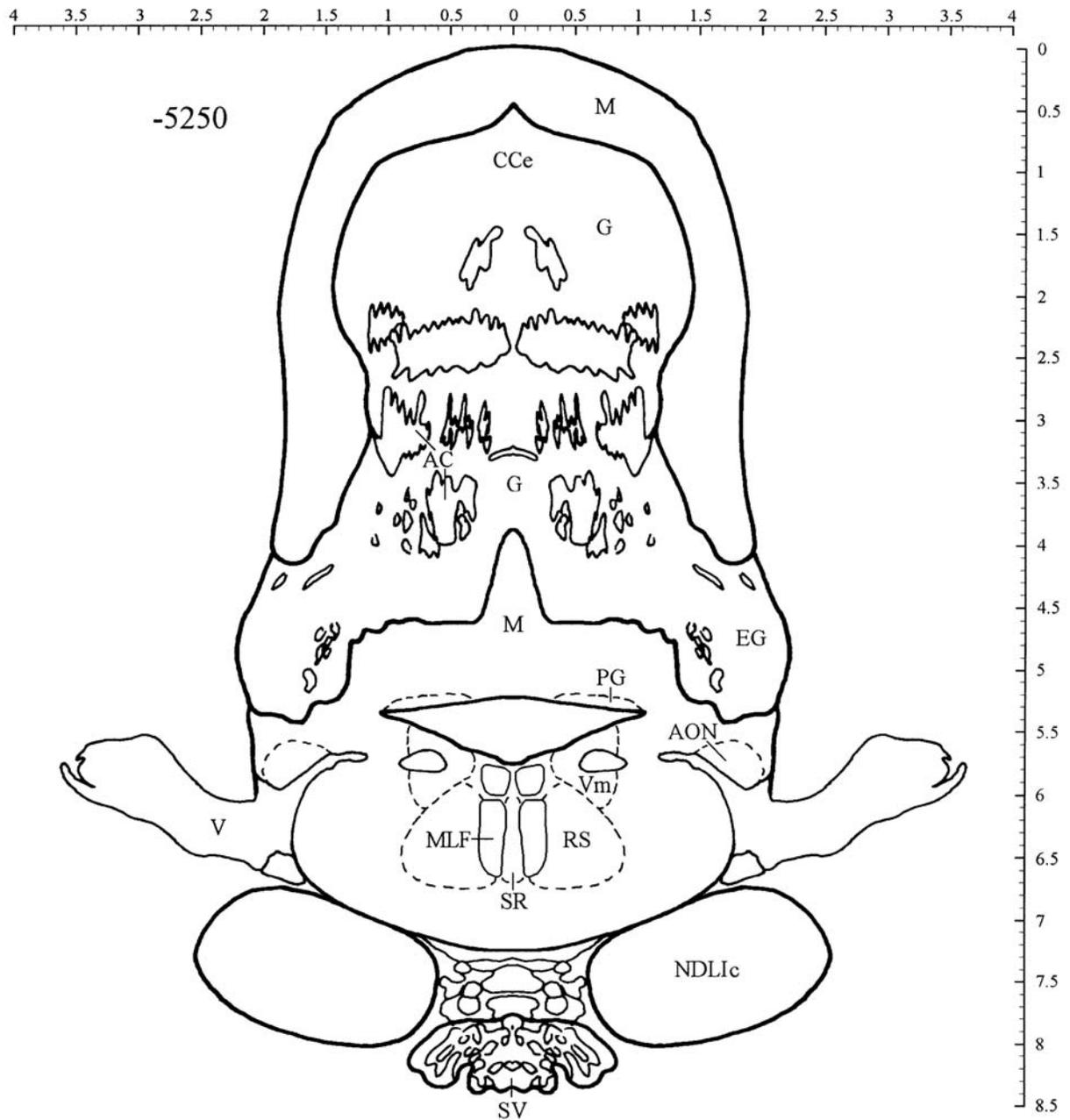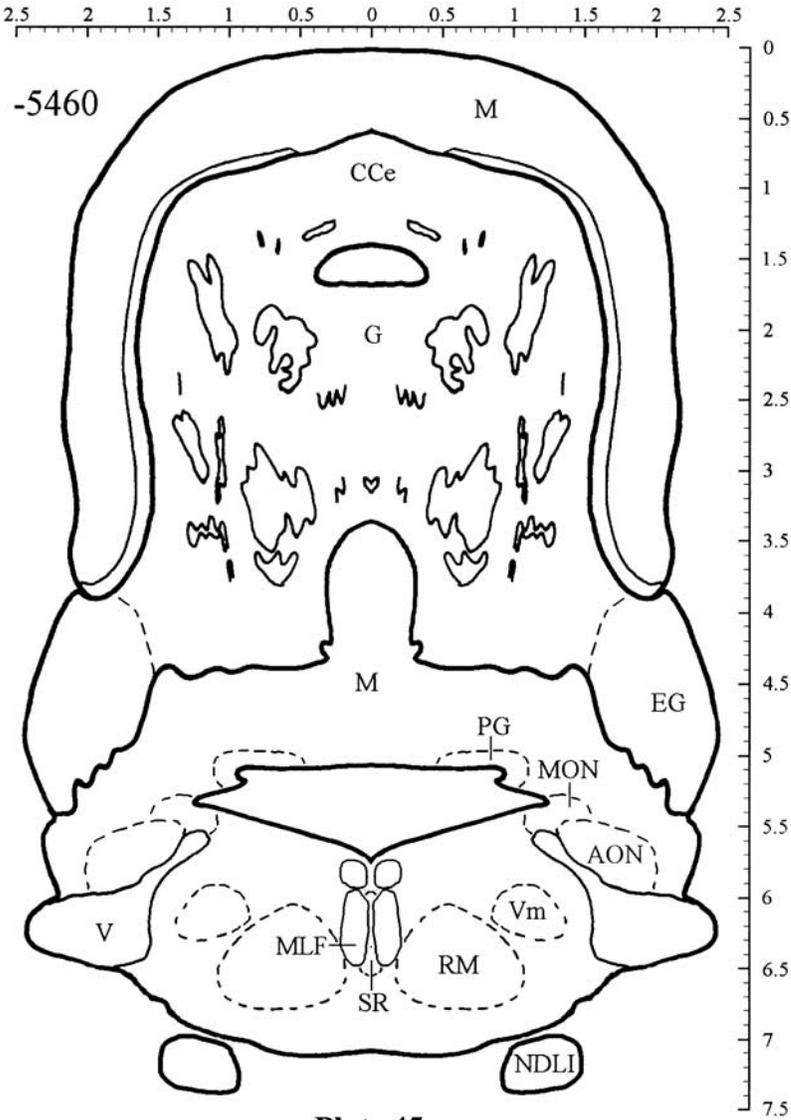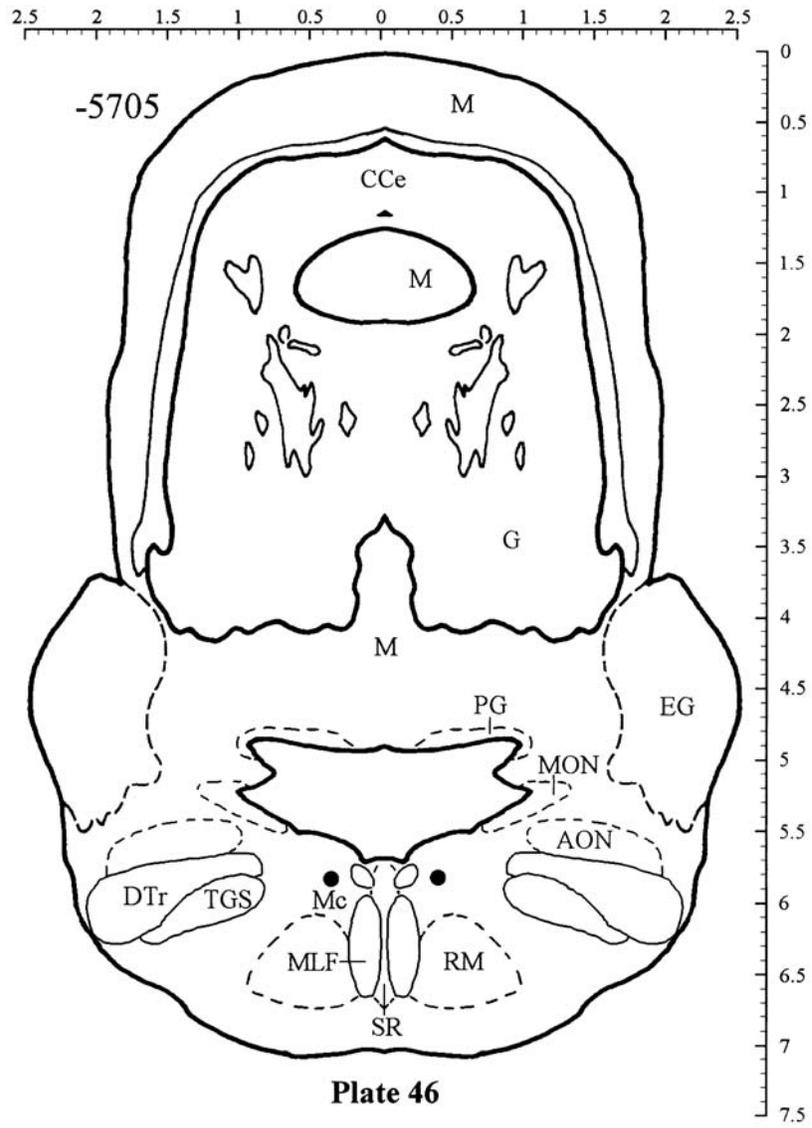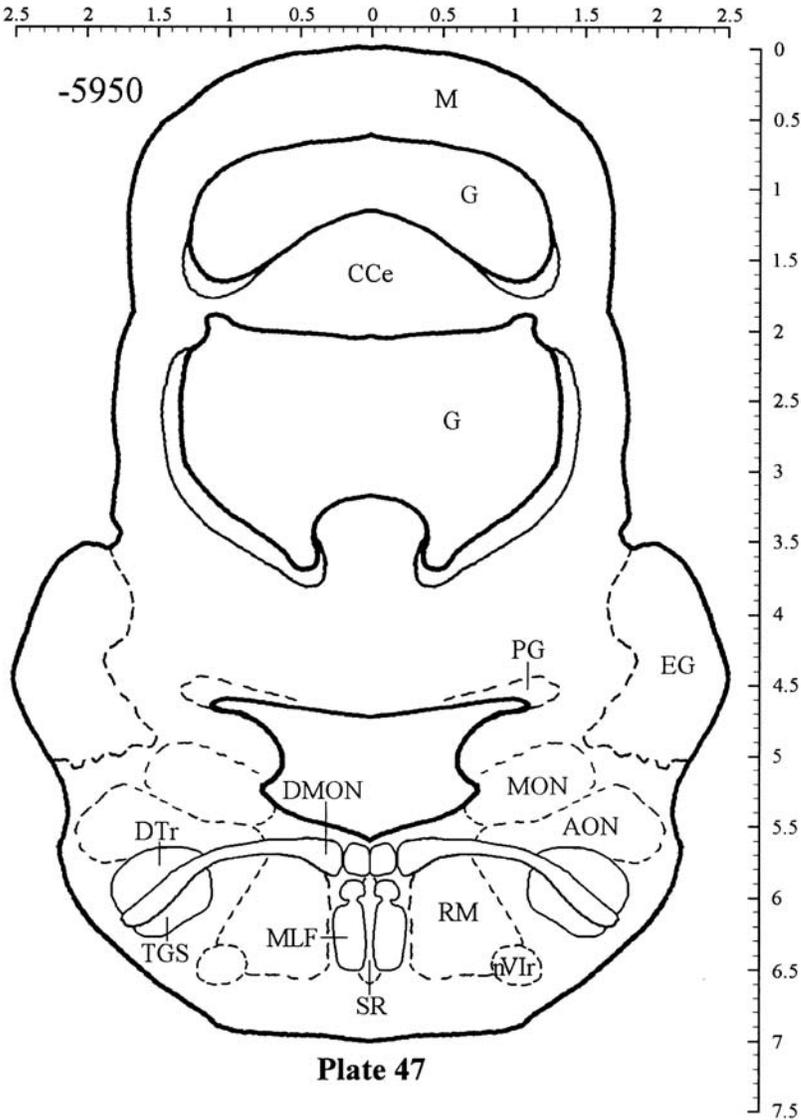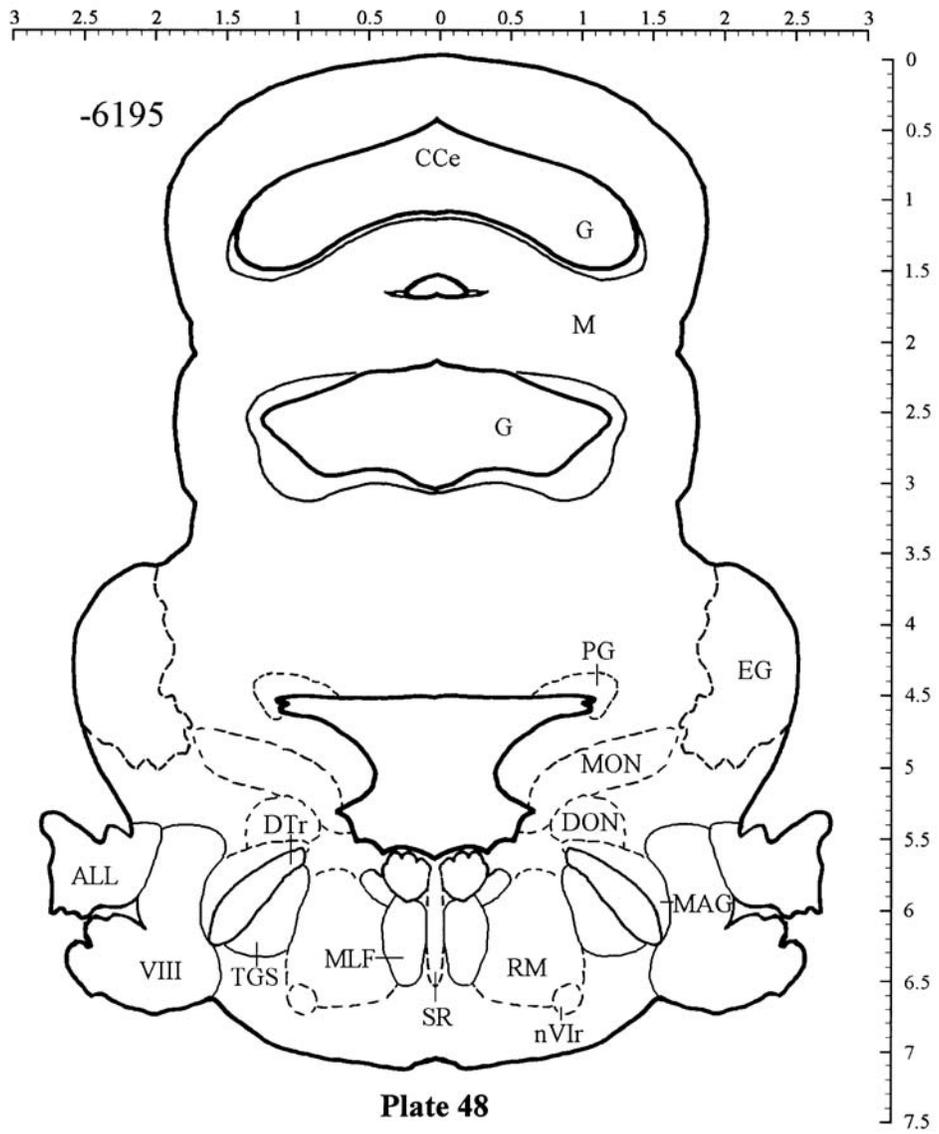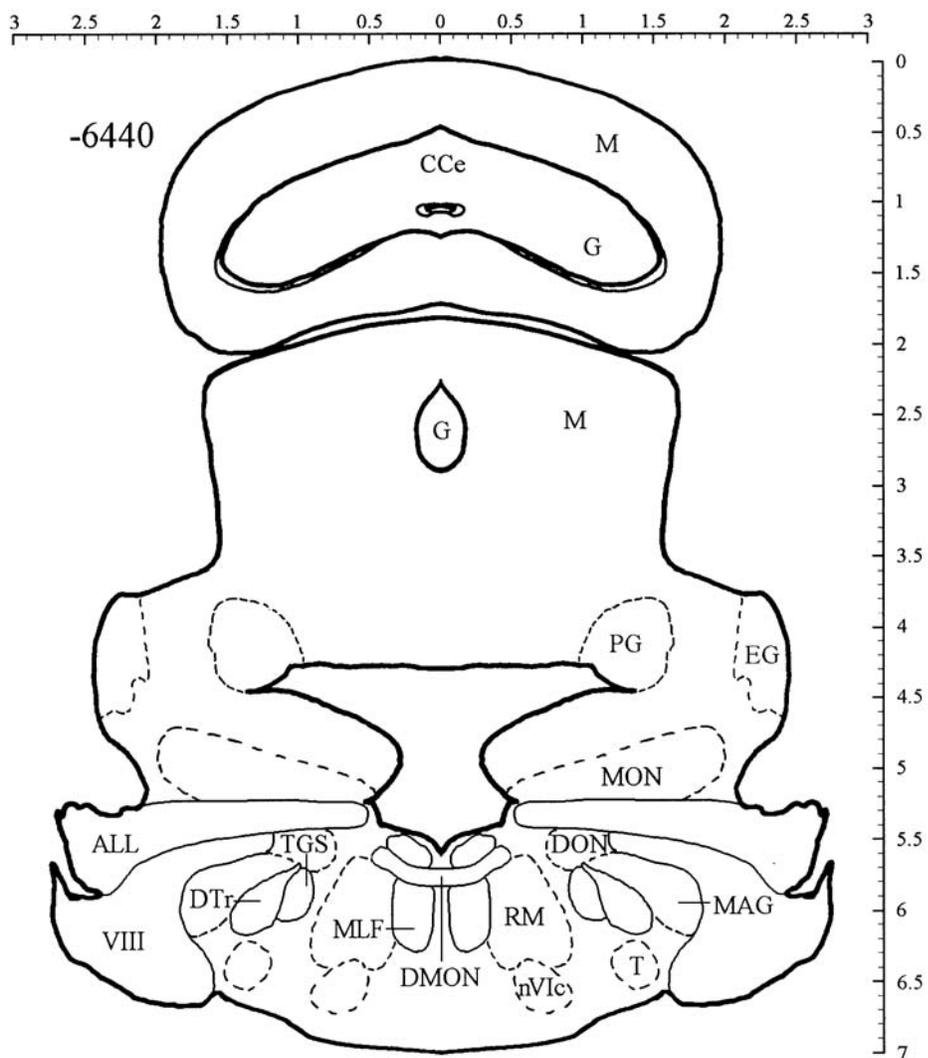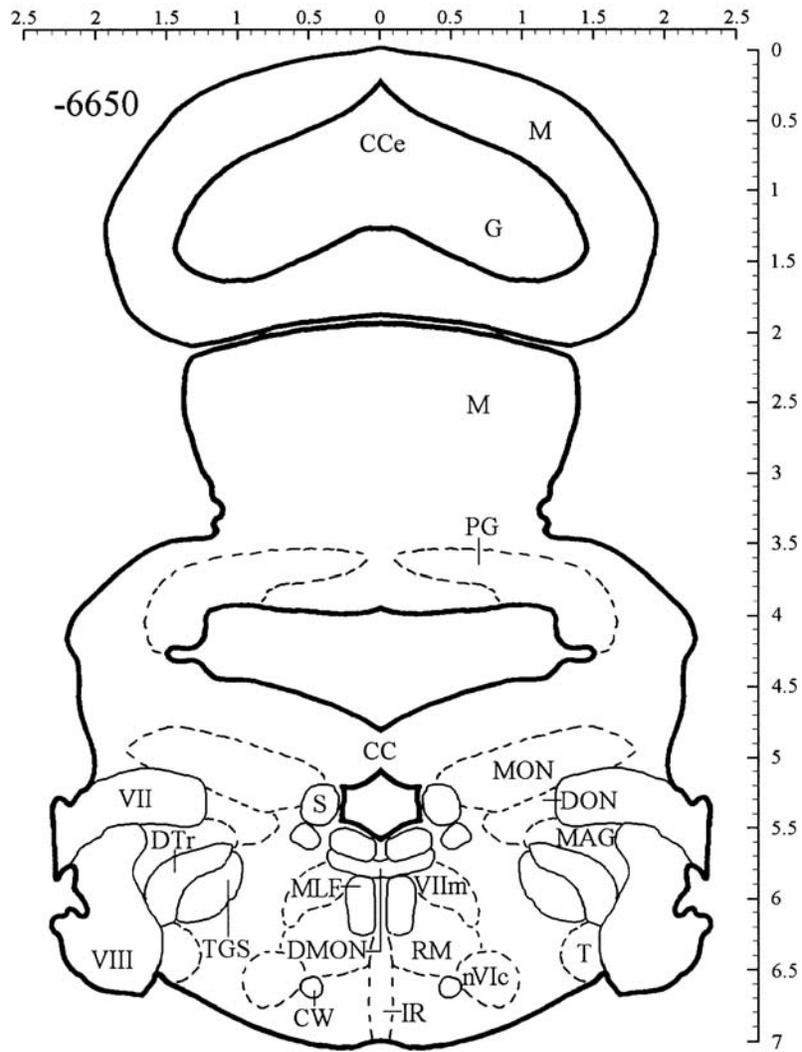
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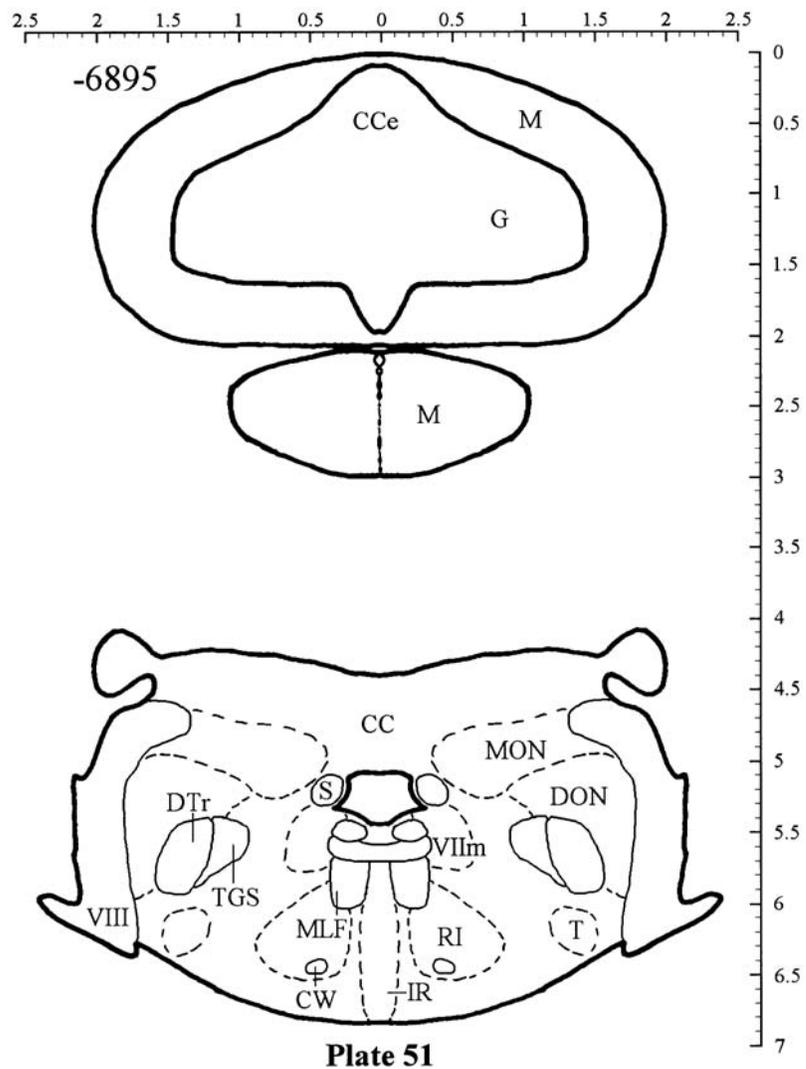
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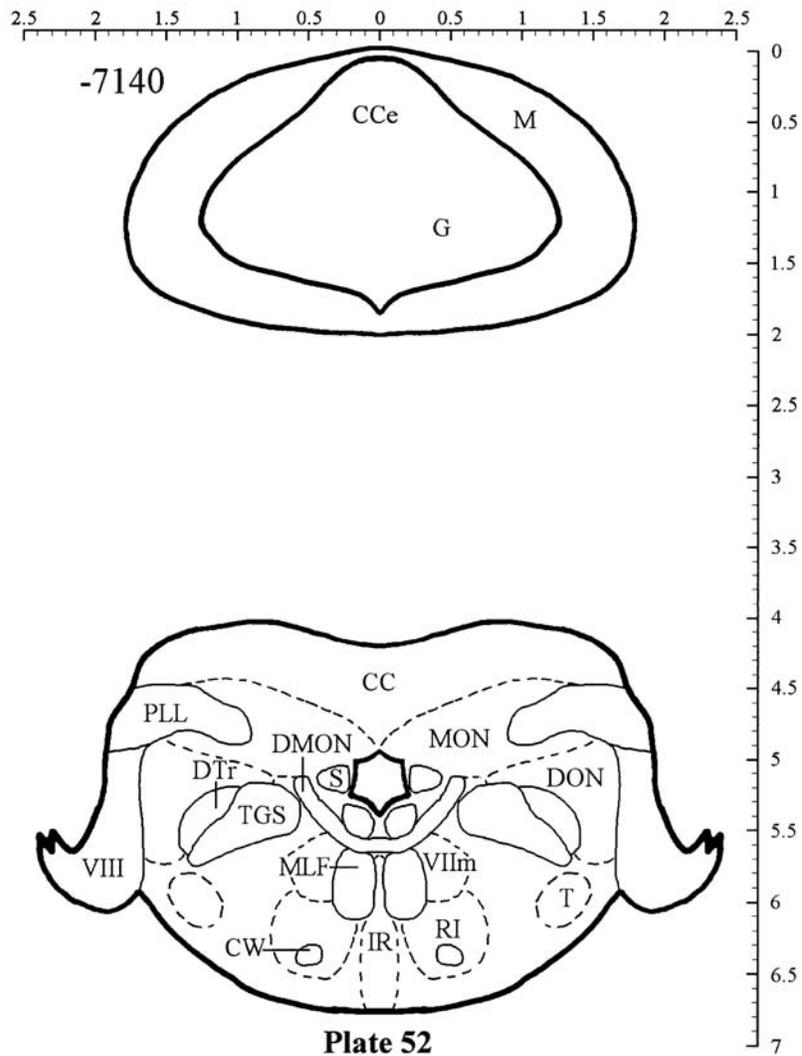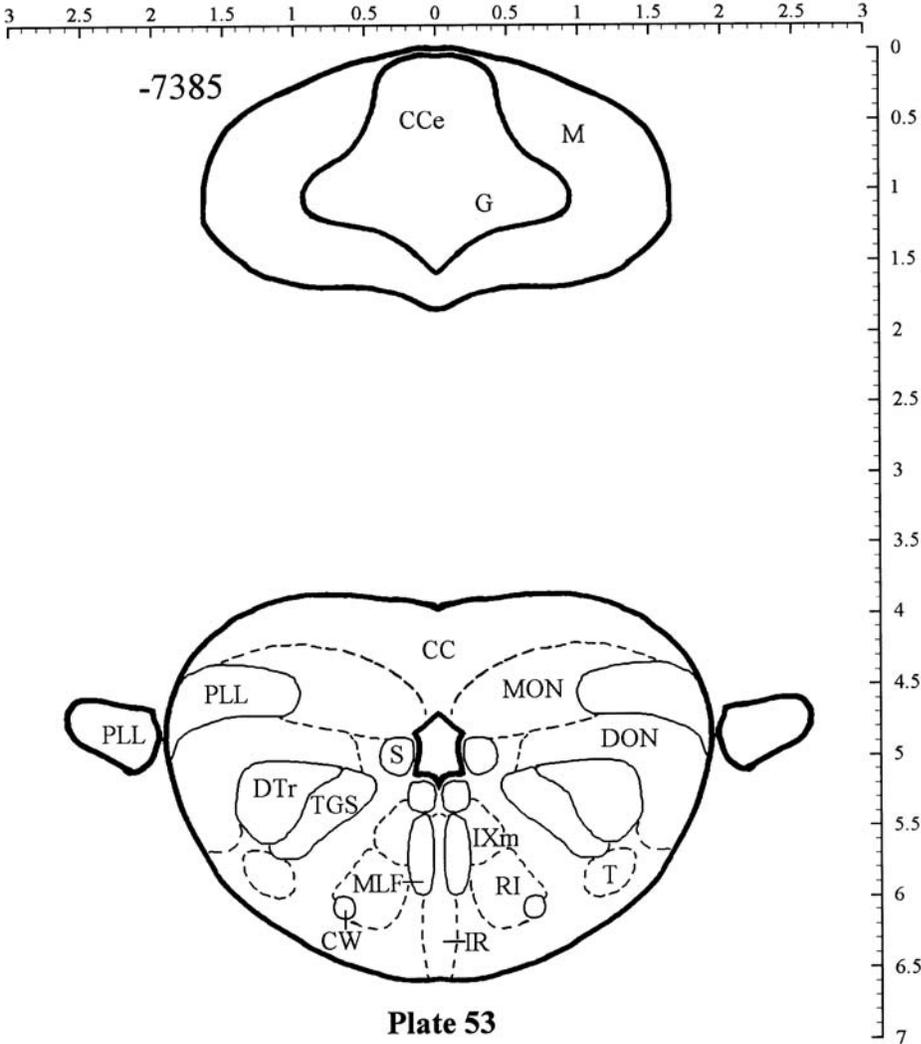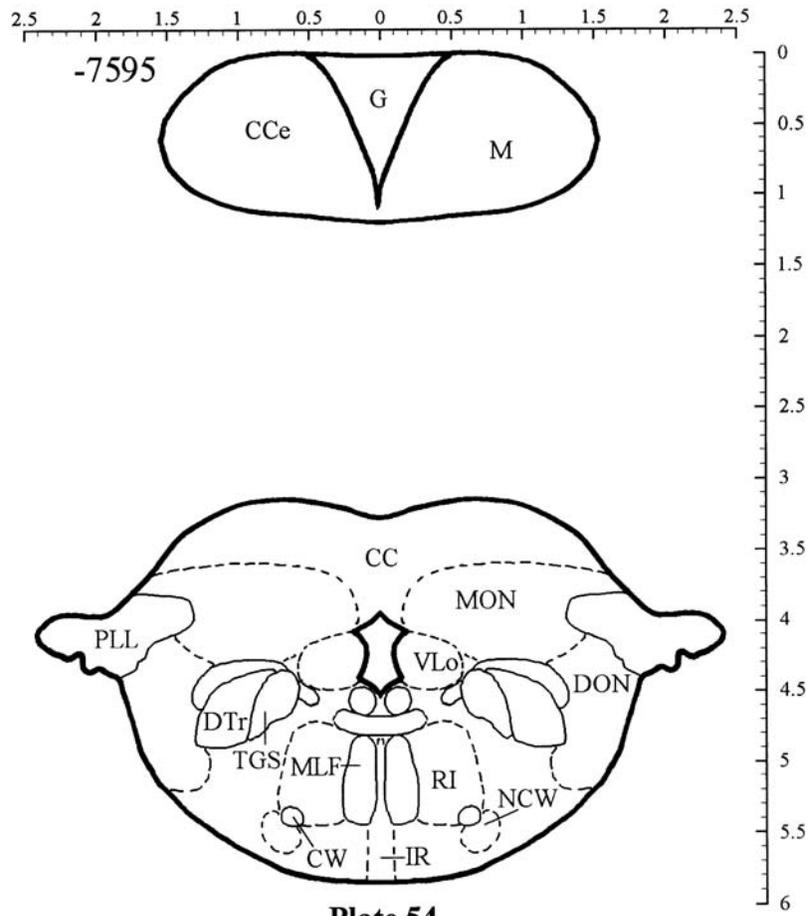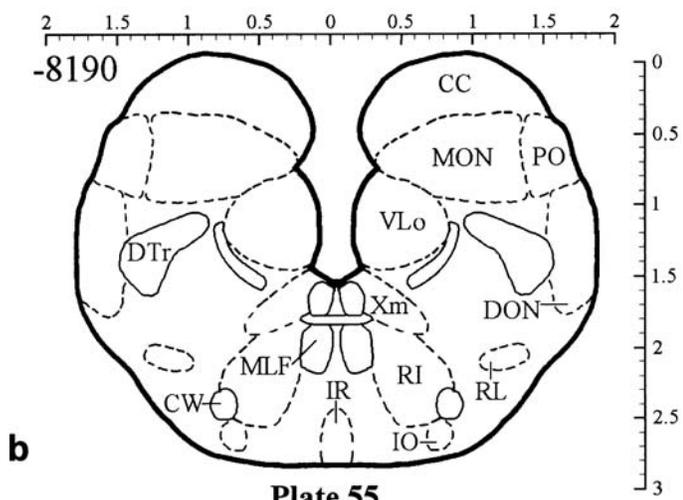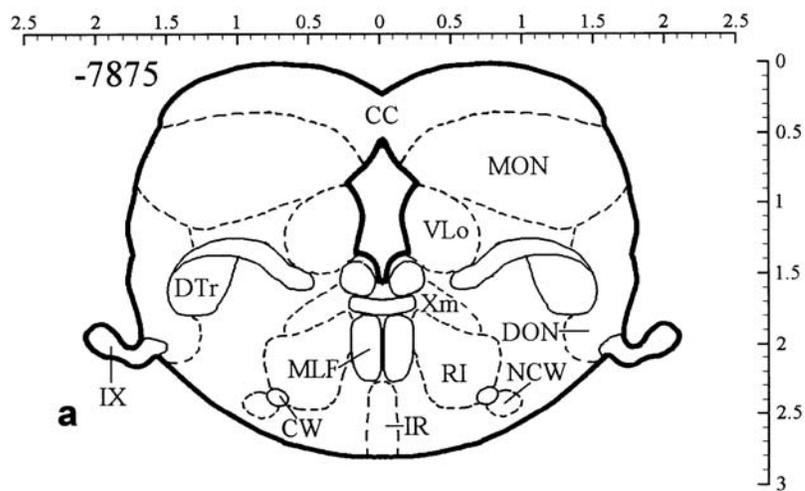
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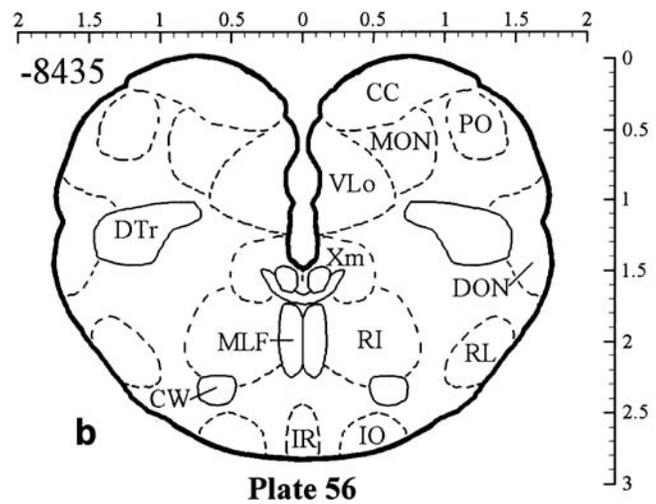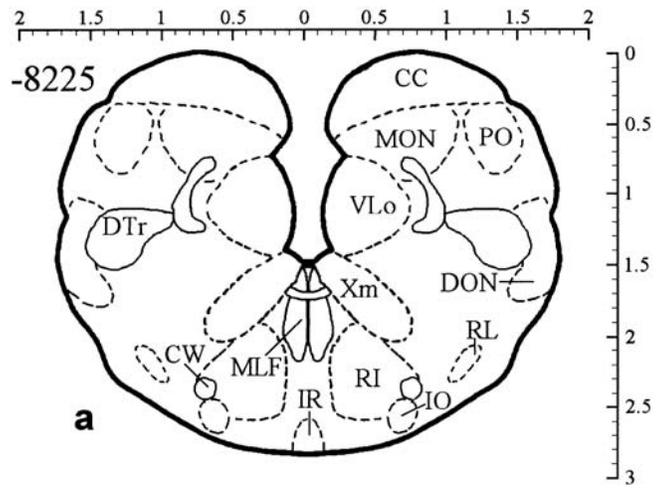
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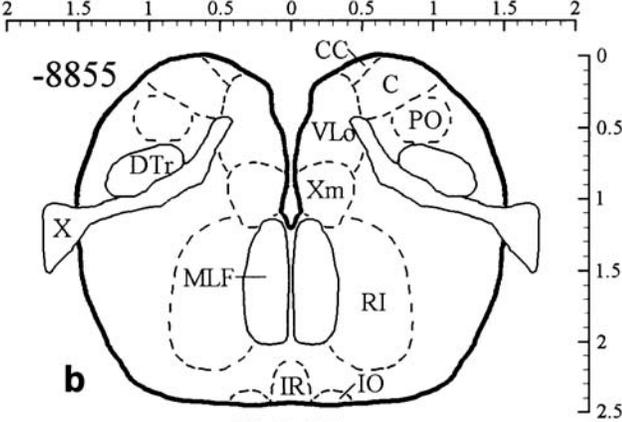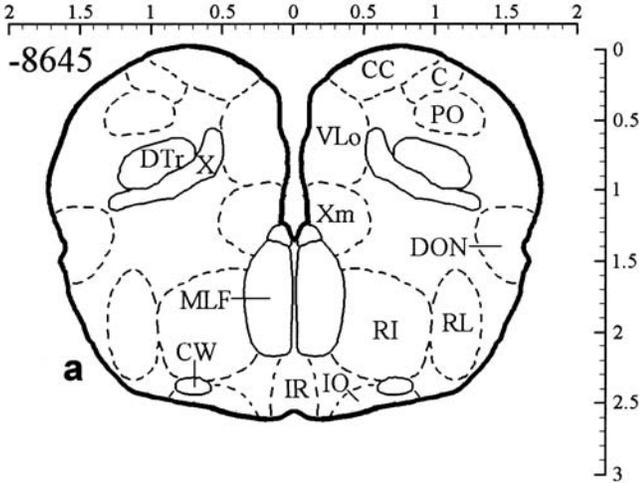
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Plate 56

Plate 57
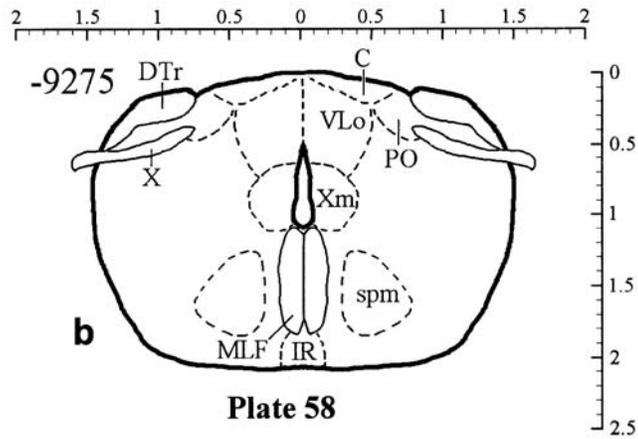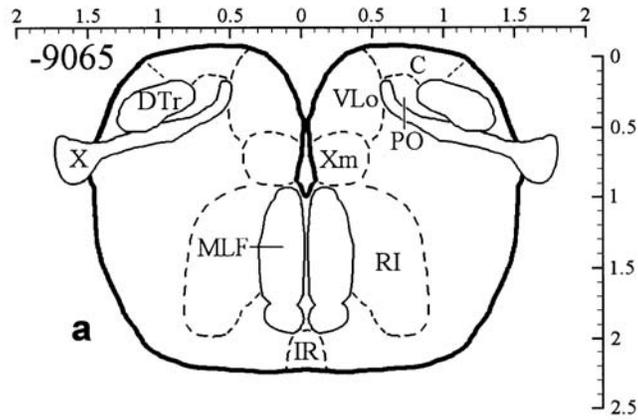
Plate 58

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