A Forebrain Atlas and Stereotaxic Technique for the Lizard, *Anolis carolinensis*

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ABSTRACT A forebrain atlas and stereotaxic neurosurgical techniques were developed for use in anatomical and behavioral experiments on the green anolis lizard (Anolis carolinensis). Green anoles are convenient and robust experimental subjects with a rich behavioral repertoire, the social components of which are partly under hormonal control.

The technique and atlas were devised to conduct neuroethological investigations of the effect of lesions on species-typical display behavior. The atlas consists of 12 transverse sections from an average size adult male. The figures (4–15) are based on Nissl material and supplemented with fiber-stained material from adjacent sections. They appear at the end of the article. Limitations on the accuracy of stereotaxic coordinates are discussed and tables of correlative nomenclature for principal telencephalic and diencephalic nuclei are provided.

Among lizards, the diurnal, visually oriented Iguanids are the most amenable to study, and of these, the green anole, Anolis carolinensis, is the most studied. This species has a rich behavioral repertoire, most of which can be elicited in seminatural laboratory habitats. and it exhibits social activity with distinctive displays (B. Greenberg and Noble, '44; Crews, '75; Greenberg, '77a) that are partly under hormonal control (Crews, '75). With the use of microtechniques, this New World lizard is also an excellent subject for combined neurophysiological and neuroanatomical investigations (Greenberg et al., '79). To facilitate such research this report describes the forebrain of A. carolinensis in stereotaxic coordinates and provides a methodology for the placement of devices in the brain.

Valuable reviews of the reptilian forebrain have been published by Goldby and Gamble ('57) and Northcutt ('78), who also provided a useful summary of the variation within the Lacertilia. An architectonic analysis of a related member of the Family Iguanidae, *Iguana iguana*, was provided by Northcutt ('67); and a schematic atlas for this species was published by Distel ('76). The diencephalon of *I. iguana* was analyzed in detail by Butler and Northcutt ('73).

Detailed archetectonic studies on the diencephalon and midbrain of *Anolis carolinensis* were published in 1933 by Huber and Crosby. Twenty years later Armstrong et al. ('53) published on the telencephalon of other species of

Anolis with special reference to the olfactory apparatus, correcting errors made by earlier authors (Crosby and Humphrey, '39). Detailed descriptions of the preoptic and hypothalmic areas of A. carolinensis were included in a comparative essay by Crosby and Woodburne ('40). The anatomy of the cranial nerves was described by Willard ('19) and the cranial motor nuclei investigated by Gillaspy ('54).

An important impediment to functional neuroanatomical studies on lizards is the lack of information about normal behavior. Specialized and time-consuming ethological techniques are required to index their behavioral patterns and to ascribe function to these with any confidence. This has been partly relieved by recent detailed ethograms and behavioral inventories (e.g., Brattstrom, '71; Distel, '78; Greenberg, '77b) and partial ethograms stressing thermoregulatory (DeWitt, '71; Greenberg, '76; Heath, '65) and social behavior (Crews, '75; Greenberg, '77a; Noble and Bradley, '33). Learning in lizards was reviewed by Brattstrom ('78) and Burghardt ('77). The behavior of A. carolinensis has been described by Crews ('75), Evans ('36, '38), B. Greenberg and Noble ('44), Greenberg ('77a), and Noble and Bradley ('33).

Anolis carolinensis are small, easy to handle, economical to maintain, and are robust subjects for surgical procedures. They are easily captured in the field or readily available from commercial suppliers. It is one of the most broadly distributed of the anoles, the largest

genus of reptiles of the Americas. It is the only member of the genus which is native to the continental United States and ranges from North Carolina to Florida, west to southeastern Oklahoma and central Texas (Conant, '75). This species may reach a maximum body size (snout-to-vent) of 75 mm. Detailed information is available about their biology, ecology, and natural history (Gordon, '56). Specimens utilized in our laboratory are from southern Louisiana, where they occur in high densities in ecotonal areas of the coastal plains (Gordon, '56).

METHODS Stereotaxic technique

A headholder for Anolis carolinensis was adapted from a Kopf Small Animal Stereotaxic instrument (Fig. 1). The apparatus provides a bite plate covered with a thin layer made of dental elastic impression material into which the lizard's teeth are pressed by a forked clamp with a rubber strap stretched between the tines as it is lowered over the animal's snout. Additional support is provided by blunt ear-bars which are freshly tipped with fast-setting dental impression material (e.g., light-bodied

permlastic, Kerr Corp., Romulus, MI) in order to avoid injuring the tympanic membrane. Since hypothermia is used to obtain anesthesia, the instrument is provided with an adjustable tray for packing the lizard's body in crushed ice.

The horizontal reference plane along the same line as the edge of the upper jaw is provided by the bite plate; anterior/posterior, and lateral measurements utilize the center of the cornea of the parietal eye located on the top of the head as a zero point (Fig. 2). Measurements on five anesthetized individuals indicate that the surface of the brain is 0.5 mm below the zero point.

Surgical techniques

Because of tail autotomy and seasonal variations in fat stores, snout-to-vent (S-V) length is more reliable than weight as an index of size and maturity in iguand lizards. Lizards initially operated on varied from 59 to 69 mm S-V. For consistency in stereotaxic coordinates and to minimize relative size effects on behavioral tests, we came to limit the size of experimental subjects to 63–65 mm S-V. To conduct surgery, a subject was placed in a bed of crushed ice for a minimum of 10 minutes. When all

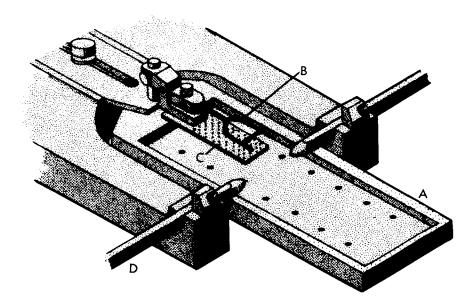


Fig. 1. Stereotaxic headholder adapted form a Kopf Small Animal Instrument. A, crushed ice tray with drain holes for

cryoanaesthesia; B, snout clamp with rubber strap; C, bite plate thinly covered with rubber; D, ear-bar.

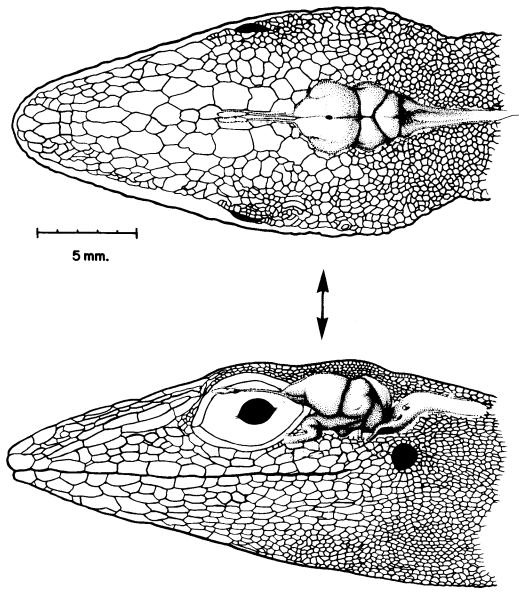


Fig. 2. Position of brain in cranium of lizard. Arrow indicates level of parietal eye used as the stereotaxic zero point.

signs of muscular activity ceased, it was transferred to the tray of the head-holder and again packed in ice. A sponge beneath a drain in the ice tray absorbed melting ice. The upper jaw of a lizard was pressed gently into the bite plate. The headholder was then adjusted until

a natural resting posture was obtained and the earbars were positioned alongside the tympanic opening. Several drops of fast-setting dental impression material were placed between the head and earbars and then the bars were tightened to within 2 mm of the tympanic

opening. The impression material conforms to the contours of an individual's head and sets in 10 minutes; after surgery it easily peels off.

Histological techniques

Lizards were sacrificed by injection with an overdose of Nembutal. To flush blood and fix tissue, transcardial perfusion of 0.9% saline followed by 10% formalin in 0.9% saline was performed with a 27-gauge needle connected by flexible tubing to a hypodermic syringe. The animals were then decapitated, the lower jaws removed, and the head skinned and placed in 10% formalin with sucrose for at least 2 days. The brains were cut in situ. Prior to embedding, a cranium was placed in 5% formic acid for 24-30 hours to decalcify, a procedure that did not compromise the quality of subsequent staining. Heads were embedded in gelatin-albumin or gelatin and transverse serial frozen sections were prepared on a freezing-sliding microtome set at 25 or 50 µm. To obtain transverse sections, the edge of the jaw was exposed and lined up with the vertical edge of a drafting triangle placed on the track of the microtome blade. Trial sections through the snout allowed correction for symmetry.

The atlas figures were prepared from the decalcified head of a 64-mm lizard imbedded in gelatin-albumin. Two guide tracks were placed beneath the jaw parallel to the horizontal plane to provide an independent horizontal reference point. Once the cranial vault was revealed, all sections were saved. Alternate sections were stained with cresyl violet for the Nissl material and the Weil stain for myelinated fibers. Several brains were prepared in the sagittal and horizontal planes for comparison. For the atlas illustrations, the left hemisphere of alternate

Nissl-stained sections were photographed alongside a mirror-image photo in which the principal nuclei were delineated. To represent fiber tracts, adjacent Weil sections were projected onto acetate sheets overlying the photographs of Nissl sections, and drawn in place.

RESULTS AND DISCUSSION Structural variability

The coordinates of three forebrain points were obtained along the anterior/posterior axis of 15 subjects (body size 63–65 mm) to indicate brain variability that might be expected in routine procedures (Fig. 3). The data indicate that an electrode can be placed in a 0.35-mm structure with high reliability. The greater variability in the coordinates of the posterior pole of the telencephalon was attributed to the relative lack of support from adjacent tissue, causing mechanical displacement of that portion of the brain during handling.

Limitations on stereotaxic accuracy

The average size of mature, vigorous males in commercial shipments was 60–68 mm. For most experimental procedures, males 63–65 mm were used. The atlas individual was 64 mm.

Since the brain grows more slowly than surrounding cranial tissue (Jerison, '73:28), the brain, supported by membranes and cartilage, becomes progressively more loosely supported within the skull. Thus the natural resting posture of the subject in the headholder is important because tension on the spinal cord can pull the entire brain caudally within the cranium.

The anterior/posterior position of the parietal eye shifts allometrically caudal as individuals grow, but within any given size class

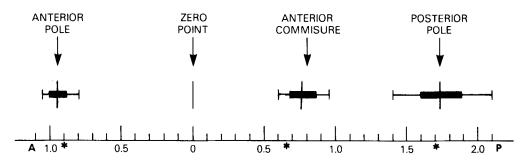


Fig. 3. Variability in the coordinates of three forebrain landmarks in 15 animals (body size 63–65 mm) relative to the zero point. The vertical line through a dark bar indicates the mean stereotaxic position of the specified landmark; the

dark bar indicates one standard deviation on each side of the mean; the entire bar indicates the complete range of variation. Asterisks beneath the scale indicate the landmark coordinates in the atlas. may be expected to be constant (J. Roth, personal communication).

Shrinkage was studied in canary brains after a similar perfusion technique, and after embedding and staining mounted sections (Stokes et al., '74). Less than 5% variation was observed when treated material was compared to fresh or perfused unstained material.

Nomenclature

Since there is as yet no complete architectonic study of the brain of Anolis carolinensis to guide the identification of telencephalic and diencephalic structures, terms were selected from recent reports on other lizards in which topological and in some cases architectonic information was sufficiently clear to allow generalization. Where ambiguity as to probable homology exists, the least specific term was utilized. For example, the nucleus of the lateral olfactory tract, identified in most lizards, is not clear in A. carolinensis although it is likely related to nucleus Al of Armstrong et al. ('53). On the other hand, nucleus sphericus (NS), conspicuous in the posterior dorsal ventricular ridge (PDVR) of most other lizards, is represented by a very small cell group that is clear in the atlas specimen and only three of 14 other brains examined. Preliminary retrograde degeneration experiments on olfactory and vomeronasal connections in A. carolinensis indicate a clear pathway that dissipates in the ventral neuropil of the PDVR at the level at which the NS would be expected (Greenberg and Switzer, unpublished data).

The reptilian DVR, the "strio-amygdaloid

complex" of several authors (e.g., Goldby and Gamble, '57; Armstrong et al., '53), often has its posterior area (PDVR) identified as amygdala, in which NS is the most prominent structure. Some recent authors continue in this conservative but flexible tradition and regard NS as one of the cell groups within the PDVR (e.g., Northcutt, '81; Voneida and Sligar, '79), while others have identified PDVR as a distinct nucleus (Northcutt, '67) sometimes within a "basal" DVR (Balaban, '78; Ulinski and Peterson, '81). Kuhlenbeck ('77) locates NS within a posterior epibasal complex. Because of the confusion latent in these alternative uses of the term, the *Anolis* atlas retains PDVR in the more conservative sense. In A. carolinensis and other species that lack a distinct sulcus neostriaticus (Ariens Kappers, '21) or cytological criteria (Northcutt, '78) to indicate the boundary between ADVR and PDVR, the area is identified by a reduced cell density, which becomes obvious caudal to the level of the anterior commissure.

Correlative nuclear nomenclature of several lizard species is provided in Tables 1 and 2 for pallial and subpallial structures. The terms indicate only a few possible ambiguities. The uncommon designation, "Zone A of the ADVR" (ZA), has been utilized to identify a distinct area on the medial margin of ADVR, distinguished by Northcutt ('78) as a target of an ascending auditory pathway in *Iguana*. The "lateral area of the ADVR" (ADVR, lat) is similarly unfamiliar and is used here to designate the subpallial component of the dorsolateral cortex (CxDL), also identified in *Iguana*

TABLE 1. Pallial nomenclature in lizards

| Current usage in Anolis carolinensis | | Armstrong | | 37 | D1 - 1 (100) | |
|--------------------------------------|--|-----------|--|------------------------------------|--|-------------------------------|
| Abbrev. | Structure | Location | et al. ('53) Anolis species | Northcutt ('67) Iguana iguana | Northcutt ('78) Iguana iguana | Distel ('76) Iguana iguana |
| CxD | dorsal cortex | A0.6-P1.4 | dorsal cortex | cortex dorsomedialis | dorsal cortex, divisions C1, C2 | cortex dorsalis |
| CxDL | dorsolateral cortex | A0.6 | | cortex dorsolateralis | , | cortex dorsolateralis |
| CxL | lateral cortex | A0.2-P1.2 | piriform cortex | cortex pyriformis | lateral cortex | cortex lateralis |
| CxM, lc | medial cortex, large-celled div. | A0.2-P1.6 | hippocampal cortex large-celled part | hippocampus, pars dorsalis | medial cortex, dorsal division (C1) | cortex dorsomedialis |
| CxM, sc | medial cortex, small-celled div. | A0.2-P1.6 | hippocampal cortex, small-celled part | hippocampus, pars dorsomedialis | medial cortex, ventral division (C2) | cortex medialis |
| DMI | dorsomedial interposition | PO.4-P1.6 | F | | dorsal cortex, division C3 | |

TABLE 2. Subpallial nomenclature in lizards

| | Current usage in Anolis carolinesis | | Armstrong et al. ('53) | Northcutt ('67) | Distel ('76) | Northcutt ('78) |
|--------------|--|------------------------|---|---|---|---|
| Abbrev. | Structure | Location | Anolis species | Iguana iguana | Iguana iguana | Iguana iguana |
| ADVR | anterior dorsal ventricular ridge | A0.6-P1.2 | hypopallium | hyperstriatum anterius | hyperstriatum anterius | dorsal ventricular ridge, anterior div |
| ADVR, lat | anterior dorsal ventricular ridge, lateral are | A0.4-P0.4 | | cortex dorsolateralis | cortex dorsomedialis [sic] | |
| AON | anterior olfactory n. | A0.6 | anterior olfactory n., pars lateralis | n. olfactorius anterior | n. olfactorius anterior | |
| BNac | bed n. of the anterior commissure | P0.6 | • | n. commissurae anterioris | n. commissurae anterioris | |
| BNhc | bed n. of the hippocampal commissure | P0.6 | | n. commissurae hippocampi | n. commissurae hippocampi | |
| BNst | bed n. of the stria terminalis | P0.6 | | | | |
| NA 1 NA 3 | n. A1 n. A3 | A0.2-P0.6 P0.2-P0.6 | amygdaloid n.1 amygdaloid n. | hyperstriatum posterius [?] neostriatum [?] | hyperstriatum posterius [?] neostriatum [?] | |
| NAcc | n. accumbens | A0.2-P0.4 | 3 paleostriatum medialis | n. accumbens | n. accumbens + [ventromedial] | n. accumbens |
| Ndb | n. diagonal band | AP0.0 | n. diagonal band | n. diagonal band of Broca | paleostriatum n. diagonal band of Broca | n. diagonal band of Broca |
| NDL Sep | n. dorsolateralis of the septum | P0.4-P0.8 | ventromedial n of paraterminal body | n. parolfactorius medialis | n. parolfactorius medialis | septal nuclei |
| NS | n. sphericus | P0.6 | amygdaloid n. 2 | n. sphaericus | n. sphaericus | n. sphericus |
| NVM Sep | n. ventromedialis of the septum | A0.2-P0.6 | dorsolateral n. of paraterminal body | n. parolfactorius lateralis | n. parolfactorius lateralis | septal nuclei. |
| PDVR | posterior dorsal ventricular ridge | P0.6-P1.2 | 200, | hyperstriatum posterius | hyperstriatum posterius | dorsal ventricular ridge, posterior div. |
| Ps | paleostriatum | A0.4-P0.4 | paleostriatum lateralis, small-celled part | paleostriatum | paleostriatum | striatum |
| Ps (lat) | paleostriatum, lateral area | P0.2-P0.4 | pari | neostriatum | neostriatum | striatum |
| Ps, lc | paleostriatum, large-celled area | AP0.0-P0.2 | paleostriatum lateralis, large-celled part | | | |
| Tub olf | olfactory tubercle | A0.6-P0.2 | olfactory tubercle | tuberculum olfactorium | tuberculum olfactorium | olfactory tubercle |
| VMN | ventromedial n. of the PDVR | P0.6-P1.0 | amygdaloid n. 4 | ventromedial nucleus | n. ventromedialis | n. ventromedialis |
| ZA | zone A of the ADVR | P0.2-P1.0 | | | | sensory zone A of ADVR |

TABLE 3. Diencephalic nomenclature in lizards

| | Current usage in Anolis carolinensis | | Butler and Northcutt | Cruce ('74) | D:-4-1 (270) | North and (270) |
|--------------|---|--------------------------------|---|--|--|--|
| Abbrev. | Structure | Location | ('73) Anolis carolinensis | Tupinambis nigropunctatus | Distel ('76) Iguana iguana | Northcutt ('78) Iguana iguana |
| DHN DLN | dorsal hypothalamic n. dorsolateral n | P1.0- P1.2 P1.0 | n. dorsolateralis hypothalami n. dorsolateralis anterior | n. dorsolateralis hypothalami n. dorsolateralis anterior | n. dorsolateralis hypothalami n. dorsolateralis anterior thalami | n. dorsolateralis hypothalami dorsolateral n. |
| DMN | dorsomedial n. | P1.0- P1.2 | n. dorsomedialis | n. dorsomedialis | n. dorsomedialis thalami | dorsomedial n. |
| Hab | habenula | P0.8- P1.4 | n. habenularis medialis [3 divisions recognized] | n. habenularis [2 divisions recognized] | n. habenularis | habenular n. [2 divisions recognized] |
| LGN | lateral geniculate n. | P0.8- P1.2 | n. geniculatis lateralis [3 divisions recognized] | n. geniculatis lateralis [2 divisions recognized] | n. geniculatis lateralis | lateral geniculate n. |
| LHA | lateral hypothalamic area | P1.4 | n. lateralis hypothalami | lateral hypothalamic area | n. lateralis hypothalami | |
| LMN | lentiform mesencephalic n. | P1.4 | n. lentiformis mesencephali | n. lentiformis mesencephali | | n. lentiformis mesencephali |
| LTN | lentiform thalamic n. | P1.4 | n. lentiformis thalami [2 divisions recognized] | n. lentiformis thalami pars plicata | n. lentiformis thalami [2 divisions recognized] | |
| MN | mammillary n. | P1.6 | G - | n. mammillaris [2 divisions recognized] | - | |
| NM | n. medialis | P1.2 | n. medialis | n. medialis pars anterior | n. medialis thalami | medial n. |
| NP | n. periventricularis | P1.4 | • | n. paraventricularis hypothalami | periventricular hypothalamic n. | |
| N Rot PHN | n. rotundus posterior hypothalamic n. | P1.2 P1.4- P1.6 | n. rotundus n. periventricularis [posterior, ventral] | n. rotundus n. posterior hypothalami | n. rotundus n. lateralis hypothalami | n. rotundus |
| PMN | premammillary n. | P1.2- P1.4 | | n. premammillaris | | |
| PGN | pretectal geniculate n. | P1.4 | n. geniculatus pretectalis | n. geniculatus pretectalis | n. geniculatis pretectalis | n. geniculatus pretectalis |
| POA | preoptic area | P0.2- P0.8 | n. preopticus | preoptic area [2 divisions recognized] n. periventricualris preopticus | n. praeopticus | |
| SCN | suprachiasmatic n. | P0.6 | | n. suprachiasmaticus | | |
| VMA | ventromedial area | P1.4 | area ventromedialis | area ventromedialis | | |
| VMH VMTN | ventromedial hypothalamus ventromedial thalamic n. | P1.0- P1.6 P1.0- P1.2 | n. ventralis hypothalami n. ventromedialis | n. ventromedialis hypothalami n. ventromedialis thalami | n. ventralis hypothalami n. ventromedialis thalami | ventromedial hypothalamus n. ventromedialis thalami |

(Northcutt, '67), that appears to merge with ADVR and become less distinct at more posterior levels. This area may be Area C of Northcutt ('78), identified as the possible recipient of visual information relayed through nucleus rotundus. Diencephalic structures are named in Table 3. Support for the identifica-

tion of the suprachiasmatic nucleus, the bed nucleus of the stria terminalis, and mammillary nuclei derives largely from Crosby and Woodburne's report on the hypothalamus ('40: Figs. 47, 51). Although several other telencephalic structures invite comparison with possible homologs in other species, the proposal

of such hypotheses must await completion of detailed architectonic studies.

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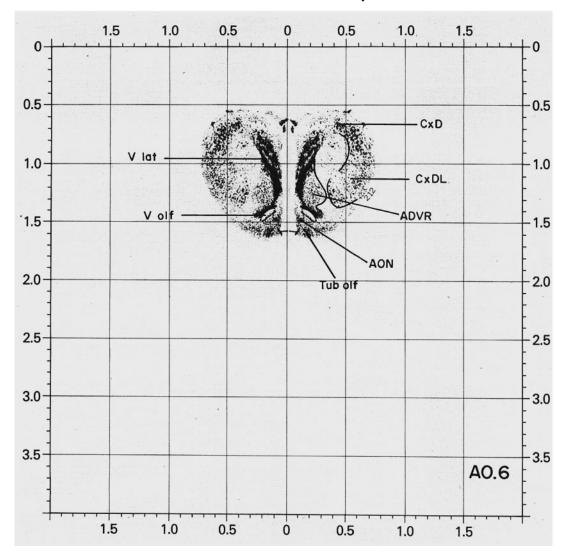


Fig. 4. Level A0.6.

| ADVR | anterior dorsal ventricular ridge | Tub olf | olfactory tubercle |
|------|-----------------------------------|---------|---------------------|
| AON | anterior olfactory nucleus | V lat | lateral ventricle |
| CxD | dorsal cortex | V olf | olfactory ventricle |
| CxDL | dorsolateral cortex | | |

Figs. 4-15. Transverse sections through the forebrain of Anolis carolinensis. Stereotaxic coordinates are in milli-

meters. Figures were prepared of sections at 0.2-mm intervals anterior (A) or posterior (P) to the zero point (AP 0.0).

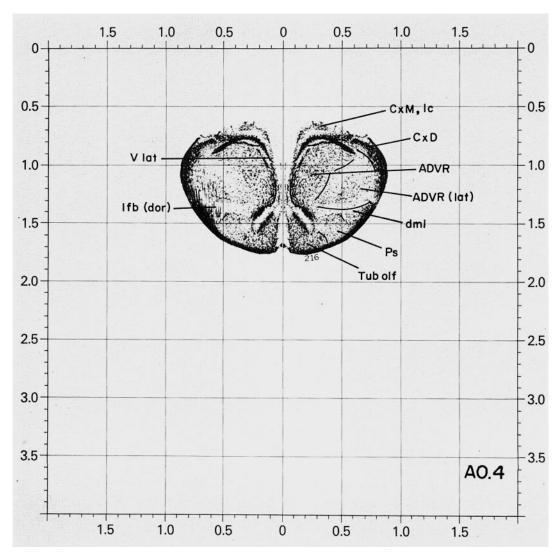


Fig. 5. Level A0.4.

| ADVR | anterior dorsal ventricular ridge | dml | dorsal medullary lamina |
|------------|--|------------------------|--|
| ADVR (lat) | anterior dorsal ventricular ridge, lateral | lfb (dor) | lateral forebrain bundle, dorsal peduncle |
| CxD CxM | area dorsal cortex medial cortex | Ps Tub olf V lat | paleostriatum olfactory tubercle lateral ventricle |

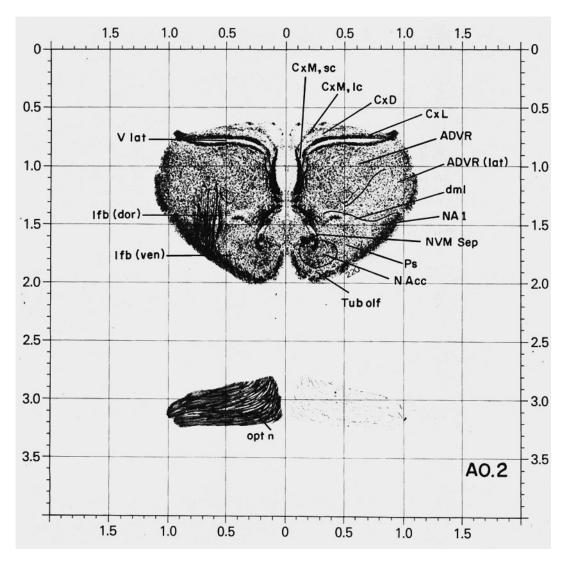


Fig. 6. Level A0.2

| ADVR ADVR (lat) CxD CxL CxM, lc CxM, sc dml | anterior dorsal ventricular ridge anterior dorsal ventricular ridge, lateral area dorsal cortex lateral cortex medial cortex, large-celled division medial cortex, small-celled division dorsal medullary lamina | lfb (ven) N Acc NA1 NVM Sep opt n Ps Tub olf V lat | lateral forebrain bundle, ventral peduncle nucleus accumbens nucleus A1 nucleus ventromedialis of the septum optic nerve paleostriatum olfactory tubercle lateral ventricle |
|---|--|--|---|
| dmi lfb (dor) | dorsal meduliary lamina lateral forebrain bundle, dorsal peduncle | v iai | lateral ventricle |

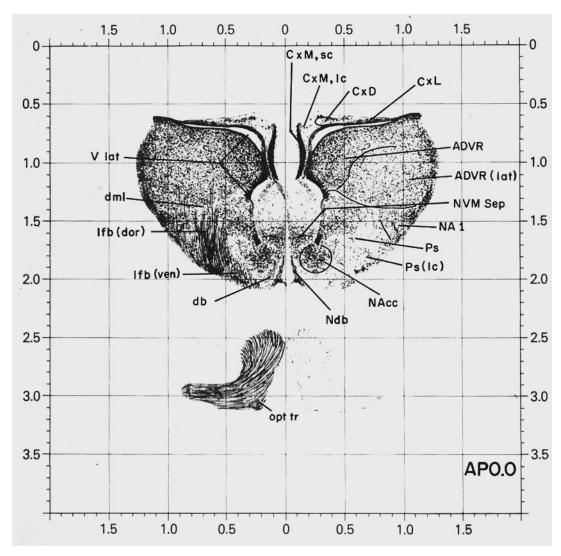


Fig. 7. Level A0.0.

| ADVR | anterior dorsal ventricular ridge | lfb (ven) | lateral forebrain bundle, ventral peduncle |
|------------|--|-----------|--|
| ADVR (lat) | anterior dorsal ventricular ridge, lateral | N Acc | nucleus accumbens |
| | area | NA1 | nucleus A1 |
| CxD | dorsal cortex | Ndb | nucleus of the diagonal band |
| CxL | lateral cortex | NVM Sep | nucleus ventromedialis of the septum |
| CxM, lc | medial cortex, large-celled division | opt tr | optic tract |
| CxM, sc | medial cortex, small-celled division | Ps | paleostriatum |
| ďb | diagonal band | Ps (lc) | paleostriatum, large-celled area |
| dml | dorsal medullary lamina | V lat | lateral ventricle |
| lfb (dor) | lateral forebrain bundle, dorsal peduncle | | |

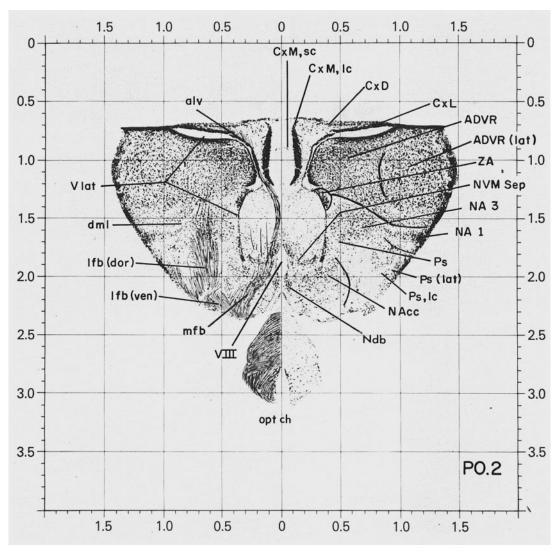


Fig. 8. Level P0.2.

| ADVR | anterior dorsal ventricular ridge | NA1 | nucleus A1 |
|------------|--|----------|--------------------------------------|
| ADVR (lat) | anterior dorsal ventricular ridge, lateral | NA3 | nucleus A3 |
| | area | N Acc | nucleus accumbens |
| alv | alveus | Ndb | nucleus of the diagonal band |
| CxD | dorsal cortex | NVM Sep | nucleus ventromedialis of the septum |
| CxL | lateral cortex | opt ch | optic chiasm |
| CxM, lc | medial cortex, large-celled division | Ps | paleostriatum |
| CxM, sc | medial cortex, small-celled division | Ps (lat) | paleostriatum, lateral area |
| dml | dorsal medullary lamina | Ps, lc | paleostriatum, large-celled area |
| lfb (dor) | lateral forebrain bundle, dorsal peduncle | V lat | lateral ventricle |
| lfb (ven) | lateral forebrain bundle, ventral peduncle | V III | third ventricle |
| mfb | medial forebrain bundle | ZA | zone A of the ADVR |
| | | | |

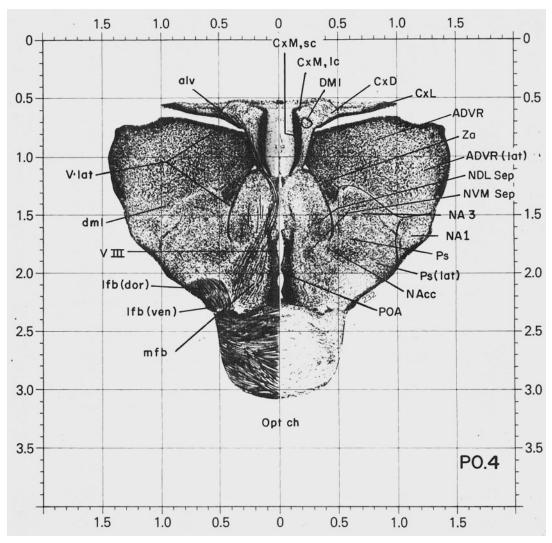


Fig. 9. Level P0.4.

| ADVR | anterior dorsal ventricular ridge, medial | mfb | medial forebrain bundle |
|------------|--|------------------------|--------------------------------------|
| | area | NA1 | nucleus A1 |
| ADVR (lat) | anterior dorsal ventricular ridge, lateral | NA3 | nucleus A3 |
| | area | N Acc | nucleus accumbens |
| alv | alveus | NDL Sep | nucleus dorsolateralis of the septum |
| CxD | dorsal cortex | NVM Sep | nucleus ventromedialis of the septum |
| CxL | lateral cortex | opt ch | optic chiasm |
| CxM, lc | medial cortex, large-celled division | POA | preoptic area |
| CxM, sc | medial cortex, small-celled division | $\mathbf{P}\mathbf{s}$ | paleostriatum |
| DMI | dorsomedial interposition | Ps (lat) | paleostriatum, lateral area |
| dml | dorsal medullary lamina | V lat | lateral ventricle |
| lfb (dor) | lateral forebrain bundle, dorsal peduncle | V III | third ventricle |
| lfb (ven) | lateral forebrain bundle, ventral peduncle | ZA | zone A of the ADVR |

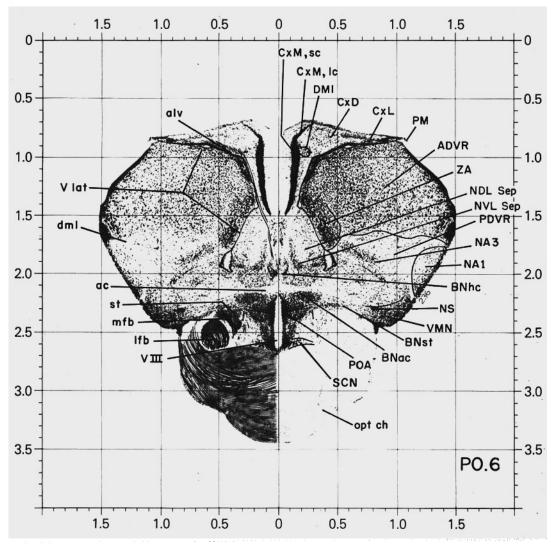


Fig. 10. Level P0.6.

| ac | anterior commissure | NA3 | nucleus A3 |
|---------|---|---------|--------------------------------------|
| ADVR | anterior dorsal ventricular ridge | NDL Sep | nucleus dorsolateralis of the septum |
| alv | alveus | NS | nucleus sphericus |
| BNac | bed nucleus of the anterior commissure | NVM Sep | nucleus ventromedialis of the septum |
| BNhc | bed nucleus of the hippocampal commissure | opt ch | optic chiasm |
| BNst | bed nucleus of the stria terminalis | PDVR | posterior dorsal ventricular ridge |
| CxD | dorsal cortex | PM | pallial membrane |
| CxL | lateral cortex | POA | preoptic area |
| CxM, lc | medial cortex, large-celled division | SCN | suprachiasmatic nucleus |
| CxM, sc | medial cortex, small-celled division | st | stria terminalis |
| DMI | dorsomedial interposition | V lat | lateral ventricle |
| dml | dorsal medullary lamina | V III | third ventricle |
| lfb | lateral forebrain bundle | VMN | ventromedial nucleus of the PDVR |
| mfb | medial forebrain bundle | ZA | zone A of the ADVR |
| NA1 | nucleus A1 | | |

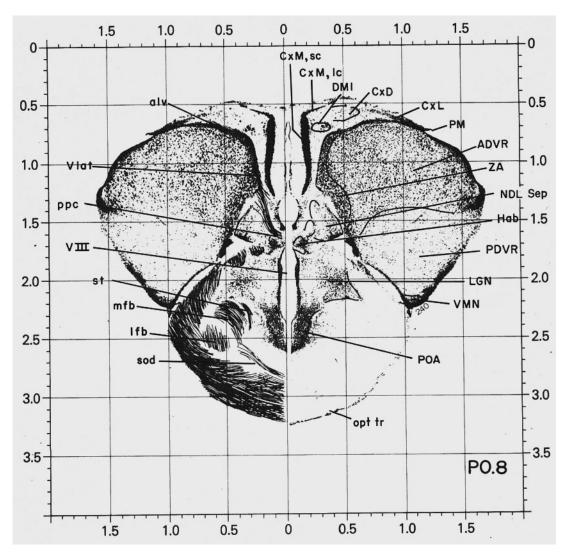


Fig. 11. Level P0.8.

| ADVR | anterior dorsal ventricular ridge | opt tr | optic tract |
|---------|--------------------------------------|--------|------------------------------------|
| alv | alveus | PDVR | posterior dorsal ventricular ridge |
| CxD | dorsal cortex | PM | pallial membrane |
| CxL | lateral cortex | POA | preoptic area |
| CxM, lc | medial cortex, large-celled division | ppc | posterior pallial commissure |
| CxM, sc | medial cortex, small-celled division | st | stria terminalis |
| DMI | dorsomedial interposition | sod | supraoptic decussation |
| Hab | habenula | V lat | lateral ventricle |
| lfb | lateral forebrain bundle | V III | third ventricle |
| LGN | lateral geniculate nuclei | VMN | ventromedial nucleus of the PDVR |
| mfb | medial forebrain bundle | ZA | zone A of the ADVR |
| NDL Sep | nucleus dorsolateralis of the septum | | |
| | | | |

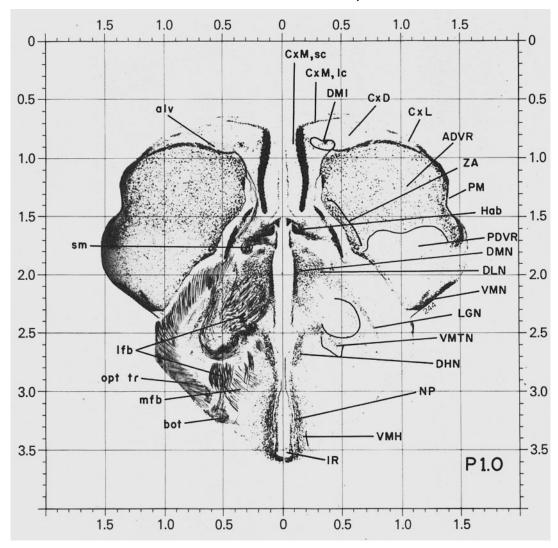


Fig. 12. Level P1.0.

| ADVR | anterior dorsal ventricular ridge | lfb | lateral forebrain bundle |
|---------|--------------------------------------|--------|------------------------------------|
| alv | alveus | LGN | lateral geniculate nucleus |
| bot | basal optic tract | mfb | medial forebrain bundle |
| CxD | dorsal cortex | NP | nucleus periventricularis |
| CxL | lateral cortex | opt tr | optic tract |
| CxM, lc | medial cortex, large-celled division | PDVR | posterior dorsal ventricular ridge |
| CxM, sc | medial cortex, small-celled division | PM | pallial membrane |
| DHN | dorsal hypothalamic nucleus | sm | stria medullaris |
| DLN | dorsolateral nucleus | VMN | ventromedial nucleus of the PDVR |
| DMI | dorsomedial interpositin | VMH | ventromedial hypothalamus |
| DMN | dorsomedial nucleus | VMTN | ventromedial thalamic nucleus |
| Hab | habenula | ZA | zone A of the ADVR |
| IR | infundibular recess | | |

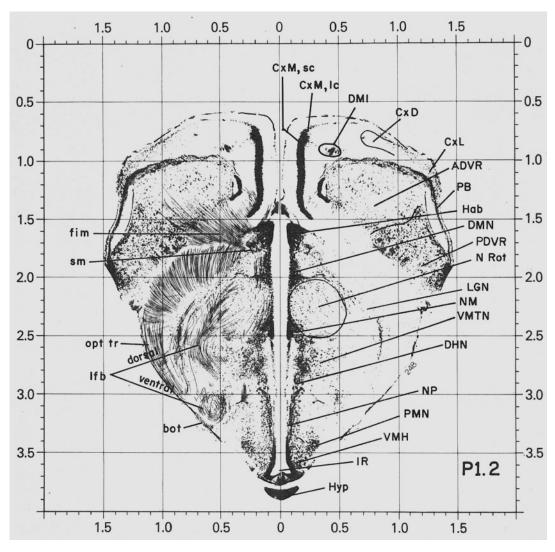


Fig. 13. Level P1.2.

| ADVR | anterior dorsal ventricular ridge | lfb | lateral forebrain bundle |
|---------|--------------------------------------|--------|------------------------------------|
| bot | basal optic tract | LGN | lateral geniculate nucleus |
| CxD | dorsal cortex | NM | nucleus medialis |
| CxL | lateral cortex | NP | nucleus periventricularis |
| CxM, lc | medial cortex, large-celled division | N Rot | nucleus rotundus |
| CxM, sc | medial cortex, small-celled division | opt tr | optic tract |
| DHN | dorsal hypothalamic nucleus | PΒ | pallial bridge |
| DMI | dorsomedial interposition | PDVR | posterior dorsal ventricular ridge |
| DMN | dorsomedial nucleus | PMN | premammillary nucleus |
| fim | fimbria | sm | stria medullaris |
| Hab | habenula | VMH | ventromedial hypothalamus |
| Нур | hypophysis | VMTN | ventromedial thalamic nucleus |
| IR T | infundibular recess | | |
| | | | |

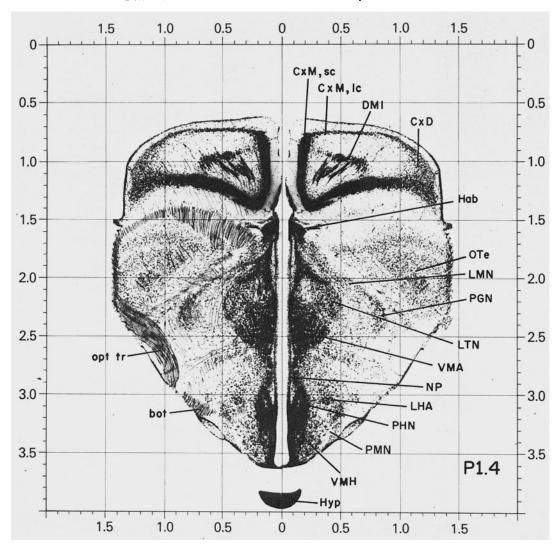


Fig. 14. Level P1.4.

| bot CxD CxM, lc CxM, sc DMI Hab | basal optic tract dorsal cortex medial cortex, large-celled division medial cortex, small-celled division dorsomedial interposition habenula hypophysis | LTN NP opt tr OTe PGN PHN PMN | lentiform thalamic nucleus nucleus periventricularis optic tract optic tectum pretectal geniculate nucleus posterior hypothalamic nucleus premammillary nucleus |
|---------------------------------|---|-------------------------------|---|
| Hyp LHA | hypophysis lateral hypothalamic nucleus | PMN VMA | premammillary nucleus ventromedial area |
| LMN | lentiform mesencephalic nucleus | VMH | ventromedial hypothalamus |

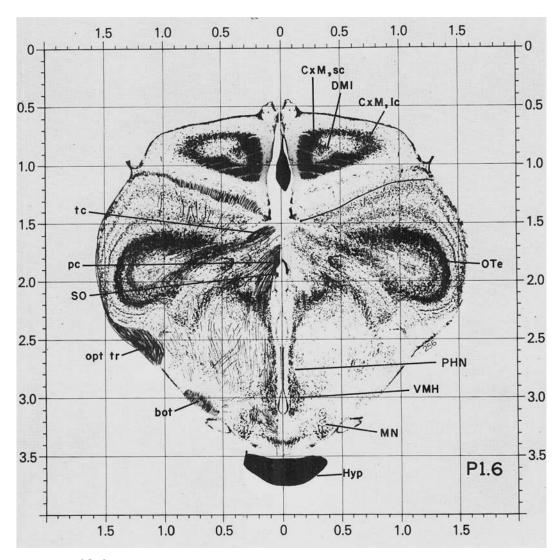


Fig. 15. Level P1.6.

| bot | basal optic tract | OTe | optic tectum |
|---------|--------------------------------------|-----|--------------------------------|
| CxM, lc | medial cortex, large-celled division | pc | posterior commissure |
| CxM, sc | medial cortex, small-celled division | PHN | posterior hypothalamic nucleus |
| DMI | dorsomedial interposition | SO | subcommisural organ |
| Hyp | hypophysis | tc | tectal commissure |
| MN | mammillary nuclei | VMH | ventromedial hypothalamus |
| opt tr | optic tract | | |