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The Telencephalon, Diencephalon, and Mesencephalon of the Canary, *Serinus canaria*, in Stereotaxic Coordinates

TEGNER M. STOKES, CHRISTIANA M. LEONARD
AND FERNANDO NOTTEBOHM

The Rockefeller University, New York, New York 10021

ABSTRACT A stereotaxic atlas of the telencephalon, diencephalon and mesencephalon of the canary, *Serinus canaria*, was prepared for use in anatomical and behavioral experiments. Canaries have a complex vocal and behavioral repertoire many of whose components are under hormonal control in the male, and are therefore useful for many physiological and anatomical experiments. They are available commercially, breed easily in captivity, are quite hardy and respond well to anesthetic and surgical procedures.

The atlas consists of 30 frontal plates from the frontal pole to the level of the motor nucleus of the trigeminus. One sagittal plate is included for reference purposes. Six birds (three males and three females) with marking lesions were used to make the atlas. Their brains were embedded in albumin-gelatin media, cut at 50 and 25 μ and stained with cresyl violet for cell bodies, Weil stain for myelinated fibers and the Fink-Schneider method for unmyelinated fibers. Plates were drawn from the cresyl violet series and labeled using all three stains.

The completed atlas was tested for accuracy by making 12 small lesions in a number of predetermined discrete loci in several birds and evaluating their placement. Eleven of these lesions were found to be within the targeted structure. The results of this test, combined with the results of experiments in over 50 birds, have shown the atlas to be accurate in 80% of all cases.

In recent years there has been growing interest in the anatomy, physiology and hormonal mechanisms of birds. They are interesting from a comparative and evolutionary standpoint as well as particularly useful in the study of sensory control over learned and species-specific behaviors. Songbirds have a complex vocal repertoire, which in some species is learned and monitored through auditory feedback (reviews in Nottebohm, '70, '72; Marler and Mundinger, '72). We have been investigating the neural pathways and hormonal systems underlying the output of vocal behavior (Zigmond et al., '73, and in preparation). A system of stereotaxic coordinates was required to place small lesions that would induce deficits in song production. The atlas contained in the following pages was prepared for this purpose.

Although the original experiments in our investigation were on the European chaffinch, *Fringilla coelebs*, the present em-

bargo on importation of foreign birds forced us to use a more available species, the canary. We have found it to be a most satisfactory experimental bird and we would recommend it to other investigators with interests in sensory systems. Canaries have highly complex vocal and behavioral repertoires which facilitate the detection of small post-operative deficits. Several pure bred strains are commercially available and canaries are easy to keep and breed in captivity; they are quite hardy and respond well to anesthetic and surgical procedures.

METHODS

Selection of plane of section and design of a headholder. The technology of preparing an atlas has grown considerably in recent years and good equipment is available from a number of companies. We chose the Kopt Small Animal Stereotaxic Instrument. The earbars used were the

non-rupturing, blunt "rat-type" supplied with the instrument. The posterior fixation point was the earbar placement in the external auditory canal of the animal.

The most complete and widely used atlas of the avian brain is that of the pigeon by Karten and Hodos ('67). They describe at length the difficulties in selecting an anterior fixation point which produces a convenient and appropriate plane of section. We used the ventral surface of the upper mandible as our anterior fixation point. In the mammal, the anterior and posterior fixation points are usually parallel to the horizontal axis of the instrument. However, because of the bird's upright posture and differing feeding habits, the brain location or cerebral axis within the skull varies in its alignment to the bill axis (Cobb, '60). As a result, the plane of section is not consistent with established mammalian anatomical relationships. Karten and Hodos used an adaptor designed by Dr. Alvin Revzin to support the anterior fixation point. This adaptor places the anterior fixation point 45° below the horizontal axis of the instrument. For our atlas, we reproduced the Revzin pigeon adaptor which is carefully described by Karten and Hodos in their book. The 45° angle of the Revzin adaptor provided an excellent perpendicular section of the forebrain laminae in the canary and made it relatively easy to demarcate forebrain structures.

Our initial headholder included a small bar to support the upper mandible. Later we discovered that this allowed considerable pivotal motion around the bar, even when the earbars were securely fastened in place. As a result, we replaced the bill bar with a bill plate which included a small clamp to attach over the upper mandible. This new bill plate with its dimensions is contained in figure 1. The placement of the head in the stereotaxic instrument, the anterior and posterior fixation points and the angle of penetration of the electrode are also depicted in figure 1.

Surgery. Adult male and female canaries, *Serinus canaria*, of the Wasserschlager breed weighing about 20 gms were used. The animals were deprived of food and water for a minimum of two

hours before surgery and then injected with 0.06–0.08 cc Equithesin.

The head of the bird is placed in the stereotaxic instrument in much the same way that is used for any small mammal or rodent. The external auditory canal is quite easily located by lifting or plucking away the feathers on the side of the head. The earbars can be gently pushed in until a slight resistance is felt and then secured. The average inter-ear distance in our breed was 8 mm. After securing the earbars the bill plate can be placed between the upper and lower mandibles and fitted into the holes in the Revzin adaptor. The clamp is then fitted over the upper mandible and the screws tightened. This draws the bill plate tightly against the upper mandible. The crescent-shaped cut-out in the center of the plate was added to prevent the tongue from touching the metal and causing a choking reflex. The notches in the plate help in centering the beak and head.

With the head placed in the holder, the calvarium was removed and the brain exposed. Marking lesions were made at a number of predetermined loci in both hemispheres using 100 μ diameter stainless uninsulated electrodes in six birds.

After surgery birds were perfused through the left ventricle with 0.9% saline followed by 10% formalin in 0.9% saline. At this time the head was replaced in the stereotaxic holder and the brain blocked with a knife held by the electrode carrier in either the transverse or sagittal plane. This insured that the plane of section was exactly parallel to the penetration of the electrodes. The brain was then removed completely from the skull and fixed in 10% formalin for 6–12 days. After the initial fixation the brain was transferred to a 30% sucrose in 10% formalin solution for three days before embedding.

Histology. The embedding medium was the egg albumin and gelatin method described by Snodgrass and Dorsey ('63) and modified in our lab. The blocked surface of the brain was placed on a platform of 5% hardened gelatin about 3 mm thick in the bottom of a cardboard disposable histo-mold (Lipshaw). The albumin-gelatin solution was added and the histo-mold with its contents placed in a dish with 1/2" concentrated formalin cov-

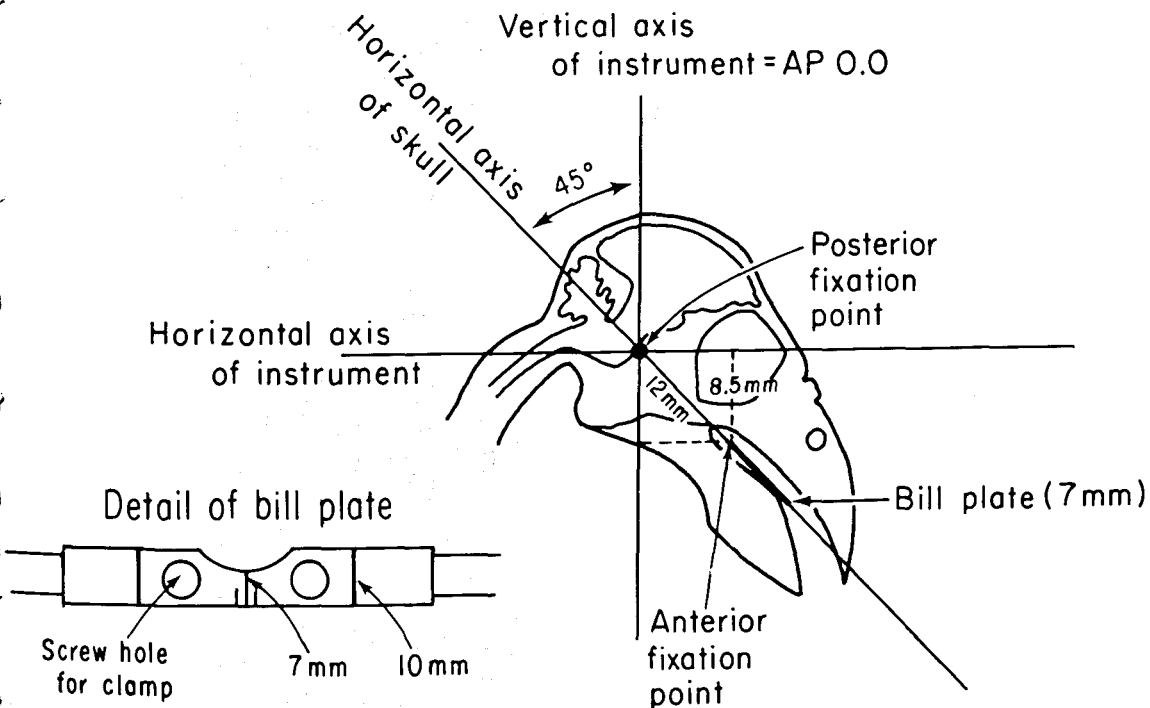


Fig. 1 A diagrammatic representation of the orientation of the skull and brain of the canary with respect to the horizontal and vertical axes of the stereotaxic instrument. If the bill was too overgrown to permit smooth closure over the bill plate, it was clipped slightly at the tip. The Revzin adaptor, which is described completely in Karten and Hodos ('67), is not shown. A top view of the bill plate is shown in the inset. The depth coordinate for lesion placement was calculated relative to the brain surface. The zero on the vertical scale of the plates does not equal ear bar zero.

ering the bottom. The dish was then put in the refrigerator for two to four days.

After the albumin had hardened, the brain was placed on the freezing stage of an A.O. Spencer sliding microtome and sectioned at $50\ \mu$ and $25\ \mu$. Two $25\ \mu$ sections were taken following two $50\ \mu$ sections to maintain a standard distance between stained sections. The $50\ \mu$ sections were collected sequentially into 50% ethyl alcohol and the $25\ \mu$ sections into 10% formalin.

The $50\ \mu$ sections were mounted immediately on chrome-alum (chromium potassium sulfate) gelatinized slides and alternating sections later stained with the cresyl violet stain for Nissl substance and the Weil stain for myelin sheath. The $25\ \mu$ sections were kept one week under refrigeration (40°F) before staining with the Fink-Schneider technique (Schneider, '69) for unmyelinated fibers and cells.

Drawings were made from the cresyl violet stained series using a Bausch and

Lomb microprojector. Major cell nuclei and fiber pathways were outlined and fine structure was filled in using the Weil and Fink-Schneider series.

To estimate the extent of shrinkage the authors compared measurements made in fresh and perfused tissue, embedded tissue, and mounted stained sections. Measurements were made by selecting a standard magnification on the Bausch and Lomb microprojector and then projecting the differently prepared tissues over one another. The numbers obtained from the projected measurements were also compared with the depths and distances of the marking electrode tracks. Less than 5% increase or decrease in size was found in the cresyl violet and Weil series when compared with the fresh or perfused unstained tissue. The Fink-Schneider series on the other hand was found to be up to 10% larger when compared with the fresh or perfused unstained tissue. Consequently these sections were never used for draw-

ing atlas plates and were adjusted when used to identify structures.

No significant difference was found in the size of the three female and three male brains used for the atlas. We hope that the transverse sections represented here are as free as possible of distortion resulting from histological procedure. To test for the accuracy of the atlas a total of 12 lesions were made in several birds. Targets were chosen which were small and represented a full range of depths and anterior-posterior levels. Eleven of these 12 lesions were found to be within the targeted structure. The results of this test, combined with the results of experiments in over 50 birds have shown the atlas to be accurate in 80% of all cases.

COMMENTS

The issue of nomenclature has been a persistent and unresolved problem in the study of the avian brain. The terminology of Huber and Crosby in their classic paper of 1929 is probably the most widely used even though it sometimes conflicts with more recent anatomical data. Many atlas authors have discussed the difficulties in applying their nomenclature (e.g., Karten and Hodós, '67; van Tienhoven et al., '62) but none-the-less it appears to have the most popularity and thus is the most easily understood.

We used this nomenclature for our atlas whenever it did not conflict with more recent findings. In cases where structures were not identified by Huber and Crosby or their nomenclature was confusing, we used the terminology of Karten and Hodós.

Both dashed and solid lines were used to outline nuclei depending on the clarity they gave an individual drawing. Where shading lines were used to indicate fibers, the direction of the lines does not always indicate the direction in which the fibers travel. In large areas where structure was quite complex (e.g., optic tectum or archistriatum) no attempt was made to label small subdivisions. In some cases where we were unable to find any relevant information in the literature about well-defined cell groups, we outlined the structure and left it without a label. It is hoped that future anatomical and physiological work will enable us and other workers to attach

names and functions to an ever increasing number of structures.

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Abbreviations

A, Archistriatum	P0.2-P1.6	FLM, Fasciculus longitudinalis	
Ac, Nucleus accumbens	A4.0	medialis	P0.6-P1.6
AL, Ansa lenticularis	A1.8-A0.6	FPL, Fasciculus prosencephali	
ANI, Nucleus annularis	P1.0-P1.2	lateralis (lateral forebrain	
AP, Area pretectalis	A0.4-P0.8	bundle)	A2.8-A0.8
APH, Area parahippocampalis	P0.6-P1.6	FRL, Formatio reticularis	
AQ, Aqueductus cerebri	AP0.0-P0.6	lateralis mesencephali	A0.6-P0.8
AVT, Area ventralis (Tsai)	A1.0-A0.6	FRM, Formatio reticularis	
B, Nucleus basalis	A6.0-A2.8	medialis mesencephali	A0.6-P0.2
BC, Brachium conjunctivum	A0.2-P1.6	GLV, Nucleus geniculatus lateralis,	
BCA, Brachium conjunctivum		pars ventralis	A2.8-A1.2
ascendens	AP0.0-P0.2	GCT, Substantia grisea centralis	AP0.0-P1.2
BCD, Brachium conjunctivum		HA, Hyperstriatum accessorium	A7.0-A1.0
descendens	P0.6-P1.0	HD, Hyperstriatum dorsale	A7.0-A2.0
BCS, Brachium colliculi superioris	A0.4-P1.2	HIS, Hyperstriatum intercalatus	
BO, Bulbus olfactorius	A7.0	superior	A7.0
Cb, Cerebellum	A0.4-P1.6	HL, Nucleus habenularis lateralis	A0.4-AP0.0
CF, Campi Foreli	A0.8-A0.6	HM, Nucleus habenularis medialis	A0.4-AP0.0
CHCS, Tractus cortico-habenularis et		HP, Hippocampus	A1.8-P0.4
cortico-septalis	A0.8-A0.4	HV, Hyperstriatum ventrale	A7.0-P1.2
CO, Chiasma opticum	A3.5-A2.0	HVdv, Hyperstriatum ventrale,	
CoA, Commissura anterior	A1.6-A1.2	dorsoventrale	A6.0-A5.0
CoS, Nucleus commissuralis septi	A1.6-A1.2	HVvv, Hyperstriatum ventrale,	
CP, Commissura posterior	AP0.0-P0.4	ventroventrale	A6.0-A5.0
CPa, Commissura pallii	A1.2	ICo, Nucleus intercollicularis	AP0.0-P1.2
CS, Nucleus centralis superior		ICT, Nucleus intercalatus thalami	A2.2-A1.8
(Bechterew)	P0.2	III, Nervus oculomotorius	A1.4-P0.6
CT, Commissura tectalis	P0.4-P0.8	IM, Nucleus isthmi, pars magno-	
CTz, Corpus trapezoideum	P0.8-P1.6	cellularis	A1.2-P1.4
D, Nucleus of Darkschewitch	A0.2-AP0.0	IN, Tractus infundibularis	A1.2-A1.0
DA, Tractus archistriatalis dorsalis	A1.0-P1.6	INP, Nucleus intrapeduncularis	A2.0-A1.0
DBC, Decussatio brachiorum		IO, Nucleus isthmo-opticus	P1.4-P1.6
conjunctivorum	P0.2-P1.0	IP, Nucleus interpeduncularis	A0.6-AP0.0
DIP, Nucleus dorsointermedius		IPC, Nucleus isthmi, pars	
posterior thalami	A0.6-A0.4	parvocellularis	A1.0-P1.4
DIV, Decussatio nervi trochlearis	P1.4	IPS, Nucleus interstitio preecto-	
DLAmc, Nucleus dorsolateralis		subpreectalis	A1.0-A0.8
anterior thalami, pars		IS, Nucleus interstitialis (Cajal)	A0.4-AP0.0
magnocellularis	A1.8-A1.6	LA, Nucleus lateralis anterior	
DLL, Nucleus dorsolateralis		thalami	A2.6-A2.4
anterior thalami, pars lateralis	A1.4-A1.0	LAD, Lamina archistriatalis	
DLM, Nucleus dorsolateralis		dorsalis	P0.4-P1.6
anterior thalami, pars medialis	A0.8-A0.6	LFM, Lamina frontalis suprema	A7.0-A2.0
DLP, Nucleus dorsolateralis		LFS, Lamina frontalis superior	A7.0-A1.0
posterior thalami	A0.2	LH, Lamina hyperstriatica (tractus	
DMP, Nucleus dorsomedialis		fronto-occipitalis)	A7.0-AP0.0
posterior thalami	A0.6-P0.2	LHy, Nucleus lateralis	
DS, Decussatio supraoptica	A2.8	hypothalami	A2.4-A1.6
DSD, Decussatio supraoptica		LL, Lemniscus lateralis	P1.2-P1.4
dorsalis	A2.6-A2.2	LLd, Nucleus lemnisci lateralis, pars	
DSV, Decussatio supraoptica		dorsalis (Groebbs)	P1.0-P1.2
ventralis	A2.4-A1.8	LM, Nucleus lentiformis	
E, Ectostriatum	A2.8-A1.0	mesencephali	A2.0-A1.8
EM, Nucleus ectomammillaris	A1.0-A0.6	LMD, Lamina medullaris dorsalis	A6.0-A0.2
Ep, Regio periectostriatalis	A1.6	LoC, Locus ceruleus	P1.4-P1.6
EW, Nucleus of Edinger-Westphal	P0.6-P1.0	LPO, Lobus parolfactorius	A6.0-A1.2
FA, Tractus fronto-archistriatalis	A4.5-P1.4	MLd, Nucleus mesencephalicus	
FDB, Fasciculus diagonalis Brocae	A2.8-A2.6	lateralis, pars dorsalis	AP0.0-P1.0

MLv, Nucleus mesencephalicus lateralis, pars ventralis	A0.6-AP0.0	RSd, Nucleus reticularis superior, pars dorsalis	A1.6
MNV, Nucleus mesencephalicus nervi trigemini	P0.6-P1.2	RSv, Nucleus reticularis superior, pars ventralis	A1.6
MPv, Nucleus mesencephalicus profundus ventralis (Jungherr)	A0.4-AP0.0	Rt, Nucleus rotundus	A2.2-A1.0
MV, Nucleus motorius nervi trigemini	P1.2	Ru, Nucleus ruber	A0.6-AP0.0
N, Neostriatum	A7.0-AP0.0	RxVM, Radix mesencephalicus nervi trigemini	P1.4-P1.6
NC, Neostriatum caudale	P0.2-P1.6	S, Nucleus septalis	A2.6-A0.8
NIII, Nervus oculomotorius	A1.4-P0.6	SAC, Stratum album centrale	P0.6-P1.6
NIV, Nervus trochlearis	P1.0-P1.4	SCE, Stratum cellulare externum	A1.6-A0.8
nIV, Nucleus nervi trochlearis	P1.2-P1.4	SCI, Stratum cellulare internum	A1.4-A0.8
nSt, Nucleus striaterminalis (Karten)	A1.6-A0.6	SGC, Stratum griseum centrale	P0.6-P1.4
OM, Tractus occipitomesencephalicus	A1.6-P1.2	SGF, Stratum griseum et fibrosum superficiale	A0.8-A0.6
OMd, Nucleus nervi oculomotorii, pars dorsalis	P0.2-P0.8	SGP, Substantia grisea et fibrosa periventricularis	A1.2-A0.6
OMv, Nucleus nervi oculomotorii, pars ventralis	P0.2-P0.8	SHL, Nucleus subhabenularis lateralis	A0.2-A0.6
OV, Nucleus ovoidalis	A1.6-A0.6	SLu, Nucleus semilunaris	A0.2-P1.2
PA, Paleostriatum augmentatum	A2.8-P0.2	SM, Nucleus septalis medialis	A2.4-A1.2
pap, Nucleus papillioformis	A0.2-P0.4	SL, Nucleus septalis lateralis	A2.4-A1.2
PD, Nucleus pretectalis diffusus	A0.6	SMe, Stria medullaris	A0.8-A0.6
PL, Nucleus pontis lateralis	P0.2-P1.0	SP, Nucleus subpretectalis	A1.2-A0.8
PLH, Nucleus lateralis hypothalami posterioris	A2.0-A1.8	SPC, Nucleus superficialis parvocellularis (nucleus of septomesencephalic tract)	A1.0-P0.4
PM, Nucleus pontis medialis	P0.2-P1.4	SpL, Nucleus spiriformis lateralis	A1.0
PMH, Nucleus medialis hypothalami posterioris	A2.2-A1.2	SpLd, Nucleus spiriformis lateralis, pars dorsalis	A0.8-A0.6
PMI, Nucleus paramedianus internis thalami	A0.4	SpLv, Nucleus spiriformis lateralis, pars ventralis	A0.8-A0.6
POA, Nucleus preopticus anterioris	A2.8	SpM, Nucleus spiriformis medialis	A0.4-P0.2
POM, Nucleus preopticus medialis (van Tienhoven)	A2.6	SRt, Nucleus subrotundus	A1.2-A1.0
PP, Paleostriatum primitivum	A2.6-A0.2	TeO, Tectum opticum	A2.6-P1.6
PPC, Nucleus principalis precommissuralis	A1.4-AP0.0	TFM, Tractus thalamo-frontalis et frontalis-thalamicus medialis	A4.0-A3.5
PPM, Nucleus preopticus paraventricularis magnocellularis (van Tienhoven)	A2.6		A2.6-A1.4
PrV, Nucleus sensorius principalis nervi trigemini	P1.6	TIO, Tractus isthmo-opticus	A2.4-P1.2
PST, Tractus pretecto-subpretectalis	A0.8	Tn, Nucleus taeniae	P0.2-P1.4
Pt, Nucleus pretectalis	A0.8-A0.6	ToS, Torus semicircularis	A0.4-A0.2
PV, Nucleus posteroventralis thalami (Kuhlenbeck)	A1.8-A1.2	TOV, Tractus nuclei ovoidalis	A1.4-A1.0
PVM, Nucleus paraventricularis magnocellularis	A2.4-A1.0	TPc, Nucleus tegmenti pedunculo-pontinus, pars compacta	A0.4-P0.4
QF, Tractus quinfofrontalis	A5.0-P0.8	TrEM, Tractus nuclei ectomamil-laris (basal optic root)	A1.2
R, Nucleus Raphes	P1.0-P1.2	TrO, Tractus opticus	A2.8-P0.2
RPgc, Nucleus reticularis pontis caudalis, pars gigantocellularis	P1.0-P1.6	TrSM, Tractus septomesencephalicus	A7.0-AP0.0
RPO, Nucleus reticularis pontis oralis	P0.4-P0.8	TT, Tractus tectothalamicus	A2.0-A1.0
		Tu, Nucleus tuberis	A1.6-A1.2
		TV, Nucleus tegmenti ventralis (Gudden)	P1.2-P1.4
		TVM, Tractus vestibulo-mesencephalicus (Papez)	P0.8-P1.0
		V, Ventricle	
		VLT, Nucleus ventrolateralis thalami	A2.4-A2.0
		VLV, Nucleus ventralis lemnisci lateralis	P0.8-P1.0

