THE ARCHISTRIATUM OF THE PIGEON: ORGANIZATION OF AFFERENT AND EFFERENT CONNECTIONS

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INTRODUCTION

The archistriatum is a large and heterogeneous nuclear mass in the caudal ventrolateral portion of the avian telencephalon. Early investigators suggested that this large and complex mass corresponds to the mammalian amygdala[1], because of (a) its seemingly extensive relationship to the anterior commissure, a notion long prevalent in regard to the mammalian amygdala as well; (b) its contribution to a tract considered equivalent to the stria terminalis of mammals; (c) its apparent relationship to the hypothalamus; and (d) assorted behavioral observations on the effects of archistriatal lesions on 'taming', egg laying, aggressive behavior, motivational behavior and similar phenomena[14]. However, little or no information is available on the cytoarchitecture, nuclear subdivisions, different origins or terminations of efferent and afferent systems of the archistriatum. A series of studies were initiated to clarify the nature and organization of this large neuronal mass. The present paper is intended to provide a general overview of the problem; more detailed accounts of the different systems will be presented in subsequent publications.

MATERIAL AND METHODS

A total of 60 pigeons sustained unilaterally either surgical lesions, electrolytic coagulation lesions or cut lesions produced with a razor blade scalpel. The animals were anesthetized with Equithesin® (0.25 ml/100 g body wt.). The head was fixed in a stereotaxic instrument. Surgical lesions were brought under visual control by sucking away the brain tissue with a pipette. All other lesions were made by stereotaxic electrolysis at loci determined by the aid of the atlas of Karten and Hodos[10]. Unipolar stainless steel electrodes (0.3 mm diameter) were used for electrolytic coagulation. An anodal DC current of 1–3 mA passed through the uninsulated tip of the electrode for 20 sec gave reliable lesions of 1–3 mm diameter. The indifferent electrode was fixed to the skin of the animal's head. Thirty-four animals received lesions in the archistriatum, and 6 animals received control lesions in the overlying hyper- and neo-

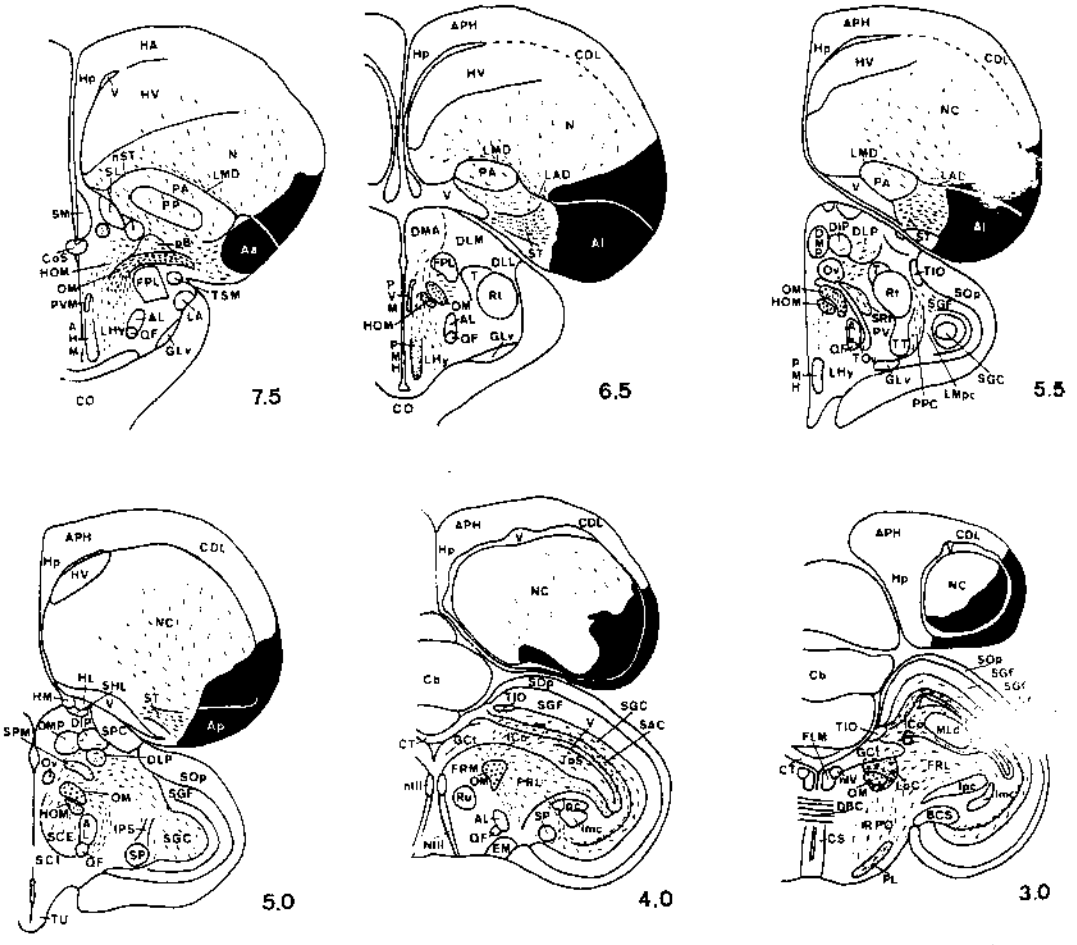

Fig. 1. Degeneration found 3 days after unilateral ablation of the archistriatum. Small lines symbolize degenerated nerve fibres, fine stipple indicates the presence of terminal degeneration and the numbers give the distance from the stereotaxic zero plane in millimeters according to the atlas of Karten-Hodos[10] in this and all subsequent figures. × 4. See Table of Abbreviations for identification of structures.

striatum. In 8 animals a horizontal cut was made with a 2 mm wide strip of razor blade inserted immediately dorsal to the archistriatum, and 9 animals sustained a vertical incision medial to the archistriatum interrupting the tractus occipitomesencephalicus. After a postoperative period of 2–20 days, the deeply narcotized animals were perfused with a physiological saline solution, followed by 10% formol-saline. The further processing was done as follows: removal of the skull and fixation in 10% formalin for 1–4 weeks, immersion for about two days in a 30% sucrose solution containing 10% formalin, embedding of the brain in albumin[16] and sectioning at 25 μm on a freezing microtome. Every 8th section was stained with the Fink–Heimer[2] modification of the Nauta–Gygax[12] method, while the adjacent sections were stained with cresylecht-violet. The charting of relevant silver sections was done with an electronic panto-

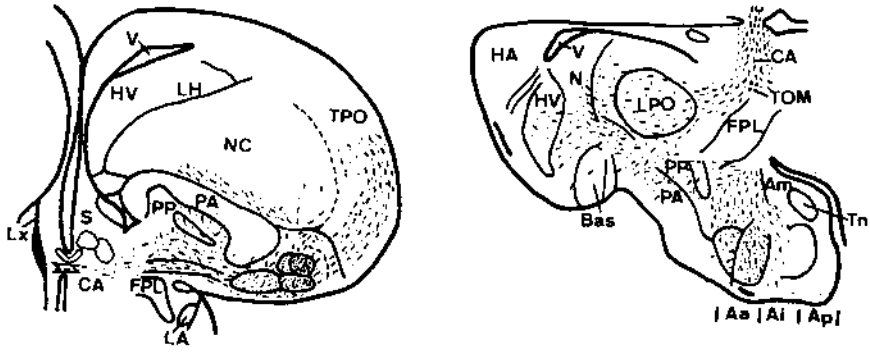

Fig. 2. Projections of the anterior commissure depicted in frontal (left) and horizontal (right) planes. Note that only the anterior part of the archistriatum receives fibers from the anterior commissure. 11 days postoperative survival time. × 5. Lx, lesion interrupting the anterior commissure. See Table of Abbreviations for identification of structures.

graph. Corresponding cresyl sections were examined in order to identify the topography and the subnuclei of the archistriatum.

RESULTS

Degenerations found after archistriatal lesions are shown in Fig. 1 charted from case PF-36 with a huge archistriatal lesion and a postoperative survival of 3 days. In the telencephalon, projections from the archistriatum terminate in the nucleus commissuralis anterior, pars bulbaris, in the nucleus of the stria terminalis and in circumscribed regions of the central, medial and lateral septa. Of all septal regions the central nucleus contains the most extensive degeneration (Fig. 1, plate 7.5). Some fibers originating from the archistriatum reach the opposite hemisphere as a component of the anterior commissure, and either terminate there in the nucleus commissuralis anterior, pars bulbaris, and to a lesser degree in the archistriatum anterior, or leave the forebrain as a crossed component of the tractus occipitomesencephalicus. This crossed pathway will be discussed below.

Distribution of the anterior commissure

Fig. 2 illustrates how the anterior commissure branches into a pars bulbaris and a pars temporalis. Fibers of the pars bulbaris terminate in the nucleus commissuralis anterior, pars bulbaris, and along its entire rostral projection which extends as far as into the lobus parolfactorius. The pars temporalis of the anterior commissure reaches the archistriatum anterior and the overlying neostriatum. However, only a moderate amount of terminal degeneration is found in the archistriatum anterior, the remaining portions of the archistriatum being completely free of degeneration.

Extratelencephalic projections of the archistriatum OM and HOM

Two descending pathways, the tractus occipitomesencephalicus (OM) and the

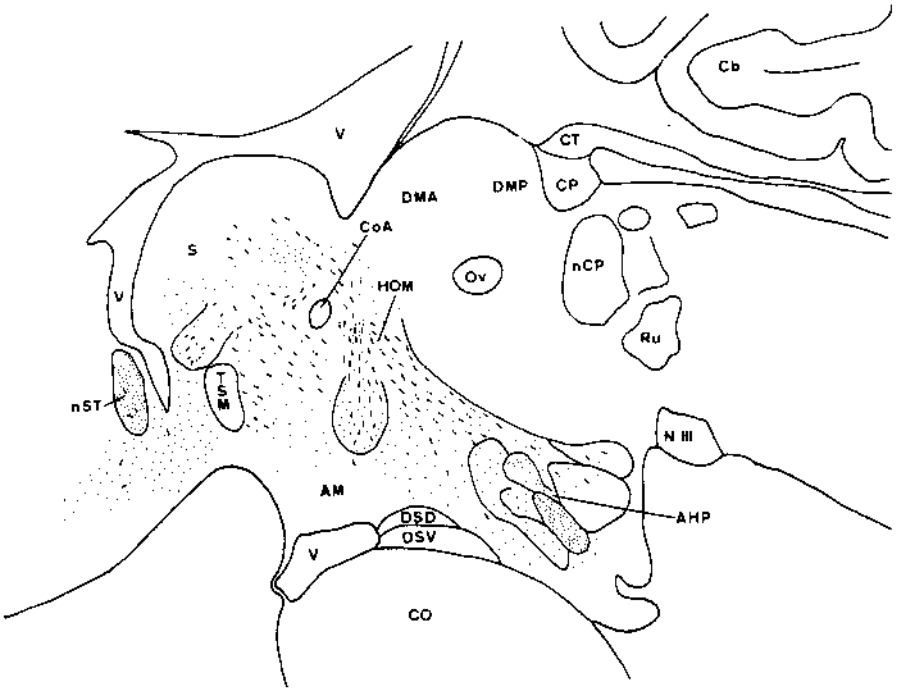

Fig. 3. Sagittal section through the medial hypothalamus showing the pattern of HOM degeneration. 4 days postoperative survival time. × 10. See Table of Abbreviations for identification of structures.

tractus occipitomesencephalicus, pars hypothalami (HOM) connect the archistriatum with subtelencephalic structures. OM is a compact bundle of thick fibers leaning caudally against the anterior commissure and accompanying this bundle toward the midline. However, it separates from the commissure before reaching the midline and sweeps down into the diencephalon. HOM on the other hand consists of thinner fibers joining OM as dorsal and caudal neighbors. Terminals can be found along the entire course of HOM. Most of the HOM fibers lead into the medial hypothalamus while the lateral hypothalamus, the stratum cellulare internum and thes tratum cellulare externum receive only a few of the HOM fibers (Fig. 1, plate 7.5, 6.5, 5.5 and 5.0). The distribution of HOM can best be seen in a sagittal section through the medial hypothalamus; Fig. 3, taken from case PF-84 with a survival time of 4 days, shows that the posterior parts of the hypothalamus, especially two outstanding nuclei, receive the densest projections.

The course of OM is also depicted in Fig. 1. OM fibers terminate in the dorsal thalamus, predominantly in posterior thalamic nuclei such as DLP and DlP (Fig. 1). Even more intense degeneration is found in the lateral part of the nucleus pirifo medialis, in the nucleus subrotundus and in the nucleus principalis precommissuralis (Fig. 1, plates 5.5 and 5.0). A significant contingent of OM fibers projects into the formatio reticularis lateralis (Fig. 1, plate 4.0; Fig. 4), into the nucleus intercollicularis (ICo: Fig. 1, plates 4.0 and 3.0) and through the stratum album centrale into the

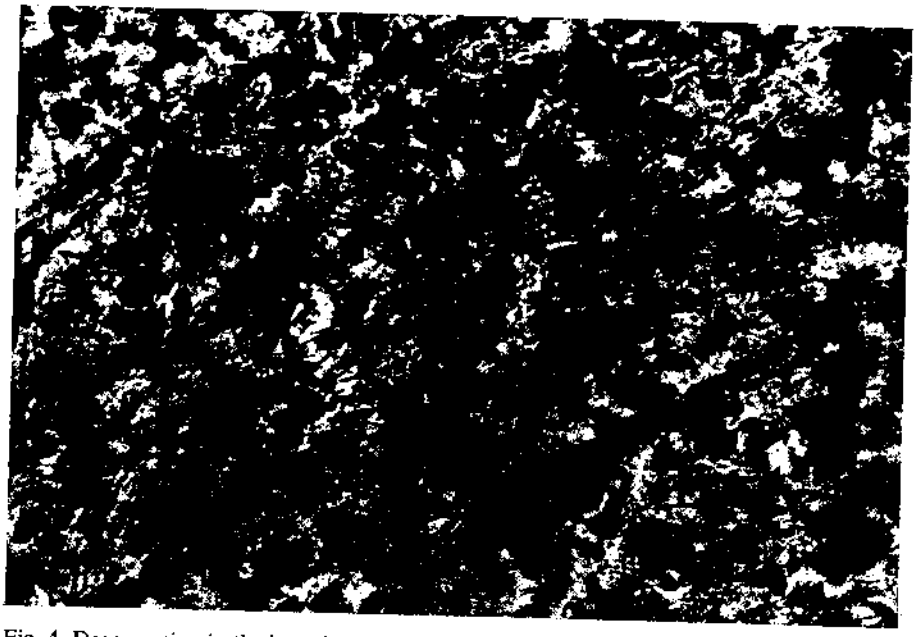

Fig. 4. Degeneration in the lateral reticular formation following an archistriatal lesion. 4 days postoperative survival time. Fink–Heimer stain. × 480.

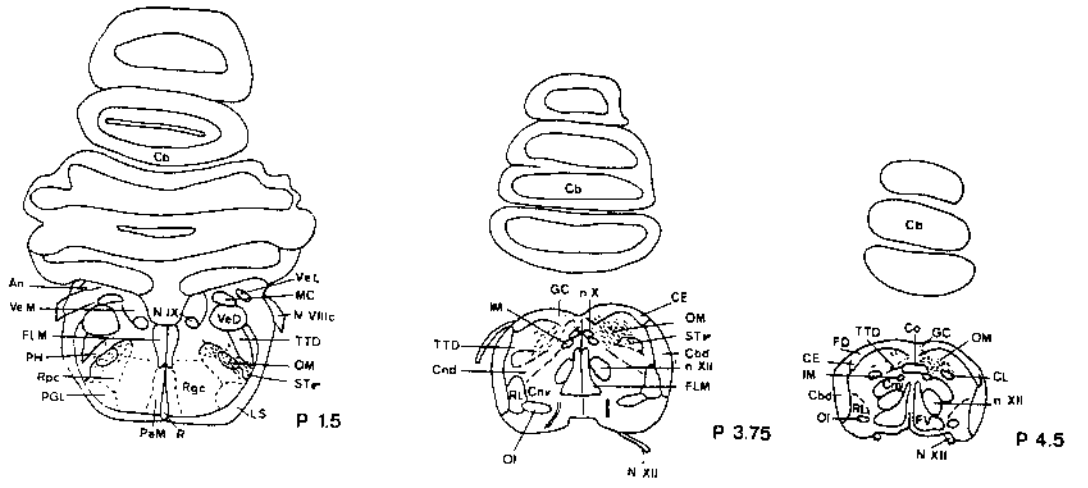

Fig. 5. Degenerations found after the tractus occipitomesencephalicus had been cut on the right side. 11 days postoperative survival time. × 4. See Table of Abbreviations for identification of structures.

stratum griseum centrale of the optic tectum. However, the outer layers of the optic tectum and the nucleus mesencephali lateralis, pars dorsalis are completely free of degeneration (Fig. 1, plates 4.0 and 3.0). In the brain stem, massive fiber degeneration is found in the locus coeruleus. Additional fiber degeneration appears in the nucleus subcoeruleus dorsalis and ventralis, and in the nucleus pontis lateralis.

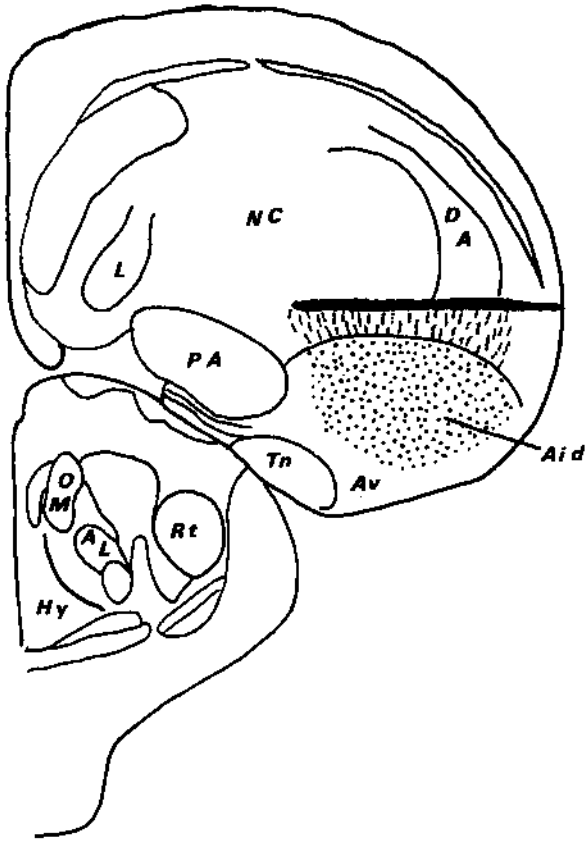

Fig. 6. Horizontal overcut dorsal to the archistriatum. After such lesions there is no evidence of degeneration of the tractus occipitomesencephalicus. The field in the center of the archistriatum with an extreme density of degeneration indicates the termination area of the tractus archistriatalis dorsalis. 6 days postoperative survival time. × 7.5. See Table of Abbreviations for identification of structures.

The continuation of OM and its crossed component is shown in Fig. 5 (case PF-97 with a survival time of 11 days). The right OM and HOM were cut with a razor blade. Degeneration is located on the ipsilateral side in the nucleus reticularis parvocellularis, nucleus subtrigeminalis, nucleus descendens nervi trigemini and in the nuclei gracilis and cuneatus. The crossed component of OM can be followed to the corresponding nuclei in the brain stem and upper cervical cord as indicated in Fig. 5. However, no degeneration is found contralateral to the lesions in HOM, stria terminalis, septum, thalamus, hypothalamus or tectum opticum.

Locus of origin of OM

The following experiment proves that OM originates exclusively from the archistriatum and not from the overlying neostriatum. A horizontal cut immediately dorsal to the archistriatum (Fig. 6) does not result in any degeneration in OM. How-

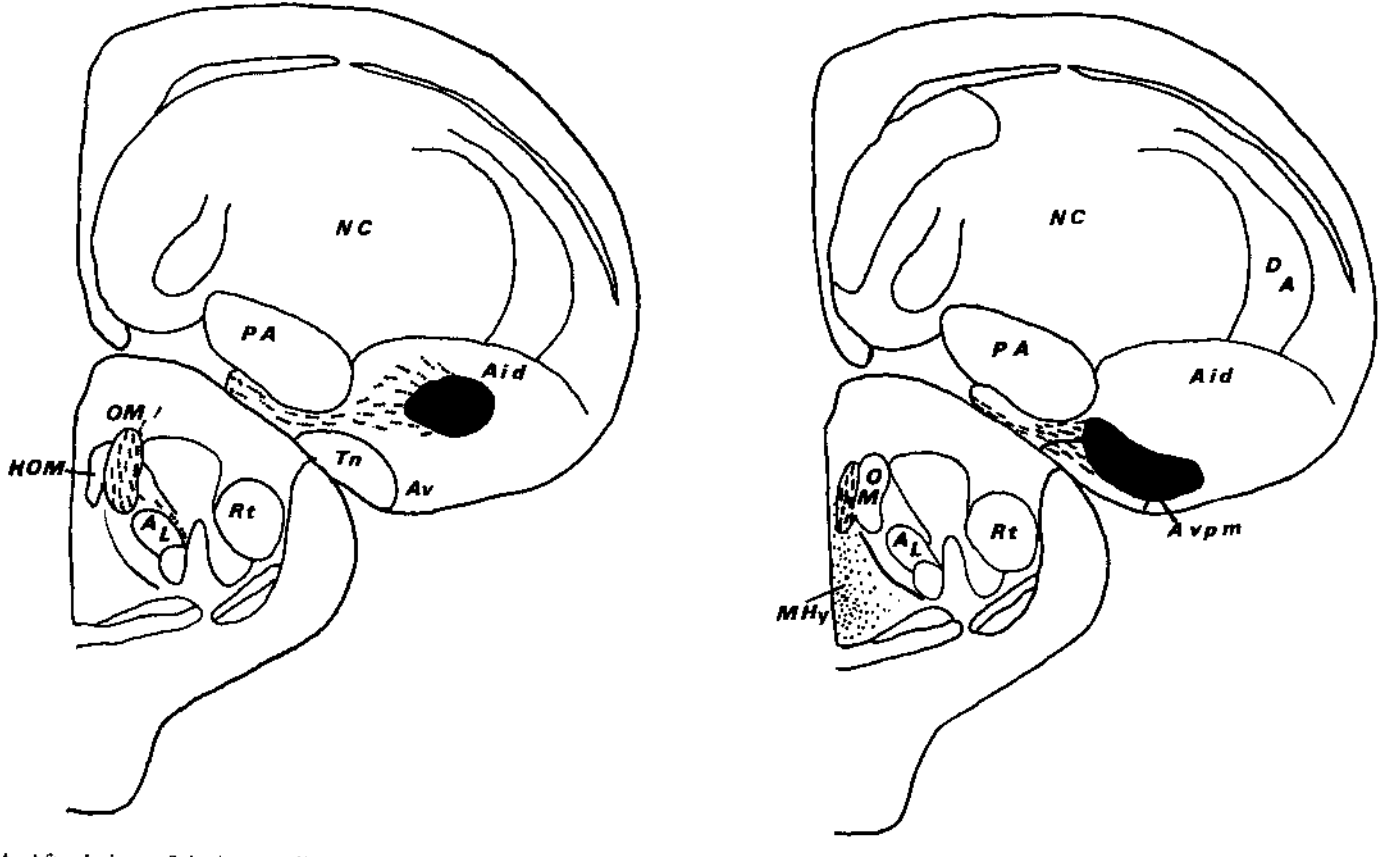

Fig. 7. A, After lesions of the intermediate region of the archistriatum, fibers of the tractus occipitomesencephalicus are degenerated. × 7.5. B, After a lesion of the postero-medial portions of the archistriatum, degeneration is confined to the HOM. × 7.5. See Table of Abbreviations for identification of structures.

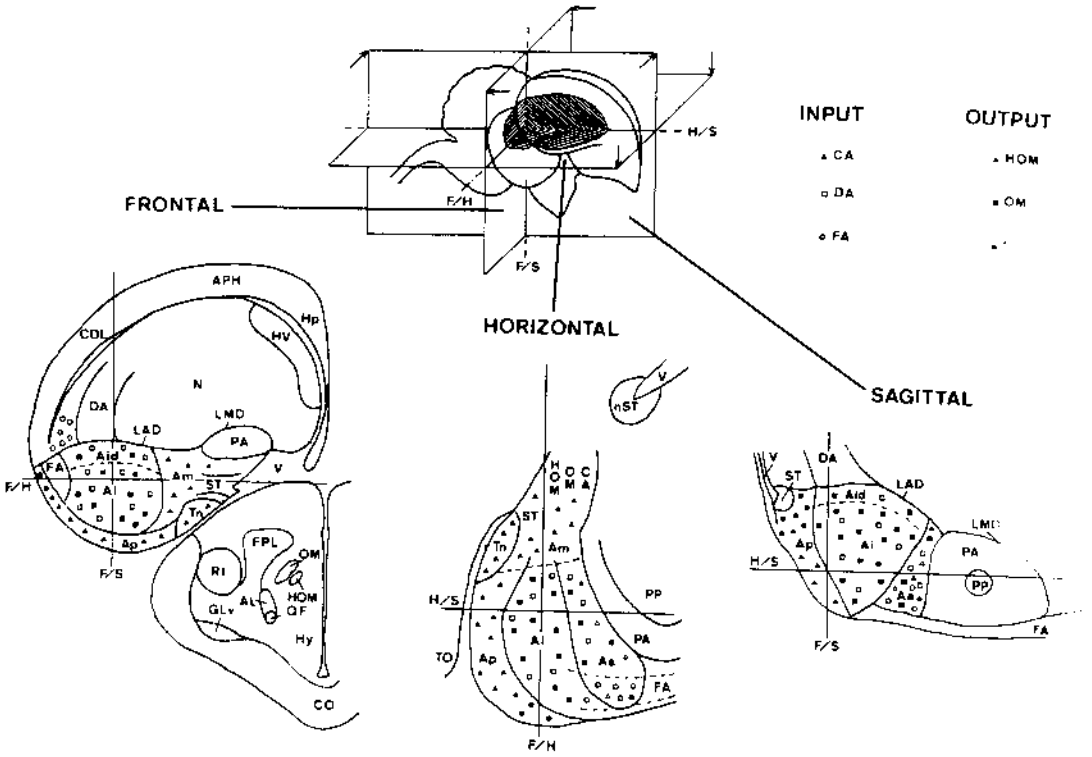

Fig. 8. Subdivisions of the archistriatum depicted in frontal (F), horizontal (H) and sagittal (S) planes with some of their afferents (input) and efferents (output). See Table of Abbreviations for identification of structures.

ever, even slight involvement of the dorsal archistriatum (Fig. 7A) results in prominent degeneration in OM, whereas HOM degenerates after lesions in the postero-medial portions of the archistriatum (Fig. 7B). In the archistriatum itself the horizontal overcuts always elicit dense terminal degeneration in a region apparently corresponding to the distribution of the tractus archistriatalis dorsalis which is unavoidably interrupted by these cuts. The evaluation of 32 cases with lesions in various regions of the archistriatum suggests a division of the archistriatum into 4 major regions: the archistriatum anterior, the archistriatum intermedium, the archistriatum posterior, including a postero-ventral portion, and the archistriatum mediale. Cytoarchitecturally, 4–8 discrete nuclei can be identified within each of these regions. The approximate boundaries of these regions and some of their afferents and efferents are shown in Fig. 8 in the frontal, sagittal and horizontal planes. The *archistriatum anterior* (Aa) is the only part of the archistriatum receiving an input from the anterior commissure (Fig. 2). A further input comes from the tractus archistriatalis dorsalis and tractus fronto-archistriatalis. The latter bundle crosses the archistriatum anterior and further projects caudally into a region of the neostriatum dorsal to the archistriatum. Efferents of the archistriatum anterior form a small component of OM. The *archistriatum intermedium* (Ai) contains most of the terminal fields of the tractus archistriatalis dorsalis

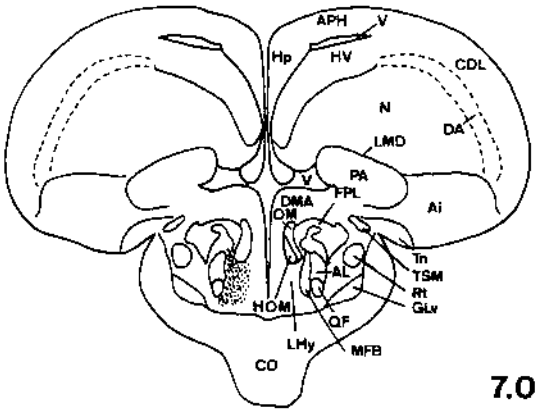

Fig. 9. Terminal field of the medial forebrain bundle in the lateral hypothalamus following an ipsilateral lesion in the lobus parolfactorius. 6 days postoperative survival time. × 4. See Table of Abbreviations for identification of structures.

and is the major source of origin of OM, with its long ipsi- and contralateral projections down to the brain stem and rostral cervical segments. Lesions in the *archistriatum posterior* (Ap) cause no degeneration in OM, but elicit degeneration in the stria terminalis which can be traced into the nucleus striae terminalis, a cell group positioned around the ventral anterior aspect of the forebrain ventricle (Fig. 1, plate 7.5), and in lesser quantity to the hypothalamus. Degeneration to these latter hypothalamic afferent fibers is found especially when the lesion involves the postero-ventral archistriatum. Lesions in the *archistriatum mediale* and in the nucleus taeniae produce a considerable amount of degeneration in the medial hypothalamus via HOM, but only scattered degeneration in the lateral hypothalamus. The lateral hypothalamus can be clearly delineated from the medial hypothalamus by the terminal field of the medial forebrain bundle. This bundle degenerates after a lesion in the lobus parolfactorius and anterior preoptic area, as illustrated in Fig. 9.

DISCUSSION

The avian archistriatum is commonly regarded as the homolog of the mammalian amygdala, and thus as an essential part of the limbic system, closely related to the hypothalamus. The present anatomical findings dispute this simple generalization, but rather suggest a division of the archistriatum into 4 major regions: the archistriatum anterior, intermedium, posterior and mediale. The posterior third and the most medial parts of the archistriatum (archistriatum posterior and mediale) are connected with the hypothalamus through the tractus occipitomesencephalicus, pars hypothalami, and thus may correspond to the mammalian amygdala. However, for a direct comparison of the subnuclei identifiable within this region with the known nuclei of the mammalian amygdala[8], more anatomical and physiological data would be needed from mammals as well as from birds. The anterior two-thirds of the archistriatum (archistriatum anterior and intermedium) form the origin of the nonhypothalamic

tractus occipitomesencephalicus. This bundle consists of fibers thicker than those of the hypothalamic projection; it projects to the thalamus, optic tectum, tegmentum, lateral reticular formation, lateral pontine nuclei, sensory nuclei of the brain stem, and to a minor extent even down to the rostral levels of the spinal cord. In its course and distribution this fiber tract strongly resembles Bagley's bundle in the goat[3], a fiber system often considered to be a variant form of the pyramidal tract of primates. This similarity suggests that the anterior two-thirds of the archistriatum may be involved in somatic rather than viscero-endocrine effector mechanisms, and may indeed, as proposed earlier by Zecha[18], be compared to the pericentral cortex of the goat and the sensorimotor cortex of primates, respectively. The most massive telencephalic afferents to the archistriatum, the tractus archistriatalis dorsalis and, to a lesser degree, the tractus frontoarchistriatalis, terminate in this somatic subdivision of the archistriatum. The path of the tractus archistriatalis dorsalis might have misled earlier investigators into the assumption that the tractus occipitomesencephalicus originates from the archistriatum and from the overlying neostriatum. However, the present study clearly refutes this assumption and supports Herrmann's[5] earlier suggestion that the tractus occipitomesencephalicus emerges exclusively from the archistriatum. Finally, fibers of the anterior commissure appear to be distributed only to the most anterior part of the archistriatum, whereas the remaining portions of the archistriatum receive no commissural connections. This finding is compatible with the results of recent studies in the rabbit[17], in the rat[15], and in the monkey[11], which suggest that commissural associations of the amygdala are also quite limited in these mammalian forms.

According to the results here reported, the most caudal and medial parts of the archistriatum can be considered 'limbic', whereas the anterior two-thirds of the archistriatum appear to be 'somatic sensorimotor' in nature. Both regions give rise to descending pathways from the telencephalon and are morphologically separated from the major primary sensory projection fields (*e.g.*, nucleus basalis, ectostriatum, Field 'L' and Wulst). In mammals, the 'somatic' efferents (*e.g.*, the pyramidal tract arising from the neocortex) and the 'limbic' efferents (*e.g.*, stria terminalis) originate from widely separated and morphologically discrete regions of the brain. The present findings in the bird indicate the existence of directly comparable paths that arise from adjacent, though equally distinct, cell groups. The long descending connections of the archistriatum to the brain stem appear to act primarily on internuncials in the lateral reticular formation and only indirectly on the medial reticular formation, *i.e.*, by polysynaptic projections. The recent study of Harting and Martin[4] on cortical projections in the armadillo demonstrates direct projections only to the lateral reticular formation, and not to the medial magnocellular reticular regions. This pattern may well represent the original mode of distribution of the long telencephalic efferents of many primitive mammals, of birds, and possibly other vertebrates. Some understanding of the apparent discrepancy in morphology of the respective zones of origin of such connections in birds and mammals may be forthcoming if we consider the embryology of selected regions of the archistriatum of birds and of the cortex of mammals. Both the archistriatum of birds and parts of the

neocortex of mammals may be derived from the hypopallial eminence of the dorsal ventricular ridge[6,7]. In a manner outlined by Karten[9] and Nauta and Karten[13] neuroblasts of the hypopallial eminence of mammals may migrate into the pallium, thus contributing to the formation of the mammalian neocortex, while the homologous neuroblast population in non-mammalian classes remains approximately *in situ* and thus comes to compose an apparently 'striatal' structure with connections and functional associations comparable to those of the mammalian neocortex, despite the difference in gross location in the telencephalon. Further comparative studies of these telencephalofugal pathways in non-mammalian vertebrates may be expected to contribute to a better understanding of the nature and evolution of the mammalian neocortex, as well as the more apparent benefits in attempts to understand the avian brain.

SUMMARY

The avian archistriatum, usually considered homologous with the mammalian 'amygdaloid complex', was studied in the pigeon by the aid of silver impregnation methods for degenerating nerve fibers and nerve endings. The results obtained suggest a subdivision of the archistriatum into 4 major regions: the archistriatum anterior, intermedium, posterior (with a postero-ventral portion) and mediale. The archistriatum posterior and mediale give rise to descending pathways terminating in the medial and lateral hypothalamus, and may therefore be comparable to the mammalian amygdala. The archistriatum anterior is the only part of the archistriatum receiving afferents from the anterior commissure and from the tractus fronto-archistriatalis, whereas the archistriatum intermedium encompasses most of the terminal fields of the tractus archistriatalis dorsalis. The anterior and intermediate regions appear to be associated mainly with the 'somatic sensorimotor' system, since they issue the long ipsi- and contralateral projections of the tractus occipitomesencephalicus to the brain stem and rostral spinal cord. These long descending connections strongly recall the picture of Bagley's bundle of ungulates, a fiber bundle often considered a variant form of part of the pyramidal tract of primates.

TABLE OF ABBREVIATIONS

Aa	= archistriatum anterior	APH	= area parahippocampalis
AH	= hypothalamus anterior	Av	= archistriatum ventrale
AHM	= nucleus anterior medialis hypothalami	Avpm	= archistriatum ventrale posterior et mediale
AHP	= area hypothalami posterioris	BCS	= brachium colliculi superioris
Ai	= archistriatum intermedium	CA	= commissura anterior
Aid	= archistriatum intermedium, pars dorsalis	Cb	= cerebellum
		Cbd	= tractus spinocerebellaris dorsalis
AL	= ansa lenticularis	CDL	= area coiticoidea dorsolateralis
AM	= hypothalamus anterior, pars medialis	CE	= nucleus cuneatus externus
		CL	= nucleus cervicalis lateralis
Am	= archistriatum mediale	Cnd	= nucleus centralis medullae oblongatae, pars dorsalis
An	= nucleus angularis		
Ap	= archistriatum posterior	Cnv	= nucleus centralis medullae oblon-

gatae, pars ventralis
CO = chiasma opticum
Co = nucleus commissuralis (Haller)
CoS = nucleus commissuralis septi
CP = commissura posterior
CS = nucleus centralis superior
CT = commissura tectalis
DA = tractus archistriatalis dorsalis
DAT = thalamus dorsalis anterior
DBC = decussatio brachiorum conjunctivorum
DIP = nucleus dorsointermedius posterior thalami
DLL = nucleus dorsolateralis anterior thalami, pars lateralis
DLM = nucleus dorsolateralis anterior thalami, pars medialis
DLP = nucleus dorsolateralis posterior thalami
DMA = nucleus dorsomedialis anterior. thalami
DMP = nucleus dorsomedialis posterior
DPT = thalamus dorsalis posterior
DSD = decussatio supraoptica dorsalis
DSV = decussatio supraoptica ventralis
EM = nucleus ectomammillaris
FA = tractus fronto-archistriatalis
FLM = fasciculus longitudinalis medialis
FPL = fasciculus prosencephali lateralis
FRL = formatio reticularis lateralis mesencephali
FRM = formatio reticularis medialis mesencephali
GC = nucleus gracilis et cuneatus
GCt = substantia grisea centralis
GLv = nucleus geniculatus lateralis, pars ventralis
HA = hyperstriatum accessorium
HL = nucleus habenularis lateralis
HM = nucleus habenularis medialis
HOM = tractus occipitomesencephalicus, pars hypothalami
Hp = hippocampus
HV = hyperstriatum ventrale
Hy = hypothalamus
IC = nucleus intercalatus
ICo = nucleus intercollicularis
IM = nucleus intermedius
Imc = nucleus isthmi, pars magnocellularis
Ipc = nucleus isthmi, pars parvocellularis
IPS = nucleus interstitio-pretecto-subpretectalis
L = Field 'L'
LA = nucleus lateralis anterior thalami
LAD = lamina archistriatalis dorsalis
LHy = hypothalamus lateralis
LMD = lamina medullaris dorsalis
LMpc = nucleus lentiformis mesencephali, pars parvocellularis
LoC = locus coeruleus
LS = lemniscus spinalis
MC = nucleus magnocellularis
MFB = fasciculus prosencephali medialis
MHy = hypothalamus medialis
MLd = nucleus mesencephalicus lateralis, pars dorsalis
N = neostriatum
NC = neostriatum caudale
NIII = nervus oculomotorius
NVIIIc = nervus octavus, pars cochlearis
NXII = nervus hypoglossus
nCP = nucleus commissura posterior
nST = nucleus striae terminalis
nIII = nucleus nervi occulomotorii
nIV = nucleus nervi trochlearis
nIX = nucleus nervi glossopharyngei
nX = nucleus motorius dorsalis nervi vagi
nXII = nucleus nervi hypoglossi
OI = nucleus olivaris inferior
OM = tractus occipitomesencephalicus
OS = nucleus olivaris superior
Ov = nucleus ovoidalis
P = posterior
PA = paleostriatum augmentatum
PaM = nucleus paramedianus
pB = commissura anterior, pars bulbaris
PGL = nucleus paragigantocellularis lateralis
PH = plexus of Horsley
PL = nucleus pontis lateralis
PMH = nucleus medialis hypothalami posterioris
PP = paleostriatum primitivum
PPC = nucleus principalis precommissuralis
PT = nucleus pretectalis
PV = nucleus posteroventralis thalami
PVM = nucleus periventricularis magnocellularis
QF = tractus quintofrontalis
R = nucleus raphes
Rgc = nucleus reticularis gigantocellularis
RL = nucleus reticularis lateralis
RPO = nucleus reticularis pontis oralis
Rpc = nucleus reticularis parvocellularis
Rt = nucleus rotundus
Ru = nucleus ruber
S = septum
SAC = stratum album centrale
SC = stratum cellulare
SCE = stratum cellulare externum
SCI = stratum cellulare internum
SGC = stratum griseum centrale
SGF = stratum griseum et fibrosum superficiale

SGP = substantia grisea et fibrosa periventricularis
SHL = nucleus subhabenularis lateralis
SL = nucleus septalis lateralis
SM = nucleus septalis medialis
SOp = stratum opticum
SP = nucleus subpretectalis
SPC = nucleus superficialis parvocellularis
SPM = nucleus spiriformis lateralis
SRt = nucleus subrotundus
ST = stria terminalis
STr = nucleus subtrigeminalis
T = nucleus triangularis
TIO = tractus isthmo-opticus
Tn = nucleus taeniae
ToS = torus semicircularis
TOv = tractus nuclei ovoidalis
TrO = tractus opticus
TS = tractus solitarius
TSM = tractus septomesencephalicus
TT = tractus tectothalamicus
TTD = nucleus et tractus descendens nervi trigemini
TU = nucleus tuberis
V = ventriculus
VeD = nucleus vestibularis descendens
VeL = nucleus vestibularis lateralis
VeM = nucleus vestibularis medialis
VH = hyperstriatum ventrale

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