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THE AMYGDALOID COMPLEX IN THE RAT

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A THESIS

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CHAPTER I

INTRODUCTION

General Consideration

Normal and experimental anatomical studies of the amygdaloid complex have been carried out by a number of investigators during this century. A variety of species have been used and different terminologies have been established in different countries. In most of these studies Nissl and normal fibre stains have been employed to define the boundaries and describe the cytoarchitecture of the different nuclei and as well to identify some amygdaloid connections.

The amygdaloid nucleus as a whole occupies a large part of the ventral aspect of the cerebral hemisphere. It extends from the posterior plane of the anterior commissure to a plane near the posterior extremity of the hemisphere. Laterally it is limited by the external capsule, claustrum and the piriform cortex. Medially it is bounded by the preoptic region, hypothalamic area and optic tract. The caudate-putamen lies dorsally. Ventrally the periamygdaloid cortex lies superficial to it. (Figs. 1 and 2).

Johnston ('23) divided the nuclei of the amygdala into two groups on the basis of embryonic origin and phylogenetic age; a basolateral complex consisting of the lateral the basal and the accessory basal nuclei and a corticomedial group composed of the

cortical, medial and central nuclei and, as well, the nucleus of the lateral olfactory tract and the anterior amygdaloid area. Fox ('40, cat) classified the last two nuclei as a separate group on the basis of their anterior position. More recently, Koikegami and his group ('63) placed the small-celled part of the basal nucleus (APM of their terminology) in the corticomedial division on the basis of their functional studies. In the present text the original terminology of Johnston will be used.

According to Johnston ('23) the corticomedial group represents the ancient olfactory area of fishes while the basal and lateral nuclei are new centers formed in the land animal by the processes of growth, cell migration and infolding of the piriform lobe. Humphrey ('68), however, in a study of the development of amygdala in the human fetus, found no evidence of any infolding or inward cell migration from the surface. According to her, the appearance of "infolding" in older fetal and adult brains represents an area in which cell migration has not progressed so far outward toward the surface as in the adjacent areas. In addition Humphrey ('68) observed that the central nucleus appears later in development than the other amygdaloid nuclei, with the exception of the nucleus of the lateral olfactory tract. She noted that if early age of development indicates primitiveness then the central nucleus and the nucleus of the lateral olfactory tract are the least primitive areas of the

amygdala. However, Johnston ('23) on the basis of phylogeny considered both of these nuclei to be members of the more primitive part. The basal nucleus is seen in reptiles and the lateral nucleus makes its first appearance in marsupials. (Johnston, '23).

Evoked potentials can be elicited throughout the whole extent of the amygdaloid complex when the olfactory bulb is stimulated (Berry et al, '52; Hugelin et al, '52). However, it is only in the corticomedial amygdaloid complex and medial portion of the basal nucleus that the latency is short (3-5 m.sec.) and there is no overlapping with other modalities. These areas can be regarded as part of the specific olfactory receiving area (Hugelin et al, '52). There is no doubt that the amygdala receives an inflow of olfactory impulses. However, the anatomical observations suggest that the amygdala as a whole cannot be related very closely to the olfactory sense. In this regard it should be noted that the completely anosmatic aquatic mammals, like the dolphin or the porpoise, possess a very well developed amygdala. Not even the corticomedial complex shows any sign of regression except for the nucleus of the lateral olfactory tract (Addison, '15; Langworthy, '32; Breathnach and Goldby, '54). Further, it has been shown that bilateral destruction of the amygdala does not affect olfactory discrimination in rats or dogs .

Physiological studies have demonstrated that evoked potentials

from stimulating all sensory modalities can be elicited in the amygdala (Gerard et al, '36; Robinson and Lennox, '51; Machne and Segundo, '56). The latency of these responses may vary from 8 to 25 m.sec. and for unitary discharges may even measure from 20 to 500 m.sec. This suggests mediation over long polysynaptic pathways. Gloor ('55a) and Shearly and Peele ('57) concluded that there is no specific functional localization existing in the amygdala. However, Ursin and Kaada ('60) and Egger and Flynn ('67) found some definite topographic organization within the amygdala with some overlapping of functional effects. Furthermore Koikegami et al ('63) could even separate "parasympathetic" and "sympathetic" zones in the amygdala.

Review of the Nuclei

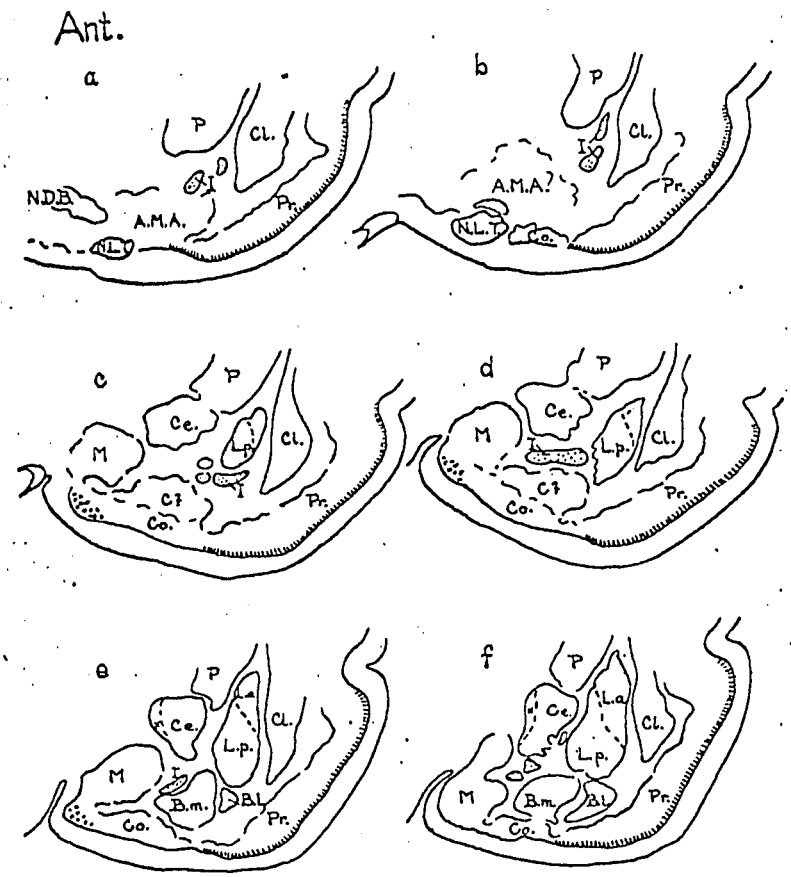
A. Anterior Amygdaloid Area (Fig. 1)

The most anterior part of the amygdaloid complex is composed of a diffusely dispersed mass of cells. The interstitial nucleus of the septal portion of the medial forebrain bundle extends into this area and contributes to its formation (Gurdjian, '28). This led Cowan et al ('65) to regard the anterior amygdaloid area as the bed nucleus for the amygdaloid component of the medial forebrain bundle. The area has a relatively similar configuration in a variety of species.

B. The Nucleus of the Lateral Olfactory Tract (Fig. 1)

This is the most circumscribed mass in the amygdaloid complex.

Figs. 1 and 2. A series of drawings of transverse sections through the amygdaloid complex of the rat. (Brodal '47)



Figs. 1 and 2 A series of drawings of transverse sections through the amygdaloid complex of the rat with equal intervals from anterior to posterior. Nissl-stain. The symbols have the following meaning: A.M.A., anterior amygaloid area. B.l., lateral, large celled part of basal nucleus. B.m., medial, small celled part of basal nucleus. C.?, the nuclear mass associated with the cortical nucleus, probably being part of this or corresponding to the accessory basal nucleus of other forms. Cc., central nucleus. Cl., claustrum. Co., cortical nucleus. E., entorhinal area, area 28. F.D., dentate fascia. H., hippocampus. I., intercalated masses, indicated by fine stipplings where not labelled. M., medial nucleus. N.D.B., nucleus of diagonal band. L.a., anterior, small celled part of lateral nucleus. L.p., posterior, large celled part of lateral nucleus. P., putamen-caudate complex. Pr., piriform cortex, area 51 with subdivisions, after Krieg. S., subiculum. V., lateral ventricle. x., the small, large celled part of the central nucleus. y., cortico-amygdaloid transition area. The coarse stipplings at the transition between medial and cortical nucleus at levels c–e indicates the presence of clumps of cells of cortical type.

Fig. 1

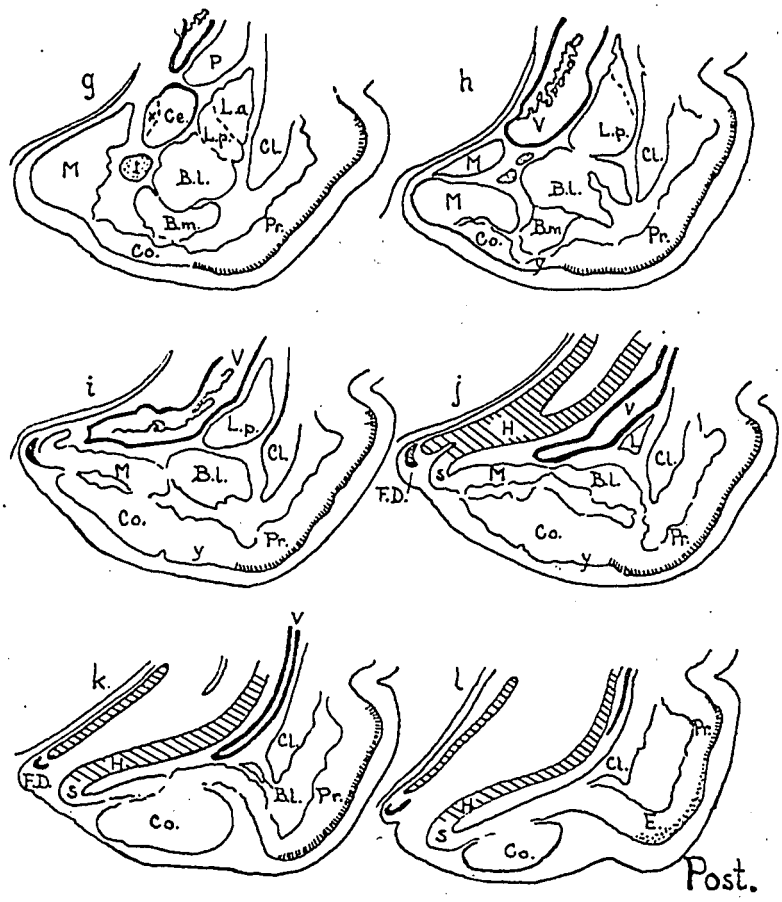


Figure 2

Fig. 2

It is always found anteriorly surrounded by the anterior amygdaloid area. However, there is some variation in the relative position of its two subdivisions. (See table I, page 10).

C. The Central Nucleus (Figs. 1 and 2)

This nucleus is similar to the putamen in cell structure and cell density. A fusion of the two nuclei has been described in many species and there is difficulty determining the boundary between them. In some species the central nucleus may consist of two parts. A summary of the description in a variety of species is given in table II, (page 11).

D. The Medial Nucleus (Figs. 1 and 2)

This is the only nucleus included in the amygdala by Von Kölliker (1896). Gurdjian ('28) described it as extending throughout the whole course of the amygdaloid complex anterioposteriorly. However, Crosby and Humphrey ('41) and Uchida ('50) recognized the medial nucleus only in the middle third of the anteroposterior extent of the amygdala. For a comparison of the descriptions by different authors see table III, (page 12).

E. The Cortical Nucleus (Figs. 1 and 2)

This nucleus is the most ventral member of the amygdaloid complex and extends from the posterior plane of the nucleus of the lateral olfactory tract to the posterior extremity of the amygdala (Gurdjian, '28). Again a variety of descriptions are present in

the literature. (See table IV, page 13).

F. The Lateral Nucleus (Figs. 1 and 2)

As can be seen from table V, (page 14), the lateral nucleus consists of one part in some species, and two parts in others. In the rat there is some disagreement concerning the inferior limit of the nucleus. Gurdjian ('28) included in the lateral nucleus what Brodal ('47) considered the large-celled part of the basal nucleus.

G. The Basal Nucleus (Figs. 1 and 2)

Gurdjian ('28) considered the basal nucleus of the rat to consist of only small cells. Brodal ('47), however, distinguished a medial small-celled part and a lateral large-celled part. Fox ('40) and Brodal ('47) observed that the lateral part of the basal nucleus has slightly larger cells than those of the lateral nucleus, but in the mouse Valverde ('62) observed in Golgi preparation that those of the lateral nucleus were largest. (See table VI, page 15).

H. The Accessory Basal Nucleus (Fig. 1)

This nucleus has not been described in some species. Gurdjian ('28), Young ('36), Fox ('40) and Brodal ('47) did not recognize it in their studies of the rat, rabbit, cat and rat respectively. (See table VII, page 16).

I. The Intercalated Masses (Figs. 1 and 2)

Gurdjian ('28) used the term nucleus intercalatus. However, Johnston ('23) and Brodal ('47) preferred the term

intercalated masses because the cells are in isolated clusters rather than in continuity. Völsch ('10) considered the masses to be glial in nature. However, Johnston ('23) identified them as true nerve cells. Fox ('40) included the intercalated masses in the anterior amygdaloid group but Humphrey ('41) and Lauer ('45) considered the masses to be part of the basolateral group.

J. The Cortico-Amygdaloid Transition Area (Fig. 2)

According to Humphrey ('68) the amygdalopiriform transition area is undoubtly present in all mammals. It has been described in the rabbit (Young, '36), man (Crosby and Humphrey, '41), monkey (Lauer, '45), porpoise (Breathnach and Coldby, '54), shrew (Crosby and Humphrey, '44) and human fetus (Humphrey, '68). Crosby and Humphrey ('44) in the shrew and Humphrey ('68) in human fetus also observed a transitional zone between amygdala and hippocampus.

TABLE I

THE NUCLEUS OF THE LATERAL OLFACTORY TRACT

SPECIES	AUTHOR	YR.	CELL SIZE	CELL TYPE	# OF SUBD.	LOCATION	STAIN
S. Am. Opossum	Obenchain	'25	N.S.	N.S.	2	Dorsal Ventral	N.S.
Rat	Gurdjian	'28	N.S.	Same as those of piriform cortex	2	Dorsal Ventral	N.S.
Rabbit	Young	'36	Small, large, similar to piriform cortex	N.S.	2	Medial Lateral	Deeply stained and lighter stained
Bat	Humphrey	'36	Small	Round or ovoid granule cells	2	Rost.	N.S.
Rat	Brodal	'47	Rather large. Similar to those of piriform cortex	N.S.	2	Dorsal Ventral	N.S.
Cat	Fox	'40	N.S.	N.S.	1	Suprf.	Deeply stained
Man	Crosby & Humphrey	'41	N.S.	Elongated	2	Rost. Caudal	Deeply stained
Shrew	Crosby & Humphrey	'44	N.S.	N.S.	2	Rost. Caudal	Deeply stained
Mink	Jeserich	'45	Resembles deep cell of piriform cortex	Resembles deep cell of piriform cortex	1	Suprf.	Deeply stained
Panda	Lauer	'49	Large	N.S.	1	Deeper	N.S.
Rat	Uchida	'50	N.S.	N.S.	2	Dorsal Ventral	N.S.

N.S.= Not Stated

TABLE II
THE CENTRAL NUCLEUS

SPECIES	AUTHOR	YR.	CELL SIZE	CELL TYPE	# OF SUBD.	FUSION WITH PUTAMEN
Opossum	Johnston	'23	Small Medium	N.S.	N.S.	±
Rat	Gurdjian	'28	Smaller cells than those of ventral part of lateral N.	N.S.	N.S.	+ also with Ant. Amygd. Area (AAA)
Rabbit	Young	'36	Medium	Fusiform	N.S.	+
Bat	Humphrey	'36	Resembles caudate-putamen	Resembles caudate-putamen	N.S.	+
Cat	Fox	'40	Small Larger	Similar to putamen	2	+
Man	Crosby & Humphrey	'41	Resembles putamen	Resembles putamen	N.S.	+
Monkey	Lauer	'45	Larger than those of medial N. Smaller than those of lat. part of basal N.	Similar to putamen	N.S.	+ (AAA, and substriatal gray)
Rat	Brodal	'47	Small Medium Large	N.S.	2	+
Rat	Uchida	'50	Medium	N.S.	N.S.	N.S.
Mouse	Valverde	'62	Medium	Stellate or fusi-form	N.S.	+ (note only medial N.)

N.S.= Not Stated

TABLE III
THE MEDIAL NUCLEUS

SPECIES	AUTHOR	YR.	CELL SIZE	CELL TYPE	# OF SUBD.	BLENDING WITH OTHER NUCLEI
Opossum	Johnston	'23	Small	N.S.	N.S.	N.S.
Rat	Gurdjian	'28	Small	N.S.	N.S.	+ (cortical N.; basal N.)
Rabbit	Young	'36	N.S.	N.S.	1	+ (cortical N.; hippocampus piriform cortex)
Bat	Humphrey	'36	Small Larger	Spindle Triangular Multipolar	2-3 layers	+ (hippocampal formation cortical N.)
Cat	Fox	'40	Medium	N.S.	N.S.	+ (AAA; hippocampus)
Man	Crosby & Humphrey	'41	Small Slightly larger	Multipolar	1	+ (AAA; substriatal gray)
Monkey	Lauer	'45	Small Medium	N.S.	N.S.	+ (AAA)
Rat	Brodal	'47	Small Medium	N.S.	2	+ (cortical N.; hippocampus)
Rat	Uchida	'50	Small Medium	N.S.	1	+ (cortical N. (?)
Mouse	Valverde	'62	Medium	Fusiform or Stellate	N.S.	+ (cortical N.; central N.)

N.S.= Not Stated

TABLE IV
THE CORTICAL NUCLEUS

SPECIES	AUTHOR	YR.	CELL SIZE	CELL TYPE	# OF SUBD.	BLENDING WITH OTHER NUCLEI
Opossum	Johnston	'23	Small	N.S.	N.S.	N.S.
Rat	Gurdjian	'28	Small	N.S.	N.S.	+ (cortical N.; basal N.)
Rabbit	Young	'36	Smaller than those of the piriform cortex	N.S.	2 (Suprf. Deep)	+ (medial N.)
Bat	Humphrey	'36	Larger than those of the medial N. Resembles the cells of piriform cortex. Smaller	Pyramidal Triangle or Multipolar	N.S.	+ (medial N.; accessory basal N.)
Cat	Fox	'40	Medium Small	Pyramidal Variety	N.S.	+ (piriform cortex; medial N.; hippocampal cortex)
Man	Crosby & Humphrey	'41	N.S.	Multipolar Pyramidal Polymorphic	N.S.	+ (cortico-amygd. transitional area; accessory basal N.)
Shrew	Crosby & Humphrey	'44	N.S.	Pyramidal	N.S.	+ (accessory basal)
Monkey	Lauer	'45	Small Medium	Pyramidal	N.S.	+ (cortex; accessory basal N.)
Rat	Brodal	'47	N.S.	Pyramidal	N.S.	+ (medial N.; basal N.)
Rat	Uchida	'50	Large Medium Small	Similar to those of piriform cortex. Pyramidal	2 (Dors. Vent.)	+ (cortical N.(?); Ammonsformation)
Mouse	Valverde	'62	N.S.	Pyramidal Double pyramids Little polymorphic	N.S.	+ (medial N.)

N.S.= Not Stated

TABLE V
THE LATERAL NUCLEUS

SPECIES	AUTHOR	YR.	CELL SIZE	CELL TYPE	# OF SUBD.	FUSION WITH OTHER NUCLEI
Opossum	Johnston	'23	N.S.	N.S.	N.S.	N.S.
Rat	Gurdjian	'28	Smaller Large	N.S.	2	+ (hippocampal formation caudate-putamen)
Rabbit	Young	'36	Large Smaller	Spindle Oval	2	+ (caudate-putamen)
Bat	Humphrey	'36	Smaller	Multipolar	1	N.S.
Cat	Fox	'40	N.S.	N.S.	1	N.S.
Man	Crosby & Humphrey	'41	Medium Smaller	Multipolar	1	+ (basal N.)
Shrew	Crosby & Humphrey	'44	Large	N.S.	1	+ (basal N.)
Monkey	Lauer	'45	Small Medium	N.S.	1	+ (basal N.)
Mink	Jeserich	'45	Large Small	N.S.	2	+ (basal N.)
Rat	Brodal	'47	Small Large	N.S.	2	+ (basal N.)
Rat	Uchida	'50	Small Large	N.S.	N.S.	N.S.
Mouse	Valverde	'62	Large	Profuse dendrites	N.S.	-

N.S.= Not Stated

TABLE VI
THE BASAL NUCLEUS

SPECIES	AUTHOR	YR.	CELL SIZE	CELL TYPE	# OF SUBD.	FUSION WITH OTHER NUCLEI
Opossum	Johnston	'23	Large Small	N.S.	2	N.S.
Rat	Gurdjian	'28	Small	N.S.	1	+ (medial N.; cortical N.)
Rabbit	Young	'36	Small Large	Elongated Similar to those of piri-form cortex	2	+ (pyriform area)
Bat	Humphrey	'36	Large Smaller	N.S.	2	+ (pyriform cortex; accessory basal N.)
Cat	Fox	'40	Large Medium	N.S.	2	+ (transitional gray; caudally)
Man	Crosby & Humphrey	'41	Large Medium Small	Multipolar	2	+ (lateral N.; cortex; accessory basal; cortico-amygdaloid trans.)
Shrew	Crosby & Humphrey	'44	Medium	N.S.	2	+ (lateral N.; cortex)
Monkey	Lauer	'45	Large Small	Multipolar	2	+ (lateral N.; accessory basal)
Rat	Brodal	'47	Small Medium Large	N.S.	2	+ (lateral N.; cortical N.)
Rat	Uchida	'50	Small Large	Spindle	2	N.S.
Mouse	Valverde	'62	Medium	Profused dendrites	N.S.	-

N.S.= Not Stated

TABLE V11

THE ACCESSORY BASAL NUCLEUS

SPECIES	AUTHOR	YR.	AUTHORS' OPINION	ACCESSORY BASAL N. RECOGNIZED
Opossum	Johnston	'23	Lateral to basal N.	+
Rat	Gurdjian	'28	N.S.	-
Rabbit	Young	'36	Medial part of the basal N.	-
Bat	Humphrey	'36	Medial to basal N.	+
Cat	Fox	'40	N.S.	-
Man	Crosby & Humphrey	'41	Small & large neurons medial to basal N.	+
Shrew	Crosby & Humphrey	'44	Ventro-medial to the large-celled part of the basal N.	+
Monkey	Lauer	'45	Last of the nuclear to disappear posteriorly	+
Mink	Jeserich	'45	Scattered cells	+
Rat	Brodal	'47	A part of the cortical N.	-

Problem Formulation

It has been noted above (see tables) that the nuclear configuration of the amygdala in the rat has been studied by Gurdjian ('28), Brodal ('47), Uchida ('50) and Girgis ('68, coypu rat). On comparing their findings certain discrepancies became evident. These are probably due to insufficiently distinctive features in the nuclei as seen in Nissl preparations. It is difficult, however, without exact definition of these nuclei to compare experimental anatomical, physiological and behavioral studies in the rat with those in other animals. The present study was undertaken in an attempt to resolve the controversies in the literature regarding the amygdala in the rat and to provide data that would allow a closer comparison with other species.

CHAPTER II

MATERIAL AND METHODS

A total of 27 albino rats of the Sprague-Dawley strain were used in this study. They were 6 weeks or 3 months of age. In each case the animal was anesthetized with an intraperitoneal injection of nembutal (5 mg. / 100 gm., body weight).

The following staining techniques were employed:

a) Nissl stain (6 brains, cut in the frontal plane.
4 brains, cut in the sagittal plane.
2 brains, cut in the horizontal plane).

b) Tungstate modification of the Golgi-Cox method
(4 brains, cut in the frontal plane.
3 brains, cut in the sagittal plane.
2 brains, cut in the horizontal plane).
The alternate sections were counterstained with cresyl violet.

c) Enzyme stain (2 brains, cut in frontal plane). The alternate sections were stained with cresyl violet.

d) Fink-Heimer stain (4 brains, cut in frontal plane).

a) Procedure for Nissl Staining

1. Rats were perfused with normal saline (0.85%) and then with 10% formalin or formolsaline.

2. Brains were then stored in formalin or formolsaline for one to ten days.
3. The brain was dehydrated through graded alcohols 50%, 70%, 90%, 96%, (one day at each concentration) and absolute alcohol (two changes, one day each).
4. The brain was put through the following solutions:
    a) absolute alcohol for 48 hrs. (one day, one change);
    b) one to one alcohol - chloroform solution from 6 hrs. to 12 hrs. (until brain sinks);
    c) into pure chloroform, two baths, each for 6 hrs.;
    d) mixture of 1 to 1 chloroform - paraffin (52°C to 58°C melting point), 6 hrs. at least;
    e) three paraffin baths, 24 hrs. in each.
5. Embedding:

    In order to avoid the formation of a deep central depression in the paraffin block, the following technique was devised. Immediately after immersing the brain in liquid paraffin, the paraffin surface was

touched briefly with an ice cube. This produces a thin layer of solid paraffin on the surface and no deep depression forms. Attention was paid to avoid overcooling as this makes the wax near the tissue very porous or even honeycombed in appearance.

6. Sections were cut at 10 μ or 15 μ .
7. Every 10th section was mounted on a slide pretreated with albumin or gelatin. Albumin gives better results.
8. The paraffin in the tissue was dissolved in xylene and the sections were then rehydrated through graded alcohols.
9. The sections were stained in thionin solution (concentration 0.01 - 0.02%) for 1.5 min. to 15 min. (Best results obtained with 10 to 12 min.).
10. They were rinsed in water before being placed in 70% alcohol for differentiation. (Best results at approximately 20 min.).
11. Sections were dehydrated, cleared and covered.

b) The Tungstate Modification of the Golgi-Cox Method

Six week old rats were used. Brains were stained according to the method of Ramon-Moliner ('64).

c) Enzyme Stain

Mature rats were used. Perfusion was carried out as in (a) above. Sections of 50 μ thickness were cut with the freezing microtome. Every other section was stained by the Mathisen and Blackstad ('64) and Blackstad ('69) procedure. One brain was stained with and one without the ethopropazine inhibitor. The alternate sections were stained with cresyl violet.

d) Fink and Heimer Technique

Three month old rats were used. Electrocoagulation was performed in the temporal region by applying a metal disc through which 20 ma current was passed for 10 sec. once or twice. The survival time was 4 or 6 days. After perfusion the material was stored in 10% formolsaline for 10 days and 30% sucrose solution for 3 days. Sections of 30 μ thickness were collected in 2% formolsaline. Staining procedure II (Fink and Heimer, '67) was followed. The cresyl violet technique was employed to verify the extent of lesion and nucleus of termination.

CHAPTER III

OBSERVATIONS

In the rat the amygdaloid complex extends from the olfactory tubercle anteriorly to a small depression at the anterior part of the entorhinal cortex posteriorly. The superior limit of the amygdala reaches the level of the rhinal sulcus. The medial border is indicated by the hemispheric fissure and the lateral border is indicated by amygdaloid fissure.

Twelve projection drawings of the amygdala as seen in Nissl preparations are given in Figs. 3-8, A-L. The levels correspond approximately to those of Brodal's ('47) Figs. 1 and 2, a-l. As Brodal's ('47) study is the reference used most frequently by authors carrying out investigations of the amygdala in rat, close reference has been made to his outline drawings. These figures have been included in Figs. 3-8 to allow comparison with the findings reported here. It should be noted that there is a slight difference in the plane of sectioning.

I. The Basolateral Complex

A. The lateral nucleus: The lateral nucleus can be divided into two parts in Nissl preparations (Figs. 9, 10, 11). As these parts are coexistensive from level E to J, the terms dorsolateral and ventromedial are considered more appropriate than anterior and

Figs. 3 to 8, A series of drawings of frontal sections of rat brain. Nissl stain.

The upper two drawings labeled with a,b,c,d,... were reproduced from Brodal's paper (⅄ 47).

The lower two drawings labeled with A,B,C,D,... are the diagrams from this investigation.

The two series are at approximately the same levels. Thus a~A, b~B, etc.

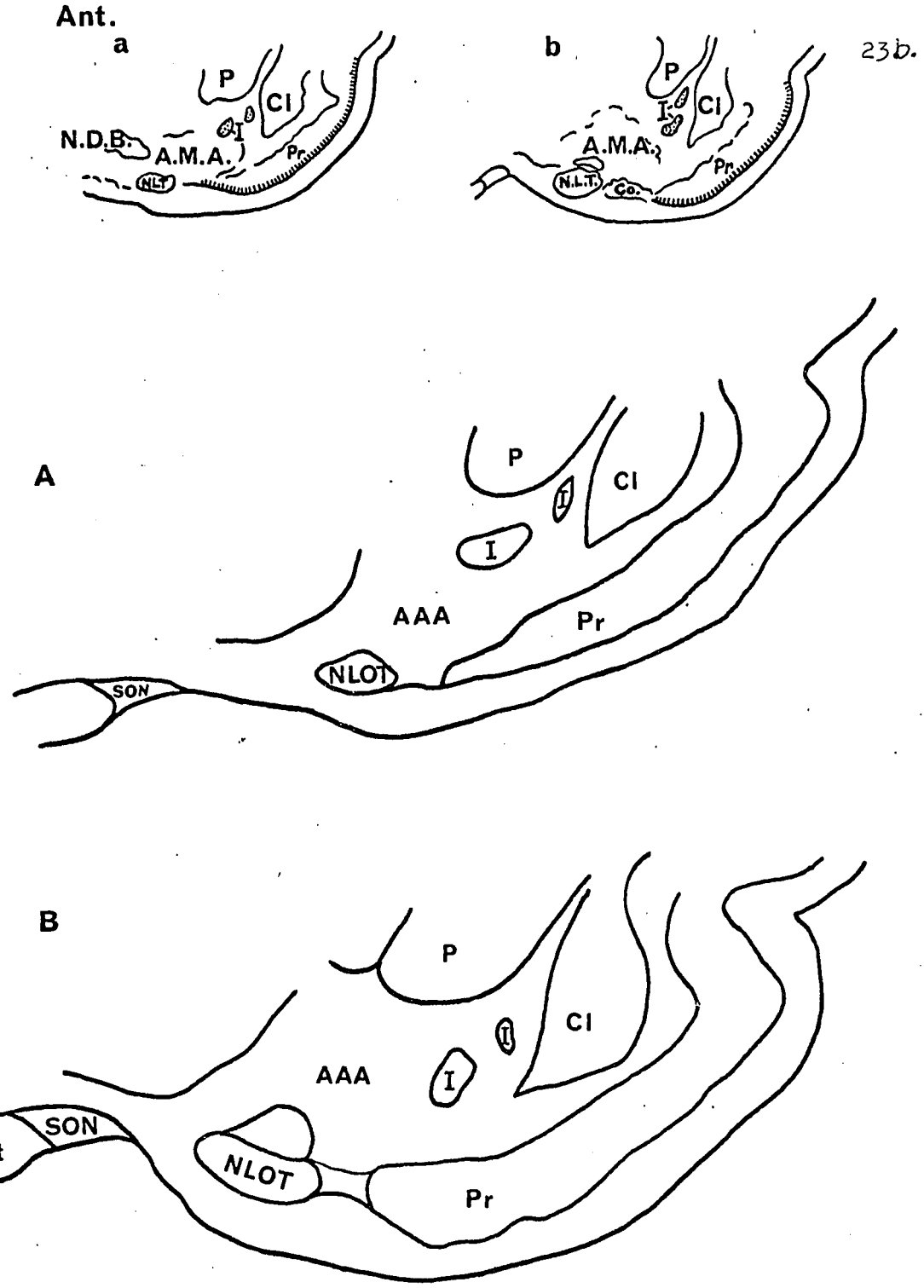

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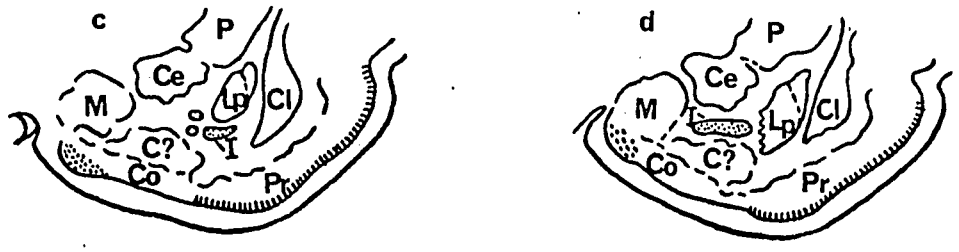
Fig. 3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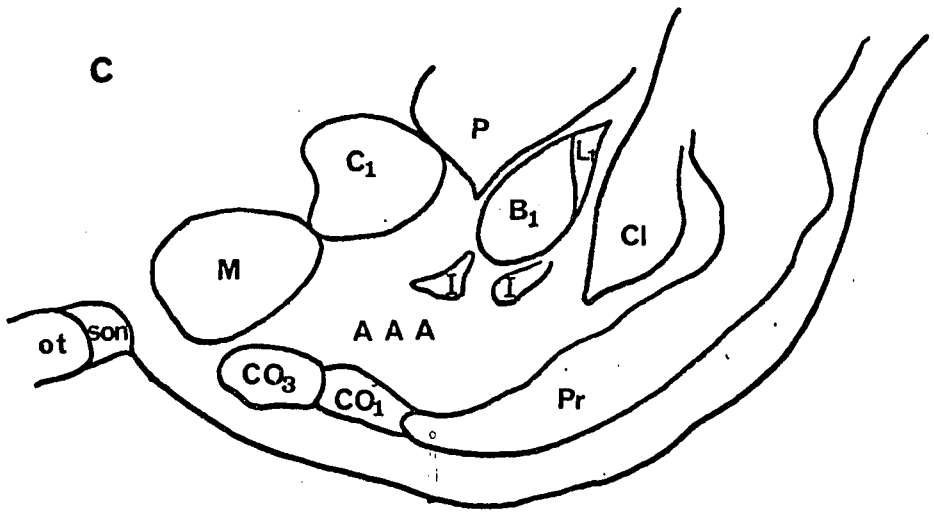
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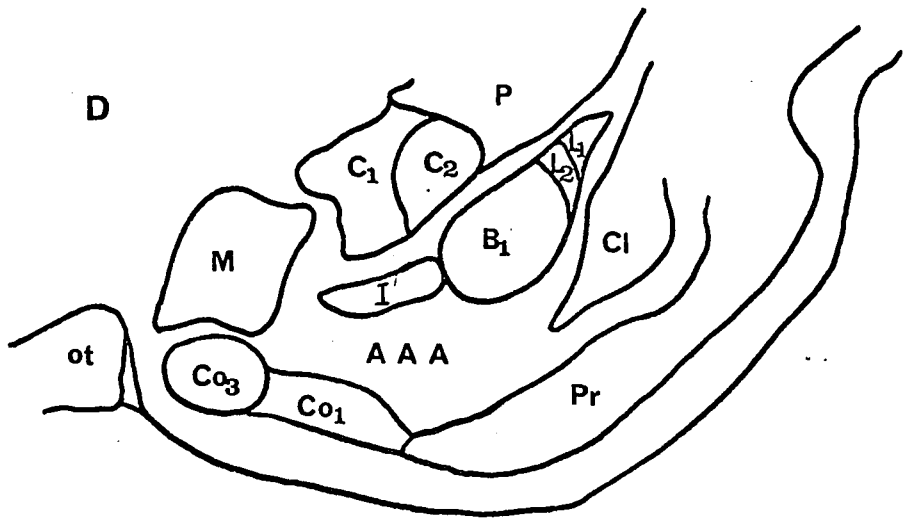
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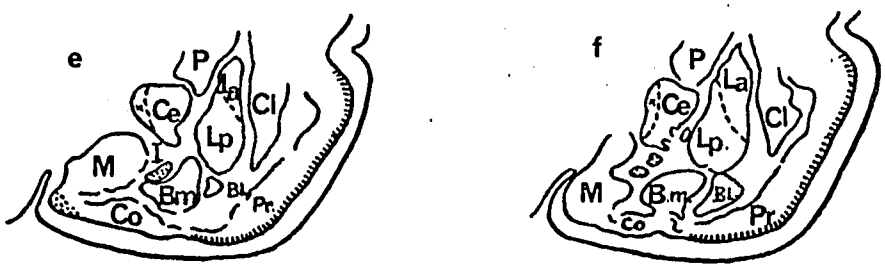
Fig. 4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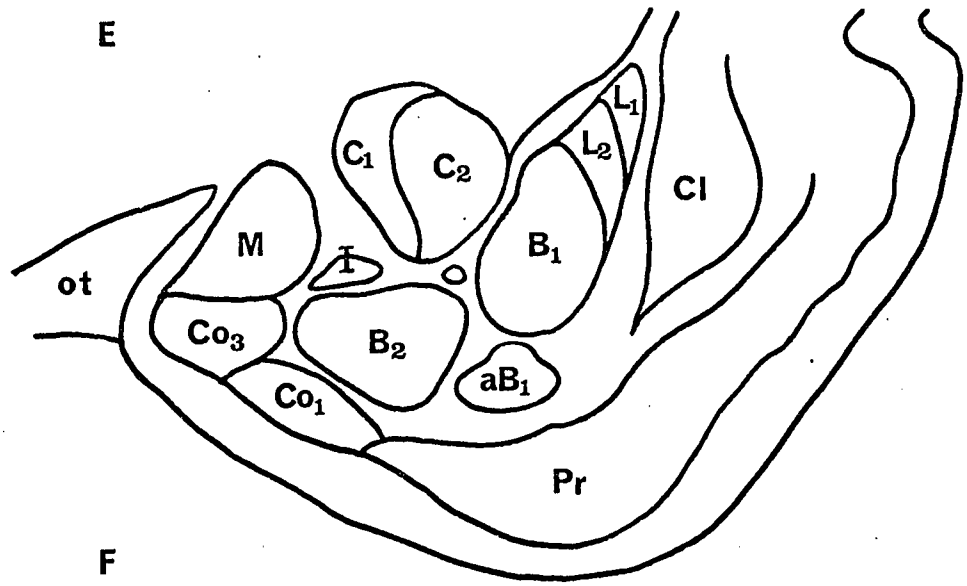
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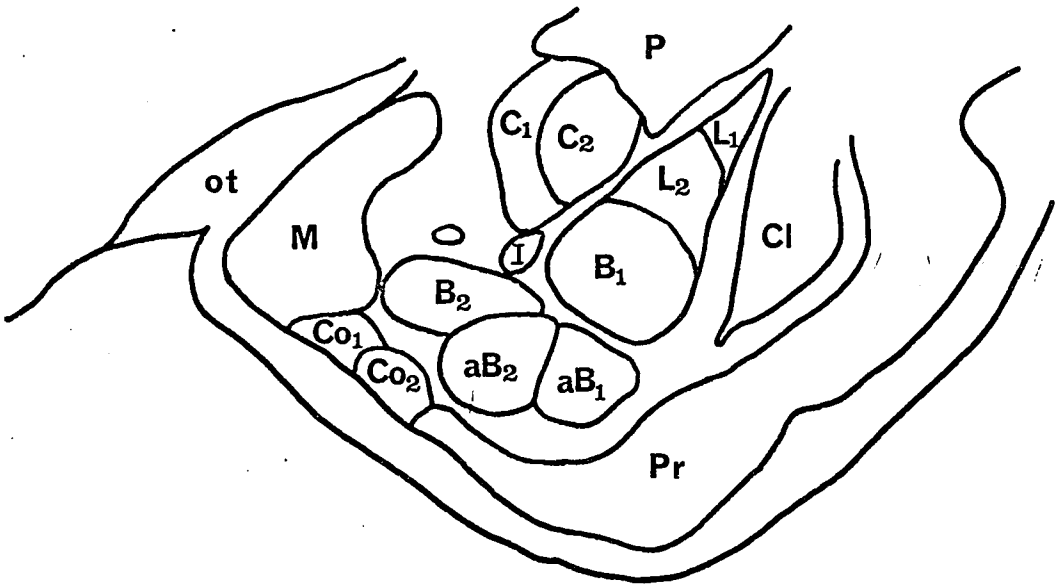
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Fig. 5

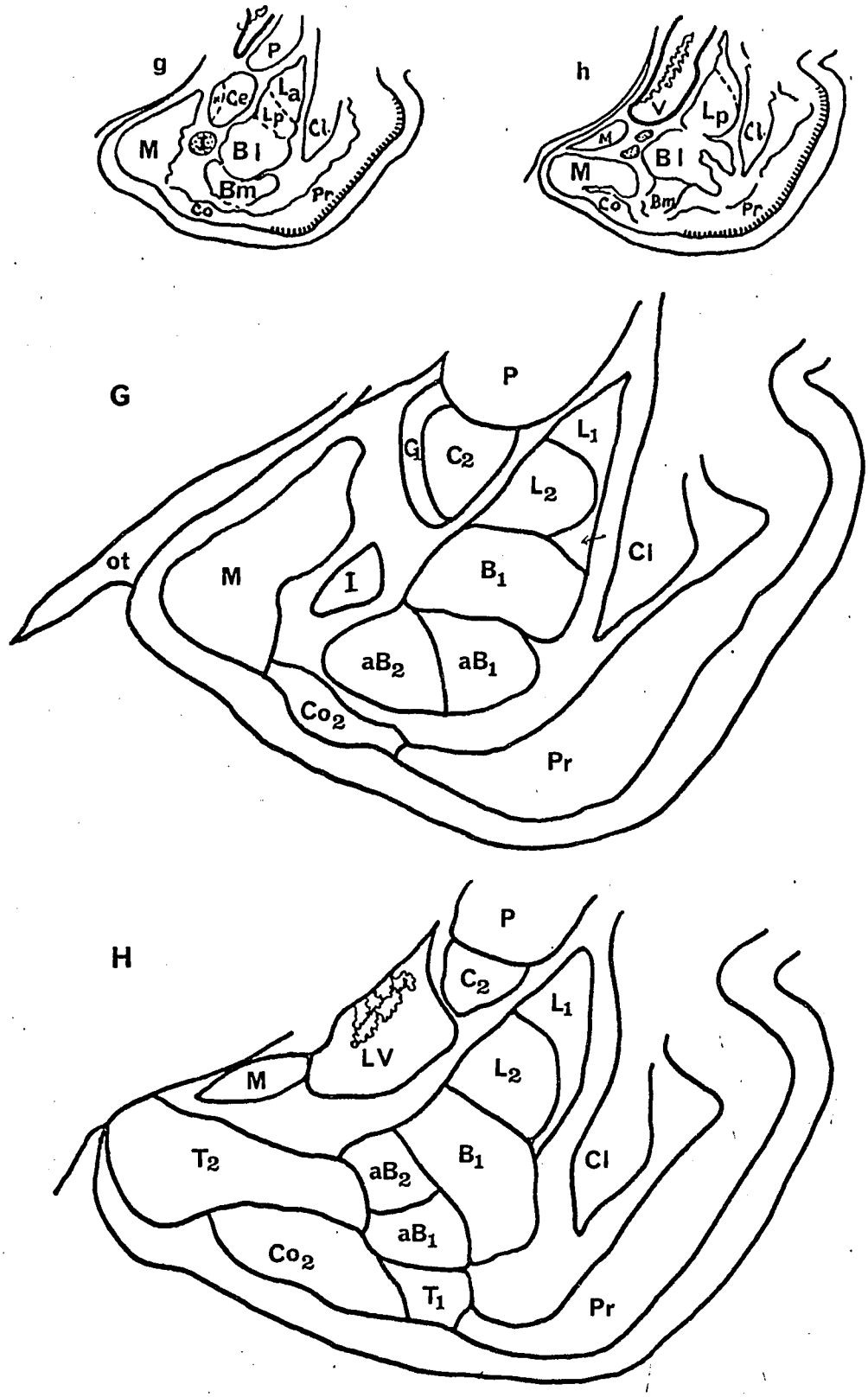
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Fig. 6

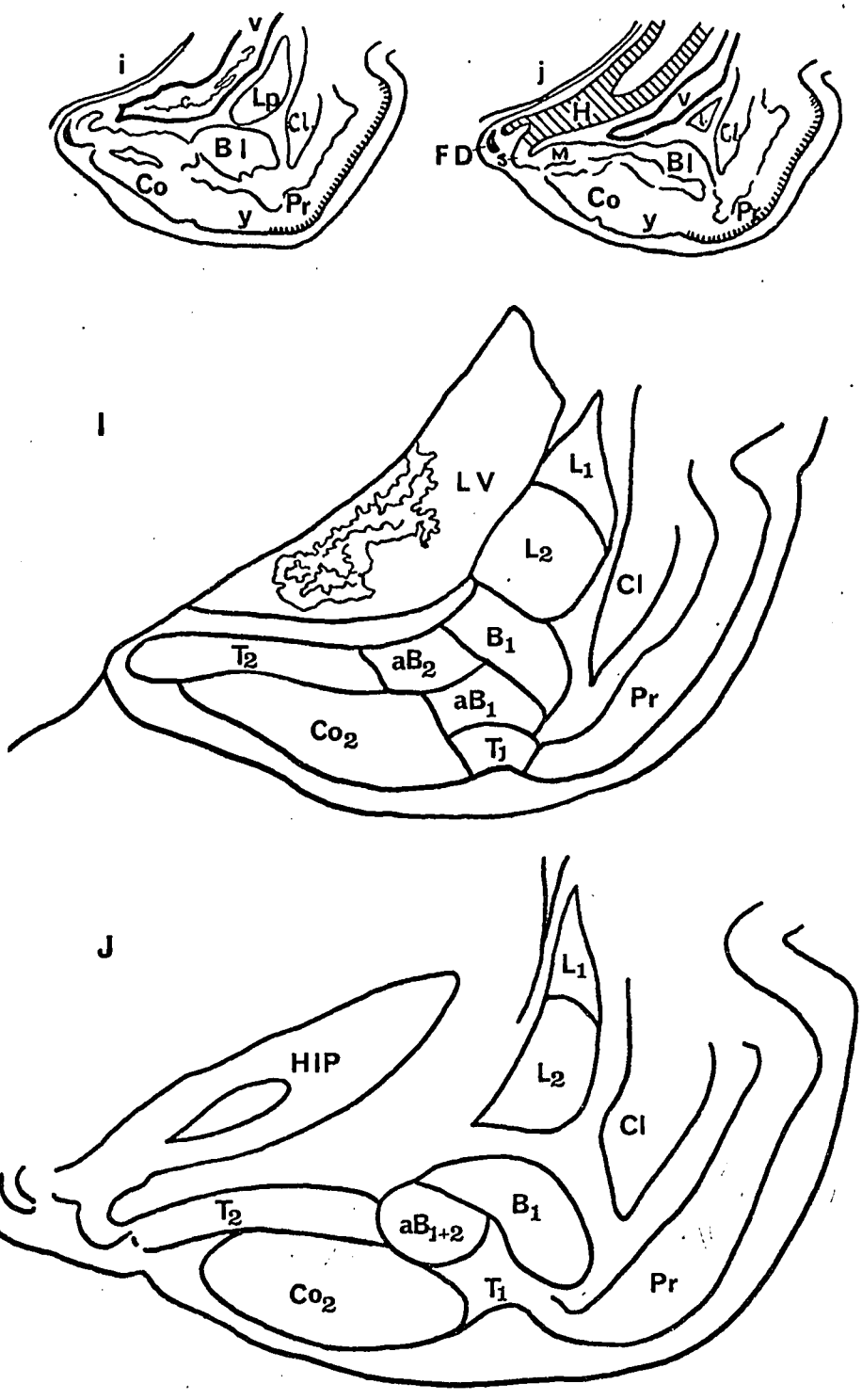
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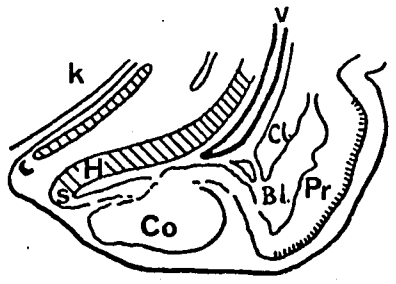
Fig. 7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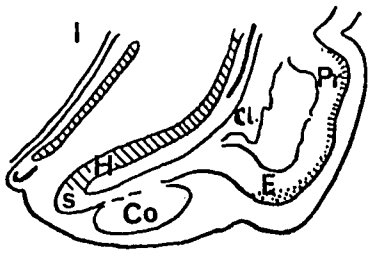
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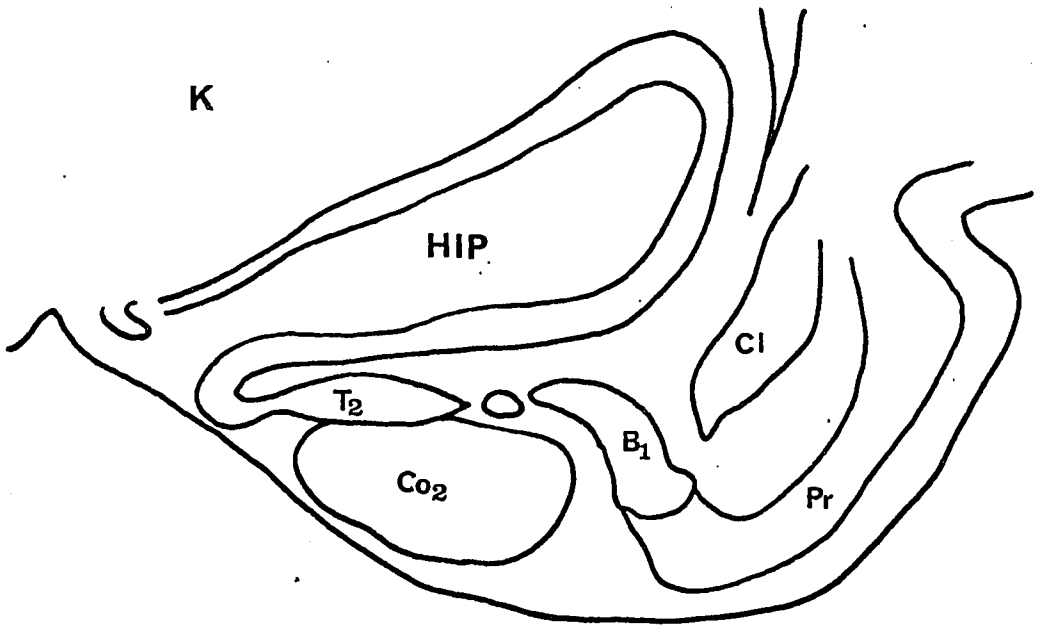
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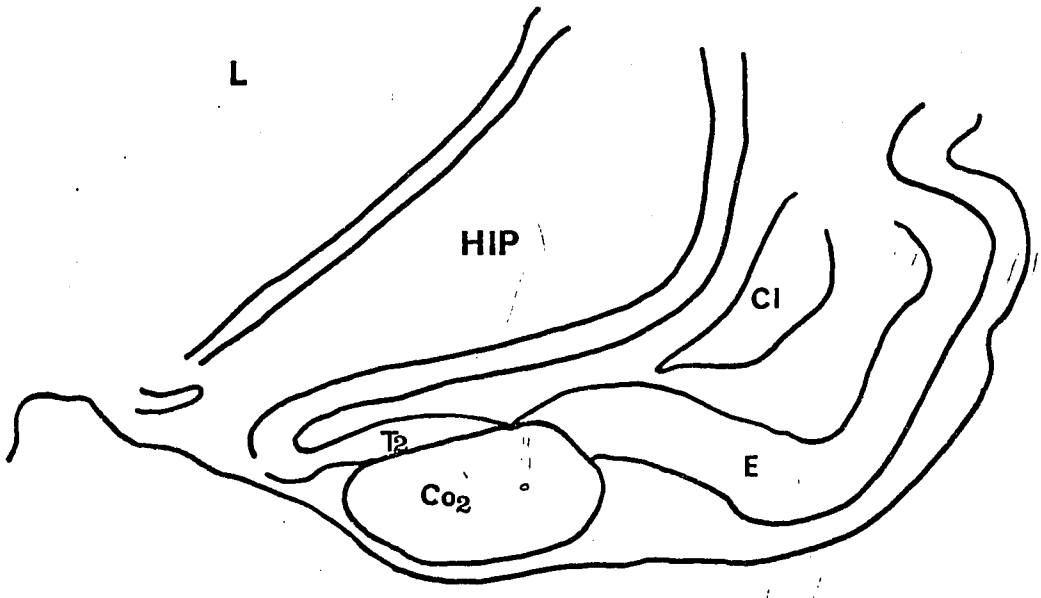
L
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Fig. 8

Fig. 9. Slide R1-366. (Dr. Sanides, Dept. of Anatomy, University of Ottawa). Frontal Section. Nissl stain. Low power view of the amygdaloid complex. L1 is the dorsolateral part and L2 is the ventromedial part of the lateral nucleus. 25x

Fig. 10. Slide RA10-9. Frontal Section. Nissl stain. The dorsolateral part of the lateral nucleus. The cells are smaller and more compact than in the ventromedial part. Compare with Fig. 11. 400x

Fig. 11. Slide RA10-9. Frontal Section. Nissl stain. The ventromedial part of the lateral nucleus. The cells are larger and more loosely arranged. 400x

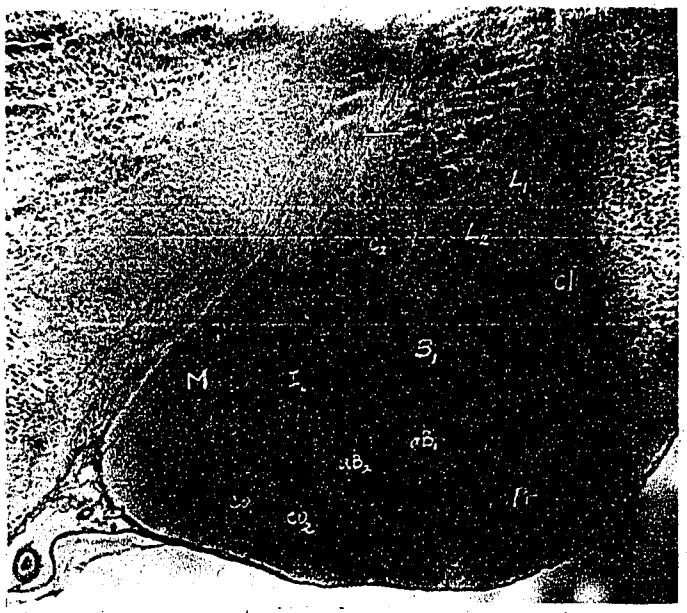


Fig. 9 25X

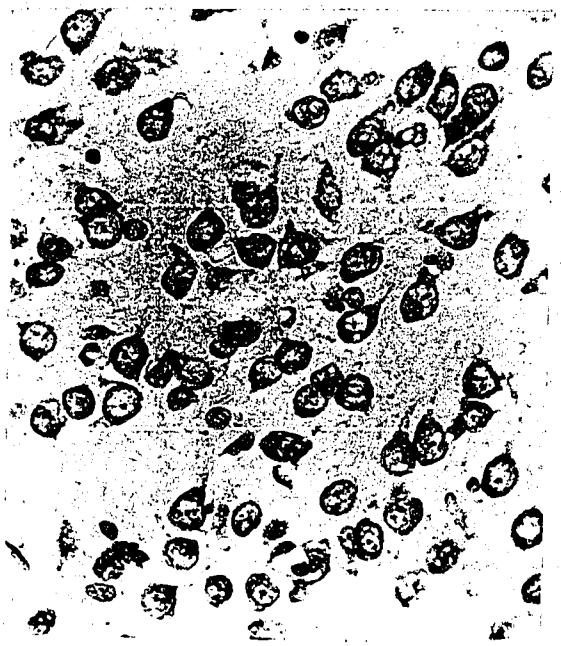


Fig. 10 400X

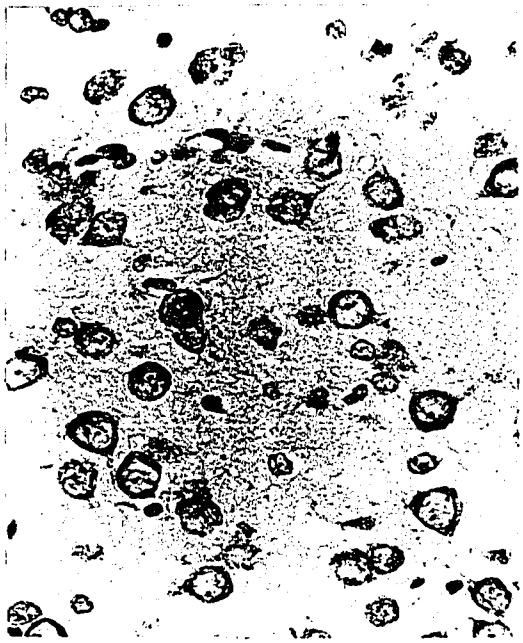


Fig. 11 400X

posterior as used by Brodal. It should be noted that there is a small triangular projection from the dorsolateral that extends ventrally to meet the basal nucleus lateral to the ventromedial subnucleus (see arrow Fig. 6 G.). In Figs. 5-8, it can be seen that the dorsolateral part is more extensive posteriorly than Brodal indicated (his anterior part). The ventromedial part is less extensive anteriorly.

The dorsolateral part is composed mainly of small and medium-sized cells with round, fusiform, triangular and polygonal bodies (Fig. 10). The round cells have relatively large nuclei surrounded by a thin ring of cytoplasm. The triangular, fusiform and polygonal cells have more cytoplasm in which deeply stained fine Nissl granules can be seen. The long axis of the cells lying in the most dorsal part of the subnucleus point dorsoventrally.

The ventromedial subnucleus is composed primarily of medium-sized cells, but occasionally larger and smaller cells are seen (Fig. 11). The shape and Nissl character of the cells are similar to those of the former group. However, the cells are more loosely arranged.

The cell sizes of the two subnuclei in the posterior portion of the lateral nucleus tend to be equal and the cells are evenly spaced. Although the dorsal part seems to be denser, it is difficult in Nissl staining to delimit the two different entities

exactly. At this level Brodal ('47) considered only the "posterior" part of the lateral nucleus to be present.

In Golgi preparations the two subdivisions cannot be distinguished. The dendrites are radiate in pattern and sometimes project into bordering fiber tracts. Throughout the lateral nucleus two cell types were seen:

Type I. The modified pyramidal cells (Figs. 12-14)

The medium-sized and larger cell bodies are pyramidal in shape. The dendritic pattern consists of a longer apical or main dendrite with a very thick primary segment and relatively shorter basal dendrites. The dendritic field is conical in shape. The primary segment of the apical dendrite is free of spines. Spines first appear on the secondary segment and gradually increase in number distally. The basal dendrites occasionally bear a spine on their proximal segment and again the spines gradually increase in number distally. The branches of the apical dendrites are more numerous than those of the basal dendrites. The apical dendrites usually have their first bifurcation within a cell diameter of their soma. Axons were occasionally seen and of these a few gave off collaterals within the dendritic field of their cell of origin. Some cells were seen which resembled the

Fig. 12. Slide RA5-16. Frontal Section. Golgi stain.
The modified pyramidal cells of the lateral nucleus.
200x

Figs. 13 and 14. Two drawings of the modified pyramidal cells.
(Lateral nucleus).

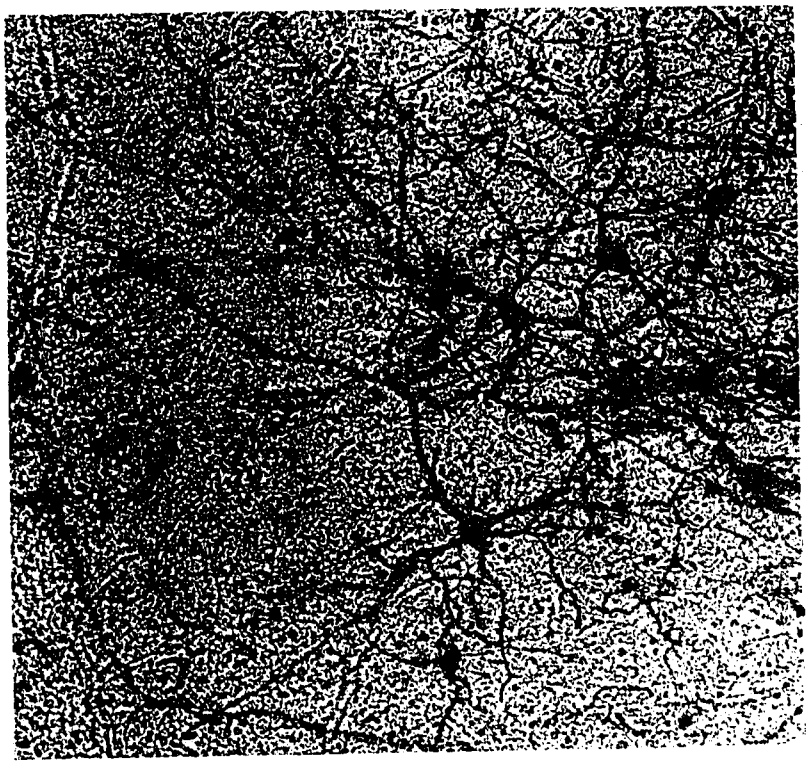
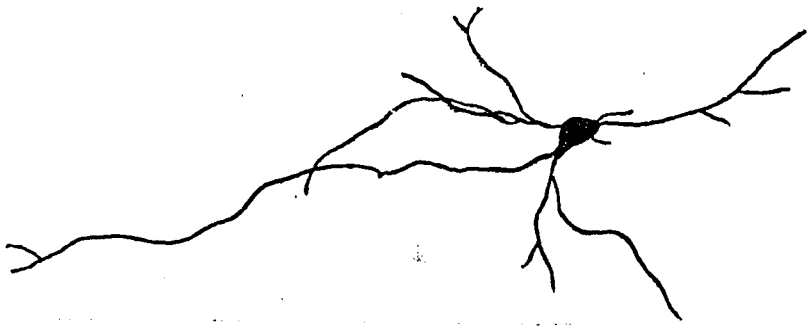


Fig. 12 200X



Spine : ++

Fig. 13

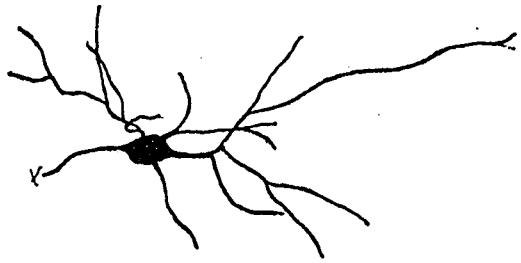


Fig. 14

Spine : +++

pyramidal type but had no apical dendrite. These were interpreted as pyramidal cells which had been cut along their short axis.

Type II. The fusiform cells

The small to medium-sized cells usually present two equally thick dendrites, one at each extremity of the soma, which branch less than those of type I. Their dendritic field is elongated. Spines are less numerous than on the dendrites of type I.

Cholinesterase staining shows moderate activity in the lateral nucleus (Figs. 16-24). The activity is greater in the dorsolateral part than in the ventromedial part. The highest activity in the lateral nucleus is seen along the supero-medial and lateral borders of the dorsolateral part. The two portions of the lateral nucleus can be distinguished relatively easily even at more posterior levels where in Nissl preparation the cells tend to be equal in size and density. Acetylcholinesterase staining (that is, the cholinesterase method with the inhibitor) shows an identical pattern.

Degeneration Studies, Rat # T3, T4

In each case the lesion involved neocortex superior to the rhinal fissure. The temporal area was destroyed and there was slight encroachment into the parietal and insular cortex. The degenerated fibres course via the external capsule into the dorsolateral

Figs. 15 to 26. Rat brain E 2. Slide No. 4, 7, 9, 11, 12, 13, 15, 16, 18, 20, 21, and 23. Frontal Sections. AChE stain. A series of photographs showing the AChE activity in the amygdaloid complex in the rat. 25x

Fig. 15 25 X

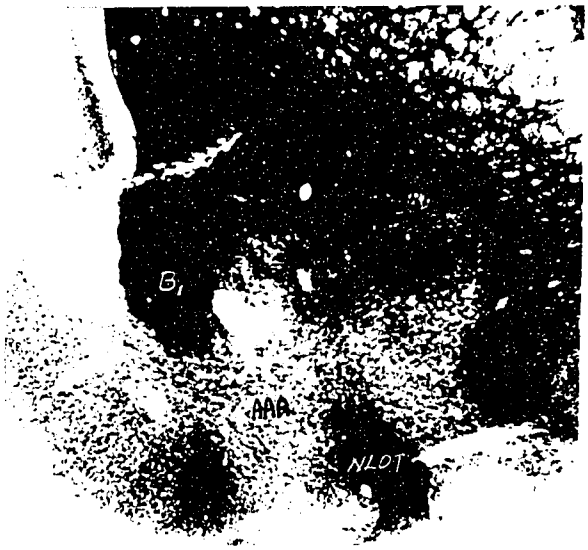


Fig. 16 25 X

Fig. 17 25X

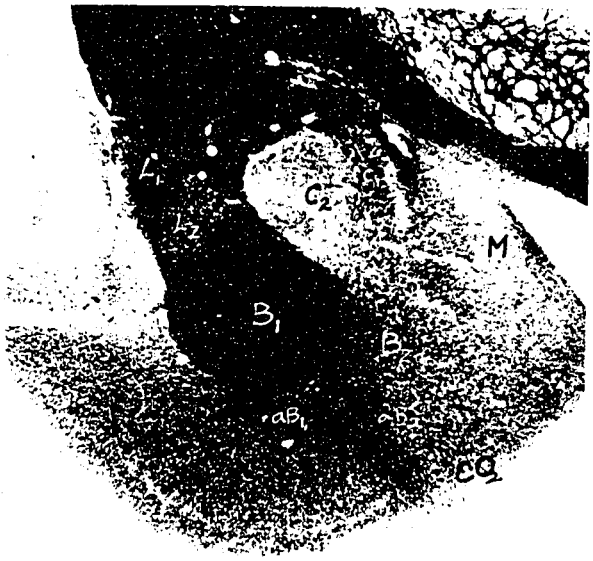


Fig. 18 25X

Fig. 19 25X

Fig. 20 25X

Fig. 21 25X

Fig. 22 25X

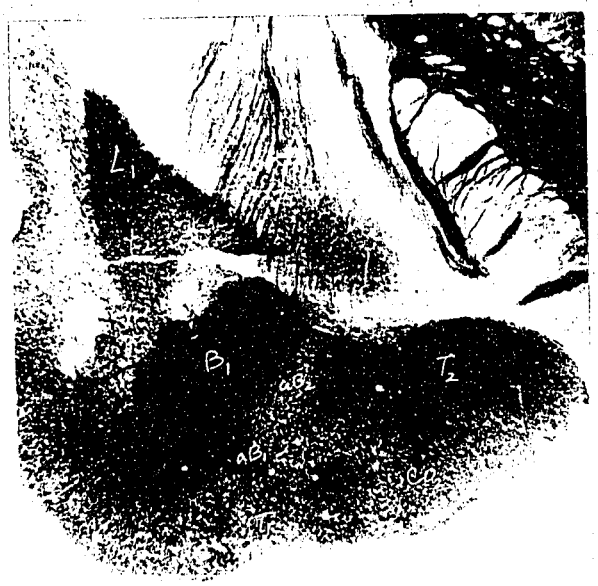


Fig. 23 25×

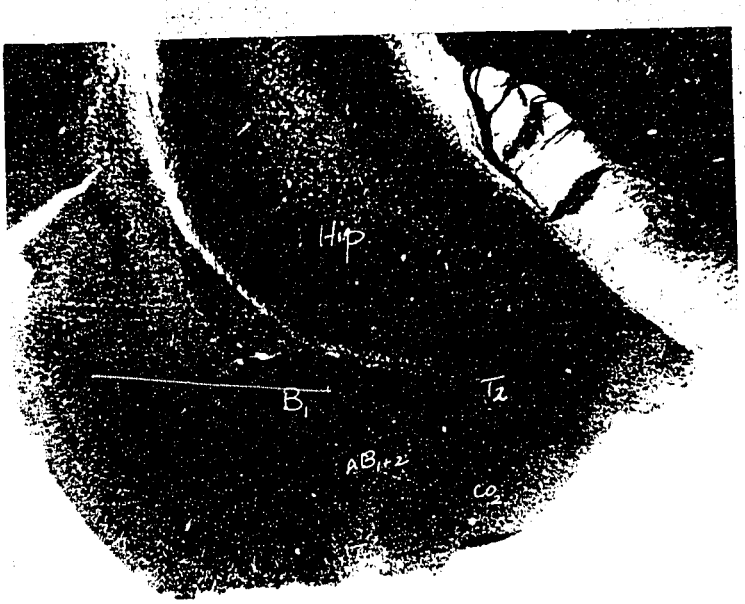


Fig. 24 25×

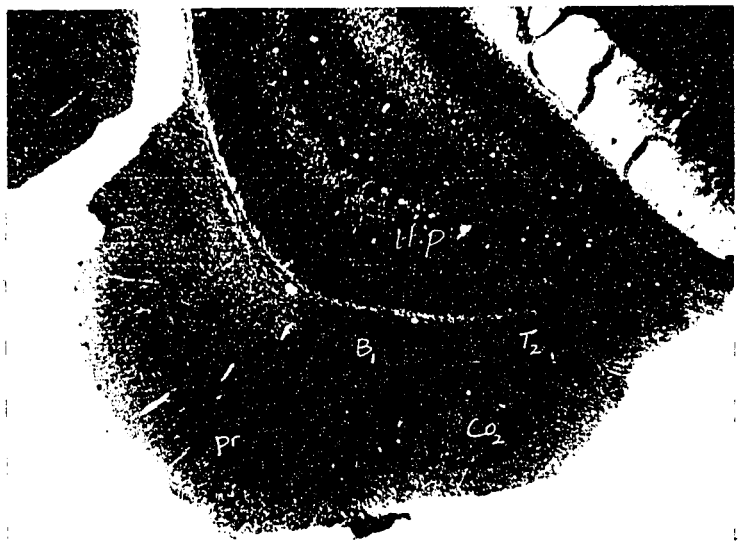


Fig. 25 25×

Fig. 26 25×

part of the lateral nucleus where they terminate (Figs. 27-29). No other amygdaloid nucleus was observed to contain degenerating fibres.

B. The basal nucleus: The nucleus is located ventromedial to the lateral nucleus and can be divided into a large-celled and a small-celled part. The large-celled part begins at about the same level as the lateral nucleus anteriorly (Fig. 4C) and extends almost as far posteriorly (Fig. 8K) as the cortical nucleus. It can be noted by comparing drawings C-F with Brodals c-f, that the large-celled part of the basal nucleus at these levels was considered by Brodal ('47) to be the "posterior" part of the lateral nucleus. The transitional area Brodal ('47) described between area La and Lp is the ventromedial segment of the lateral nucleus in this study. Small intercalated cell masses are sometimes interposed between the lateral and basal nuclei and may be useful in delimiting them.

The large-celled part of the basal nucleus (Figs. 9, 30) is composed predominantly of very large cells. Some medium-sized and small cells are also present. Among each size group round, fusiform, triangular and polygonal shape were seen in Nissl preparations. The large cells contain more cytoplasm than those of the lateral nucleus and their Nissl granules are denser (Fig. 31). In the posterior extremity there is some blending of neurons with those of the entorhinal cortex.

Fig. 27. Rat brain T4. Slide No. 13. Frontal Section. Nissl stain. The shaded area shows the lesion superior to the rhinal fissure.

Fig. 28. Rat brain T2. Slide No. 7. Frontal Section. Fink and Heimer stain. On the left, degeneration in the dorsolateral part of the lateral nucleus on the ipsilateral side. On the right, it can be seen that the contralateral field is free of degeneration. 800x

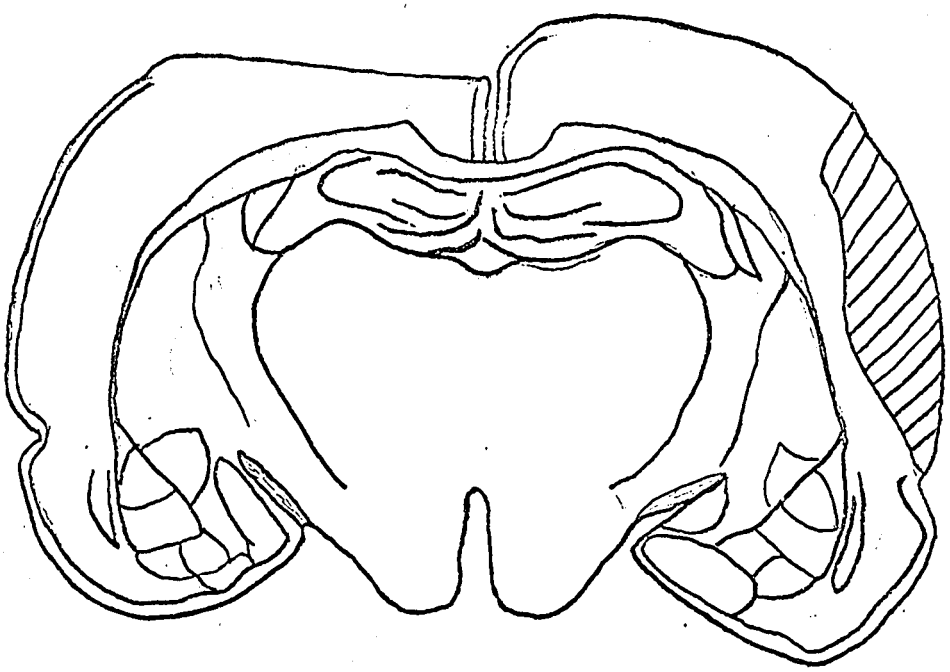


Fig. 27

The site of the lesion

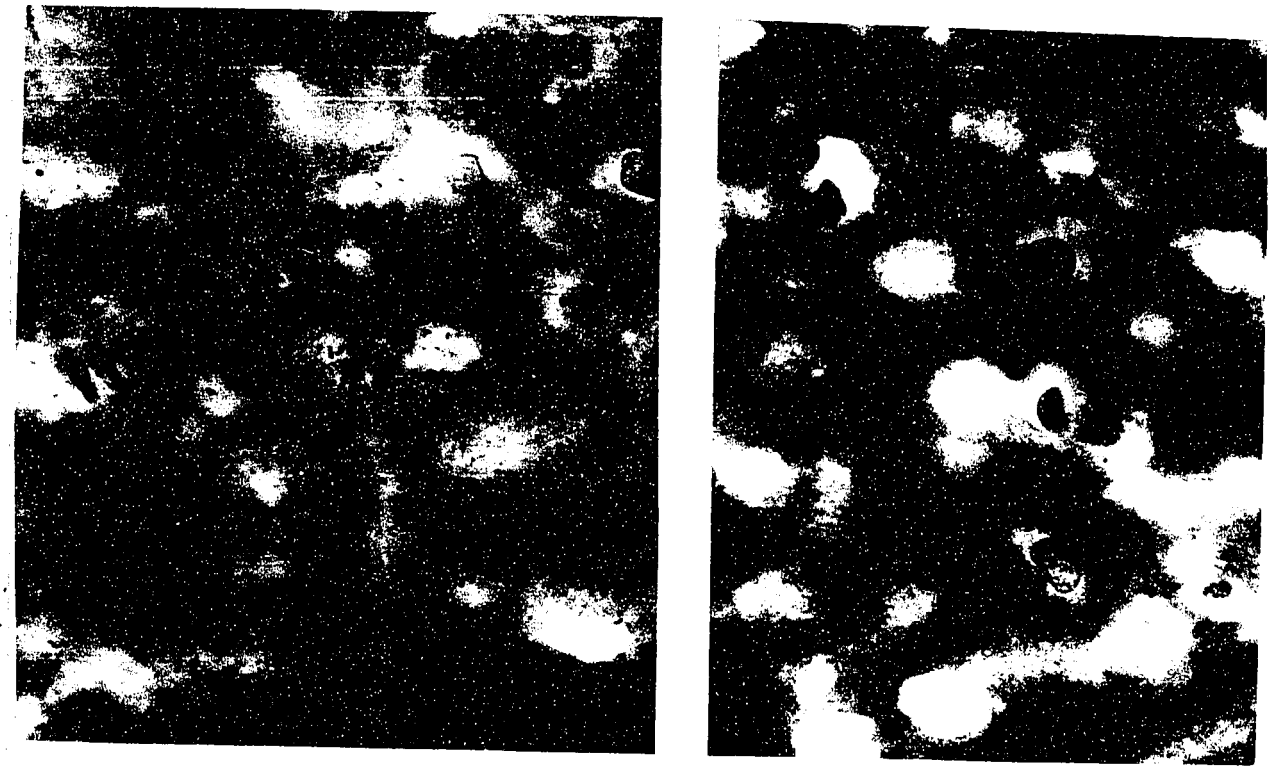


Fig. 28 The ipsilateral side and the contralateral side 800x

Fig. 29. Rat brain T4. Slide No. 13. Frontal Section. Fink and Heimer stain. On the left, degeneration in the dorsolateral part of the lateral nucleus on the ipsilateral side. On the right, it can be seen that the contralateral field is free of degeneration.

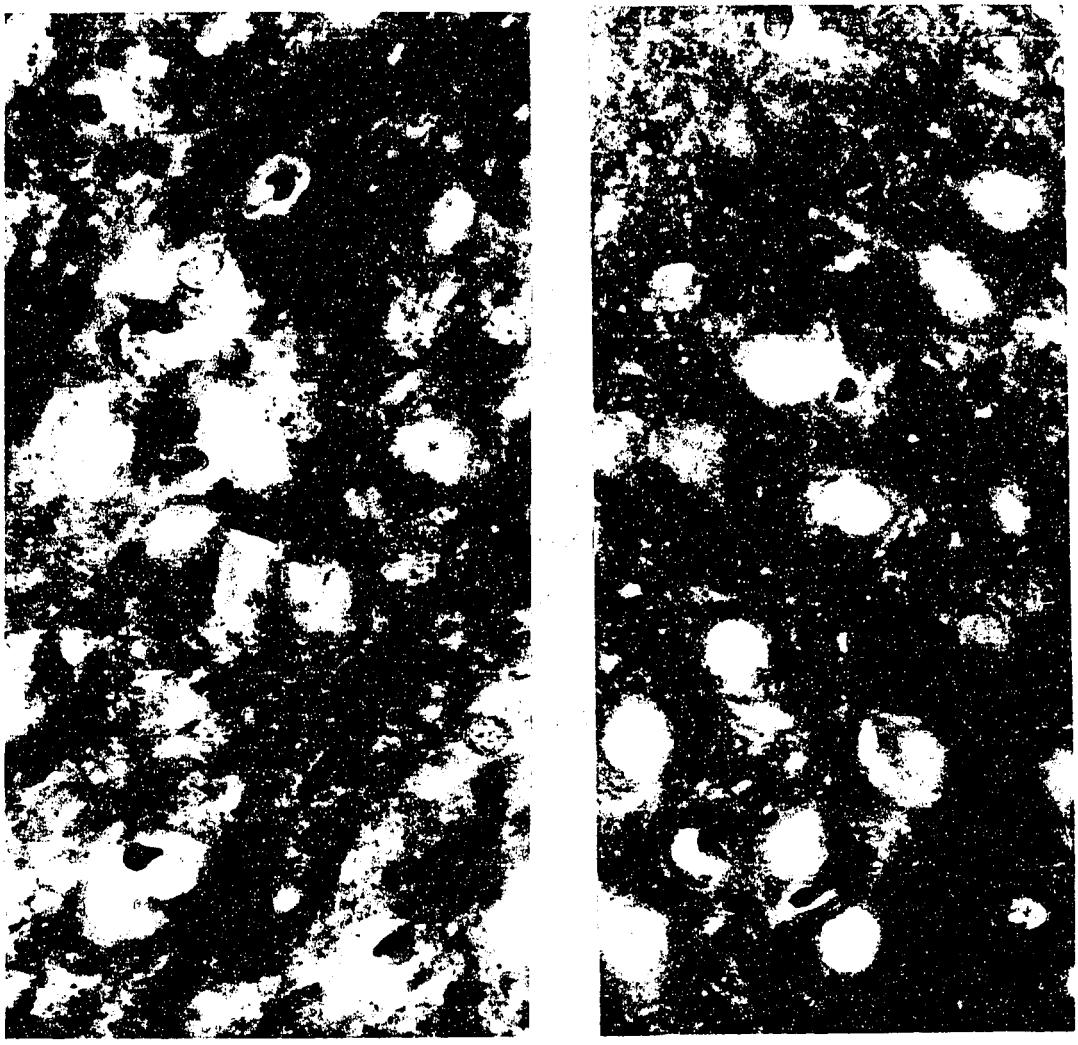


Fig. 29. The ipsilateral side and the contralateral side 800×

Fig. 30. Slide R1-366 (Dr. Sanides). Frontal Section. Nissl stain. B1 shows the anterior extremity of the large-celled part of the basal nucleus. 25x

Fig. 31. Slide RA10-9. Frontal Section. Nissl stain. The cells in the large-celled part of the basal nucleus. 400x

Fig. 32. Slide RA10-9. Frontal Section. Nissl stain. The cells in the small-celled part of the basal nucleus. 400x

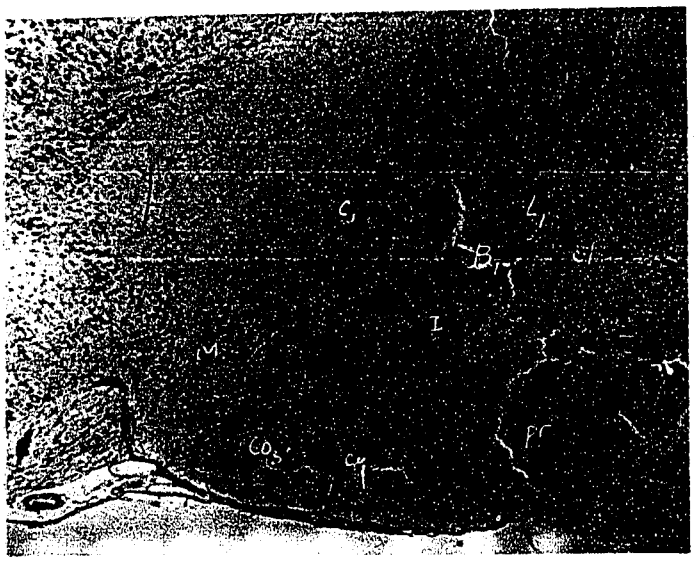


Fig. 30 25x

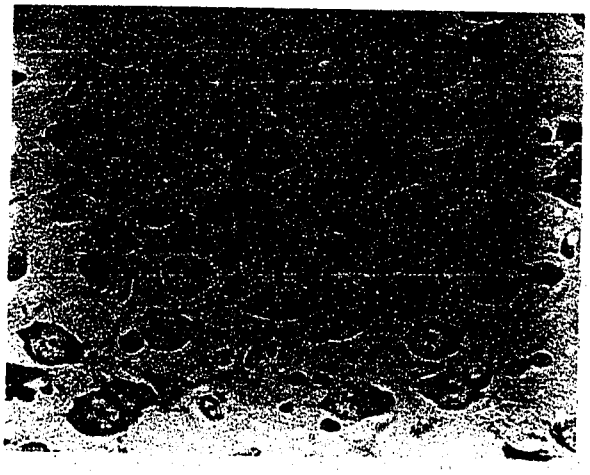


Fig. 31 400x

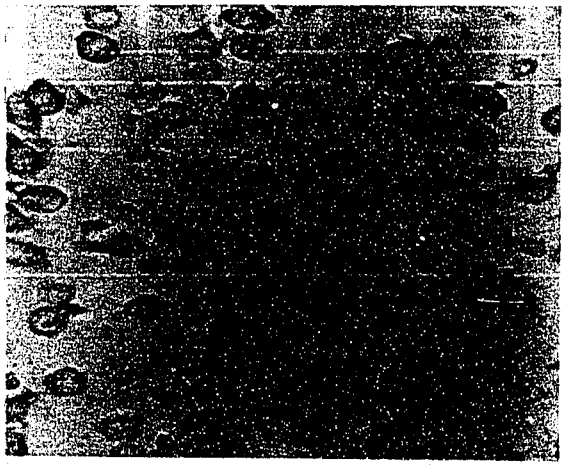


Fig. 32 400x

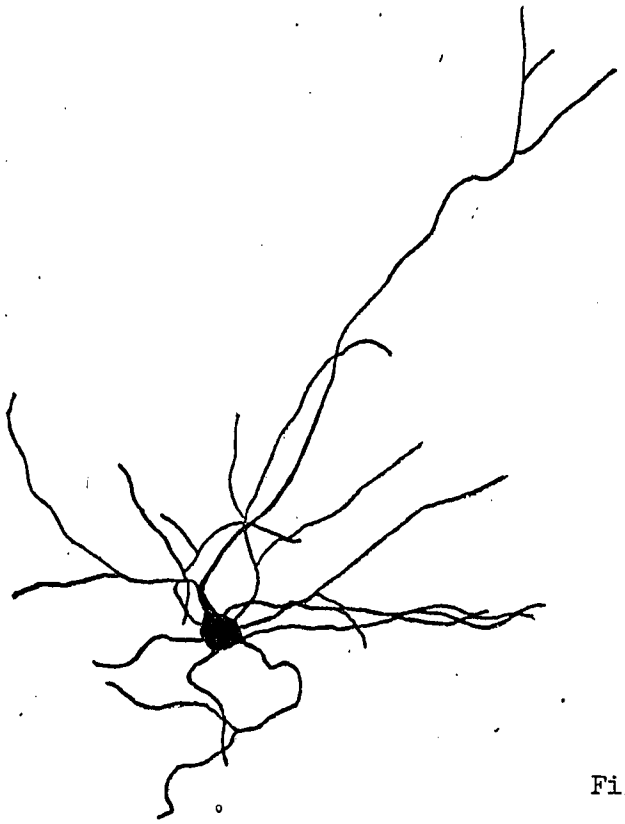
The small-celled part of the basal nucleus (Fig. 32) lies ventromedial to the large-celled part. It is made up predominantly of small cells but also contains a few medium-sized cells. This part of the basal nucleus extends for only 500 μ to 600 μ antero-posteriorly (Fig. 5E, F). In the horizontal sections it appears denser in structure than the anterior amygdaloid area. Nissl granules in the cytoplasm are less distinct than in the large-celled part.

In Golgi material the dendritic arborization is radiate. Clustering of the cells was seen occasionally. The cell types found in the basal nucleus are similar to those found in the lateral nucleus (Figs. 33 and 34). However, the cells in the large-celled part of the basal nucleus tend to have more branches and spines than those in the lateral nucleus. The cells of the small-celled part of the basal nucleus have fewer dendrites bearing fewer spines.

The highest cholinesterase activity in the amygdala was found in the large-celled part of the basal nucleus (Figs. 16-25). It was as dense as that seen in the caudate-putamen. In the posterior extremity of this part of the basal nucleus the staining density gradually diminishs toward adjacent slightly stained entorhinal cortex. The area occupied by the small-celled part of the basal nucleus shows low cholinesterase activity (Fig. 18).

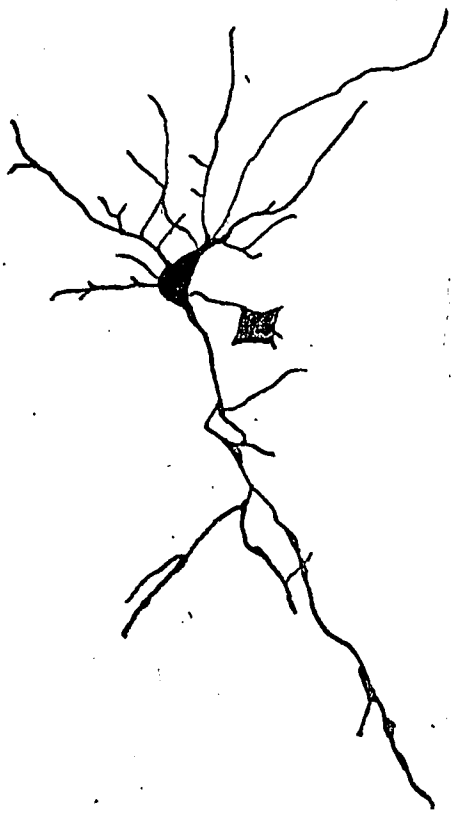
C. The accessory basal nucleus: Johnston ('23) stated that the accessory basal nucleus is closely related to the amygdaloid

Figs. 33 and 34. Two drawings of the modified pyramidal cells seen in the basal nucleus. Golgi stain.



Spine : +++

Fig. 33



Spine : +++

Fig. 34

fissure in the opossum. Both Gurdjian ('28) and Brodal ('47) could not find this nucleus although Brodal ('47) did make a tentative suggestion regarding its possible location (his area C?, Fig. 4, c, d). In this study the accessory basal nucleus was identified and it was observed to have two parts, a large-celled mass (Fig. 5, E and F) and a smaller-celled mass (Fig. 5, F). The former group lies ventral to the large-celled part of the basal nucleus. The latter group lies more posteromedially. At some levels the small-celled part of the basal nucleus described by Brodal ('47, compare Fig. 6G and H with g and h) is equivalent to the small-celled group of the accessory basal nucleus in this investigation.

The cells of both groups range from round to triangular, fusiform and polygonal in shape in Nissl preparations (Figs. 35, 36, 37). Other cellular characteristics found in the accessory basal nucleus are similar to those found in the basal nucleus. The accessory basal nucleus is always in close relation to the amygdaloid fissure.

It was observed in the Golgi material that the dendrites of the accessory basal nucleus may project ventrally to the cortical nucleus (Fig. 38). The nucleus is composed of pyramidal and fusiform cells similar to those found in the basal nucleus.

Low activity is seen in the accessory basal nucleus with cholinesterase staining (Figs. 18-25). This feature aids in distinguishing the large-celled part of the accessory basal from

Fig. 35. Slide R1-356 (Dr. Sanides). Frontal Section. Nissl stain. The anterior level of the accessory basal nucleus. 25x

Fig. 36. Slide RA10-9. Frontal Section. Nissl stain. The cells in the larger-celled part of the accessory basal nucleus. 400x

Fig. 37. Slide RA10-11. Frontal Section. Nissl stain. The cells in the smaller-celled part of the accessory basal nucleus. 400x

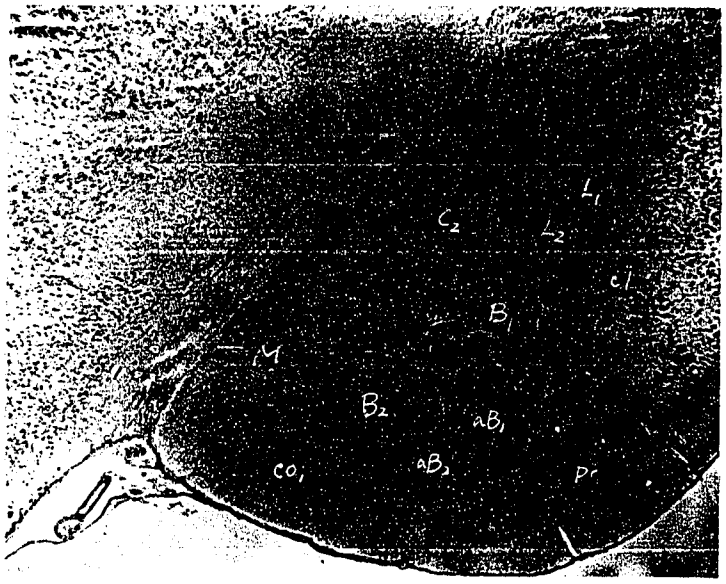


Fig. 35 25x

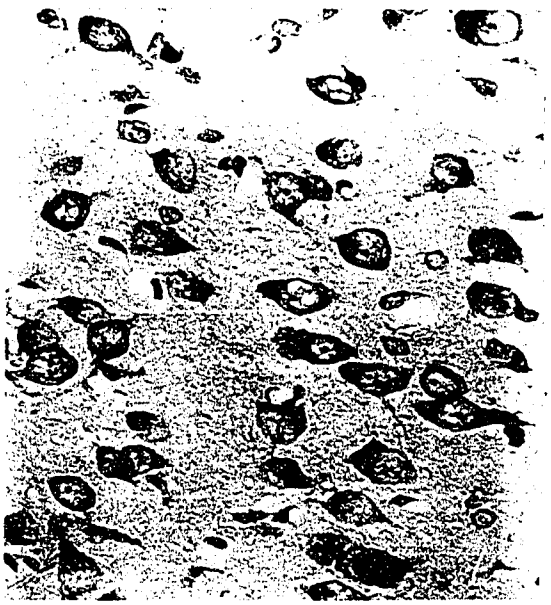


Fig. 36 400x

Fig. 37 400X

Fig. 38. Slide RA5-15. Frontal Section. Golgi stain. The dendrites of the cells in the accessory basal nucleus project superficially. 200x

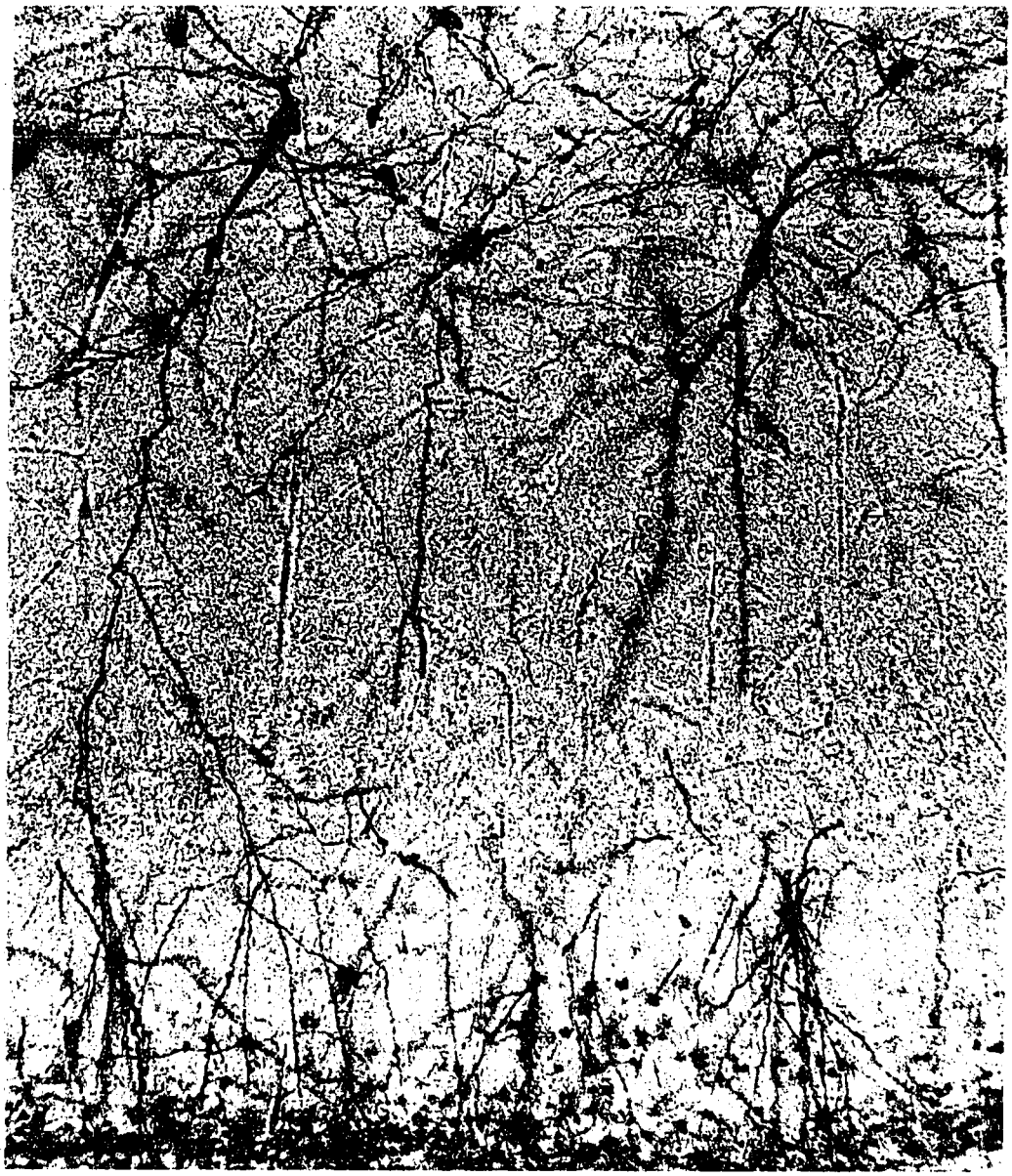


Fig. 38 200x

the large-celled part of the basal nucleus.

II. The Corticomedial Complex

A. The cortical nucleus: This is the most ventral of the amygdaloid nuclei in the rat (Figs. 9, 30, 35). It extends almost the whole length of the amygdaloid complex (Figs. 4-8, C-L) and can be divided into three parts. More anteriorly a medial and lateral group are seen. More posteriorly a third group appears. The anteriorly located medial area corresponds to what Brodal ('47) described in his paper (p. 9) as "a small group of cells at the medio-ventral angle of the common corticomedial nuclear mass". The cell somas of the cortical nucleus are round, fusiform or triangular in shape. Nissl granules are fewer in number and less distinct than those found in the cells of the piriform cortex.

In the Golgi preparations the majority of the cells in the cortical nucleus are found to be of the pyramidal type. The apical dendrites of these cells tend to be directed superficially, but are not so distinctly perpendicular to the surface as those of the pyriform cortex. They carry numerous spines. Some small bouquet-like cells are found close to the surface. Their dendrites spread out in the plexiform layer and may reach to the subpial surface. Again, many spines are distributed on the dendrites with the exception of the primary segment. The axons of both cell types are directed dorsally and extend beyond the dendritic field of

their cell of origin. An occasional fusiform and stellate cell with few dendritic branches and spines are also present in the cortical nucleus (Figs. 39, 40).

The cortical nucleus is low in cholinesterase activity (Figs. 16-26).

B. The medial nucleus: The nucleus lies in the ventromedial angle of the amygdala immediately lateral to the optic tract (Figs. 9, 35). It extends about one third the length of the amygdaloid complex (Figs. 4-6, C-H) and terminates after the appearance of the inferior horn of the lateral ventricle. The description given here includes only the "main mass" of the medial nucleus described by Brodal ('47). The nucleus is composed of many small and a few medium-sized cells that are round, triangular or fusiform in shape (Fig. 41). Relatively little cytoplasm surrounds the nuclei and Nissl granules are not abundant.

In Golgi material two types of cells can be found (Figs. 42, 43). The fusiform cells have two main dendrites coursing in opposite directions. Additional slender dendrites may be given off from the circumference of the body. They may carry few or no spines at all. They divide usually only twice or three times. The stellate cells usually have three to five thin branches radiating directly from the cell bodies. They may or may not branch and may carry a few to a moderate number of spines. Some cells in the dorsal portion

Figs. 39 and 40. Slides RA5-15, RA6-17, and RA6-19.
Frontal Section. Golgi stain.
These photographs show the cell types
found in the cortical nucleus.
The modified pyramidal cells,
Stellate cells, fusiform cells and
bouquet-like cells. 200x

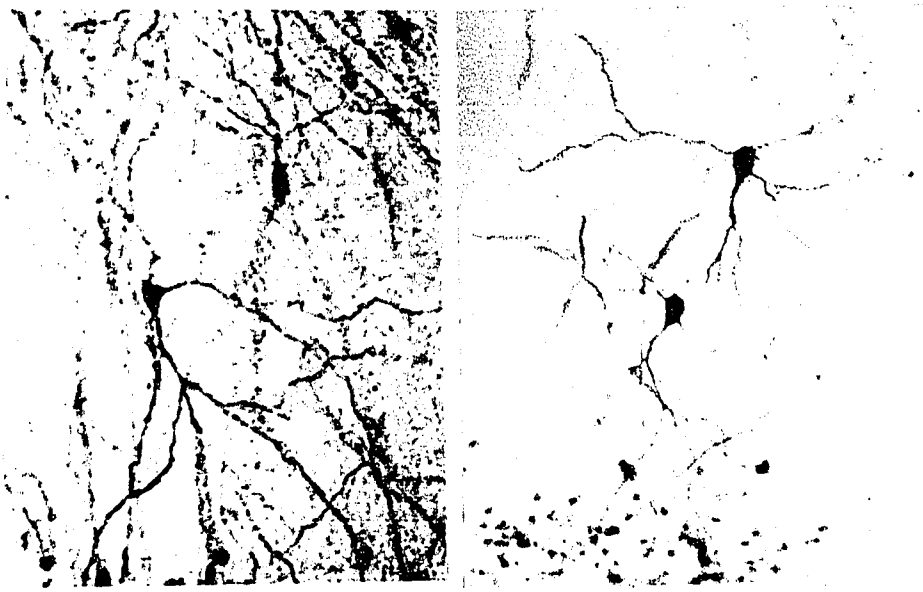


Fig. 39 200X

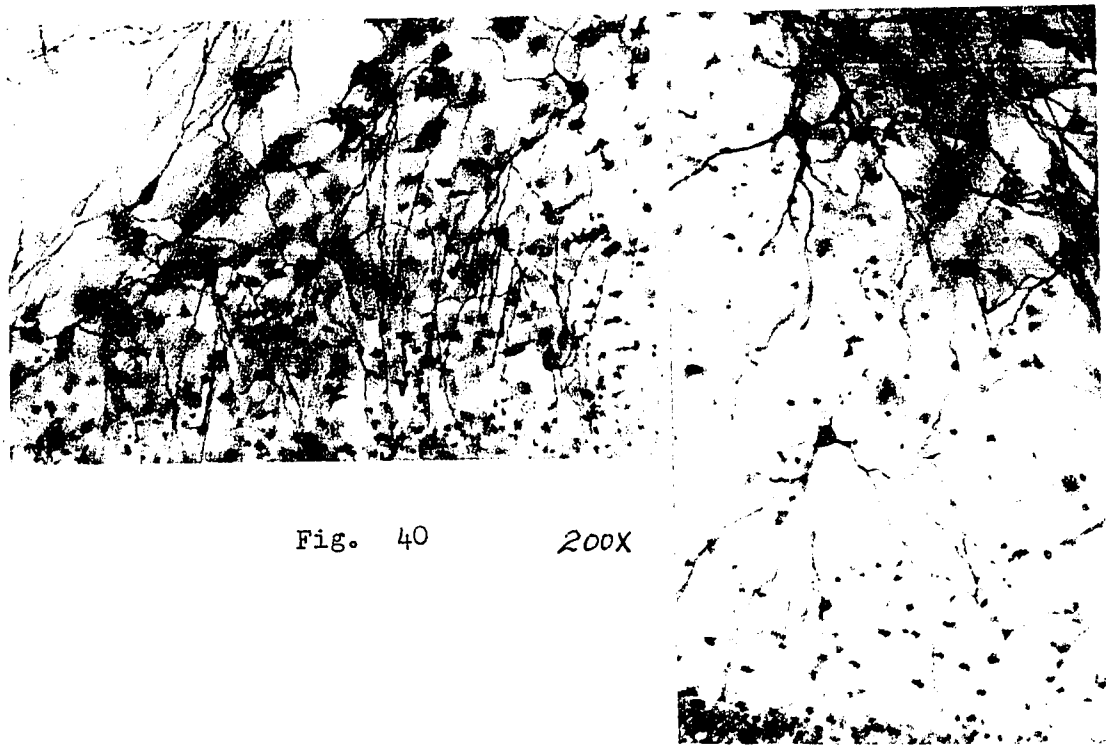


Fig. 40 200X

Fig. 41. Slide RA10-9. Frontal Section. Nissl stain. Cells in the medial nucleus. 400x

Figs. 42 and 43. Slides G31-R-16, and G31-R-15. Frontal Sections. Golgi stain. Stellate and fusiform cells in the medial nucleus. 200x

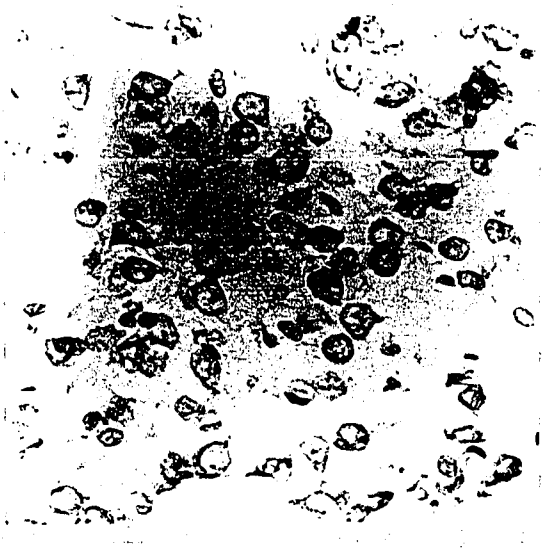


Fig. 41 400x

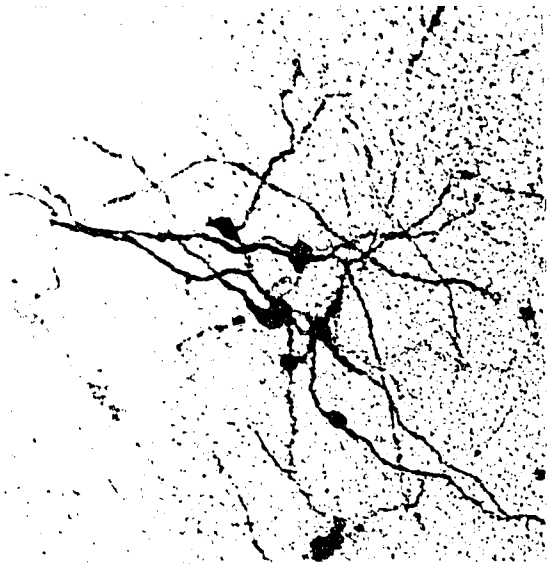


Fig. 42 200x

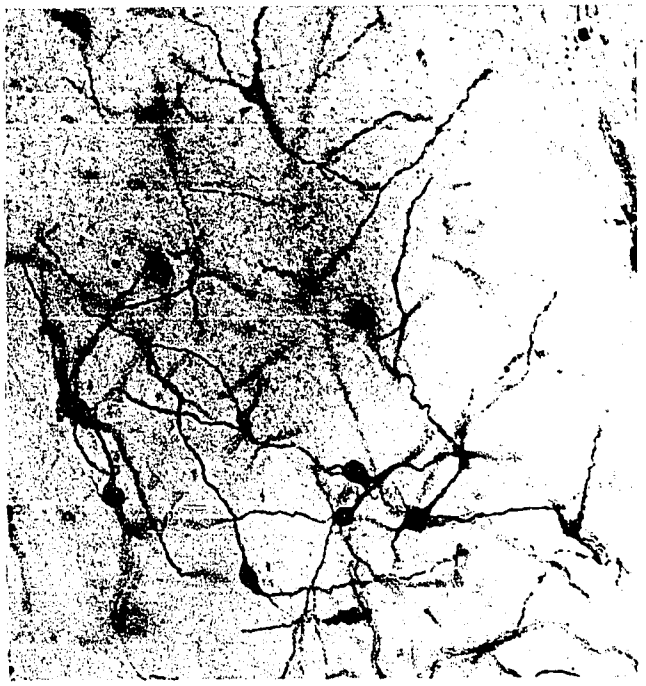


Fig. 43 200x

project their dendrites into the stream of the stria terminals.

The enzyme study shows the lowest cholinesterase activity in the medial nucleus (Figs. 17-22).

C. The central nucleus: This nucleus is not situated, (as its name would imply), in the central part of the amygdala in the rat but is located in its dorsomedial angle (Figs. 4-6, C-H). It can be divided into two parts, a medial and a lateral. The former is composed primarily of medium-sized cells (Fig. 45) that are round, fusiform or triangular in shape. They are more loosely arranged than those of the lateral part of the central nucleus. Nissl granules are more distinct in the cytoplasm of the larger cells. The cellular components of the medial part of the central nucleus are similar to those of the bed nucleus of the stria terminalis and the anterior amygdaloid nucleus.

Just posterior to the anterior extremity of the central nucleus the better circumscribed or lateral part of the central nucleus appears (Figs. 4D, 5E, F). The cells are smaller than those of the medial division (Fig. 44), and contain little cytoplasm. The Nissl granules are very palely stained. This part of the central nucleus is similar to cytoarchitecture of the caudate-putamen complex and they are sometimes hard to separate. This difficulty has been reported in many species including rat (Gurdjian, '28; Brodal, '47), rabbit (Young, '36), bat (Humphrey, '36), cat (Fox, '40), monkey

Fig. 44. Slide RA2-6. Frontal Section. Nissl stain.
The cells in the lateral part of the central nucleus.

Fig. 45. Slide RA2-6. Frontal Section. Nissl stain.
The cells in the medial part of the central nucleus.
640x

Fig. 46. Three drawings of the cells in the central nucleus.
Golgi stain.

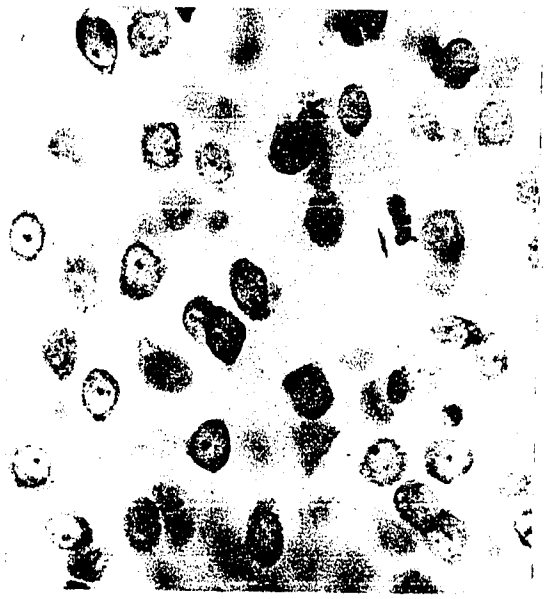


Fig. 44 640x

Fig. 45 640x

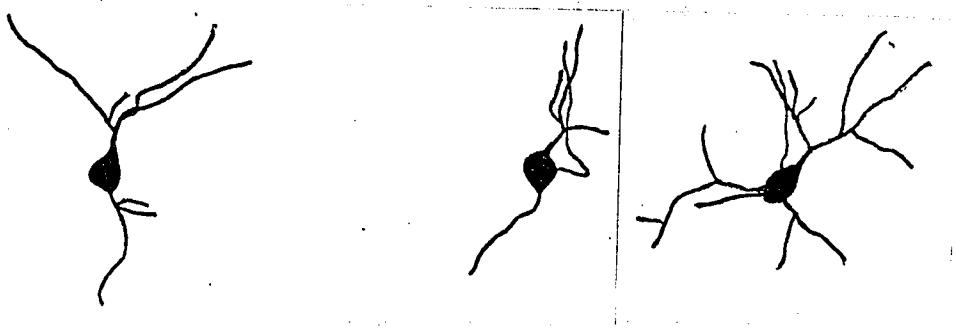


Fig. 46 Spine: +

(Lauer, '45), man (Crosby and Humphrey, '41). The cells in the lateral part of the central nucleus are rather uniform in size and density compared with those of the other nuclei in the amygdala. They may be smaller in size than those of the caudate putamen complex.

In Golgi stained sections the cells near the stria terminalis appear to project their dendrites into the stream of the stria. The lateral part of the central nucleus is relatively well circumscribed.

Two types of cells have been seen in the Golgi material. Those are stellate and fusiform. The stellate cells are small and medium-sized. Their dendrites are of the radiate pattern and carry varying numbers of spines. Some of them are almost free of spines while others may have many spines. A low branching order of the dendrites are noted. The dendritic field is round or elongated. The fusiform cells, small and medium-sized, usually have two main dendrites sent out from the tapered ends. There are few spines on the dendrites.

The lateral part of the central nucleus shows extremely low enzyme activity while the medial part shows a little higher activity in cholinesterase study (Figs. 17-20). Because of the high cholinesterase activity in the caudate-putamen complex, the central nucleus can be distinguished easily in this type of preparation.

D. The nucleus of the lateral olfactory tract: The extent

of this nucleus can be seen in (Fig. 3A, B). It can be divided into a dorsal and a ventral part. The ventral main mass is well circumscribed and the easiest of the amygdaloid nuclei to identify (Fig. 47). It has a disc-like shape which can be most clearly seen in horizontal sections. The A-P dimension in this investigation is around 600 μ. However, the A-P extent of the ventral main mass indicated in König and Klippel's rat atlas is not less than 890 μ. The length of the ventral main mass together with a cell group posterior to it (medial part of cortical nucleus in this study) is around 900 μ. The cells in this part are small to medium in size and round, oval or triangular in shape. The cytoplasm is deeply stained and fine. Nissl granules can be seen with high power magnification (Fig. 48). The cells are densely packed and evenly spaced. The dorsal sub-nucleus is shaped like a low cone resting on the ventral main mass. It is composed primarily of medium-sized cells. These are round, fusiform and triangular in shape. Nissl granules aggregate in the polar regions of the cytoplasm (Fig. 48).

In Golgi preparations a special pyramidal type of cell is seen in the ventral main mass of the nucleus of the lateral olfactory tract (Fig. 49). It has one long very thick dendritic directed superficially and several thin basal dendrites which are wavy and sometimes tufted. All the dendrites carry a dense spine population. Axons were identified arising from the cell bodies and coursing

Fig. 47. Slide R1-311 (Dr. Samides). Frontal Section. Nissl stain. NLOT indicates the nucleus of the lateral olfactory tract. 25x

Fig. 48. Slide RA10-6. Frontal Section. Nissl stain. High power view of the NLOT. The cells in the dorsal part are larger while those in the ventral part are smaller. 400x

Fig. 47 25x

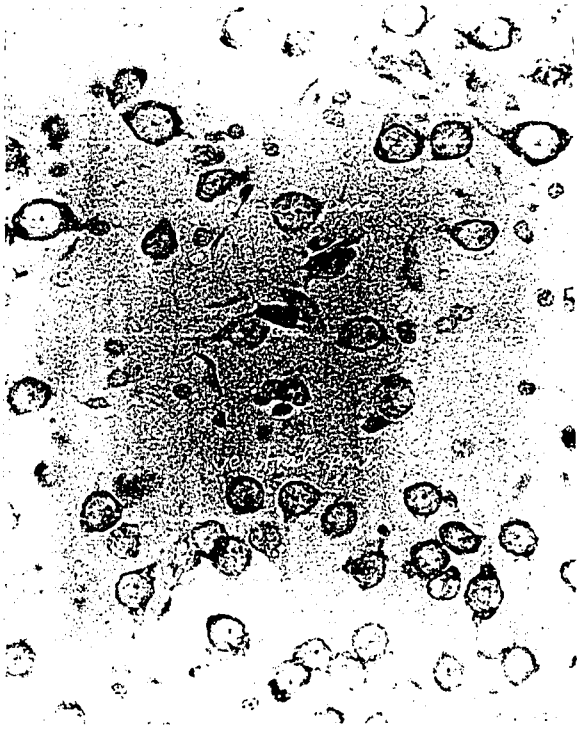
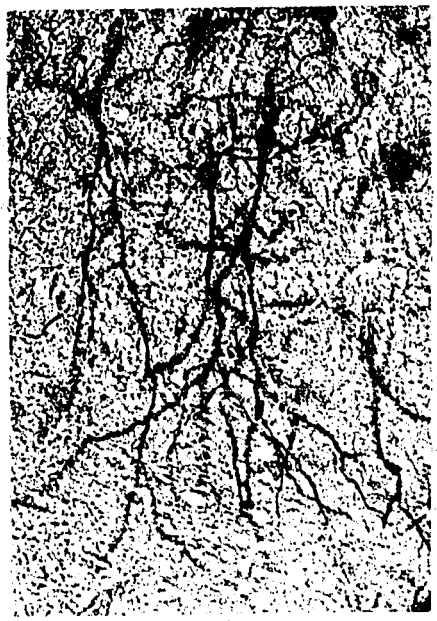


Fig. 48 400x

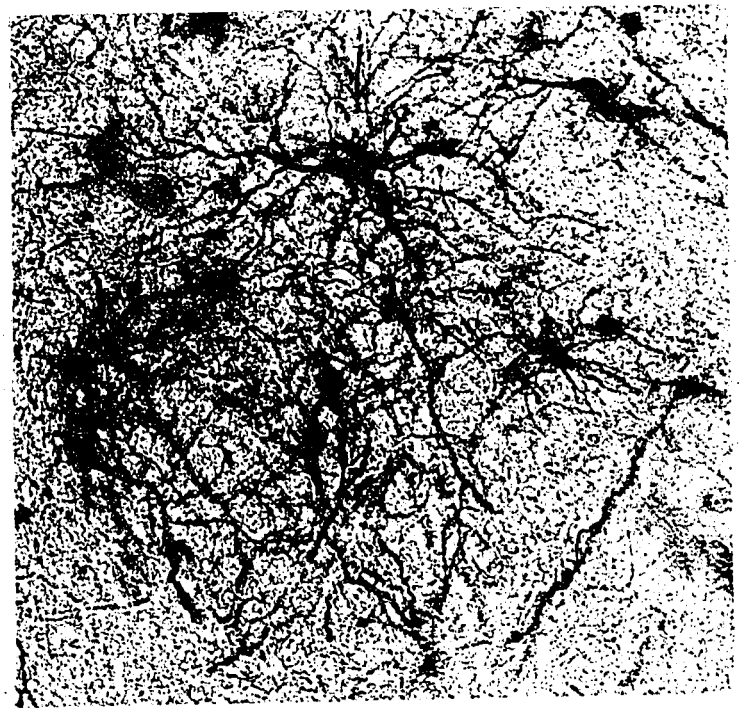
Fig. 49. Slide G33-L-13. Frontal Section. Golgi stain. The typical cells in the ventral part of the nucleus of the lateral olfactory tract (NLOT). 200x

Fig. 50. Slide G33-L-13. Frontal Section. Golgi stain. The cells seen in the dorsal part (single arrow) and the ventral part (double arrow) of the NLOT. 200x



ventral part

Fig. 49 200X



Dorsal part

ventral part.

Fig. 50 200X

dorsally beyond the dendritic field.

In the dorsal subnucleus another kind of cell can be found (Fig. 50). This type has a large polymorphic body and many dendrites carrying a moderate number of spines.

The cholinesterase activity in the nucleus of the lateral olfactory tract is as high as that in the large-celled part of the basal nucleus (Figs. 15, 16). The active area extends dorsally to include the dorsal subnucleus and ventrally to the fibrillar layer. The distribution of enzyme activity gradually fades out both ventrally and dorsally.

E. The anterior amygdaloid area: This is a diffusely scattered cellular area located at the anterior portion of the amygdaloid complex (Figs. 3, 4, A-D; Fig. 47). It consists of the same kind of cells as are seen in the medial part of the central nucleus in Nissl preparations.

In Golgi preparations stellate, fusiform and some modified pyramidal types of cells can be seen. The large cells are similar to those found in the dorsal part of the nucleus of the lateral olfactory tract. The small and medium-sized stellate and fusiform cells resemble those found in the central nucleus. Medium-sized modified pyramidal cells were noted also.

Low to moderate cholinesterase activity in the anterior amygdaloid area was noted (Figs. 15, 17).

F. The intercalated mass: These cell masses are very discrete and located mainly in the region between the basolateral and the corticomedial group (Fig. 9). They are composed of very small round cells that are compactly arranged. Their presence may sometimes be useful in assessing the level and the point of junction of different nuclei (Figs. 3-6, A-G). They contain very little cytoplasm and the Nisal granules are barely seen (Fig. 51).

In Golgi preparations they appear as small stellate cells with thin dendrites carrying a few spines on their distal portions.

In the enzyme study there is very low activity in the intercalated masses (Figs. 17, 20).

G. The cortico-amygdaloid transitional areas: These are the areas of transition from the piriform and hippocampal cortex to the amygdaloid complex. The former is related to the lateral part of amygdaloid fissure (Figs. 6, 7, H-J). The latter is related to the medial limb of the amygdaloid fissure.

The amygdalopiriform transitional area shows a gradual change in staining intensity from the piriform cortex to the cortical nucleus (Figs. 9, 35). The cells become more irregularly arranged as the cortical nucleus is approached. Small and medium-sized pyramidal and stellate cells are seen in the region.

Cholinesterase activity in the amygdalo-piriform transitional cortex is the same as that in the cortical nucleus.

Fig. 51. Slide RA10-9. Frontal Section. Nissl stain.
The cells of the intercalated mass.
400x

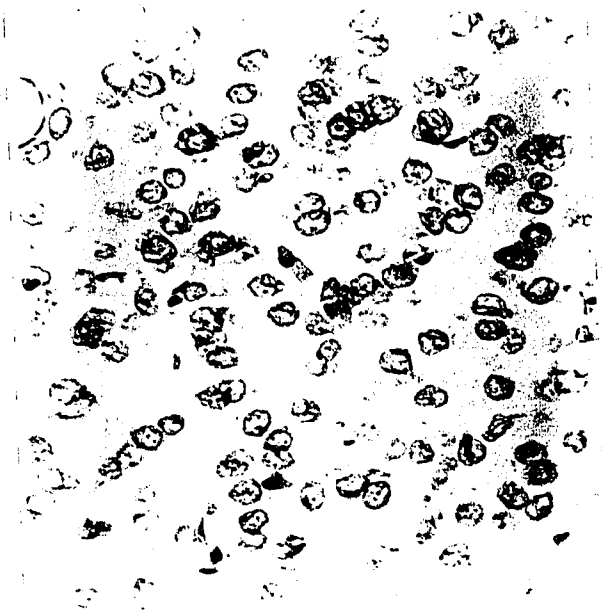


Fig. 51 400X

The amygdalo-hippocampal transitional area in this investigation (Figs. 6-8, H-L) is the one that Brodal ('47) described as the posterior prolongation of the medial nucleus. In this investigation it is not included in the medial nucleus for the following reasons. Firstly the cellular components are large and usually pyramidal in type. Secondly there is a very definite separation of these two masses by a fiber bundle.

In the Golgi material, one sometimes sees the same kind of modified pyramidal cell in the amygdalo-hippocampal transitional area as in the cortical nucleus and hippocampus. The amygdalo-piriform transitional area contains more of these cells and more closely resembles the cortical nucleus.

In the cholinesterase preparations there is moderate activity similar to that in the hippocampal region (Figs. 22-26).

A list of abbreviations

AAA	-	The anterior amygdaloid area.
aB_1	-	The large-celled part of the accessory basal nucleus.
aB_2	-	The smaller-celled part of the accessory basal nucleus.
B_1	-	The large-celled part of the basal nucleus.
B_2	-	The small-celled part of the basal nucleus.
C_1	-	The medial part of the central nucleus.
C_2	-	The lateral part of the central nucleus.
Cl	-	Claustrum.
Co_1	-	The lateral group of the anterior cortical nucleus.
Co_2	-	The posterior cortical nucleus.
Co_3	-	The medial group of the anterior cortical nucleus.
E	-	The entorhinal cortex.
Hip	-	Hippocampus.
I	-	Intercalated mass.
L_1	-	The dorsolateral part of the lateral nucleus.
L_2	-	The ventromedial part of the lateral nucleus.
LV	-	The lateral ventricle.
M	-	The medial nucleus.
NLOT	-	The nucleus of the lateral olfactory tract.
ot	-	The optic tract.
P	-	Caudate-putamen.
Pr	-	Piriform cortex.

S - Subiculum.

SON - The supraoptic nucleus.

T_1 - The amygdalo-piriform transitional area.

T_2 - The amygdalo-hippocampal transitional area.

CHAPTER IV

DISCUSSION

The amygdaloid complex is usually divided into two major groups. In the observations based on phylogeny Johnston ('23) included the central nucleus and the nucleus of the lateral olfactory tract in the corticomedial part. The lateral, basal and accessory basal nuclei were included in the baso-lateral portion. This kind of classification, however, was not supported by ontogenetic studies (Humphrey, '68). In human fetus Humphrey ('68) found that the central nucleus and the nucleus of the lateral olfactory tract developed even later than the basolateral group. This is an example that phylogeny does not always reflect ontogeny. Fox ('40) put the anterior amygdaloid area and the nucleus of the lateral olfactory tract into a third group.

The classifications mentioned above are not supported by the studies of the adult rat brains. The cell types in the cortico-medial group are not homogenous. Those of the cortical nucleus and the nucleus of the lateral olfactory tract are predominantly modified pyramidal in type. They are more similar to those of the basolateral group than the corticomedial group. In the histo-chemical study the large-celled part of the basal nucleus and the nucleus of the lateral olfactory tract have the same high acetyl-

cholinesterase activity. Other members of the amygdaloid complex have lower activity. According to Shute and Lewis ('63) there is a cholinesterase containing system in the rat brain. The two nuclei with the high acetylcholinesterase activity in the amygdala were included in this system. However, the authors interpreted the densely stained part of the basal nucleus as the "pars ventralis of the lateral amygdaloid nucleus". In these areas they noted that the staining was so dense that the precise location of enzyme is difficult to determine. From the physiological point of view, Koikegami et al ('63) observed that stimulation of the "medial principal nucleus" (which appears to correspond to the small-celled part of the basal nucleus) like the nuclei of the corticomedial group resulted in sympathetic effects. Other members of the basolateral group were related to parasympathetic function. Thus it can be seen that different approaches yield different classifications. As there is no way of knowing which method of subdividing the nuclei is the most significant, perhaps it is wisest at present to consider them individually.

Regarding the central nucleus of the amygdala, Johnston ('23) used the Weigert stain and noted that the putamen was richer in myelinated fiber network than the central nucleus, and on this basis the separation of the two areas was said to be fairly clear. By using this criterion Fox ('40) found difficulty separating the central

nucleus and the putamen in certain levels in the cat. Other authors including Gurdjian ('28), Young ('36), Humphrey ('36), Crosby and Humphrey ('41) and Brodal ('47) have been aware of the difficulty in delimitation of the central nucleus. On comparison of the acetylcholinesterase activity in the caudate-putamen complex and the central nucleus, a surprising difference was noted. The caudate-putamen complex acquires much higher acetylcholinesterase activity than does the central nucleus. The contrast is sharp enough to be used as a criterion to separate them. The validity of the method applied in other species needs further confirmation. Although there were similar findings in the guinea pig and man by De Giacomo ('60). Koelle's paper ('54) indicated that the central nucleus of the amygdala acquired the same intense staining in rat as does the caudate-putamen and the nucleus of the lateral olfactory tract. This may be due to the different indentification of the central nucleus of the amygdala. As no illustration was given in his report, the results cannot be compared.

The similarity of the cellular components of the medial part of the central nucleus, the bed nucleus of the stria terminalis and the anterior amygdaloid area agrees with Johnston's finding ('23) that the bed nucleus of the stria terminalis expands caudad into the central and medial nuclei of the amygdala. It is also in agreement with the hypothesis of Cowan et al ('65) that the anterior amygdaloid

area be considered as a bed nucleus for the anterior amygdaloid component of the medial forebrain bundle and that the stria terminalis is a displaced component of the medial forebrain bundle.

The cortical nucleus does not seem to have a homogenous cellular structure. Three subdivisions have been suggested in this study. The significance of the groupings is not clear. Valverde ('62) postulated the cortico-baso-lateral linked system according to his theory that the afferents from the olfactory bulb terminate in the cortical nucleus by giving off dorsally running collaterals from the anteroposteriorly directed fibers (p.162; Figs. 2, 13). Heimer ('68, '69) studied the synaptic distribution of the centripetal and centrifugal nerve fibres in the olfactory system of the rat and pointed out that the termination of olfactory fibers in the cortical nucleus shows a massive monolaminar pattern in the superficial part of the plexiform layer and there does not seem to be any degeneration deep to the superficial part of the plexiform layers. In the Golgi preparations there are many cells sending their apical dendrites superficially to reach the superficial part of the plexiform layer. These dendrites can be considered receiving the terminals from the olfactory bulb fibers. This observation is in agreement with experimental material, and Girgis's observation ('68) based on normal material. However, the possibility that collaterals extend from the secondary olfactory area to the deeper part of the cortical nucleus as illustrated by

Valverde ('62) cannot be ruled out.

The amygdalo-hippocampal transitional area in this investigation corresponds to the posterior portion of the medial nucleus described by Brodal ('47). This area in the rat seems to be homologous to the amygdalo-hippocampal transitional area indicated by Crosby and Humphrey ('44) in the shrew. The medial nucleus, therefore, is confined to the anterior portion described by Brodal ('47). In early development the medial nucleus of the human embryo passes over into the anlage of the gyrus dentatus directly and the cortical nucleus is clearly continuous with the primordial cornu ammonis. Later in development the relationship is obscure and a transition zone intervenes. In the older fetuses, this area either lies between the primordial cornu ammonis or the anlage of the gyrus dentatus on one side and the cortical nucleus or medial nucleus on the other. However, the specific relationship is no longer constant (Humphrey, '68). The later stage of the ontogenetic development (Humphrey, '68) is comparable to that in the shrew (Crosby and Humphrey, '44) and in the adult rat in this investigation. Posteriorly, the accessory basal nucleus and the basal nucleus also lie next to the amygdalo-hippocampal transitional area in the shrew (Crosby and Humphrey, '44) and in the adult rat in this investigation.

The nucleus of the lateral olfactory tract may be single

mass as in the cat (Fox, '40) and mink (Jeserich, '45), or two masses, medial and lateral, as in the rabbit (Young, '36), rostral and caudal, as in the bat (Humphrey, '36) and dorsal and ventral, as in the rat (Gurdjian, '28; Brodal, '47). These various relative position and the union or separation of these two parts may not signify a functional difference. The various arrangements in the different species might mean the mutual adjustment of the cells and fibres to the space available relative to the surrounding. In the coypu rat Girgis ('68) only sometimes recognized two rounded masses. However, in the albino rat used in this investigation two parts in the nucleus can always be identified. Krieg ('46) in the albino rat designated 51h as the nucleus of the lateral olfactory tract and described it as minute ovoid compact group of the dark cells at the caudal end of the olfactory tubercles. This finding may be interpreted as applying only to the ventral main mass of the nucleus in the present study. AchE staining shows high activity in the nucleus. The location of AchE is not clear. Shute and Lewis ('63) suggest that it is from part of the "olfactory radiation" derived from lateral preoptic area and olfactory tubercle. However, the possibility that the AchE is in the cells of the nucleus of the lateral olfactory tract cannot be excluded. At these levels the medial part of the piriform cortex near the anterior amygdaloid area shows high AchE activity too. This area is in the pathway of the

"amygdaloid radiation" as seen in Shute and Lewis's diagram ('63).

The large-celled part of the basal nucleus is much more extensive anteriorly than that described by Brodal ('47). AchE staining shows high activity. In human and guinea pig it has been reported that AchE staining is confined to the basal nucleus (De Giacomo, '60). Preliminary studies by Wakefield ('69) have shown the distribution of the AchE activity in the basal nucleus is the same in the cat. Therefore the area stained intensely in the rat is homologous to that of human, guinea pig and cat. The large-celled part of the basal nucleus in the rat appears at the same level anteriorly as the lateral nucleus and ends posteriorly just before the termination of the cortical nucleus. At its posterior extremity the cells intermingle with those of the entorhinal cortex. AchE staining gradually diminishes in intensity toward the lightly stained entorhinal cortex. This phenomenon can be explained by Johnston's hypothesis ('23) that the basolateral amygdaloid complex forms as a result of infolding of the amygdaloid fissure or Humphrey's proposal ('68) that there is a migration of cells from the deep portion of the developing amygdala cortex. Whether the migration occurs in an outward or inward direction, the resulting cell continuity would appear the same.

As far as the sites of AchE activity are concerned they might be in the Nissl substance of neurons (Fukada and Koelle, '59),

in endoplasmic reticulum or possibly in mitochondria (Giacobini, '60) or in axons (Shute and Lewis, '63). De Robertis et al ('63) showed that AchE is associated with the membrane of nerve endings while Ach and cholinacetylase are located in synaptic vesicles (after Koelle, '62). Friede ('66) summarized several enzyme patterns found in nerve cells: (1) high enzyme activity is often present in cytoplasm, dendrites and axons; (2) little enzyme activity can occur in the cytoplasm of nerve cells, with a strong granular reaction in the terminal boutons on the cell membrane or in the neuropil surrounding the perikarya; (3) both patterns may occur in combination.

Most authors investigating the amygdala did not recognize the existence of the large-celled part of the accessory basal nucleus and included this area in the large-celled part of the lateral nucleus (Gurdjian, '28) or in the large-celled part of the basal nucleus (Brodal, '47; Girgis, '68, coypu rat). According to Johnston ('23) in opossum the accessory basal nucleus is closely related to the amygdaloid fissure. In the rat there is a large-celled mass ventral to the large-celled part of the basal nucleus. The AchE staining of the former is quite different from the latter group. This area with large cells and low AchE activity is thought to be the large-celled part of the accessory basal nucleus in the present study of the amygdaloid complex.

The lateral nucleus of the amygdaloid complex makes its

first appearance at the level of the opossum in the phylogenetic scale and apparently exists in all mammals. The relative position of this nucleus is rather constant. As far as the cell size is concerned, the lateral nucleus is variable from the smaller cells in the bat (Humphrey, '36), the small and medium-sized cells in the monkey (Lauer, '45) and man (Crosby and Humphrey, '41) to the largest cells in the mouse (Valverde, '62). These variations may be due to the different descriptive criteria, delimitation problem, real species difference or artifact. The largest cells in the amygdala of the mouse (Valverde, '62) are in the lateral nucleus. This is not the case in the rat. Gurdjian ('28) included the large-celled part of the basal nucleus and the accessory basal nucleus of this investigation in the lateral nucleus. Brodal ('47) excluded the large-celled part of the accessory basal nucleus from the lateral nucleus and included it in the large-celled part of the basal nucleus. As can be seen from their illustration, Girgis ('68, coypu rat) and Brodal ('47) delimited the large-celled part of the basal and lateral nuclei in a similar manner. However, it should be noted that both of them admitted the difficulty of separating these nuclei at some levels.

Close observation revealed that the cellular components of the large-celled part of the basal nucleus extended into most of the large-celled part of the lateral nucleus designated by Brodal ('47)

anteriorly. These two parts just mentioned are impossible to separate and should be put together as the large-celled part of the basal nucleus. This interpretation of the material is supported by the cholinesterase staining which shows the same high activity in both areas.

Dorsal and dorsolateral to the large-celled part of the basal nucleus is the lateral nucleus. The lateral nucleus still has two parts in the interpretation presented here. The large-celled or ventromedial part of the lateral nucleus occupies the area corresponding to the transitional area between the large-celled part and the small-celled part of the lateral nucleus shown as a dotted line by Brodal ('47) in his diagram. This area shows lower cholinesterase activity than the small-celled part of the lateral nucleus. As the cytoarchitecture of both the lateral and the basal nucleus compares well with the enzyme activity as described in this report. The delimitation of the nuclei is considered more adequate than that of previous authors.

The pattern of AchE distribution in the amygdala and the putamen in the rat has been recorded by Ishii ('57 b) in the table XVll. In this table the "lateral nucleus" of the amygdala and putamen maintain the same value of AchE activity from the 30 days old to the adult rat. Koelle ('54) reported similar findings in the "lateral nucleus" of the amygdala and the putamen. Shute and Lewis ('63) described and showed in their diagram that the densely

stained areas in the amygdala were "pars ventralis of the lateral amygdaloid nucleus", and the nucleus of the lateral olfactory tract. In these accounts the so-called "pars ventralis" of the lateral nucleus of the amygdala must be the large-celled part of the basal nucleus of this investigation.

A degeneration study was done because preliminary evidence in the cat (Lescault, '69) suggested that the degeneration pattern resulting from neocortical lesions could be useful in defining the dorsolateral part of the lateral nucleus. In the cat the degeneration terminates in the supero-lateral segment of the lateral nucleus. In the rat it is distributed to the comparable part of the lateral nucleus. These findings support the cytoarchitectural description of the dorsolateral part of the lateral nucleus as described in this study, rather than that of Brodal ('47).

The delimitation of the amygdaloid nuclei in Nissl stained material and the confirmation of these findings with AchE staining, and Fink and Heimer's technique provide a new and more solid basis for comparison of the individual amygdaloid nuclei in different species. In addition it is anticipated that this study will allow a more exact analysis of both the afferent and efferent connections of the amygdala in the rat and provide the basis for a clearer presentation of the phylogeny of these projection systems.

CHAPTER V

SUMMARY

1. The nuclear subdivisions of the amygdala were studied in Nissl, Golgi, acetylcholinesterase (AchE) and experimental preparations.

2. Although the two parts of the lateral nucleus were identified, their delimitation differs from that of Gurdjian ('28) and Brodal ('47) so that the nucleus as a whole is less extensive anteriorly.

3. Concomitantly the large-celled part of the basal nucleus is more extensive anteriorly. Confirmation of these findings in Nissl preparations was obtained from AchE material where the large-celled part of the basal nucleus shows very high activity compared to the adjacent cell groups.

4. Contrary to previous studies, an accessory basal nucleus was observed.

5. The central nucleus, which is difficult to delimit from caudate-putamen in Nissl preparations, stands out clearly in AchE preparations because of its very low level of activity.

6. The medial nucleus of this study corresponds closely to the "main mass" of the medial nucleus described by Brodal ('47).

7. A transitional area between amygdala and hippocampal has been identified.

8. A subdivision of the cortical nucleus is suggested.

9. The nucleus of the lateral olfactory tract shows approximately the same high AchE activity as that of the large-celled part of the basal nucleus.

10. The degeneration resulting from the neocortical lesions in this study terminates in the dorsolateral part of the lateral nucleus.

11. It is anticipated that this analysis of the nuclear subdivisions of the amygdala will allow a more exact comparison of experimental anatomical, electrophysiological, and ablation studies with those carried out in different species.

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