

# STUDIES OF THE VERTEBRATE TELEENCEPHALON

## II. THE NUCLEAR PATTERN OF THE ANTERIOR OLFACTORY NUCLEUS, TUBERCULUM OLFACTORIUM AND THE AMYGDALOID COMPLEX IN ADULT MAN

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### INTRODUCTION

The present paper is an attempt to correlate the finer nuclear configuration of the anterior olfactory nucleus, tuberculum olfactorium and the amygdaloid complex in adult man with that of the corresponding centers in various mammals. The study is based on a single series of adult material which had originally been fixed in formalin and then treated with the Huber trichloroacetic fixative before staining by the routine method for toluidin blue. The series was prepared in the Department of Anatomy of the University of Michigan

through the aid of a grant from the Horace H. Rackham School of Graduate Studies of this University, to whom the writers wish to express their sincere thanks. The work was greatly furthered by the use of a special binocular research microscope provided by a Carnegie Trust grant in aid of research to the Department of Anatomy of the University of Aberdeen. The study has been carried on partly in the American Universities with which the authors are associated and partly in the Anatomy Department of Marischal College, University of Aberdeen in which both observers have worked. The writers are very appreciative of the many courtesies showed them in the pursuance of this program by the directors and members of the Departments of Anatomy of these respective Universities.

#### GENERAL SURVEY OF THE PERTINENT LITERATURE

The literature pertinent to the discussion of the various sections of this paper will be considered under the appropriate subdivisions. Brief mention will be made here only of certain contributions which deal with these areas in the human brain. The gross relations are adequately handled in most of the standard neuroanatomical texts and gross anatomies. Von Kölliker in 1896 and later Tilney and Riley ('21) and Rose ('27 b, area retrobulbaris) made reference to a gray mass in man which obviously is representative of nucleus olfactorius anterior of other mammalian forms (see p. 311), but did not describe it in any detail. The present writers (Humphrey and Crosby, '38; Crosby and Humphrey, '39 a, '39 b) identified and figured the bulbar portion of the anterior olfactory nucleus but did not include a complete account of this complex. That portion of the human anterior perforated space which is the tuberculum olfactorium of the comparative neurologist has been referred to by various workers and described for certain subprimate forms but has not received complete description for man, although von Kölliker (1896) Ramón y Cajal ('11), Beccari ('12) and Rose ('27 a and '27 b) gave it some consideration. The amygdaloid complex is almost in-

variably designated in gross and microscopic sections passing through the appropriate area. Foix and Nicolesco ('25) and Hilpert ('28) have described this nuclear mass in adult man. Their subdivisions do not correspond with those given for other mammals. In the present account an attempt will be made to present an analysis of this nuclear gray which will permit the correlation of the human material with the descriptions in subprimates and thus the utilization of data gathered from experimental studies.

#### DESCRIPTION OF THE NUCLEAR GROUPS

##### Nucleus olfactorius anterior

Studies of the human olfactory formation (von Kölliker, 1896; Humphrey and Crosby, '38; and others) show that although typical in structure it is relatively small as compared with that of many mammals (Crosby and Humphrey, '39 b) and that in adult man no accessory olfactory formation has as yet been recognized although its presence, differentiation and ultimate disappearance have been traced in a series of human embryos by Humphrey ('40). Nevertheless the secondary olfactory areas extend well forward into the olfactory bulb, being represented by the bulbar portion of nucleus olfactorius anterior (fig. 1).

In the toluidin blue preparations the cells of this nucleus are larger and more deeply stained than those of the internal granular layer, among which they make their appearance, and so are easily differentiable. The neurons of nucleus olfactorius anterior are rounded in outline, although multipolar, and are intermediate in size between the mitral and the granule cells. They appear first well rostral in the bulb as a clump of rather sharply circumscribed gray in the lateral but deeper part of the internal granular layer (fig. 1), and so separated from the mitral cells by neurons of this layer. This group persists for from .2 mm. to .25 mm. in the right bulb and then disappears entirely or is represented only by two or three neurons, so that the general appearance is that of a

## ABBREVIATIONS

- a, ventral extension from medial island of Calleja toward neopallial cortex and tuberculum olfactorium  
ant.amyg.a., anterior amygdaloid area  
b, a deeper strand of granule cells from medial island of Calleja suggesting boundary of caudate nucleus and then extending laterally as c  
c, intercalated masses of neurons between the tuberculum and the caudate nucleus  
cap.int., capsula interna  
com.ant., commissura anterior  
cor.prepyr., cortex prepyriformis  
cort.-amyg.tr.a., cortico-amygdaloid transition area  
d, characteristically large neurons of polymorph layer of tuberculum olfactorium  
ep., ependyma  
fil.olf., fila olfactoria  
fis.amyg., fissura circularis amygdalae (fissura semiannularis of Rose)  
fis.amyg.acces., fissura circularis amygdalae accessoria  
fis.endorh., fissura endorhinalis  
fis.long., fissura longitudinalis  
g.am., gyrus ambiens  
g.sem., gyrus semilunaris  
g.subcal., gyrus subcallosus  
glob. pal., globus pallidus  
isl.Cal., island of Calleja  
glom., lamina glomerularis  
l.gran.ext., lamina granularis externa  
l.gran.int., lamina granularis interna  
l.mit.e., layer of mitral cells  
l.molec.ext., lamina molecularis externa  
l.molec.int., lamina molecularis interna  
lob.pyr., lobus pyriformis (regio entorhinalis of Hilpert)  
mas.interc., massa intercalata  
med.isl.Cal., medial island of Calleja  
mit.e., mitral cells  
n.ac., nucleus accumbens  
n.amyg.bas.p.lat., nucleus amygdalae basalis, pars lateralis  
n.amyg.bas.p.med.(deep part), nucleus amygdalae basalis, pars medialis (deep portion)  
n.amyg.bas.p.med.(superf. part), nucleus amygdalae basalis, pars medialis (superficial portion)  
n.amyg.bas.acces.p.lat., nucleus amygdalae basalis accessorius, pars lateralis  
n.amyg.bas.acces.p.med., nucleus amygdalae basalis accessorius, pars medialis  
n.amyg.cent., nucleus amygdalae centralis  
n.amyg.cort., nucleus amygdalae corticalis (periamygdaloid cortex of Rose)  
n.amyg.lat., nucleus amygdalae lateralis  
n.amyg.med., nucleus amygdalae medialis  
n.caud., nucleus caudatus  
n.diag.b.Broca, nucleus of the diagonal band of Broca  
n.olf.ant., nucleus olfactorius anterior  
n.olf.ant.,p.dors., nucleus olfactorius anterior, pars dorsalis  
n.olf.ant.,p.lat., nucleus olfactorius anterior, pars lateralis  
n.olf.ant.,p.med., nucleus olfactorius anterior, pars medialis  
n.tr.olf.lat., nucleus tractus olfactorii lateralis  
neopal., neopallium  
precom.sept., precommissural septum  
put., putamen  
str.alb., stratum album  
sub.in., substantia innominata  
substr.g., substriatal gray  
tra.a., area of transition from cortical amygdaloid nucleus to pyriform lobe cortex  
tub.olf.,plex.l., tuberculum olfactorium, plexiform layer  
tub.olf.,polym.l., tuberculum olfactorium polymorph layer  
tub.olf.,pyram.l., tuberculum olfactorium, pyramidal cell layer  
v.lat., ventriculus lateralis  
X, indications of folding in the cortical layer of tuberculum olfactorium  
Z, area showing superficial resemblance to accessory olfactory formation

greatly attenuated nuclear mass. After an interval of .25 mm. to .3 mm. another cell cluster of nucleus olfactorius anterior, of approximately similar extent and appearance to that of the more rostral group, is found among the neurons of the internal granular layer. At the caudal end of this second group (fig. 2) there is again a decrease in the number of cells in the nucleus so that some sections have one or two neurons although others lack them entirely. Later a third portion of this nucleus is present and continues caudalward into the region of the crus (fig. 3 A). In the left olfactory bulb there is a similar pattern for the nucleus with perhaps less inter-connection between adjacent subdivisions. It is altogether

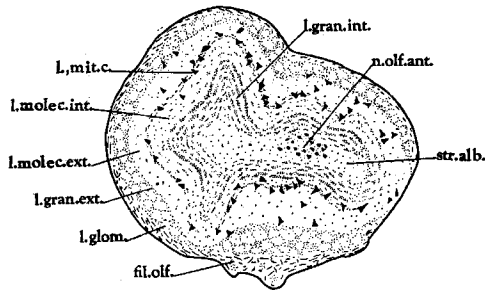


Fig.1 Drawing of a transverse section of the human olfactory bulb through the rostral end of nucleus olfactorius anterior. Toluidin blue preparation.  $\times 12.5$ .

probable that the separate portions were once part of a discrete nuclear mass, having so few cellular elements that it separated into distinct groups with the spreading forward of the olfactory formation. Granting that such be the case, one might expect considerable variation in the number and in the continuity of the neuron groups in the olfactory bulbs of different individuals.

No pars externa of nucleus olfactorius anterior has been found in the available adult human material, a fact which correlates with the lack of an accessory bulb and the poor differentiation of the olfactory formation in the adult, since differentiation of secondary centers must be greatly influenced by the richness and the variety of the incoming primary

impulses. However, as the bulb narrows down into the crus, the remnants of a pars externa can be seen in that region which, denuded of olfactory formation, marks the position of the accessory olfactory bulb in other adult forms (Crosby and Humphrey, '39 b, Y of fig. 6 E) and in the human embryo (Humphrey, '40). This trace of a pars externa is indicated by a slight medial grouping of neurons, smaller than those of the main mass of nucleus olfactorius anterior, and by a band of four or five scattered cells extending laterally (fig. 2). The mass is so small that it is of more theoretical than practical interest in the adult.

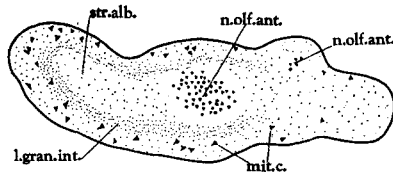


Fig. 2 Illustration of a transverse section through the caudal end of the olfactory formation, showing a second portion of nucleus olfactorius anterior in man. Toluidin blue preparation.  $\times 12.5$ .

In the rostral part of the crus, the main portion of nucleus olfactorius anterior is well developed at most levels, but patches of cells are separated rostrocaudally by areas in which such neurons are reduced to a minimum or entirely absent, so that, in essentials, the pattern of the bulbar portion of nucleus olfactorius anterior is repeated in the frontal part of the crus. The dorsal eminence on the olfactory bulb (fig. 1) and crus (fig. 3, A and B), which fits into the olfactory sulcus on the ventral surface of the hemisphere, early loses its olfactory formation and is regarded then as representing the position of the accessory olfactory bulb of other forms (Crosby and Humphrey, '39 b, text and fig. 6 E). This dorsal eminence is occupied in the crus region by a mass of somewhat scattered, relatively large, multipolar neurons (fig. 3, A and B) which probably represents the cephalic tip of pars dorsalis. These neurons constitute a secondary olfactory center for a very considerable distance within the crus. Like other portions of

nucleus olfactorius anterior, this mass varies in its degree of development from section to section as if it too had thinned out in the elongation of the olfactory stalk.

In the region illustrated in figure 3 A the crus shows a marked dorsoventral compression, retaining the slight dorsal eminence seen in more cephalic levels. This eminence no longer occupies the midportion of the crus, however, but is nearer the lateral tip, so that a longer medial and a shorter lateral extension are visible. Pars dorsalis lies in the dorsal eminence. Gradually this cephalic portion of the nucleus thins out, although scattered neurons of secondary type, in varying number and in size from small to medium, occupy the medial extension of the crus. At about this level a conspicuous rounded group of somewhat smaller, more darkly staining, and more compactly arranged cells constitutes a third subdivision of nucleus olfactorius anterior and occupies the middle of the lateral extension. This subdivision persists for some time as the

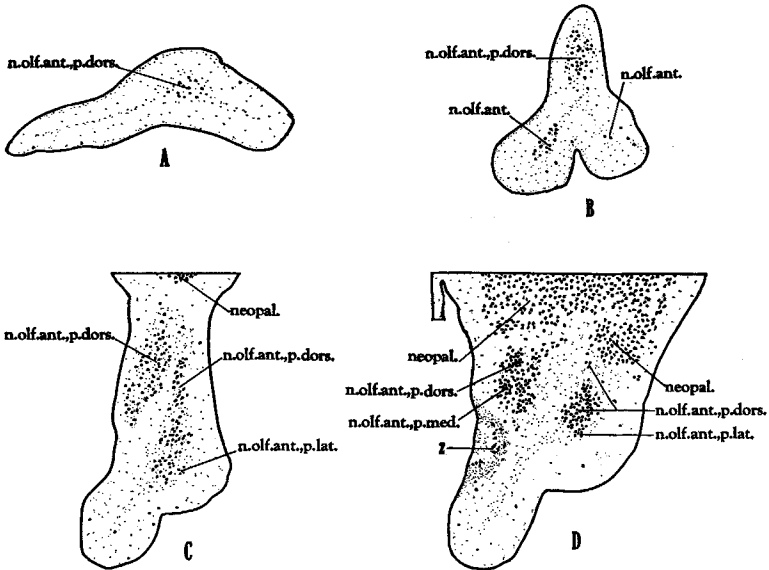


Fig. 3 Drawings of transverse sections through various levels of the human olfactory crus, arranged in order from rostral (A) to caudal (D). Throughout the series the positions of the various subdivisions of nucleus olfactorius anterior are indicated. Letter Z in figure D draws attention to a specially differentiated portion of this secondary gray (see p. 319). Toluidin blue preparation.  $\times 12.5$ .

sections are followed rostrocaudalward and, during its extent, is frequently more conspicuous than is pars dorsalis, which latter is fairly continuous throughout but which shows wide variability of development from section to section. As the crus becomes still smaller, the secondary center in the lateral extension vanishes, leaving only pars dorsalis and certain supplementary scattered neurons through other areas (fig. 3 A). There are places throughout this region in which pars dorsalis is absent, only to reappear subsequently. The main mass of the crus is occupied by fiber bundles with some intermingled granule and neuroglial elements.

During the next .36 mm. the crus assumes a trifoliate outline (fig. 3 B) with the medial and lateral extensions from the dorsal eminence of approximately equal length. Pars dorsalis continues caudalward in the same relative position but with a variable number of cells from level to level. The lateral leaflet of the trifoliate crus shows nuclear groups twice throughout this extent. The more rostral of these neuron masses has slightly smaller neurons but resembles in general appearance the group described farther forward in the lateral extension. The more caudal group, although in line with the frontal cell mass, is composed of slightly larger cells. Between the discrete masses in the lateral leaflet there are, at many levels, groups of scattered neurons which at least suggest an earlier continuity in the gray.

In the medial leaflet (fig. 3 B) there are, likewise, two discrete nuclear masses, connected frontocaudally by scattered neurons. In addition to these nuclear groups, single nerve cells or groups or small clusters of neurons, of a size comparable to those in the dorsal leaflet, are found in various parts of the crus. Sometimes they are near the periphery and sometimes in the depths of the gray, but they follow no definite pattern from section to section. These scattered cells are illustrated in various figures throughout the crus and labeled in figure 2. Smaller, less deeply stained neurons also lie in the crus region, clustered along the fibers of passage (fig. 3 B) and occasionally forming a rather definite



layer ventral to the main fiber bundle, but for them too there is no common configuration characteristic for all levels. These medial and lateral cell groups of the olfactory crus and the previously mentioned secondary olfactory nuclear mass of the olfactory bulb seem to belong with the major group in the dorsal eminence as forward extensions of pars dorsalis of nucleus olfactorius anterior. However, only the portion in the dorsal eminence is so labeled since evidence for the allocation of the remaining groups to pars dorsalis is not conclusive.

Gradually, as the series is followed caudalward, with the exception of smaller neurons with no special arrangement, the crus loses all its secondary gray other than that portion of pars dorsalis which occupies the dorsal eminence. Still farther caudalward groups of neurons again reappear and disappear in the medial and lateral leaflets, but the main mass of pars dorsalis retains its same general position and size until the crus becomes continuous with the hemisphere. There pars dorsalis forms an inverted V-shaped mass with the apex directed toward the hemisphere. Soon this mass breaks up into medial and lateral divisions (fig. 3 C), both of which pass over into the neopallial cortex. Before the medial division of pars dorsalis is completely united with the neopallial cortex, a differentiated, smaller-celled group (fig. 3 D) appears within its rostromedial portion and then becomes separated from it to continue into the area of junction of the crus with the main mass of the hemisphere (fig. 4), at which level it disappears. Its position and its cell type suggest that it represents the crural portion of pars medialis of nucleus olfactorius anterior. It is not surprising that, in the adult material available, it has been impossible to establish cell continuity of pars medialis with the anterior continuation of the hippocampus. The inability to do this probably depends upon the reduced state of the rostral end of the hippocampus on the one hand and on the enormous development of the neopallium on the other, as well as on the reduction of pars medialis.

Before the union of the lateral limb of pars dorsalis with the neopallium, there appears intermittently along this limb,

as it continues caudalward, a group of smaller neurons, the rostral continuation of pars lateralis (figs. 3, C and D, and 4). As the lateral portion of pars dorsalis becomes continuous with the neopallial cortex, similar discontinuous groups of neurons are found at the ventral border of the cortex, as far lateralward as the band of prepyriform gray which passes in turn into continuity with the pyriform lobe cortex around the endorhinal fissure. Both the prepyriform gray and its medial continuation, as represented by these discontinuous small-celled patches, fall within nucleus olfactorius anterior pars lateralis (or prepyriform area or anterior continuation of the pyriform lobe of other forms, Crosby and Humphrey, '39 b. See Craigie, '41, concerning its cortical character).

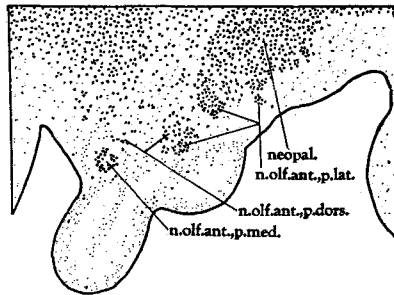


Fig. 4 An illustration of the human anterior olfactory nucleus as seen in a transverse section through the base of the hemisphere. This level shows particularly well the relation of pars dorsalis to the neopallial cortex and the extension lateralward of pars lateralis. Toluidin blue preparation.  $\times 12.5$ .

No clear-cut periventricular ring of gray (see also Rose, '27 b), such as was first described by Herrick ('24) in the opossum, Obenchain ('25) in *Caenolestes*, and Sonntag and Woollard ('25) in *Orycteropus* and has since been repeatedly documented by numerous observers in various mammals, is demonstrable for the human nucleus olfactorius anterior. However, suggestions of this relationship may be obtained by connecting the various discontinuous gray masses by imaginary lines. If the enormous elongation of the olfactory crus be taken into account, it is evident that only embryologically could such a ring be complete. It is of interest that in the

macaque material available this ring of gray is also inevident (Crosby and Humphrey, '39 b).

Pars ventralis is represented only by diffusely arranged cells which increase slightly to form a small gray mass caudal to the plane of figure 4. The relations resemble those described for the macaque (Crosby and Humphrey, '39 b). In view of the limited development of the frontal portion of the human tuberculum olfactorium (or anterior perforated space, see p. 320), with the polymorphic layer of which pars ventralis comes into relation, the small size of this portion of nucleus olfactorius anterior is to be expected.

Before closing this account of the anterior olfactory nucleus, attention should be called to a curious little group of larger neurons (Z in fig. 3 D) found on the medial side of the crus at the point at which it is widening out into the hemisphere. This cell group, which persists for only a short distance, is made up of scattered, medium-sized, darker staining, multipolar neurons, intermingled medially with smaller, lighter staining neurons and bounded laterally by a band of gray in which the smaller cells are linearly arranged and faintly stained. For a short distance this mass forms a tiny bulge on the wall of the crus. There is not the least evidence of entering nerve fibers or a glomerular layer, but there is a slight superficial resemblance to a minute accessory olfactory bulb. It seems probable, from the evidence at hand, that this area belongs to the general gray of nucleus olfactorius anterior. It does not appear comparable to the accessory olfactory bulb found in human embryos (Humphrey, '40) and occasionally represented in the young macaque (Crosby and Humphrey, '39 a, '39 b).

Rose ('27 b) described an area retrobulbaris in the human brain, which area in general corresponds to the nucleus olfactorius anterior of other vertebrates and of the present account for man. This observer regarded it as cortex, classifying it as "cortex totoparietinus holoprotoptychos bistratificatus." He described two laminae in this region, stressed its development through subprimates and related its attenua-

tion in primates to the great forward development of the frontal pole. Those interested in Rose's account should consult his 1927 b paper (Rose, '27 b, Taf. 76, Abb. 1 and 3).

### Tuberculum olfactorium

In the region of the basal hemisphere wall, caudal to the attachment of the olfactory bulb, lies the anterior perforated space of human anatomy, so named from the perforation of its gray by numerous small blood vessels, clearly visible in both gross preparations and microscopic sections. The number of such vessels, and consequently the rostrocaudal extent of the perforations, shows some variation from brain to brain, a fact which may account for the differences in opinion regarding the boundaries of this space. These vessels lie at the depths of the folds which characterize its outer surface (see p. 325).

The positions of tuberculum olfactorium and the anterior perforated space are indicated on ventral surface views of the brain in practically all standard texts of gross and neuroanatomy, but the limits and subdivisions are not always the same. Retzius (1896) placed "Tuber olfactorium" in the region of the olfactory trigone and termed the area caudal to it the anterior perforated space. Apparently he included in this latter the region of the diagonal band (see Retzius, 1896, p. 72) which he described as showing less perforation. Ramón y Cajal ('11) stated that the anterior perforated space of man was comparable to tuberculum olfactorium of other mammals, but the region he designated includes all the area between the base of the olfactory bulb and the optic chiasm. Beccari ('12) placed in the human anterior perforated space the entire region from the plane of attachment of the olfactory stalk to the optic chiasm, including in it the olfactory trigone, the parolfactory eminence and the region occupied by the diagonal band and nucleus. C. and O. Vogt ('19) subdivided the anterior perforated space into tuberculum olfactorium (corresponding to the olfactory trigone in general), substantia

perforata and area diagonalis (the nucleus and tract of the diagonal band).

Rose ('27 b) recognized in the anterior perforated space (1) three portions of tuberculum olfactorium, beginning with the olfactory trigone and extending to the region of the diagonal band and nucleus, and (2) area diagonalis. At the base of the olfactory stalk, in front of the olfactory trigone and extending out into the crus, was his area retrobulbaris

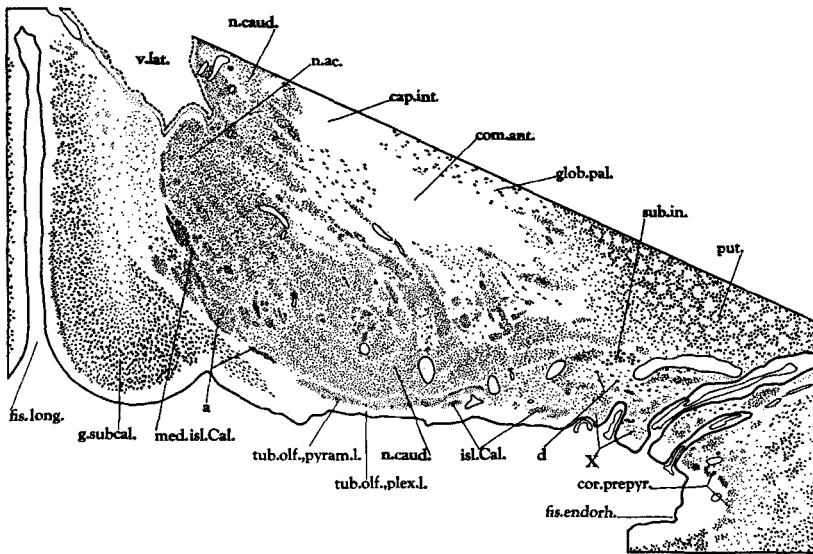


Fig. 5 Illustration of a transverse section through the less well differentiated rostral end of the human tuberculum olfactorium. Toluidin blue preparation.  $\times 4$ .

which apparently corresponds to the anterior olfactory nucleus of our account (see p. 319). The present writers are employing essentially the same subdivisions as those made by Rose although using for the anterior olfactory nucleus the terminology applied to that area in other mammalian forms. Consequently the term tuberculum olfactorium is used for that portion of the human basal hemisphere wall which corresponds directly to the similarly designated region in other

mammals, but not to tuberculum olfactorium of Retzius (1896) or of C. and O. Vogt ('19). The diagonal band and nucleus are not included in the tuberculum as Ramón y Cajal ('11) had done, but constitute its caudal boundary in man as in other mammals (Gurdjian, '25; Loo, '31; Humphrey, '36 and many others).

Tuberculum olfactorium, then, of the present account corresponds to the combined "trigono olfactorio" and "eminenzia paraolfactoria" described for the human brain by Beccari

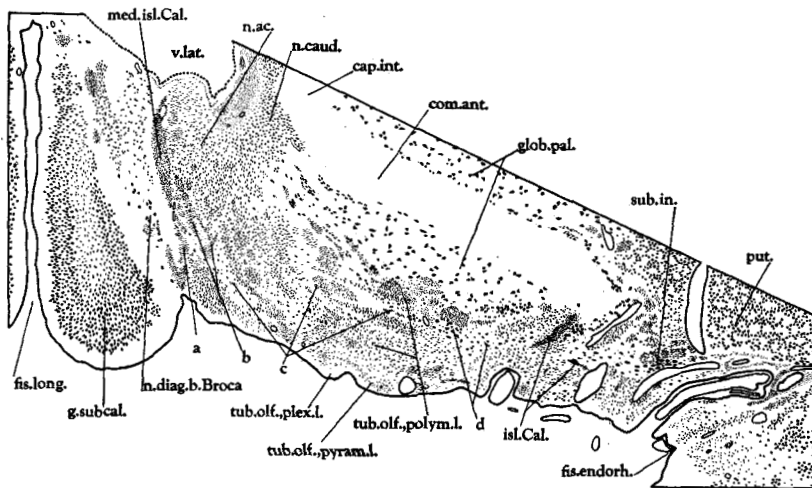


Fig. 6 Drawing showing the midportion of the human tuberculum olfactorium. In this region the structure is most typical and the layers are best developed. Toluidin blue preparation.  $\times 4$ .

('12), who bounded this region caudally by the diagonal sulcus. This observer recognized masses of granule cells which are presumably islands of Calleja and differentiated the three layers characteristic of the tuberculum. Much of his account is concerned with a description of the cell types as seen in Golgi material. Rose ('27 b) regarded the area in man as being extremely rudimentary in structure (particularly anteriorly). He designated it as "cortex striatalis" or "semiparatinus," a classification apparently not in agreement

with that of von Economo and Koskinas ('25) who did not regard this region as a cortical area. Rose divided the tuberculum into three fields, an anterior, an intermediate and a posterior field, and described large cell nests composed of small neurons and scattered large pyramidal cells. He made no specific mention of islands of Calleja and did not describe the large medial island.

In the material available for study *pars ventralis* of the anterior olfactory nucleus grades over rostrally into the deep or polymorph layer (see p. 319) of *tuberculum olfactorium* without distinct delimitation. The latter area enlarges very rapidly lateralward along the course of the lateral olfactory tract, replacing the frontally situated neopallial cortex (fig. 5). Somewhat later in the series it extends medialward to substitute for the medial extension of the neopallial gray (figs. 6 and 7). Dorsally *tuberculum olfactorium* underlies, in the usual fashion, the lower portion of the caudate nucleus and nucleus accumbens (figs. 5 and 6) and, as it replaces the cortex, follows the curve of nucleus accumbens toward the ventricle, showing in this position the characteristic large medial island of Calleja (fig. 6) observed in other mammals (Young, '36; Humphrey, '36; Fox, '40 and others). At certain levels, fiber bundles with intercalated cells belonging to *tuberculum olfactorium* separate its gray quite clearly from nucleus accumbens and the caudate nucleus. In many planes the boundary between these areas is very indistinct. As it spreads far lateralward (figs. 5 to 7) the *tuberculum* approaches the pyriform lobe area, its cortical layer displacing the more laterocaudal extension of *pars lateralis* of nucleus olfactorius anterior. The caudal boundary of *tuberculum olfactorium* is formed by the nucleus of the diagonal band of Broca (figs. 6 and 7) as the latter gray mass appears at levels through the caudal pole of the medial island of Calleja. This island disappears with the increased size of the nucleus of the diagonal band, which swings sharply across the field from medial to lateral in such close apposition to the *tuberculum*

that the gray of the region is intermingled with the fibers and cells of the diagonal band (fig. 7).

In favorable planes the three layers characteristic of tuberculum olfactorium of lower mammals—the plexiform, the pyramidal and the polymorph layers—are demonstrable in man. This is particularly true through the middle portions of the region (fig. 6). Rostrally, inside of the plexiform layer, the gray of the area is grouped into masses of intermingled pyramidal and smaller cells with only occasionally traces of

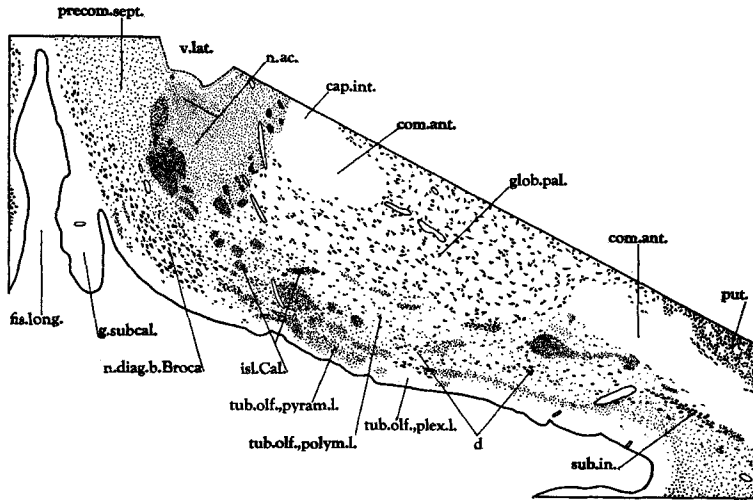


Fig. 7 Illustration of the caudal pole of tuberculum olfactorium of adult man at levels in which it is gradually being replaced by the nucleus of the diagonal band of Broca. Toluidin blue preparation.  $\times 4$ .

a cortical band, although where present in man it shows some folding (fig. 5, X). A large island of granule cells is found in the tuberculum medial to nucleus accumbens. This probably corresponds to the "masse di cellule granuliformi" of Beccari ('12, fig. 4, *m*). From the ventrolateral border of this island of Calleja (fig. 6) a strand of cells extends ventralward into relation with the neopallial cortex (fig. 5, *a*) and, behind this bit of cortex, lateralward to become continuous with the poorly differentiated cortical layer of tuberculum



olfactorium (fig. 6, *a*). A deeper strand of granule cells (fig. 6, *b*) suggests the boundary between tuberculum olfactorium and the caudate nucleus and then finds representation in intercalated masses of neurons (fig. 6, *c*) scattered along the fiber bundles imperfectly delimiting the boundary between these areas; for here, as at other levels where adjacent, there is some intermingling of neurons contributing to tuberculum olfactorium and the caudate nucleus. The polymorph layer contains some of the characteristically large neurons (figs. 5 to 7, *d*) seen in other mammals and there are occasional tiny patches of granule cells which appear to represent islands of Calleja (figs. 6 and 7, *isl. Cal.*). Still farther caudalward the medial island and its extensions disappear although intercalated cell masses are found along the deeper part of tuberculum olfactorium and large neurons are present in the polymorph layer. This is a correction to the statement in Ariëns Kappers, Huber and Crosby ('36) that there are no distinct islands in adult man. According to Johnston ('23) there are islands in the human embryo. In some places the cortical layer is demonstrable for a part of the mediolateral extent of the area and may be fairly clear and well folded toward the region of the pyriform lobe, but it is not constant for all levels or for the whole field at any given level. At the caudal pole of tuberculum olfactorium the nucleus of the diagonal band of Broca intermingles with and ultimately replaces the cortical and polymorph layers. The numerous small blood vessels which penetrate tuberculum olfactorium and give an irregular contour to its surface apparently have some relation to the folds of the cortical layer wherever these are visible, since the folds on the surface of the region correspond to those of the cortical layer. From the foregoing account it is evident that the tuberculum may be divided, on the basis of differences in differentiation, into rostral, middle and caudal regions, comparable in general to those recognized by Rose ('27 b).

Ventral to ansa lenticularis, interspersed in part with its fibers and in part overlying the tuberculum, are patches of

large, multipolar neurons to which the name of *substantia innominata* of Reichert has been given. Numerous terms have been applied to this nuclear region; some of these refer only to the large neurons and others include also smaller cells of the area (for the homologies see Foix and Nicolesco, '25, p. 398, and Ariëns Kappers, Huber and Crosby, '36, p. 1444). The gray of *substantia innominata* at certain levels appears to be continuous with that of the diagonal band. This relationship will be discussed later in connection with the septal areas in man.

#### The amygdaloid complex

The human amygdaloid complex has received little consideration from research workers, although many texts show its position in the cross sections of the human brain. Among the earlier observers who noted this area may be mentioned Burdach (1819-1826; quoted from Hilpert, '28), Meynert (1872), Mondino (1885), von Kölliker (1896), Déjérine (1895-1901), and de Vries ('10). A brief review of these and certain other older papers is to be found in the contribution by Hilpert ('28). Völsch ('06, '10), Landau ('19), Dart ('20), Johnston ('23), Holmgren ('25), Ariëns Kappers, Huber, and Crosby ('36) and others have considered the phylogeny of the primate amygdala. More detailed references to the pertinent literature will be found in connection with the accounts of the various nuclei.

All of the amygdaloid nuclei customarily described for mammals are identifiable in the adult human material. Most of these are relatively highly developed, particularly the basal nucleus. The most notable exception is the nucleus of the lateral olfactory tract. For purposes of description basolateral and cortico-medial groups, an anterior amygdaloid area and a cortico-amygdaloid transition area are recognized.

The names here applied to the subdivisions are based on those used by Humphrey ('36) and Fox ('40). In general this plan follows that of Johnston ('23), who divided the amygdala into two portions in accordance with his interpretation of the

origin and phylogenetic age of the nuclei. Thus he (Johnston, '23, p. 456) recognized "primitive or little modified central, medial, cortical and nucleus of the lateral olfactory tract; and the new nuclei formed by infolding or immigration of cells: basal and lateral." It must be remembered, however, that Johnston ('23, p. 459) considered the cortical nucleus to be "formed from the cortical layers of the pyriform lobe medial to the sulcus endorhinalis." Holmgren ('25) likewise recognized two portions of the amygdaloid complex. He allocated the lateral, medial and lateral basal amygdaloid nuclei to the pallial portion but regarded the remaining portions of the amygdaloid complex including the cortical nucleus as of subpallial origin. Johnston ('23) considered the cortical nucleus as of pallial origin. Berkelbach van der Sprenkel ('26) divided the amygdala into an anterior and medial part and a posterior and lateral part. His classification differs in that he placed the cortical nucleus in his posterior and lateral portion of the complex, which otherwise corresponds to the baso-lateral group of this account and the homologous division of Johnston. Rose ('26 and '27) and others have termed the cortical nucleus periamygdaloid cortex. For convenience in description Fox ('40) in his study of the cat amygdala placed the nucleus of the lateral olfactory tract with the anterior amygdaloid area in an anterior group. The remaining nuclear masses he subdivided into a lateral (the baso-lateral of Humphrey, '36) and a medial amygdaloid group.

Consideration will be given first to the baso-lateral amygdaloid group. In the description of the nuclear masses the account begins at the rostral pole of the amygdala.

#### *Baso-lateral amygdaloid group*

To this group belong the lateral amygdaloid, the basal amygdaloid and the accessory basal amygdaloid nuclei. All of these gray masses are large and relatively distinctly delimited although they tend, at selected levels, to grade over into each other. In many planes they are separated for

portions of their extent by intercalated cell masses in the course of fiber bundles. Such an intercalated mass is found in the encapsulating fibers over the dorsolateral border and the dorsal peak of the lateral nucleus for a considerable part of its extent.

*Lateral amygdaloid nucleus.* The lateral amygdaloid nucleus was recognized by Johnston ('23) in human foetal material. It had been described earlier by Völsch ('10) for Lemur and macaque under the letter *M*. Hilpert ('28) discussed it briefly and figured it for the human brain under the name of the ventral amygdaloid nucleus. The cephalic tip of the lateral amygdaloid nucleus appears at the frontal pole of the complex and continues caudally for approximately three-quarters of the extent of the amygdala. Rostrally it consists of groups of cells intercalated among the fibers of the external capsule (also seen in fig. 8). Soon it becomes a more discrete cell mass as it increases rapidly in size and the poorly differentiated cephalic pole of the basal amygdaloid nucleus appears along its ventromedial tip. A slight distance farther caudalward the medial and then the lateral portions of the basal nucleus make their appearance (fig. 8) forming the medial boundary of the lateral amygdaloid nucleus and indenting its medial surface so that the elongated oval which characterized its contour more rostrally changes to an irregular polygonal form (fig. 9). In planes through the rostral tip of the basal nucleus the scattered cells appear which mark the anterior continuation of the medial amygdaloid nucleus, and which are here considered an anterior amygdaloid area. They soon lie dorsal to the lateral part of the basal nucleus (fig. 8) and in this position in relation to the dorsomedial aspect of the lateral nucleus (fig. 8). Soon, however, the lateral part of the basal nucleus spreads dorsalward between the anterior amygdaloid area (fig. 8; and a little farther caudalward the most cephalic tip of the medial amygdaloid nucleus, fig. 9) and the lateral amygdaloid nucleus and for the remainder of the extent of the lateral nucleus the medial and lateral portions of the basal nucleus form its medial boundary except that

they are separated by fiber fascicles which at certain levels contain intercalated cell masses (fig. 10). Laterally the lateral amygdaloid nucleus, at this level as throughout its extent, is bounded by the external capsule in which intercalated cell masses are present at many levels except where (as in figs. 9 and 10) it comes to the surface of the ventricle. With the increase in size of the basal amygdaloid nucleus the lateral nucleus changes its shape and becomes smaller but somewhat

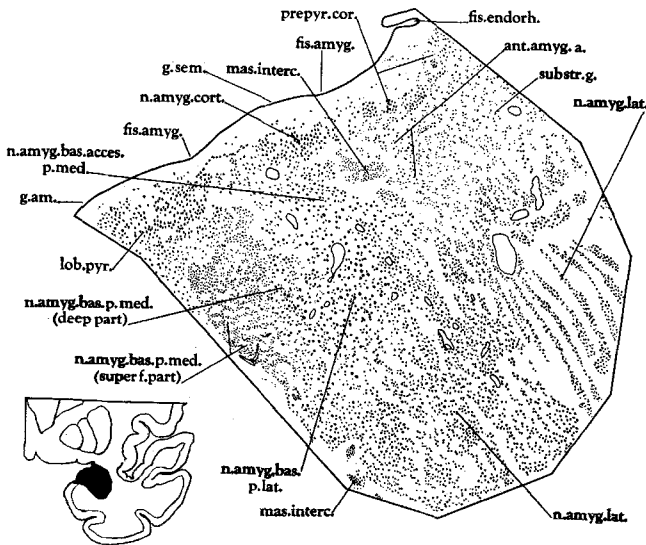


Fig. 8 Drawing of a transverse section near the rostral end of the human amygdala. The orientation of the figure is indicated by the key drawing. For prepvr.cor. compare page 318 and Rose, '27 b, Taf. 50. Toluidin blue preparation. X 5.

elongated with the ventromedial tip extending into relation with the medial portion of the basal nucleus (fig. 10). It gradually decreases in size beginning dorsalward (compare figs. 9 and 10) and at its caudal tip is represented by a narrow band of cells intervening between the ventricular surface and the basal nucleus and finally by scattered clusters of neurons of this type which then disappear.

Throughout its extent the lateral nucleus is made up of intermingled medium-sized and smaller cells, the constituent

neurons being obviously smaller than those of the adjacent lateral part of the basal nucleus (figs. 8 to 10). These neurons are multipolar in type with a round to oval nucleus, a distinct nucleolus, and well stained but rather small Nissl granules. Particularly at its ventromedial tip the cells of the lateral nucleus at many levels (fig. 8) are lined up along fiber bundles, apparently those passing to the anterior commissure. Elsewhere there is no specific arrangement of the neurons in the material available for study. It might be added that the limits of the nucleus are more easily established through its midportion and that it grades over both frontally and caudally into the adjoining gray of the basal nucleus.

*Basal amygdaloid nucleus.* The basal nucleus is divisible into a pars lateralis and a pars medialis (figs. 8 to 10). The pars lateralis is comparable to the lateral large-celled portion of the basal nucleus described in the human foetus (Johnston, '23) and in mammals such as the rabbit (Young, '36) and the bat (Humphrey, '36), to the nucleus *T'* identified by Völsch ('10) for certain subhuman primates, and to the nucleus centralis noted by Hilpert ('28) in man. The medial small-celled part of the basal nucleus corresponds to that described by Johnston, Young and Humphrey, to *T* of Völsch and to the nucleus granularis of Hilpert. This medial part of the basal nucleus is divisible into deep and superficial portions (with respect to the amygdala). The deep portion passes gradually, as elsewhere, into the lateral part of the basal nucleus. The superficial portion of the pars medialis shows special modification cytologically and is characterized further by its fusion with the cortex on the one hand and with the tip of the lateral nucleus on the other, as well as by its intimate relation with the deep portion of pars medialis (figs. 9 and 10). Hilpert ('28) made no secondary separation of his nucleus granularis although his photomicrographs show differences between the deep and superficial portions of the nucleus.

The lateral large-celled portion of the basal nucleus makes its appearance slightly behind the rostral pole of the lateral amygdaloid nucleus, appearing first as scattered cells inter-

mingled with those of the lateral nucleus but characterized by their larger size. Soon this lateral part of the basal nucleus becomes a relatively discrete nuclear mass, resting in a pocket formed on the one side by the lateral amygdaloid nucleus and on the other by the medial part of the basal amygdaloid nucleus. Slightly farther caudalward, with the greater increase of the basal amygdaloid complex, the lateral part of

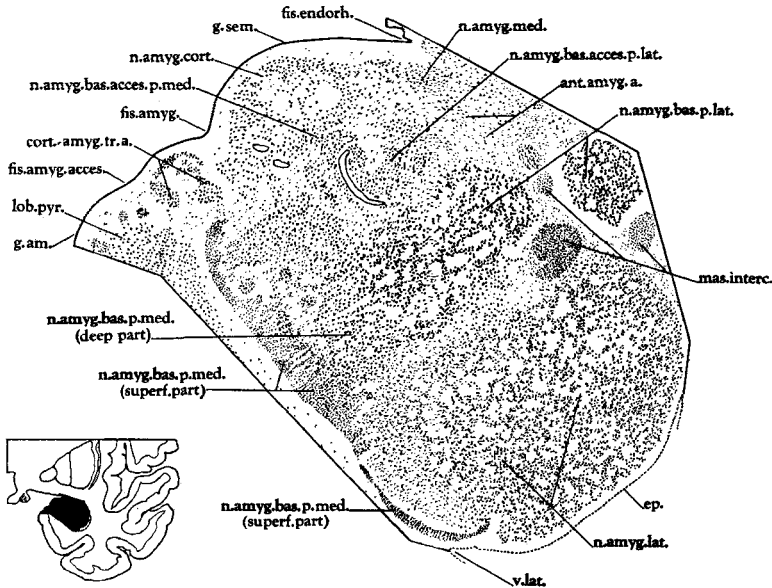


Fig. 9 Illustration of a transverse section through the human amygdala taken slightly caudal to the plane of figure 8. This and the following figure indicate particularly well the interrelations of the cortico-amygdaloid transition area to the surrounding gray, including certain of the amygdaloid nuclei. Toluidin blue preparation.  $\times 5$ .

the basal nucleus lies dorsal to the medial portion and is bounded medially by the accessory basal nucleus (fig. 8). It elongates dorsally, its dorsal extension lying between the medial and lateral amygdaloid nuclei, and its dorsal tip being separated for some time (fig. 9), in the series studied, from the main mass of the nucleus but uniting secondarily with it in planes just in front of the rostral pole of the central

amygdaloid nucleus. At such levels, and caudal to them (fig. 10), the basal amygdaloid complex is relatively very large and is encroaching steadily on the position occupied farther forward by the now diminishing lateral amygdaloid nucleus. Through these fields the nucleus is relatively sharply delimited except that no distinct boundary can be established between this lateral portion and the medial part of the basal nucleus (figs. 9 and 10). Maintaining the same general relations but varying somewhat in outline from section to section, the nucleus continues toward the caudal end of the amygdaloid complex. It remains large through much of its extent but in sections passing through the caudalmost tip of the lateral amygdaloid nucleus the basal amygdaloid nucleus has begun to show definite reduction in size in both its lateral and medial portions. It persists to approximately the caudal end of the amygdaloid complex, although at the most caudal levels of the accessory basal nucleus the lateral part of the basal is represented by only a few cells (fig. 11). This lateral part is characterized by the presence of multipolar neurons, at least as large as any found in the amygdaloid complex. These cells have wide spread dendrites which show, even in toluidin blue preparations, well marked and deeply stained Nissl granules and neuraxes which enter fiber bundles, particularly those of the anterior commissure and, more caudally, the stria terminalis.

The medial part of the basal nucleus is divisible into deep and superficial portions with respect to the surface of the amygdala. The deep (figs. 8 to 11) portion appears approximately at the same level as does the cephalic tip of the lateral part of the basal nucleus. It continues back to planes just in front of the caudal pole of the amygdaloid complex. Throughout its extent it lies in intimate relation with the lateral part of the basal amygdaloid nucleus dorsolaterally and is intermingled with the superficial part of the medial division of the basal nucleus ventromedially. Its medial tip approaches the accessory basal nucleus in those planes in which both nuclear groups are found (figs. 8 to 10) and at



many levels is not sharply delimitable from the accessory basal area. The deep part of pars medialis is distinguishable from pars lateralis through differences in the general cytological picture, in that it is composed of intermingled medium-sized and small neurons with a preponderance of the smaller type. Thus it gives a general impression of being a smaller celled nuclear mass although it contains neurons of a size and appearance directly comparable to those of the lateral division of the basal nucleus (see figures).

The superficial portion of pars medialis is distinguishable from the deep portion through the much more dense arrangement of its constituent neurons as well as by the marked preponderance of smaller cells (figs. 8 to 10). This density of arrangement is correlated with the fact that, although the deep portion is traversed by numerous large fiber fascicles the superficial portion obviously carries no bundles of considerable size. There are certain other relations which characterize this superficial portion. In midregions of the amygdaloid complex at appropriate levels the cortico-amygdaloid transition area (fig. 10), which is in continuity with the pyriform lobe cortex, is directly continuous with this superficial portion of pars medialis. At other planes not far from this level the lateral border of this superficial portion also grades over into the ventromedial tip of the lateral amygdaloid nucleus (fig. 9). Thus these neurons of the superficial portion form a cellular continuity between the pyriform cortex and the basal amygdaloid complex, a fact in line with the phylogenetic, and supposedly with the ontogenetic, development of these regions. The superficial portion of the pars medialis (figs. 8 to 10) appears just cephalic to the frontal tip of the remainder of the basal amygdaloid nucleus and extends well toward the caudal pole of the latter nucleus, disappearing before the caudal tip of the basal nucleus (fig. 11) is reached. This superficial portion is very sparsely represented rostrally and caudally but throughout most of its extent is a band-shaped mass of neurons which, although not large, is conspicuous because of the deep staining and close arrangement of its constituent elements.

*The accessory basal nucleus.* The cephalic tip of the accessory basal amygdaloid nucleus (fig. 8) appears caudal to the rostral pole of the basal nucleus. Throughout much of the amygdala the accessory basal (together with the cortical nucleus; see p. 337) occupies the eminence delimited by the circular amygdaloid fissure (figs. 8 to 10). At certain planes, however, this eminence is invaded by an extension of the medial division of the basal nucleus (fig. 10). The accessory basal nucleus continues to the caudal pole of the amygdaloid

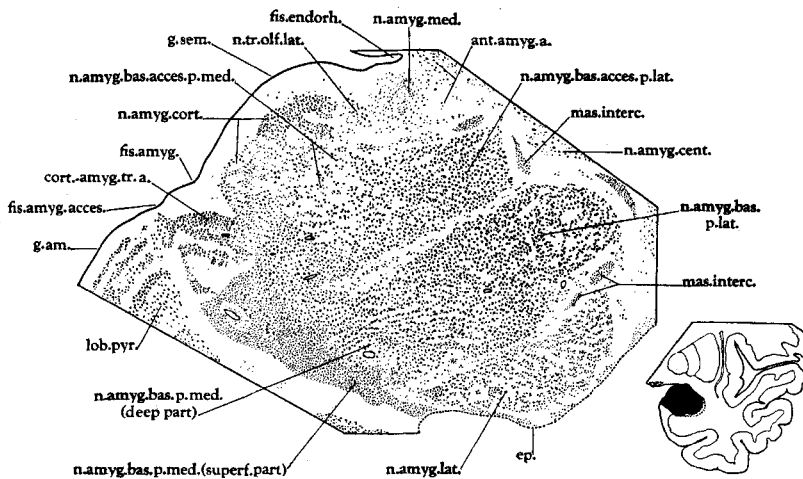


Fig. 10 Drawing illustrating a transverse section of the human amygdala through its most highly differentiated region. At this level not only all of the amygdaloid nuclei but also all of their secondary subdivisions are demonstrable. The central nucleus is not completely shown. The key drawing orients the figure. Toluidin blue preparation.  $\times 5$ .

complex (fig. 11). The accessory basal nucleus intervenes between the lateral part of the basal nucleus lateralward and ventrolateralward, the cortical nucleus dorsomedialward, and the medial part of the basal nucleus ventralward and ventromedialward. For the midportion of its extent (figs. 9 and 10) it is overlaid by the medial amygdaloid nucleus.

Rostrally a secondary subdivision of the accessory basal nucleus is not very evident but in the middle third of the

amygdaloid complex (fig. 10) medial and lateral portions of this nucleus can be recognized. Such secondary subdivisions become relatively more clear as the complex is traced toward its caudal pole; there distinct medial and lateral portions can be identified (fig. 11). Hilpert ('28) described the accessory basal complex as two separate nuclear masses. His two nuclei—the nucleus dorsalis and the nucleus medio-dorsalis—correspond in general to the lateral and medial portions respectively of the present account, although the limits given by him do not agree completely with those established in this paper.

The medial part of the accessory basal nucleus alone forms its frontal pole (fig. 8). It lies in intimate relation with the cortical amygdaloid nucleus (see p. 338 and figs. 9 and 10) and at many levels is not clearly separable from the medial portion of the basal nucleus (for example, fig. 8). It contains an intermingling of small and larger neurons but appears to be, on the whole, a smaller celled area than the lateral part of the nucleus, because of the preponderance of smaller neurons.

The lateral portion of the accessory basal nucleus (figs. 9 to 11) is located between the medial portion of the complex and the lateral portion of the basal. It lies lateral and dorso-lateral to the medial portion and resembles greatly in general appearance the lateral portion of the basal nucleus (fig. 10). It appears very slightly behind the rostral pole of the medial part of the accessory basal nucleus and continues to approximately the caudal end of the amygdaloid complex (fig. 11). It begins and ends as scattered neurons but through midportions of its extent forms a relatively discrete polyhedral mass of gray (fig. 10) varying slightly in general contour from level to level. It is fairly clearly demarcated from the basal nucleus by intervening fiber bands containing intercalated cell groups but is less clearly separable from the medial part of the accessory basal nucleus except caudally.

*Intercalated cell masses.* Between the various constituent nuclei of the baso-lateral amygdaloid complex and around its

outer border, especially on the ventricular surface and between the basal nuclear complex and the central nucleus but elsewhere as well, groups of small neurons are found in the course of fiber bundles. These intercalated cell groups are shown in figures 8 to 10 and referred to in the account of the lateral amygdaloid nucleus. Consequently they require no further description other than the statement that they are especially numerous in the human amygdaloid complex. Völsch

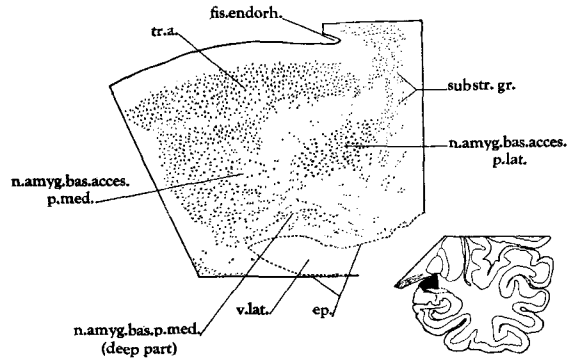


Fig. 11 An illustration of a transverse section taken near the caudal extreme of the amygdaloid complex. Again the plane of the section is indicated on the key drawing. Toluidin blue preparation.  $\times 5$ .

('10) apparently regarded these cell clusters as glial elements (in Lemur and Macacus, for example). They appear to be included by Hilpert ('28) in the nucleus granularis of his account of the human amygdala. Intercalated cell masses have been described also for various subprimate forms (Johnston, '23; Berkelbach van der Sprenkel, '26; Humphrey, '36; Young, '36; Fox, '40 and others).

#### *Cortico-medial amygdaloid group*

The cortical and medial amygdaloid nuclei, the nucleus of the lateral olfactory tract and the central amygdaloid nucleus have been allocated to the cortico-medial amygdaloid group. This classification corresponds to that employed by Humphrey ('36) in the study of the amygdaloid complex of the bat and

to that used by Fox ('40) in his description of the amygdala of the cat except that, in the latter case, the nucleus of the lateral olfactory tract, because of its position, was placed with the anterior amygdaloid area. With the exception of the cortical nucleus, which is well differentiated in man and shows in certain respects relations to the cortex similar to those of the lateral amygdaloid nucleus (see p. 341), the nuclear masses of the cortico-medial group are neither so large nor so clearly delimited as in many mammals, a fact in line perhaps with the small size of the human lateral olfactory tract.

*Cortical amygdaloid nucleus.* This amygdaloid nucleus extends for somewhat more than two-thirds of the total length of the amygdaloid complex and grades over (figs. 8 and 11), both caudally and rostrally, into the adjacent cortex, which replaces it without any clear-cut demarcation. Its caudal pole is slightly in front of the posterior extreme of the amygdaloid complex and its frontal end extends well into the rostral third of the amygdala. Throughout its extent it has a superficial position, being separated from the brain surface by a cell free area which might be considered its molecular zone. Its outer cell layer is composed primarily of multipolar and for the most part pyramidal neurons which are relatively closely arranged (figs. 8 to 11). This cell layer is continuous at the frontal and caudal extremes of the amygdala around the circular amygdaloid fissure with the pyriform cortex (fig. 8). At various other places throughout its extent the cortical nucleus shows a corresponding relation to this pyriform cortex by its continuity with the mass of cells which is here termed the cortico-amygdaloid transition area (figs. 9 and 10). This area (see p. 341) intervenes between the cortical, basal and lateral amygdaloid nuclei on the one hand and the pyriform cortex on the other hand (figs. 9 and 10). There are regions, however, in which such continuity is not evident. Internal to this outer corticoid band of cells of the cortical amygdaloid nucleus there are scattered neurons, some of which are pyramidal and some polymorphic in shape. These

pass over into the accessory basal nucleus (figs. 9 and 10) so that at numerous levels any line drawn between the accessory basal and cortical amygdaloid nuclei must be more or less arbitrary. For about two-thirds of its extent the cortical nucleus is separated from the tip of the rhinal fissure by the medial amygdaloid nucleus and, for a very brief interval, by the nucleus of the lateral olfactory tract (fig. 10). Caudally, behind the medial nucleus it borders on the substriatal gray. Frontally, rostral to the cephalic tip of the medial amygdaloid nucleus the cortical nucleus comes into relation with the anterior amygdaloid area (fig. 9) and gradually extends up to the rhinal fissure.

The cortical nucleus as just described corresponds to the cortical nucleus of Hilpert ('28) and in general to the periamygdaloid cortex of Rose ('27 a, '27 b). However, Rose's area actually includes more than that allocated to the cortical nucleus by Hilpert or the present writers. It extends farther forward (Rose's frontal part not lying within the cortical nucleus of these other workers) and includes at least a considerable part of both the area designated "sem" (sem<sub>2</sub>) by Hilpert and the cortico-amygdaloid transition area (see p. 341) of this account. Rose ('27 b) described the shift in position of the periamygdaloid region through a series of mammals to man, stressed its location on the dorsal surface in the human temporal lobe, and emphasized its greater differentiation in primates than in lower mammals. He regarded it as a semiparietal or striatal cortex, and separated it from the prepyriform cortex, with which Brodmann ('09) had included it as area prepyriformis (see also Rose, '27 b), on the basis of its different cytoarchitecture. Rose ('27 b) separated his area into oral and caudal portions, the latter lying in gyrus semilunaris, and each of these in turn into medial and lateral parts. In the series available for study slight differences in layer arrangement through the field suggest the secondary subdivisions of Rose. The cortical nucleus had been described briefly and figured by Johnston ('23) in human foetal material and even earlier by Völsch as

*B* in *Macacus rhesus* (Völsch, '10, fig. 27) and as *B'* in *Lemur* (Völsch, '10, fig. 23).

*Medial amygdaloid nucleus.* The medial amygdaloid nucleus occupies about the middle third of the amygdala. It is composed throughout of small, multipolar neurons with an occasional intermingling of slightly larger cells. Caudally it fades out into the substriatal gray and frontally into the anterior amygdaloid area (fig. 9). Throughout its extent it occupies a position near the surface of the brain, between the rhinal fissure and the cortical nucleus. It is bordered dorso-laterally by fibers of passage which separate it from the central amygdaloid nucleus (fig. 10) and in which are intermingled cells of the striatal area caudally and the anterior amygdaloid area frontally. Ventrolaterally lies the accessory basal nucleus (fig. 10 and elsewhere). The medial amygdaloid nucleus varies from an irregular oval to a polyhedral shape.

Compared with the similarly designated nucleus of the bat (Humphrey, '36) and the cat (Fox, '40) it is relatively smaller, less clearly delimited and less conspicuous. This nucleus was designated by Völsch ('10) under the letter *D* and was identified as the medial nucleus by Johnston ('23) in the human foetus. It was not recognized by Hilpert ('28) although his photomicrographs (for example, Abb. 19) indicate its presence.

*Nucleus of the lateral olfactory tract* (fig. 10). In planes toward the rostral end of the medial amygdaloid nucleus as it lies in relation with the anterior amygdaloid area, the poorly developed nucleus of the lateral olfactory tract makes its appearance within the amygdaloid complex. It lies in close relation with the medial nucleus at the place in which the latter borders on the cortical amygdaloid nucleus. The nucleus of the lateral olfactory tract is the least well developed of the amygdaloid nuclei in man. It consists of a small patch of deeply stained, elongated neurons which are few in number but which tend to outline the fiber bundles so that the shape of the nucleus of the lateral olfactory tract is preserved in man although the number of neurons is greatly reduced. Traces of this nucleus are discernible through about 1.2 mm.

although an occasional section shows practically no cells of this type. Cells of a similar appearance are found farther forward after an interval of about .4 mm. This group of cells extends for about .2 mm. and suggests a second nucleus of the lateral olfactory tract such as has been described in the bat (Humphrey, '36).

Although the nucleus of the lateral olfactory tract has been identified in various subprimates (Humphrey, '36; Fox, '40 and others), it was not recognized by Völsch ('10, p. 468) in the macaque. Although it is not shown on his figures, the text (see Völsch, '10, p. 451) appears to imply its presence in Lemur. Hilpert ('28) apparently did not find it in his adult human material, although earlier Johnston ('23) had described and figured it in an 8 months human foetus in which it is evidently better developed, judging from the photomicrographs, than in our adult material.

*Central amygdaloid nucleus.* The gray termed the central nucleus in this account is homologous to the cell mass similarly designated in certain other mammals (see Young, '36; Humphrey, '36; and Fox, '40), but not to the central nucleus as described for man by Hilpert. His nucleus is representative of the lateral part of the basal and apparently he has not recognized the central nucleus of other authors. Quite probably a portion of the area termed substantia innominata (see Hilpert, '28, *S. i.*, Abb. 19) falls within the central nucleus of the present writers. In his human foetal material Johnston ('23) apparently included the anterior amygdaloid area with the central nucleus as a common cell mass, applying to it the latter term.

The central nucleus of the present account (fig. 10) has a rostrocaudal extent of slightly less than half that of the amygdaloid complex. It is found through the midportion of the complex but approaches nearer the caudal than the frontal pole. Frontally it is replaced by the anterior amygdaloid area and caudally by the striatal gray, although its caudal tip is continuous with the putamen. Because of its similarity in cytological appearance and its intimate relation at both



extremes with the striatal gray it is very difficult to set any sharp caudal or frontal boundary for it. Throughout most of its extent, however, the nucleus is fairly discrete except for its intimate relations with the striatum. Except at its extremes it is round to oval in outline and is composed of rather sparsely arranged neurons intermingled with fiber fascicles. These neurons resemble those of the putamen and are intermediate in size between the cellular constituents of the lateral amygdaloid and the medial amygdaloid nuclei but distinctly smaller than those of the basal amygdaloid complex. The central nucleus, for most of its extent, lies in the dorsal angle between the basal amygdaloid and the accessory basal amygdaloid nuclei (fig. 10) from which it is separated by fiber fascicles. Dorsolateral and dorsal to it lie the striatal and the substriatal gray. Dorsomedially are fiber bundles which separate it, throughout the extent of that cell mass, from the medial amygdaloid nucleus (fig. 10). Such fiber bundles are infiltrated caudally by striatal gray. Frontally they are invaded by cells of the anterior amygdaloid area which in some places almost replaces them and spreads out over the frontal pole of the central amygdaloid nucleus, the two cell masses being related by scattered neurons.

*Cortico-amygdaloid transition area.* In the human amygdaloid area a most interesting relationship is evident between the baso-lateral amygdaloid group and the cortical amygdaloid nucleus on the one hand and the pyriform cortex on the other. At the medial tip of the pyriform cortex a mass of cells of pyramidal type and sometimes (although not at all levels) showing traces of lamination can be seen throughout the mid-portions of the amygdaloid complex (figs. 9 and 10). This mass of neurons is connected with the pyriform cortex by strands of cortical cells. At various although not at all levels it is continuous with the superficial part of pars medialis of the basal amygdaloid nucleus and this portion grades over directly into the lateral amygdaloid nucleus (figs. 9 and 10). Thus the lateral and the basal amygdaloid nuclei through the intermediation of the superficial portion of the pars medialis

of the basal amygdaloid nucleus and the cortico-amygdaloid transition area are in cellular continuity with the pyriform cortex. Likewise the cortico-amygdaloid transition area is continuous at many levels with the cortical amygdaloid nucleus (fig. 10) so that cellular continuity between the pyriform lobe cortex and the cortical amygdaloid nucleus is established through the intervention of this cortico-amygdaloid transition area. There are levels through the midportion of the amygdaloid complex at which the relations of the baso-lateral amygdaloid group and the cortical nucleus are demonstrable in the same section (fig. 10) thus establishing through this cortico-amygdaloid transition area cellular continuity between the baso-lateral complex and the cortical amygdaloid nucleus. These facts are in line with the studies of Johnston ('23) on the development of the amygdaloid complex, since this observer regarded the basal, lateral and cortical nuclear groups as developing phylogenetically by an ingrowth of the pyriform cortex in the region of the endorhinal fissure. Holmgren ('25), however, placed the cortical nucleus in the subpallial portion of the amygdaloid complex.

The cortico-amygdaloid transition area forms a macroscopic eminence on the surface of the brain (figs. 9 and 10). It is bounded medially by the lateral portion of the circular amygdaloid fissure. Rostrally it appears between the circular amygdaloid fissure (semiannular fissure of Hilpert, '28) and a fork of the same, or an accessory amygdaloid fissure. These two fissures diverge through the middle of the amygdala, in which region the cortico-amygdaloid transition area is most extensive (fig. 9), and then the accessory fissure approaches the main fissure again (fig. 10) but disappears in the material studied before reuniting with it. The lateral part of the main circular amygdaloid fissure is frequently the region of invasion of blood vessels. Moreover, it marks the place of infolding of the proliferation zone which turns into the amygdaloid area or bends about to pass over into the cortical nucleus. This arrangement is apparent in the amygdaloid region of the

cat as is evident from the figure in the paper on this carnivore by Fox ('40, see fig. 21).

The cortico-amygdaloid transition area has been recognized by Hilpert ('28) and a relation to the underlying amygdaloid complex and cortical amygdaloid nucleus similar to that just described has been mentioned by him. However, although the eminence which it forms shows in certain of his figures (see Hilpert, '28, Abb. 11, 16 and 19), this swelling has not been mentioned and his area, as seen from the surface, appears to be included in the base of the sulcus semiannularis. The cortico-amygdaloid transition area was designated by Völsch ('10, fig. 23) as *B* in his illustration of the brain of the lemur.

*Anterior amygdaloid area.* The anterior amygdaloid area (figs. 8 to 10) is that portion of the amygdaloid complex which has not differentiated into specific nuclear masses. It lies at the cephalic pole of the amygdaloid region intervening between the lateral and basal amygdaloid nuclei and the striatal area in planes in which this area is invaded by cells of the diagonal band of Broca. Slightly farther caudalward (fig. 8) it is bordered ventrolaterally by the lateral amygdaloid nucleus and ventromedially by pars lateralis of the basal and the medial portion of the accessory basal nucleus. Separating it at such a level from the brain surface is the prepyriform cortex. The area still grades over dorsolaterally into substriatal gray. The central amygdaloid nucleus gradually encroaches upon the anterior amygdaloid area laterally and then the medial amygdaloid nucleus replaces the area medially (fig. 10). The anterior amygdaloid area becomes more and more infiltrated with fibers of passage and, as the medial and central amygdaloid nuclei become larger, the anterior amygdaloid area gradually disappears. It has no specific arrangement, but is composed of small and medium-sized neurons of a character comparable to that of the surrounding gray but interspersed with numerous fibers of passage.

The anterior amygdaloid area was designated by Völsch as *E*<sup>2</sup> in his 1910 paper (fig. 27 of *Macacus rhesus*). Johnston

('23) apparently did not recognize it as a special area distinct from the central nucleus of the human foetus (see p. 340).

#### DISCUSSION

##### Nucleus olfactorius anterior

In man, as in other mammals, a secondary olfactory center, nucleus olfactorius anterior (area retrobulbaris of Rose, '27 b, see p. 319), finds representation in the olfactory bulb, the olfactory crus and the base of the hemisphere. Cytologically this nucleus is made up of neurons intermediate in size between the mitral and granule cells. The nucleus does not consist of a single gray mass but is represented, both in the bulb and in the crus, by cell clusters. The most nearly continuous of these is the portion constituting pars dorsalis. Lack of continuity of these cell masses is probably the result of a stretching out of the nucleus by a forward spread of the olfactory formation.

The caudal relations of nucleus olfactorius anterior are on the whole comparable with those established for other forms but with differences in emphasis. The fusion of pars dorsalis with the neopallial cortex is extremely broad although the continuation of nucleus olfactorius anterior with olfactory cortical areas is greatly reduced as compared with that in macrosmatic mammals. Thus pars lateralis breaks up into widely separated and very attenuated patches of gray which spread out to the pyriform lobe cortex and no definite cellular continuity between pars medialis and the hippocampus is demonstrable. Pars ventralis is very poorly developed in man, but grades into the polymorph layer of tuberculum olfactorium as in other mammals.

The broad area of fusion of the anterior olfactory nucleus with the neopallial cortex is in line with the increasing importance of this cortical area in man, but the relationship is expressive of a very primitive condition which dates back in phylogeny at least to tailed amphibians (Herrick, '33). The reduction in the cellular continuity of pars lateralis through

the prepyriform cortex with the pyriform lobe gray is in harmony with the relative decrease of the primary olfactory areas in these forms and is influenced further by the attenuation of pars lateralis and the prepyriform gray through the increase in the neopallial cortex. Similarly the inability to trace pars medialis into direct relationship with the anterior continuation of the hippocampus is correlated on the one hand with the reduced state of development of the rostral pole of the hippocampal gray and the decrease in pars medialis and on the other hand with the relatively enormous neopallial cortex. The great reduction in pars ventralis and also the poor differentiation of the rostral pole of tuberculum olfactorium (see p. 323) are related to the decrease in primary and secondary olfactory centers and connections.

Attention may be called again to two further differences between nucleus olfactorius anterior of man and that of many other mammals. In the first place there is no clean cut differentiation of a human pars externa. If there be any representation of this portion of nucleus olfactorius anterior it is to be found in scattered cells at various levels of the crus. This lack of development of what in many forms is a conspicuous portion of the nuclear complex is probably related to the absence of an accessory olfactory bulb in adult man. Such an accessory bulb appears in the human embryo, but undergoes regression during foetal life (Humphrey, '40). In the second place the gray constituting the various portions of the anterior olfactory nucleus does not form a complete periventricular ring such as that which characterizes its arrangement in most mammals. The fact that such a ring is suggested by the discontinuous masses of gray indicates that again the difference is based on the elongation forward of the olfactory formation and the reduction of the cellular content within nucleus olfactorius anterior itself.

#### Tuberculum olfactorium

The limits and boundaries of tuberculum olfactorium have been discussed previously and the pertinent literature re-

viewed. Those interested are referred to pages 320 to 326. The tuberculum in adult man has the structure characteristic for the homologous area of mammals but with certain peculiarities to be expected in the reduced state of development of the olfactory bulb and crus and of pars ventralis of nucleus olfactorius anterior, with which the rostral part of the polymorph layer of the tuberculum is continuous.

The tuberculum has plexiform, pyramidal or cortical, and polymorph layers comparable to those in the corresponding region of other mammals. The cortical layer is most readily demonstrable in the middle portion of the tuberculum but traces of it are found at more frontal and more caudal levels. In some places in which a cortical band cannot be shown, masses of intermingled pyramidal and granule cells suggest the area. Through part of its extent, and most conspicuously lateralward, the cortical lamina has foldings which are associated with the irregular contour given to the surface by the perforation of small blood vessels. A typical large medial island of Calleja is demonstrable in man and has the usual relations. There are also smaller islands of Calleja, composed partly of granule cells and partly of small pyramidal cells. As a whole, then, the cortical layer is less well developed and less clearly differentiated from the polymorph layer in man than in many of the subprimates reported in the literature. The adult condition suggests that, in its formation, the region has been stretched out by the developing cortical masses on either side, losing thereby something of its usual appearance. Clusters of granule cells and scattered large and medium-sized neurons characterize the polymorph layer of the human tuberculum. It has a very intimate relation to the neighboring gray, particularly to the nucleus of the diagonal band of Broca, which replaces it caudally. It is also less clearly differentiated from the cortical layer in man than is usual in other mammals. Relatively it more nearly approaches in development the corresponding layer in other forms than does the cortical lamina. Unlike the rabbit (Young, '36) and the cat (Fox, '40), but like the bat, the less differentiated

portion of the human tuberculum olfactorium is its frontal end, a fact possibly in line with the relatively small size of the olfactory bulb both in the bat (Humphrey, '36) and in man (Humphrey and Crosby, '38).

### The amygdaloid complex

Within the amygdaloid complex of man all the nuclear groups and all of the secondary subdivisions of these groups which have been recognized for subprimates are differentiable. In the preceding account the writers have endeavored to apply to these various portions of the complex the nomenclature which has been employed for subprimate forms, rather than use the terminology and subdivisions utilized by Foix and Nicolesco ('25) and Hilpert ('28). This interpretation of the human amygdala permits not only morphologic correlations between primate and subprimate forms but also places at the disposal of the student of human material data obtained from experimental research.

The amygdaloid complex in man has been subdivided, for purposes of description, into the following nuclear groups: a baso-lateral (including the lateral, basal and accessory basal nuclei), a cortico-medial (including the cortical, medial and central nuclei and the nucleus of the lateral olfactory tract), an anterior amygdaloid area and a cortico-amygdaloid transition area. The nuclear masses of the baso-lateral group are relatively and actually more highly developed in man than in the subprimates studied. The lateral nucleus, which extends for about two-thirds of the amygdaloid complex, is a very prominent part of this region in man, although it shows no secondary groupings. The basal and accessory basal nuclei are secondarily differentiable into more or less clear-cut subdivisions. Thus the basal nucleus has the large-celled lateral part (*pars lateralis*) and the small-celled medial part (*pars medialis*) characteristic of this nucleus in various mammals. In addition the *pars medialis* is further differentiated into deep and superficial portions, the latter of which is fused with the cortico-amygdaloid transition area at one end and

the lateral amygdaloid nucleus at the other. The accessory basal nucleus also falls into two portions, a lateral and a medial part. No subdivisions of the accessory basal nucleus have been described for other mammals, however (for example the bat, Humphrey, '36), and in some cases the nucleus is entirely lacking (cat, Fox, '40). It is fairly obvious, then, that greater differentiation—possibly an indication of greater specificity of connections—occurs in the baso-lateral complex of primates as compared with that of subprimate forms.

Although the baso-lateral amygdaloid complex is relatively increased in man, the cortico-medial group is considerably decreased and some of its nuclei are actually very small and not well differentiated. Thus the medial nucleus is poorly developed and its limits are ill-defined although its relations are typical of those of mammals in general. The nucleus of the lateral olfactory tract is represented by a very few cells but the position of these neurons and their arrangement make identification of the nuclear mass fairly easy. Particularly interesting is the presence of a tiny cell group rostralward suggesting an anterior nucleus of the lateral olfactory tract such as has been described for the bat (Humphrey, '36). If this latter identification be correct, man, like the bat, may have two nuclei of the lateral olfactory tract on one side of the brain. The central nucleus has no outstanding characteristics but resembles in general the similarly designated cell mass in various other mammals.

In contrast with the limited development of the medial nucleus and the nucleus of the lateral olfactory tract, the cortical nucleus is relatively highly developed in man, so much so that it has been classed by several authors as cortex (periamygdaloid cortex of Rose, '27 a and '27 b, and others). A molecular layer, a layer containing some pyramidal cells and an underlying zone of more or less scattered neurons give justification to such a classification. For purposes of comparison with subprimates, however, the present writers prefer to retain the name of cortical amygdaloid nucleus. Within this nucleus secondary subdivisions on the basis of its varia-



tions in differentiation can be made as was done by Rose. Its intimate relation with the cortico-amygdaloid transition area has been stressed on the preceding pages.

The anterior amygdaloid area is an ill-defined zone of undifferentiated gray in the course of fibers of passage. It is found in the rostral part of the amygdaloid complex in close relation with the substriatal gray and the central and medial amygdaloid nuclei. It is directly comparable with the anterior amygdaloid area described for the rabbit by Young ('36) and for the cat by Fox ('40).

The cortico-amygdaloid transition area is the name used to designate the mass of intermingled pyramidal and polymorph cells which lies beneath the slight eminence formed by the lateral part of the circular amygdaloid fissure and the accessory part of this fissure. It intervenes between the pyriform lobe cortex and the cortical amygdaloid nucleus on the one hand and between these areas and the superficial portion of pars medialis of the basal nucleus on the other hand. It lies, then, in the region in which Johnston ('23) considered an infolding had occurred to form the baso-lateral amygdaloid complex. In this connection he stressed the relations of the pyriform lobe area with the caudal part of the dorsal ventricular ridge in the turtle (Johnston, '23 and earlier). It is equally conceivable that the pyriform cortex migrated out from a region of undifferentiated central gray but retained its cellular continuity with the underlying neuron masses. In either case, then, both the part which is situated at the surface and the deeper lying portions must have much in common functionally. Moreover, in both of these areas further increase in size may well occur at the region of junction of the two as well as within the cell masses. Thus the cortical area on the surface, as represented by the pyriform cortex and the cortical nucleus is probably supplemented in function by gray (the baso-lateral amygdaloid complex) serving as vicarious cortex but having its position along the ventricular wall. Therefore, the deeper portion is directly comparable to the surface pallium except that it has a periventricular position and lacks

the laminae characteristic of fully developed cortex. This baso-lateral amygdaloid complex is to be regarded, then, as vicarious cortex in the same sense as the hypostriatal and possibly the neostriatal areas in the bird are vicarious cortex (see Huber and Crosby, '29) and are supplementary in function to the poorly developed neocortical areas in that animal. On the contrary the medial amygdaloid nucleus, the nucleus of the lateral olfactory tract and probably the central nucleus are related in function and in grade of development to the basal olfactory areas of the hemisphere as the various studies on the mammalian amygdaloid complex and its connections indicate.

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