STUDIES OF THE VERTEBRATE TELENCEPHALON

III. THE AMYGDALOID COMPLEX IN THE SHREW (BLARINA BREVICAUDA)

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EIGHT FIGURES

INTRODUCTION

Certain unusual features characterize the amygdaloid complex in the shrew (Blarina brevicauda), although the general pattern is that typical of the region in mammals. In part the peculiarities are due to the compression which is clearly evidenced in the structure of the shrew brain as a whole. In part the relations seen in the amygdala of the shrew illustrate important intermediate stages in the shifting of the various nuclei of the amygdaloid complex accompanying changes in the temporal pole region of the hemisphere during phylogeny.

The purpose of the series of studies of which this paper is a part is to present the interrelations and variations of the various telencephalic centers throughout the mammalian phylum so that experimental and anatomic data may be coordinated. For such a series the intermediate relations presented here in the amygdaloid complex of the shrew are of considerable importance.

MATERIAL AND METHODS

The material used in this study consists of a transversely cut and a horizontally cut series of the brain of Blarina brevicauda. Both series are stained with toluidin blue. These preparations belong to the Huber Neurological Collection of the University of Michigan and were prepared by the late Professor G. Carl Huber. The photomicrographs were made by George J. Smith, research technical assistant in the Department of Anatomy of the University of Michigan.

The pertinent literature is considered in the discussion. This has been done in order to show the significance of the amygdala of the shrew in the phylogenetic scale.

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NUCLEAR PATTERN OF THE AMYGDALOID COMPLEX

Lateral amygdaloid nucleus (figs. 3 to 6). At the rostral end of the lateral amygdaloid nucleus is a group of smaller, very closely arranged, deeply staining neurons. They form a cap over the rostral pole of the lateral amygdaloid nucleus and continue for a short distance caudally, dorsal and ventral to it. Such cells might be considered a part of the lateral amygdaloid nucleus or, as in the present paper (figs. 2 and 3), an intercalated cell mass. This group of small cells persists for only a short distance and then is gradually replaced, beginning ventrally, by the less densely arranged, larger neurons constituting the lateral amygdaloid nucleus (fig. 3). Rostrally the nucleus is round or oval (fig. 3), but it soon spreads out in various directions, particularly dorsally and medially, so that it acquires an irregularly quadrilateral outline (fig. 4). Ventral and ventromedial to it, and in structural continuity with it, appears the larger-celled lateral part of the basal amygdaloid nucleus (fig. 4). The two nuclei are intimately associated until the caudal pole of the hemisphere is reached. There the larger-celled part of the basal amygdaloid nucleus becomes continuous with the cortex (fig. 7). Rostrally the lateral amygdaloid nucleus is relatively distinctly separated from the putamen (fig. 4), to which it is immediately ventrolateral. Throughout their extents (figs. 3 to 6) these two areas can be definitely distinguished from each other. Caudally the putamen is separated completely from the amygdaloid complex by the widening out of the ventricle (fig. 7). The lateral amygdaloid nucleus, at its caudal end, becomes so intimately fused with the larger-celled part of the basal nucleus that it is not possible at all levels to delimit them (fig. 6). However, the lateral amygdaloid nucleus terminates rostral to the caudal pole of the basal nucleus.

Basal amygdaloid nucleus (figs. 3 to 7). As compared with the lateral, the basal amygdaloid nucleus has a lesser frontal extent and is not so well defined, being one of the more difficult of the amygdaloid nuclear groups to delimit in the shrew. There is no great range in size among the neurons constituting the basal amygdaloid nucleus. Most of them are of medium size and the designation of larger-celled and smaller-celled portions is purely relative.

The larger-celled lateral part of the basal amygdaloid nucleus begins in intimate relation with the more ventral portion of the lateral amygdaloid nucleus, the rostral pole of the basal (fig. 3) lying at about the plane of disappearance of the caudal nucleus of the lateral olfactory tract in the series studied. This relationship with the lateral nucleus is maintained throughout most of the extent of the larger-celled portion

of the basal, so that at some levels the boundary between them is relatively clear and at others it is very difficult to establish, particularly caudally where any delimitation is arbitrary. This larger-celled lateral portion of the basal nucleus persists to the caudal pole of the amygdaloid complex (fig. 7).

Ventrolateral and lateral to the larger-celled part of the basal (fig. 5), in planes through its rostral pole, between it and the cortex and dorsolateral to the accessory basal, lies the smaller-celled portion of the basal amygdaloid nucleus. Laterally the superficial part of this smallercelled area extends beneath the lateral amygdaloid nucleus and then curves dorsalward to become continuous with the outer, more scattered cells of this latter nucleus (for example, see figs, 5 and 6). There is no sharp delimitation between the two areas. Medialward the smallercelled portion of the basal nucleus fairly rapidly replaces the accessory basal nucleus (fig. 6) and, still farther caudalward, the ventral part of the medial amygdaloid nucleus to become continuous with the cortex (figs. 6 and 7). This smaller-celled portion may be indefinitely divided into two parts (fig. 8, A and B). One of these is a fairly closely arranged cell mass, somewhat more deeply situated between the accessory basal amygdaloid nucleus and the larger-celled part of the basal amygdaloid nucleus, from which it is not sharply separated. The other (fig. 8, A and B, b') is a more superficial portion, lying ventrolateral and ventral to the basal amygdaloid nucleus and ventral and then lateral to the lateral amygdaloid nucleus and characterized further by the arrangement of its constituent cells along fiber fascicles. These two portions suggest the secondary division of the smaller-celled part of the basal amygdaloid nucleus (fig. 8, C) as described by Crosby and Humphrev ('41) in man.

Accessory basal amygdaloid nucleus. The larger-celled portion of the basal nucleus, soon after its appearance rostrally, is bounded ventro-medially by the slightly smaller celled accessory basal amygdaloid nucleus (figs. 4 and 5), which at first shows a somewhat closer arrangement of its neurons. Although easily recognizable, this latter nucleus (figs. 4 to 6) passes over without sharp demarcation into the surrounding areas, so that its limits are difficult to determine. It appears, however, to extend medially into the angle formed by the medial and the cortical amygdaloid nuclei (fig. 5). The caudal pole of the accessory basal nucleus lies in intimate relation with the basal amygdaloid nucleus, but as the accessory basal disappears from the field its position is taken by the smaller-celled part of the basal (which extends medialward into the region) and by the most ventral part of the medial

amygdaloid nucleus (compare figs. 5 and 6 with fig. 7). Thus the basal amygdaloid nucleus rather than the accessory basal comes into relationship with the cortex of the area, in planes in which the pyriform lobe cortex swings around toward the hippocampus (fig. 7). It should be emphasized that, in the shrew, the occessory basal amygdaloid nucleus is relatively small and poorly differentiated even in those regions in which it is most clearly recognizable.

A subdivision of the accessory basal nucleus of the shrew into the two portions which are recognized in certain primates (Crosby and Humphrey, '41; Lauer, '44) is suggested in the available material by the cell arrangement and size at some levels (figs. 4 to 6, A and B) but is not clearly demarcated as it is in primates. Indeed, identification of these subdivisions in the amygdala of the shrew is dependent largely on a knowledge of their presence in other forms.

Anterior amygdaloid area (figs. 1 to 4). The rostral part of the anterior amygdaloid area in the shrew lies in planes through the caudal pole of the tuberculum olfactorium (fig. 1). Throughout its extent it occupies the region ventral to the striatum from which it is separated, at more frontal levels, by the nucleus of the diagonal band of Broca. Rostrally it consists of scattered gray, which soon differentiates indistinctly into a deep part and a superficial portion. Both the scattered gray and the rostral part of the deep portion are intermingled with the nucleus of the diagonal band of Broca (fig. 1). Caudally the superficial portion of the anterior amygdaloid area is replaced in part by the rostral nucleus of the lateral olfactory tract (fig. 1). Then the cortical amygdaloid nucleus (fig. 2) appears in the gray between the nucleus of the lateral olfactory tract and the pyriform lobe cortex. Behind this level the superficial gray occupying the ventromedial angle of the hemisphere takes on the character of a medial amygdaloid nucleus (figs. 2 and 3). The deep portion of the anterior amygdaloid area is replaced medially by the medial amygdaloid nucleus (fig. 3) and laterally by the larger-celled part of the basal nucleus and by the accessory basal nucleus (figs. 3 to 5). In all of these instances the transitions are gradual.

Nuclei of the lateral olfactory tract. There are two nuclei of the lateral olfactory tract in the shrew — a rostral and a caudal nucleus. The rostral nucleus (figs. 1 and 2) is distinct and relatively very large for the size of the amygdala in this mammal. Its neurons are closely arranged and deeply stained. It varies in cross-sectional outline from round to semilunar, with a dorsal hilus (fig. 2) at planes in which the fiber bundles leave it. This rostral nucleus is found near the frontal end of the amygdaloid complex, appearing close to the periphery of the

hemisphere in the ventromedial portion of the anterior amygdaloid area. Through most of its extent it is bounded medially by the medial amygdaloid nucleus and laterally and caudally by the cortical amygdaloid nucleus.

The caudal nucleus of the lateral olfactory tract (fig. 3) lies dorsal to the caudal tip of the rostral nucleus, immediately adjacent to and in continuity with it, this continuity being more marked on one side of the brain than on the other. It, too, is distinct although smaller than the rostral nucleus. The cells of the caudal nucleus of the lateral olfactory tract are even smaller and more closely arranged than are those of the rostral nucleus.

The presence of two nuclei of the lateral olfactory tract is in line with the condition found in certain other mammals, such as the bat and man. In these animals the rostral and caudal nuclei are separated by only a few sections. Their overlapping and continuity in the shrew is the reflection probably of the compression which has modified the brain in this insectivore.

Cortical amygdaloid nucleus. Lateral to the rostral nucleus of the lateral olfactory tract (fig. 2), a small band of differentiated, cortexlike gray consisting of deeply stained pyramidal neurons — the cortical amygdaloid nucleus - appears in the region occupied rostrally by the anterior amygdaloid area (fig. 1). As the rostral nucleus of the lateral olfactory tract is followed caudalward, the cortical nucleus gradually increases both in medical extent and in clearness of differentiation. Through the region of the caudal nucleus of the lateral olfactory tract, the cortical amygdaloid nucleus already shows a lateral part consisting of more closely arranged neurons and a medial portion in which the cells are farther apart (fig. 3). This medial portion has replaced the rostral nucleus of the lateral olfactory tract (compare figs. 2 and 3) and is ventral and ventrolateral to the caudal nucleus of that tract (fig. 3). Behind the caudal nucleus of the lateral olfactory tract, both portions enlarge at the expense of the medial amygdaloid nucleus, which lies medial and somewhat dorsomedial to it (fig. 4). Thus in the middle third of the amygdaloid complex, the cortical nucleus occupies a considerable part of the ventral surface of the hemisphere, medial to the pyriform lobe cortex, but never quite reaches the ventromedial angle (fig. 6). As the cortical nucleus extends caudalward, its two portions become more cortex-like in appearance and resemble each other more closely, but are relatively sharply separated, the only connection being through scattered cells (fig. 4). As the accessory basal amygdaloid nucleus appears in the field, it grades over directly into the cortical nucleus (fig. 4), its relation to the medial portion becoming particularly intimate (fig. 5). Still farther caudalward, the smaller-celled portion of the basal amygdaloid nucleus gradually supplants the accessory basal and becomes directly continuous with the medial part of the cortical nucleus. This relationship persists for a relatively long distance (fig. 6) and then the cortical nucleus gradually disappears from the field, rostral to the caudal pole of the amygdaloid complex.

Medial amygdaloid nucleus. Shortly after the rostral nucleus of the lateral olfactory tract has appeared in the peripheral portion of the anterior amygdaloid area, the area enlarges and becomes more differentiated in appearance on the medial and particularly on the lateral aspect of this nucleus. The medial mass is the rostral tip of the medial amygdaloid nucleus (fig. 2), which in this region consists of rather scattered neurons. The medial tip of this medial nucleus then enlarges (fig. 3), forming an almost circular mass in cross section (fig. 4), and extends dorsally so that the nucleus occupies the ventromedial angle of the hemisphere. There it consists of an outer, more differentiated band of gray and inner, more scattered cells. As the accessory basal amygdaloid nucleus appears in the field and the cortical amygdaloid nucleus increases in extent medialward, the ventral portion of the medial nucleus gradually disappears (fig. 5), but the dorsal portion continues caudally until it is replaced by the cortex, from which it is separated by scattered cells.

Central amygdaloid nucleus. The central amygdaloid nucleus (figs. 4 and 5) differentiates from the surrounding gray as a slightly more closely arranged mass of neurons in the anterior amygdaloid area, at levels approximately through the rostral tip of the lateral amygdaloid nucleus. It enlarges slowly (fig. 4), tending to keep a circular outline as it is followed caudalward. As the basolateral amygdaloid complex develops, the central amygdaloid nucleus lies ventral to the medial tip of the putamen, which, with a massa intercalata (D), separates it from the lateral amygdaloid nucleus. At substantially the same levels, substriatal gray, which in the more rostral planes lies dorsomedial to the central nucleus, begins to intervene between it and the putamen (fig. 4). Dorsolaterally at these levels the two nuclear masses are separated by a small intercalated cell mass which increases caudally (fig. 5, D), persists to just behind the caudal end of the central nucleus and serves as an indicator of the approximate dorsal boundary of the central nucleus. The substriatal gray, however, serves to separate the central nucleus from the putamen for only a short distance and then the two become directly continuous with each other. At its caudal pole, the

central nucleus (fig. 5) is again clearly distinguishable from the putamen. Due to the deeper staining and greater condensation of its constituent neurons and to the presence of the associated intercalated cell mass, the central amygdaloid nucleus is more clearly differentiable in the shrew than in some other mammals.

Intercalated cell masses. In planes through the rostral end of the amygdaloid complex (fig. 1), a heavily stained band of cells is seen among the fibers of the external capsule (fig. 1, C). At the ventromedial border of this cell band lies a less deeply stained group of neurons (figs. 1 and 2, Mas. Interc. A + B). This cell group, which constitutes an intercalated mass in the amygdaloid complex, continues caudalward, being separated into a dorsal (A) and a ventral (B) part by the more lateral fibers of the anterior commissure. Behind the commissure the dorsal and ventral groups incompletely merge but, within a few sections. as the series is followed caudalward, are separated by the rostral pole of the lateral amygdaloid nucleus which appears between them (fig. 3). As this lateral nucleus enlarges, the ventral part gradually disappears, beginning laterally, and ultimately fades out into the anterior amygdaloid area. With the growth of the lateral amygdaloid nucleus, the dorsal part of this intercalated mass (figs. 4 and 5) also slowly reduces in size and finally disappears by turning ventromedially into another well developed intercalated area (figs. 4 and 5) between the central nucleus and the putamen (fig. 4, D). A lateral strand of cells of this intercalated gray (fig. 3, Mas. Interc. L) can be traced for a considerable distance along the outer border of the lateral amygdaloid nucleus. Throughout its extent it varies considerably in size and shape, at some levels showing a well developed dorsal tip.

In planes which show the central amygdaloid nucleus, the intercalated mass mentioned in the foregoing paragraph as lying at the boundary between the central nucleus and the putamen can be seen. It lies in the fiber capsule between the lateral amygdaloid nucleus and the central nucleus (figs. 4 and 5, D) and continues for a considerable distance, serving as a landmark in establishing the approximate region of fusion of the putamen and the central amygdaloid nucleus. In addition to these relatively discrete intercalated masses, scattered neurons are found in the course of fiber bundles associated with the amygdaloid complex.

DISCUSSION

In the short-tailed shrew, Blarina brevicauda, the essential nuclear pattern of the amygdaloid complex corresponds to that found in marsupials (Johnston, '23; van der Sprenkel, '26), rodents (Gurdjian,

'28; Young, '36), insectivores (Ganser, 1882; Völsch, '06; '10) chiropters (Spiegel, '19; Humphrey, '36), carnivores (Fox, '40; Jeserich, '44) and primates (Völsch, '06, '10; Crosby and Humphrey, '41; Riley, '43; Lauer, '44). Throughout the mammalian series variations in the amygdaloid nuclei appear to fall into two general categories. In the first place, the individual nuclei differ in size and in degree of differentiation in relation with variations in the development of other parts of the nervous system, not only with changes in the olfactory centers but also with differences in non-telencephalic regions, such as the hypothalamic areas. In the second place, the nuclei making up the amygdaloid complex differ in positional relations to each other depending upon the degree of development of the cerebral cortex and the consequent medial rotation of the temporal pole, modifications which become progressively more pronounced in passing from lower to higher mammals.

In all mammals considered in this discussion, the lateral amygdaloid nucleus is well developed and intimately related with the basal amygdaloid nucleus. It varies in position, lying, in levels through the middle of the amygdaloid complex, dorsal to the basal nucleus in the bat and the shrew, lateral to the basal in the cat and ventrolateral to the basal in man, although in all these forms the relations vary somewhat frontally and caudally. In the rabbit and the cat, the lateral nucleus is the largest and longest nucleus in the amygdaloid complex. In the bat, the lateral is not clearly separable from the basal rostrally in cell preparations, although pyridine silver material indicates that it begins slightly farther forward. Caudalward it terminates in front of the basal in the free-tailed bat (Tadarida mexicana; Humphrey, '36) but in the fruiteating bat (Pteropus; Spiegel, '19), although the basal nucleus is the larger, the lateral extends farther caudalward. In man, the lateral amvgdaloid nucleus, which is the ventral amvgdaloid nucleus of Hilpert ('28), merges frontally and caudally with the basal nucleus. It begins slightly rostral to this latter nucleus but disappears from the field before the caudal pole of the basal is reached. The lateral amygdaloid nucleus in the shrew is closely related to the larger-celled lateral portion of the basal, extending in front of this latter nucleus but terminating just rostral to its caudal pole. Its rostrocaudal relations resemble those of the human lateral amygdaloid nucleus, but the lateral nucleus in the shrew is proportionately smaller (fig. 8), although it has a relatively somewhat greater caudal extent.

The basal amygdaloid complex includes not only the basal nucleus but also the accessory basal in those mammals in which it is present. The

basal nucleus has been divided, in many mammals, into a larger-celled lateral part lying close to the lateral amygdaloid nucleus and a smallercelled part which is frequently medial or ventromedial in position. Such medial and lateral parts were described for rodents by Young ('36, rabbit) and for carnivores by Fox ('40, cat). In the opossum Johnston ('23) recognized a basal and an accessory basal amygdaloid nucleus. Masses similarly designated were identified in the brain of a South American marsupial (Caenolestes) by Obenchain ('25) and in that of the opossum (Didelphys virginiana) by van der Sprenkel ('26). It seems probable that the accessory basal nucleus, as described by Obenchain and van der Sprenkel, does not correspond to the area so termed by Johnston, but is directly comparable to the accessory basal nucleus of the bat (Humphrey, '36). In the bat, Humphrey recognized a lateral, large-celled and a medial, small-celled portion of the basal nucleus and a medially situated mass resembling more nearly the lateral part of the basal, but with a tendency for the cells to be arranged in clusters with an intermingling of smaller cells and fibers. This third part of the basal amygdaloid complex she termed the accessory basal nucleus. In the rabbit (Young, '36) and the cat (Fox, '40) no differentiable accessory basal nucleus has been identified. In the mink (Jeserich, '44), however, an accessory basal nucleus is represented, although it is small and indefinite in outline. The present study of the basal complex in the shrew indicates that there are larger-celled and smaller-celled portions of the basal nucleus and that an accessory basal nucleus which might be subdivided into two parts, as it is in primates — can be demonstrated. Large basal and accessory basal nuclei, each clearly divisible into two parts, have been described and illustrated for the macaque (Lauer, '44) and for man (Crosby and Humphrey, '41, and Riley, '43).

The medial amygdaloid nucleus has a marked extent in certain mammals. It is the largest nuclear mass of the cortico-medial amygdaloid group in carnivores (Fox, '40). In the free-tailed bat (Humphrey, '36), in which no delimitable anterior amygdaloid area was recognized, it begins far forward in the amygdala but does not extend to the caudal pole of the complex. In the large fruit-eating bat (Pteropus; Spiegel, '19), however, its caudal end fuses with the hippocampus, as it does in the rabbit (Young, '36) and in the mole. With the decrease in size of the olfactory system in primates, the medial nucleus becomes less well differentiated and, although present (Crosby and Humphrey, '41), is not conspicuous in man, so that Hilpert ('28) did not recognize it in the human amygdaloid complex.

The cortical amygdaloid nucleus is well developed in all mammals here considered, but least so in the bat (Humphrey, '36). In some rodents (rabbit; Young, '36) it appears to have, for part of its extent, a subcortical position, but subcortical portions were not present in the carnivores (Fox, '40) or the bat (Humphrey, '36). Secondary subdivisions occur in the caudal two-thirds of the cortical amygdaloid nucleus in man (Hilpert, '28; Crosby and Humphrey, '41) as they do in the shrew.

Nuclear gray of the lateral olfactory tract, which differentiates between the cortical and the medial amygdaloid nuclei, in close relation with the anterior amygdaloid area where this area is present, shows a wide range of variations throughout the mammalian series. In the carnivores (Fox, '40) it is a spherical, deeply-staining cell mass showing no subdivisions. In the rat (Gurdjian, '28) it has dorsal and ventral portions, in the rabbit (Young, '36) medial and lateral portions, in the bat (Humphrey, '36) frontal and caudal parts and in the shrew a rostral, more ventrally situated portion and a caudal, more dorsal part. In man, extremely minute rostral and caudal representatives of this gray are found (Crosby and Humphrey, '41).

The intercalated cell masses are characteristic of the amygdaloid complex of all forms studied. Certain of these are relatively constant, particularly those between the central and the basal and dorsal to the lateral and the basal amygdaloid nuclei.

The anterior amygdaloid area is found in most mammals in the rostral part of the amygdaloid complex. It represents gray which is relatively unorganized, having not differentiated into the more specific nuclear masses. It does not appear to be present in the bat (Humphrey, '36), has fair representation in the rabbit (Young, '36) and the cat (Fox, '40) and has a considerable rostrocaudal extent in the shrew and in man (Crosby and Humphrey, '41).

The cortico-amygdaloid transition area is a region of intermingling of the pyramidal cells of cortical type with those cells characteristic of the baso-lateral amygdaloid complex and the cortical amygdaloid nucleus. This area of transition has been seen by several students of the region (Johnston, '23; Hilpert, '28; Crosby and Humphrey, '41; Lauer, '44, and others). Its significance was discussed by Johnston ('23), who believed it was due to an infolding of the pyriform lobe cortex to form the baso-lateral amygdaloid complex. Further studies, particularly on the embryology of the region, are needed to make clear the exact way in which this relation between the cortex and the underlying amygdala is established, but the relation suggests that the baso-lateral amygda-

loid complex in general may function as vicarious cortex (Crosby and Humphrey, '41) in much the same way as do the hyperstriatal and, possibly, the neostriatal areas of the avian forebrain (Huber and Crosby, '29).

In figure 8 an attempt has been made to show the actual resemblances existing between the various nuclear components present in the amygdala of the shrew and that of man. The outstanding difference between these two nuclear masses is their orientation with reference to the midplane of the cerebral hemisphere. With the great development of the temporal region, the human amygdala is oriented at an angle of approximately 140° as compared with the orientation of the corresponding area in the shrew. An attempt has been made to show this in figure 8. In A of this figure, the various nuclear components of the amygdala of the shrew are indicated in their normal position. B shows the entire amygdala of the shrew after it has been rotated medially, through approximately 140°, without disturbing the nuclear pattern. This diagram thus demonstrates the resulting hypothetical orientation of the nuclear masses after such a rotation. Figure C illustrates the nuclear constituents of the human amygdaloid complex in their norinal position. The striking resemblances existing between the relative positions of the nuclear masses after the 140° rotation in the shrew and those of the normally placed human amygdala can be seen by a comparison of these diagrams. From such an examination, it will be evident that the differences between the human amygdala and that of the shrew are due not to changes in fundamental pattern but to differences in orientation of the human amygdala, brought about by the great development and consequent medial rotation of the temporal lobe region of the hemisphere in man.

Although certain parts of the amygdala are both relatively and actually better developed in man than in the shrew, the increase in the amygdala is not commensurate with the increase in size of the cerebral hemisphere in man. Nevertheless, a comparison of the amygdala of the shrew (fig. 8, A and B) with that of man (fig. 8, C) shows that the lateral, basal and accessory basal nuclei occupy proportionately a much larger part of the human amygdaloid area. On the contrary, the medial nucleus and the nuclei of the lateral olfactory tract—those portions of the amygdala which contribute particularly to stria terminalis and which are important recipients of olfactory impulses—are relatively considerably reduced in man. The cortical and the central amygdaloid nuclei are fairly constant in proportionate size in the two forms.

This common pattern of the amygdaloid complex, seen here in the shrew and in man and undoubtedly constant in mammalian forms, has an importance for human anatomy. Such constancy in pattern is significant in that it permits the application of results obtained through experimental studies to the understanding and solution of clinical cases and contributes to the appreciation of the normal functioning of the amygdala in man.

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ABBREVIATIONS

V., ventricle

ANT. AMYG. A., anterior amygdaloid area C, cell band along fibers of external capsule CAP. EXT., external capsule COM. ANT., anterior commissure CORT.-AMYG.TR.A., cortico-amygdaloid transition area FIS. AMYG., amygdaloid fissure FIS. ENDORHIN., endorhinal fissure G. P., globus pallidus HIP., hippocampus MAS.INTERC. A, B, D and L, various intercalated cell masses (see text) N. AMYG. BAS. ACC. A, basal accessory amygdaloid nucleus, deep portion N. AMYG. BAS. ACC. B, accessory basal amygdaloid nucleus, superficial portion N.AMYG.BAS.P.M., larger-celled portion of basal amygdaloid nucleus

N.AMYG.BAS.P.P., smaller-celled portion of basal amygdaloid nucleus N.AMYG.CENT., Central amygdaloid nu-N.AMYG.CORT., cortical amygdaloid nu-N. AMYG. LAT., lateral amygdaloid nucleus N. AMYG. MED., medial amygdaloid nucleus N. DIAG. B., nucleus of the diagonal band of N.TR.OLF.LAT.P.ROST., rostral nucleus of the lateral olfactory tract N.TR.OLF.LAT.P.CAUD., caudal nucleus of the lateral olfactory tract PUT., putamen PYR. LOB. COR., pyriform lobe cortex S.G., substriatal gray T. OLF., tuberculum olfactorium

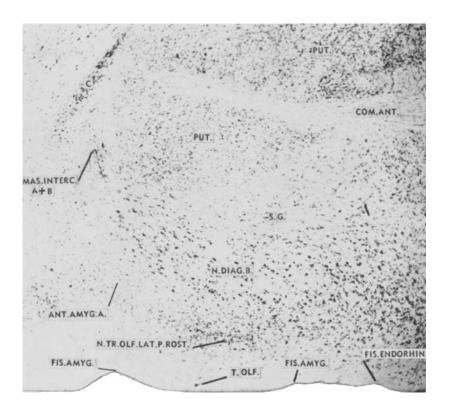


Fig. 1 A transverse section through the frontal end of the amygdaloid complex to show the relations of the rostral nucleus of the lateral olfactory tract with the anterior amygdaloid area. Toluidin blue preparation. \times 60.

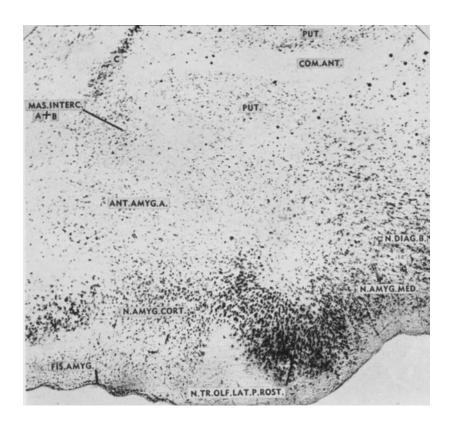


Fig. 2 A photomicrograph of a transverse section through the middle of the large rostral nucleus of the lateral olfactory tract. Toluidin blue preparation. \times 60.

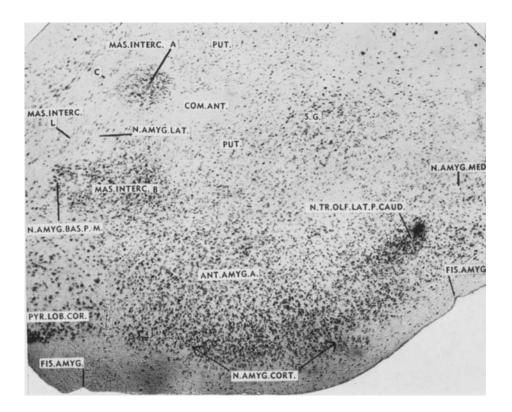


Fig. 3 A photomicrograph of a transverse section through the small caudal nucleus of the lateral olfactory tract. Toluidin blue preparation. \times 60.

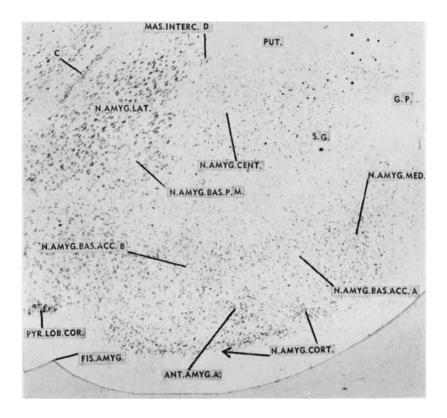


Fig. 4 A photomicrograph of a transverse section through the amygdaloid complex of the shrew at levels which show the central amygdaloid nucleus. Toluidin blue preparation. \times 60.

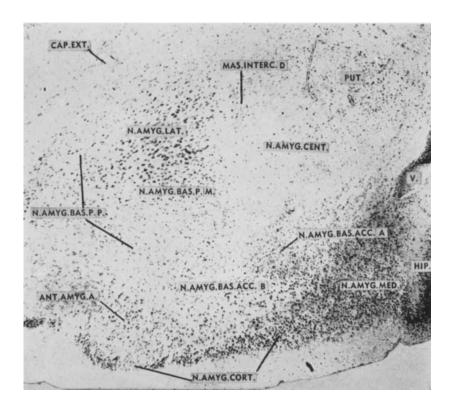


Fig. 5 A photomicrograph of a transverse section slightly caudal to that indicated in figure 4, showing the rostral part of the cortico-amygdaloid transition area. Toluidin blue preparation. \times 60.



Fig. 6 A photomicrograph of a transverse section through the caudal portions of the accessory basal and cortical amygdaloid nuclei. Toluidin blue preparation. \times 60.

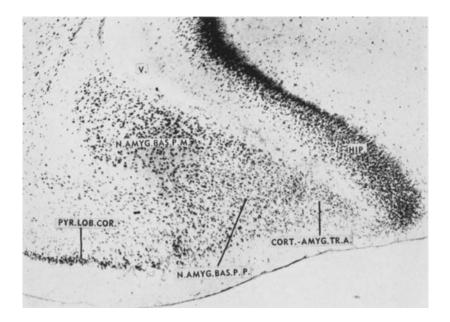


Fig. 7 A photomicrograph of a transverse section through the caudal pole of the amygdaloid complex. Toluidin blue preparation. \times 60.

Fig. 8 Diagrams of the amygdaloid complex of the shrew and of man. A. The amygdala of the shrew in its normal position as seen in transverse sections through the hemisphere (see A', key figure to show the normal position of the amygdala). \times 30. B. The amygdala of the shrew with its position changed to indicate a medial rotation of approximately 140° \times 30. C. The human amygdaloid complex as seen in transverse section through the hemisphere (see C', key figure to illustrate the position of the human amygdala). \times 5.

ABa, accessory basal nucleus — lateral portion in man, deep portion in the shrew; ABb, accessory basal nucleus — medial portion in man, superficial portion in the shrew; Ba, basal nucleus, larger-celled portion; Bb, basal nucleus, smaller-celled portion; b', the external portion (so-called superficial part in man) of the basal nucleus outside of the lateral nucleus; C, cortical nucleus; CE, central nucleus; I, intercalated cell mass; L, lateral nucleus; M, medial nucleus; O, nucleus of the lateral olfactory tract.

