THE AMYGDALOID NUCLEI, HIPPOCAMPUS AND OTHER PARTS OF THE RHINENCEPHALON IN THE PORPOISE (*PHOCAENA PHOCAENA*)

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INTRODUCTION

It is well known that the porpoise (*Phocaena phocaena*) is an anosmatic mammal, and that it does not possess an olfactory bulb. One might regard its condition as representing the end results of a phylogenetic removal of the olfactory bulb, and it is clearly of interest to compare these results with those of short-term experimental removal in mammals with a fully functioning olfactory apparatus. They will naturally be sought primarily in the 'rhinencephalon', and in a previous paper (Breathnach, 1953) the condition of the prepyriform cortex, olfactory tubercle ('area désert') and the nuclei of the precommissural region or septum were described. These are all parts of the 'rhinencephalon', but it was found that only the prepyriform cortex and the cortex of the olfactory tubercle showed any obvious deficiency. Both these structures have been shown experimentally to receive fibres direct from the olfactory bulb in osmatic mammals. It was noted that all the nuclei of the precommissural region, which have not been shown to receive such fibres in any mammal which has been adequately investigated, were well developed.

The purpose of the present paper is to extend this survey to the remaining parts of the brain which are commonly included under the term 'rhinencephalon'. The most important of these are the amygdaloid complex of nuclei, the hippocampal formation and the entorhinal cortical area. The cortex of the cingulate gyrus, the habenular nuclei, the mamillary region of the hypothalamus and the anterior thalamic nuclei have also been described as rhinencephalic; they will be considered, but more briefly than the three structures first mentioned.

MATERIALS AND METHODS

The same material was used as in the previous study (Breathnach, 1953), namely the brains of two adult porpoises (*P. phocaena*), fixed in 10% formalin and cut serially at 20μ in celloidin. In the two series the planes of section were approximately at right angles to each other; alternate sections were stained with thionin and by Weil's modification of the Weigert method. The plane of section, in relation to the hemisphere as a whole of the series from which most of the observations and illustrations in this paper were made, is shown in text-fig. 7 of the previous paper.

Similar serial sections from the brains of a sheep, rat and a phalanger (*Trichosurus vulpecula*), and of the human hippocampus were available for comparison.

OBSERVATIONS

Amygdaloid complex

Johnston (1923) divided the nuclear components of the amygdaloid complex into two groups, cortico-medial and baso-lateral, and in general the terminology used for the description of the mammalian amygdala is based on his work. It was applied to the human amygdala by Crosby & Humphrey (1941), and has been found equally suitable for the porpoise. Although the amygdala as a whole is usually included in the rhinencephalon, it should be pointed out that only the cortico-medial group of nuclei have been shown to receive direct connexions from the olfactory bulb (Clark & Meyer, 1947; Meyer & Allison, 1949).

Baso-lateral amygdaloid nuclei

These form a prominent cell mass throughout almost the whole extent of the amygdala. The components are:

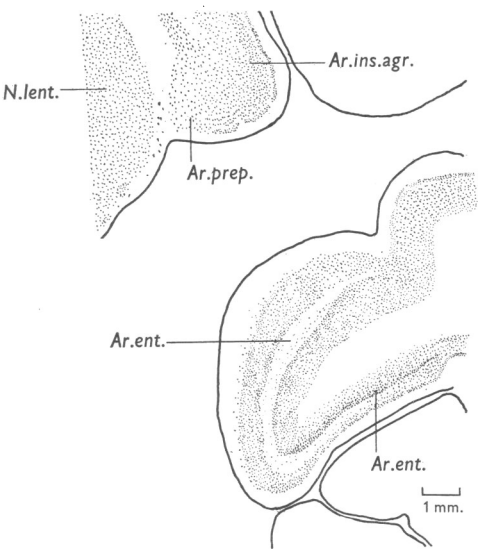
Lateral nucleus (Pl. 1, fig. 1; Text-figs. 2–7). This is the most lateral as well as the largest of the amygdaloid nuclei, and is recognizable throughout almost the whole antero-posterior extent of the complex. Its cells vary in size from medium to small and are rounded or fusiform in shape. Although slight regional variations in cell density can be seen, the general impression is of greater homogeneity than in most other amygdaloid nuclei.

Throughout, the nucleus is related laterally to the fibres of the external capsule. Posteriorly it is completely surrounded by fibres and lies in the roof of the lateral ventricle (Text-fig. 6). Except in this region the lateral nucleus has the lateral part of the basal nucleus on its medial side, and although there is some intermingling of cells where the two nuclei are adjacent, the basal nucleus can easily be distinguished since it consists of large multipolar cells, which stain deeply (Pl. 1, fig. 1). The basal and lateral nuclei are not separated by fibres except for a short distance anteriorly. Posteriorly the lateral nucleus comes to lie ventro-lateral to the central nucleus, which separates it from the lentiform nucleus.

It is clear that the lateral nucleus in the porpoise is very similar to the nucleus so named in the fin-whale (Jansen & Jansen, 1953), in man (Crosby & Humphrey, 1941) and in many other mammals (e.g. the cat, Fox, 1940). Its characteristic relationship to the external capsule and to the large-celled part of the basal nucleus as well as its topographical position make its identification reasonably certain.

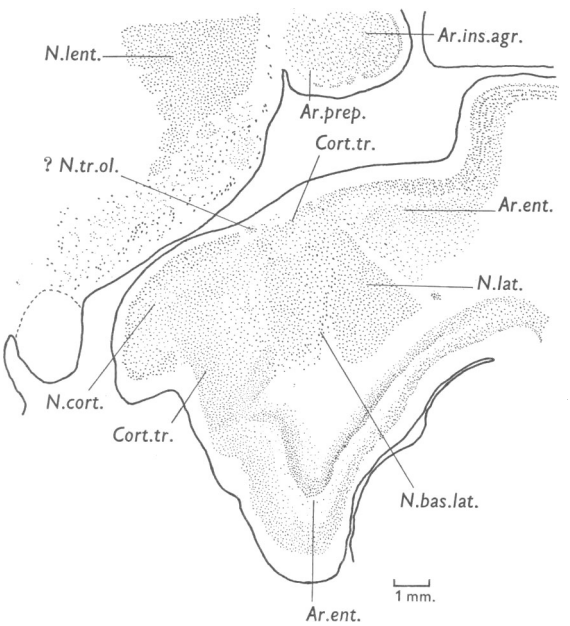
Basal and accessory basal nuclei. The basal nucleus as a whole is situated in the medial part of the amygdala (Pl. 1, fig. 1). The lateral or large-celled part is the most conspicuous and clearly defined; it is easily recognized by the size of its cells and their deep staining reaction, and it extends through the whole length of the basal mass (Text-figs. 2–5); posteriorly it is replaced by the central nucleus. Ventrally a few fibres from the stria terminalis enter it, and in doing so separate a small group of the characteristic cells from the ventro-medial angle of the main part of the nucleus (Text-fig. 4).

The medial part of the basal nucleus and the accessory basal nucleus are more difficult to define. They lie in the anterior third of the amygdala (Text-fig. 3; Pl. 1, fig. 1) deep to the cortical nucleus and the cortico-amygdaloid transition area, and



Text-fig. 1.

Text-figs. 1–7. These figures are drawings of a series of sections cut in the coronal plane and stained with thionin, passing cranio-caudally from the tip of the temporal pole to the caudal extremity of the amygdaloid complex. Parts of the hippocampus and adjacent cortical areas and the corpus striatum are shown in addition to the amygdaloid nuclei. For the list of abbreviations see p. 291.



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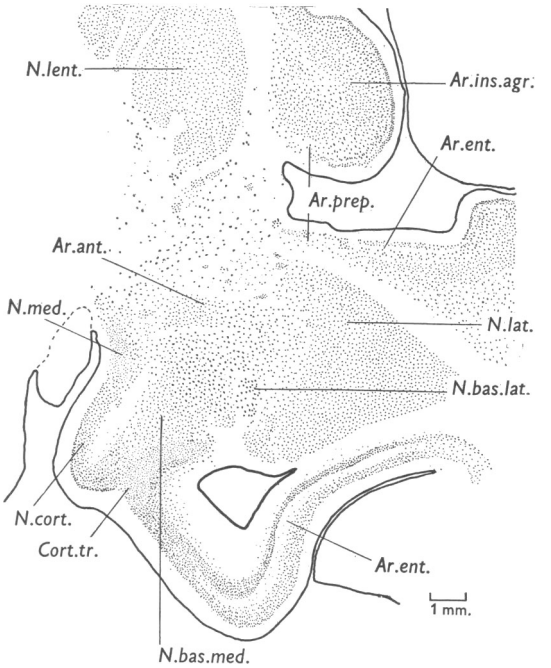

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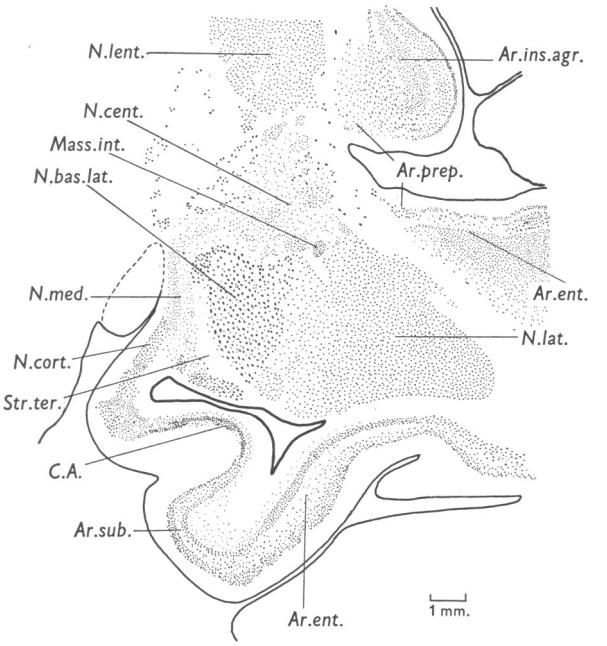

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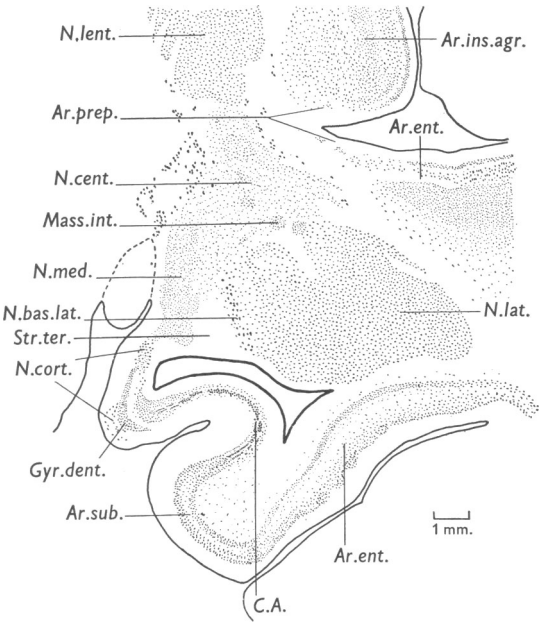

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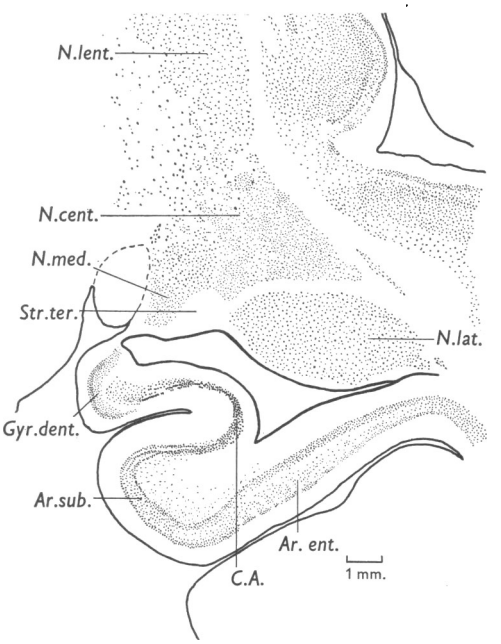
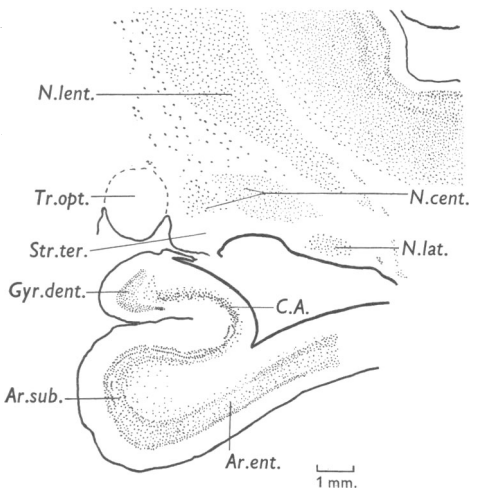


Text-fig. 6.

are closely related to fibres which appear to be derived mainly from the stria terminalis system. The medial part of the basal nucleus is divided in man into superficial and deep parts (Crosby & Humphrey, 1941). Indications of a similar subdivision can be seen in the porpoise; small cells, immediately deep to the cortico-amygdaloid transition area, may represent the superficial part and larger cells, which stain poorly, situated just ventral to the lateral part of the basal nucleus, a deep part. The significance of these very ill-defined subdivisions is doubtful.



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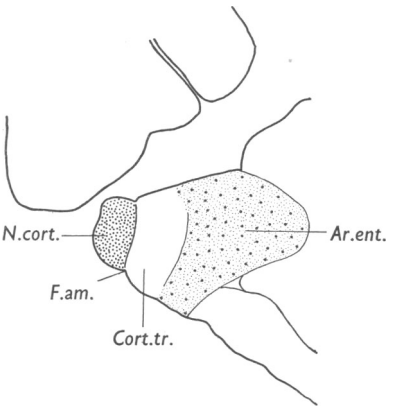


Text-fig. 8.

Text-fig. 8. A diagram showing the cranial aspect of the medial side of the left temporal pole; the cut surface of the frontal lobe is shown in the upper part of the diagram separated by the Sylvian fossa from the temporal pole. Parts of the surface extent of the cortical amygdaloid nucleus, cortico-amygdaloid transition area and the entorhinal cortical area are indicated.

The accessory basal nucleus is probably represented by a more or less discrete group of medium-sized cells, immediately deep to the cortical nucleus (Pl. 1, fig. 1) and separated from it by a layer of fibres.

Intercalated cell-masses. These are discrete islands of small cells which have been described in the amygdala of most mammals between the main nuclei. In the porpoise they are found in association with the lateral nucleus, mostly on its dorsal aspect between it and the central nucleus (Text-figs. 4, 5). An occasional group may be found between the lateral and basal nuclei. Their appearance is similar to that described by Jansen & Jansen (1953) for the fin-whale.

The features of the basal nuclei of the porpoise are clearly very much the same as those described for the region similarly named in other mammals. This applies particularly to the large-celled or lateral basal nucleus, which is easily recognized and defined, and appears to be one of the most striking features of the amygdala in most, perhaps in all mammals. Of the medial part and the accessory basal nucleus it can be said only that they constitute an ill-defined mass of cells in which regional variations in cell size and density can be recognized; while the mass as a whole is probably comparable from one mammal to another, it is uncertain if the regional

variations form a definite enough pattern for more detailed comparisons to be valid. It may be noted that Jansen & Jansen (1953) were unable to distinguish an accessory basal nucleus in the fin-whale, but apart from this, their account corresponds very closely with that given above.

Cortico-medial amygdaloid nuclei

In general, these nuclei occupy a position close to the surface and dorso-medial to the baso-lateral group. The main constituents are the cortical, medial and central nuclei and the nucleus of the lateral olfactory tract. In the anterior part of the amygdala the medial and central nuclei are replaced by a region in which there is no differentiation of nuclear groups, but where numerous small cells are present scattered irregularly among bundles of fibres (Text-fig. 3). This region, which lies dorsal to the baso-lateral group of nuclei and immediately ventral to the putamen, is the 'anterior amygdaloid area' of Crosby & Humphrey (1941) and of other authors. There is also a cortico-amygdaloid transition area.

Cortical nucleus. This nucleus forms a small elevation on the medial side of the temporal lobe (Text-fig. 8) and is surrounded by the shallow amygdaloid fissure. Its structure (Pl. 1, fig. 1) is very similar to that of prepyriform cortex. There is a superficial or molecular layer, free of cells, but containing fine myelinated fibres. This is succeeded by a narrow intermediate layer of fairly closely packed pyramidal cells which passes without any defined boundary into a broader third layer containing cells similar in type but more scattered in their arrangement. Anteriorly there is no boundary between these deeper cells and the adjacent medial basal nucleus; posteriorly a layer of fibres, probably part of the stria terminalis system, intervenes. On the surface posteriorly the cortical nucleus is replaced by the small cells of the dentate gyrus (Text-figs. 4–6).

The cortico-amygdaloid transition area (Pl. 1, fig. 1; Text-figs. 2, 3 and 8) lies between the cortical nucleus and the entorhinal area. Its cells, which are mainly pyramidal or fusiform in shape, are somewhat concentrated towards the surface from which they are separated by a molecular layer; they are not clearly separated from the cells of the underlying medial basal nucleus where the cells become smaller.

In sections through the anterior part of the amygdala a few scattered cells are found closely associated with the dorso-lateral edge of the cortical nucleus (Text-fig. 2), a situation similar to that occupied by the nucleus of the lateral olfactory tract in Primates (Crosby & Humphrey, 1941; Lauer, 1945). These cells appear to be the only possible representative of this nucleus in the porpoise, and if so, it is so poorly developed as to be barely recognizable. It is of interest to note that Jansen & Jansen (1953) found it quite well defined in the fin-whale.

The correspondence between the cortical nucleus in the porpoise and the same nucleus as described by Crosby & Humphrey (1941) in man, by Lauer (1945) in the macaque, Fox (1940) in the cat, and by other authors in other mammals, is very close. It is represented by Brockhaus's (1938) periamygdala and Rose's (1927) areas *Pam*, 2 and 3. In the porpoise it is well differentiated, and probably rather better defined than in Primates. No indication could be found of a division into dorsal and ventral parts as described by Jansen & Jansen (1953) in the fin-whale, nor was the

more superficial of its two cellular layers lacking in any situation, as these authors found.

Medial nucleus. This is found on the surface between the optic tract and the basal nucleus (Text-figs. 3–6). Ventrally it is directly related to the cortical nucleus, and dorsally extends laterally over the basal nucleus to come into relation with the central nucleus. Anteriorly it gradually becomes smaller, cell density falls off and it blends with the anterior amygdaloid area. Posteriorly it increases in size, cell density increases and it disappears by merging with the central nucleus. The cells are predominantly small in type, smaller, for instance, than those of the lateral nucleus, but, here and there, especially towards the posterior end, scattered cells of a larger size are encountered.

Central nucleus (Text-figs. 4–7). This is probably the least well defined of any of the amygdaloid nuclei. It consists of cells, mostly of medium size, generally slightly larger than those of the medial nucleus, irregularly scattered among fibre bundles. Throughout, it lies ventral to the lentiform nucleus from which it is not clearly separated although the cells of the latter are somewhat larger. It merges with the medial nucleus, and anteriorly, without any obvious boundary, the anterior amygdaloid area. Posteriorly it is continuous with the bed nucleus of the stria terminalis, and in this region there is a concentration of rather large cells towards its medial side. These may correspond with the large-celled part of the central nucleus described by Brodal (1947*b*) and Fox (1940) for the rat and cat respectively.

It seems clear that the whole region of the medial and central nuclei and the anterior amygdaloid area could be described as a field containing diffusely scattered cells in which ill-defined regional variations in cell density and size occur, and that it is a continuation forwards of the bed nucleus of the stria terminalis. So far as the medial and central nuclei are concerned, this was indeed Johnston's (1923) suggestion when he described these nuclei as an enlargement of the bed nucleus of the stria. The region is very similar in all mammals, including the porpoise; one gets the impression in this animal that the part called 'medial nucleus' contains fewer cells than in most macrosmatic mammals, especially anteriorly, and that the 'central nucleus' is perhaps larger than in Primates (cf. figures in Crosby & Humphrey, 1941; and Lauer, 1945), but in the absence of clearly defined boundaries these comparisons can have little significance.

Stria terminalis. This consists of finely myelinated fibres, accompanied by the cells of its bed nucleus, which can be followed in the usual position around the lentiform nucleus. These fibres are closely related to the basal, central and medial amygdaloid nuclei, but precise details of connexions within the amygdala cannot be established in material of the kind available. The system does not appear to be significantly different from what can be seen in similar material from the sheep.

One may sum up this account of the amygdala in the porpoise by stating that its nuclear configuration conforms to the general mammalian plan, all nuclei being present with the probable exception of the nucleus of the lateral olfactory tract. Its differentiation, and particularly that of the baso-lateral complex, resembles very closely what is found in the Primates (Crosby & Humphrey, 1941; Lauer, 1945). We have found a closely similar pattern in the sheep, and Fox's description (1940) shows that the condition in the cat is also much the same. It is clear that the

amygdala of the fin-whale (Jansen & Jansen, 1953) does not differ significantly from this general pattern, which is indeed remarkably constant in all the animals mentioned.

In relatively smooth-brained mammals such as the rat (Gurdjian, 1928; Brodal, 1947*b*), bat (Humphrey, 1936), shrew (Crosby & Humphrey, 1944), oppossum (Johnston, 1923), rabbit (Young, 1936), the position is not quite the same. Most authors have in fact distinguished and named the same nuclei as we have described in the porpoise, and Johnston, who introduced this terminology, based it on the condition he found in *Didelphys*. One finds, however, that Gurdjian's and Brodal's interpretations in the rat differ significantly from one another; that Young (in the rabbit) finds the lateral nucleus divisible into an anterior large-celled and a posterior small-celled part, while in the rat the condition is reversed (Brodal, 1947*b*). The figures published by Crosby & Humphrey (1944) for the shrew show very little in the way of well-defined nuclei, and suggest that the material on which they are based might reasonably be open to more than one interpretation. We have made no detailed study of the amygdala in mammals of this kind, but a preliminary examination of serial sections of the rat's brain and of the brain of the phalanger, *Trichosurus*, show that the difficulties of interpretation in terms of the subdivisions of the amygdala usually made, are real, and very much greater than in mammals with larger and more highly convoluted brains.

Main interest, of course, centres on the question whether the absence of olfactory bulbs and tracts in the porpoise can be related to any morphological differences between the amygdala in this animal and in mammals in which the olfactory apparatus is well developed. The virtual absence of the nucleus of the lateral olfactory tract is clearly the most obvious of these differences. All other amygdaloid nuclei are present in the porpoise, and if the loss of olfactory connexions has had any effect on their morphology it can be only in altering the degree of development of some or all of them relative to the size of the brain as a whole or to each other.

Morphological studies, such as those of Crosby & Humphrey (1941) and Lauer (1945) indicate that in microsmatic mammals like the Primates, where the non-olfactory cortex is very extensive, the nuclei of the cortico-medial group are much smaller than those of the baso-lateral, a disproportion which is said to be less evident in the brain of macrosmatic mammals such as the rat. It is implied that a progressive increase in this disproportion accompanies the development of the microsmatic condition, and, *a fortiori*, it should be the more evident in an anosmatic brain. While simple inspection of sections may give this impression it is difficult to make allowance for the fact that some nuclei may appear only or mainly in one part of a series, where other nuclei may not be visible at all. Moreover, quite small differences in the orientation of the amygdala (or of the plane of section) may alter appearances very greatly. We ourselves felt that in the sheep, an animal with a well-developed olfactory apparatus, the cortico-medial nuclei were rather better developed and proportionately larger than in the porpoise, although the difference was not very striking. We found, however, that in the bat, with a well-developed olfactory bulb, and with a poor development of the non-olfactory cortex, Humphrey (1936) described the baso-lateral complex as 'relatively very much larger than the cortico-medial'.

For these reasons it seemed desirable to supplement visual impressions as far as possible with objective measurement, and we have chosen the sheep's brain for comparison with that of the porpoise, since the general similarity in the differentiation of the amygdaloid nuclei is so marked that there is no difficulty in identifying the same nuclei in the two animals. It would be much more difficult to institute valid comparisons with the smaller smooth-brained mammals mentioned above, although many of these show the macrosmatic character to a higher degree than the sheep.

On the complete series available, the antero-posterior length, maximum width and total volume of the amygdala have been measured, and also the volume of the baso-lateral group of nuclei. All measurements of course apply to the fixed and embedded brain. The maximum width in the porpoise was taken from the surface of the cortical nucleus to the most lateral point on the lateral nucleus; owing to a difference of the orientation of the complex as a whole, the corresponding measurement in the sheep is almost vertical. Volumes were estimated by planimetry, using the method of Dornfeld, Slater and Scheffé (1942).

Dimensions of amygdala

	Antero-posterior length (mm.)	Maximum width (mm.)	Total volume ($mm.^3$)	Volume of baso-lateral nuclei ($mm.^3$)
Porpoise	12	12	2590	1480 (57 %)
Sheep	6	10	690	380 (55 %)

It will be seen that the total volume of the amygdala in the porpoise is about 4 times that of the sheep; the total brain weight (including brain stem and cerebellum) of the porpoise was about 500 g., and the sheep's brain varies from about 100 to 120 g. (the exact weight of the brain from which the sections were made was not known); that is to say the total brain weight of the porpoise is from 4 to 5 times that of the sheep, and one may say that the increase in volume of the amygdala in the porpoise is about proportionate to the total increase in brain weight. It appears, therefore, that the loss of olfactory connexions has had no great effect on the total size of the amygdala, compared to the size of the brain as a whole. Some figures given by Jansen & Jansen (1953) for the fin-whale are also relevant to this question. They give the maximum length and width of the amygdala as 25 and 20 mm. respectively. Jansen (1952) gives the total brain weight in this animal as 6850 g. The linear dimensions of the amygdala in the fin-whale are therefore about twice those in the porpoise, suggesting that the volume would be increased about 8 times. Total brain weight in the fin-whale is nearly 14 times that of the porpoise, so that the increase in size of the amygdala is considerably less than that of the brain as a whole, in spite of the presence of olfactory connexions in the fin-whale.

When the relative volumes of baso-lateral and cortico-medial nuclear groups are considered, it is found that there is practically no difference between the porpoise and the sheep. In both, the volume of the baso-lateral is greater than that of the cortico-medial group, the actual figure being between 50 and 60 % of the total volume of the amygdala. Since the sheep is macrosmatic and the porpoise anosmatic this is a surprising finding, and throws doubt on the idea that, in large-brained mammals at least, the presence or absence of olfactory tract connexions has any great effect on the relative sizes of these different parts of the amygdala.

It must of course be admitted that the volume measurements we have given are very approximate. The fact that so much of the amygdala is made up of 'nuclei' with very ill-defined boundaries, introduces a serious uncertainty into any measurements of area made in transverse sections, and it is on these measurements that the estimates of volume are based. Moreover, the boundary between the amygdala as a whole and the lentiform nucleus is by no means clear cut. Small differences in volume, which might have important functional significance, obviously could not be detected in material of this kind. One can only say that previous estimates, based simply on the inspection of sections, are open to at least as much uncertainty and are more likely to be affected by subjective bias. From our own findings we feel that it is fair to conclude that so far, no correlation between the relative size of the cortico-medial group of nuclei as a whole and the abundance or absence of olfactory tract connexions has been established, at least in mammals such as the sheep and porpoise with relatively large brains.

THE HIPPOCAMPAL FORMATION

Though traditionally a part of the 'rhincephalon', the hippocampus is now regarded as having only a remote association with olfaction, if indeed it has any at all (Brodal, 1947*a*; Kaada, 1951; Allison, 1953). One of the subsidiary arguments advanced in support of this view is the fact that the anosmatic cetacea possess a recognizable hippocampus. It has also been noted, however, that the cetacean hippocampus is small, a fact accepted by some authors (e.g. Addison, 1915) as suggestive evidence that the larger hippocampus of other mammals is at least partly concerned with olfaction. For these reasons it is clearly desirable to investigate the structure of the cetacean hippocampus in greater detail than has been done previously, and, if possible, to obtain estimates of its absolute and relative size.

In the account which follows the parts included under the term hippocampal formation are the dentate gyrus, cornu ammonis, and the subicular cortex, together with the extension of these structures above the corpus callosum as the induseum, which ends in the rudimentary anterior hippocampal cortex above the septum. There are also the associated fibre systems of which the fornix is the most important.

General form

The same parts and general relations are found as in other mammals. A typical dentate gyrus and cornu ammonis are found on the medial side of the temporal lobe (Pl. 1, fig. 4) extending posteriorly from the region of the cortical amygdaloid nucleus. As the splenium of the corpus callosum is approached these structures become considerably smaller, and the differentiation between them is lost (Pl. 1, fig. 5). There is no subcallosal 'hippocampal flexure' (Elliot Smith, 1897), and the formation can be followed directly round the splenium into continuity with a well-marked induseum (Pl. 1, fig. 6).

Cytoarchitecture

Dentate gyrus. Where this is clearly differentiated from the cornu ammonis transverse sections show a typical curved lamina of 'granule' cells (Pl. 1, fig. 4), superficial to which is a molecular layer containing a very few scattered cells. The

granule cells stain rather lightly in our preparations, and are less densely packed than in most mammals, especially those in the dorsal limb of the curve. At some levels, looser packing of the more deeply situated cells suggests a division into two laminae. Deep to the granular lamina is a region containing sparsely scattered cells of varying type; this region is included in the dentate gyrus as the polymorph layer by some authors, while others regard it as belonging in whole (Rose, 1926) or in part (Lorente de No, 1934) to the cornu ammonis. A typical dentate gyrus of this form extends over only a short distance. Anteriorly the granular layer loses its curvature, becomes orientated vertically (Text-fig. 5) and is replaced by the cortical amygdaloid nucleus (Text-fig. 4). Posteriorly the orientation becomes horizontal, and the granular lamina is reduced to a slender tail of small cells directly continuous with the small cornu ammonis (Pl. 1, fig. 5). Some distance anterior to the splenium even this vestige of the dentate gyrus is lost and in the induseum behind the splenium and above the corpus callosum nothing can be seen to represent it.

Cornu ammonis. On the basis of preparations in which fibres as well as cells were stained, six or more layers have been distinguished in the cornu ammonis (Lorente de No, 1934, and others). In our material only the main cellular layer, the stratum pyramidale, can be investigated in detail. The stratum radiatum, lacunosum and moleculare superficial to it and the stratum oriens on its deep aspect, require silver impregnation or Golgi material for their adequate investigation. Our Weigert preparations were not suitable, although they showed the alveus layer of fibres clearly enough.

The stratum pyramidale (Pl. 1, fig. 4) consists of large cells which are rather less frankly pyramidal in shape than in other mammals, being somewhat rounded. They have the appearance of being less closely packed than usual and the superficial and deep surfaces of the stratum are not very clearly defined. There is a noticeable scattering of the cells into the stratum oriens. It must be admitted, however, that direct comparison with sections of the human hippocampus does not show any conspicuous differences in these respects.

The stratum pyramidale extends from the concavity of the dentate gyrus to the subiculum, but the subicular border is indefinite. In Pl. 1, fig. 4, we have placed it at the point marked with an arrow, where a frankly bilaminar character becomes apparent, a point which can be recognized in all sections through the fully differentiated part of the hippocampus. Within the cornu ammonis defined in this way the following fields can be differentiated:

(*a*) The scattered cells within the hilum of the dentate gyrus. In the porpoise there are considerably fewer than in most mammals, and it may be that they should be classed as a polymorph layer of the dentate gyrus rather than with the cornu ammonis (see above).

(*b*) A fairly broad, ill-defined lamina of cells, many of which appear to be bipolar in type. These cells are more loosely packed than those in other parts of the cornu ammonis.

(*c*) A large area occupying the main convexity of the cornu in which cells of the same type form a more closely packed, thinner and better defined lamina than in (*b*). In a few sections a break can be seen in this lamina (*X*, Pl. 1, fig. 4) separating it from the next area.

(*d*) A smaller area in which the cell lamina again broadens and begins to show signs of a bilaminar character. As stated above, the point where the bilaminar character becomes definite has been taken as the boundary of the cornu ammonis. It is quite possible however that the field (*d*) corresponds with the prosubiculum of Lorente de No (1934), but the criteria available in Nissl preparations alone cannot decide this point.

This description applies only to that short length of hippocampus in which the dentate gyrus and cornu ammonis show the characteristic form illustrated in Pl. 1, fig. 4. Posteriorly, and before the level of the splenium is reached, the stratum pyramidale becomes much less extensive (Pl. 1, fig. 5). It begins beneath the fimbria, adjacent to the few small cells which represent the granular stratum of the dentate gyrus. From this point, it can be followed round the convexity of the cornu, gradually increasing in depth, and showing more and more evidence of subdivision until a fully laminated cortex is reached. Presumably part of the region of transition is subicular, but the absence of any abrupt change makes the placing of precise boundaries impossible, and any attempt to describe different fields within the stratum entirely arbitrary. Behind this level the stratum pyramidale can be followed round the splenium into the induseum (Pl. 1, fig. 6). Apart from a further and very marked decrease in size, and the complete disappearance of the granule cells of the dentate gyrus, it does not show any further change in structure until the anterior hippocampal cortex is reached above the septum (Breathnach, 1953).

Subicular cortex. This is a transition area between the cornu ammonis and the entorhinal cortical area, or, more posteriorly the general isocortex, without clearly defined morphological features which distinguish it sharply from adjacent areas. It occupies most of the summit of the hippocampal gyrus (Pl. 1, fig. 4). In Pl. 2, fig. 8, its structure is illustrated from a region which, in our judgement, lies about mid-way between well-defined entorhinal cortex and the cornu ammonis, and where five laminae are distinguishable. The first (molecular) contains a considerable number of fine myelinated fibres, which may represent part of the 'perforant path' of Lorente de No (1934). The second, third and fourth are made up of similar cells, pyramidal or fusiform in shape and of moderate size. These cells are more closely packed in the second and fourth lamina than in the third. The fifth lamina is a broad zone of rather small, scattered polymorphous cells.

Traced from the cornu ammonis this kind of cortex seems to be formed by a splitting up of the stratum pyramidale; in the entorhinal area, the lamination pattern becomes slightly more complex and more clearly defined (Pl. 1, fig. 2). We could find no structural criteria by which the subicular area could be divided into a number of different fields such as the pre-subiculum, para-subiculum, etc., of Lorento de No (1934), although more detailed analysis in silver and Golgi preparations might show that they exist. It must also be admitted that the subiculum in the porpoise bears only a superficial resemblance to the various subicular areas illustrated by Rose (1926) and Lorente de No (1934). It might be possible to fit the scheme of lamination adopted by either of these authors to the condition in the porpoise, but this could probably be done in quite a number of cortical areas. The identification of subiculum depends essentially on its topographical position between the cornu ammonis and the entorhinal area. Whether the term should be extended

to include transitional cortex in the posterior part of the hippocampal formation (Pl. 1, fig. 5) or the induseum (Pl.1, fig. 6), must, in the absence of intrinsic structural criteria, be left an open question.

Induseum griseum. This is quite well developed in the porpoise. It is shown in Pl. 1, fig. 6, and no further description is necessary. The size and structure illustrated are preserved with little or no change throughout the whole length of the corpus callosum.

Fibre systems

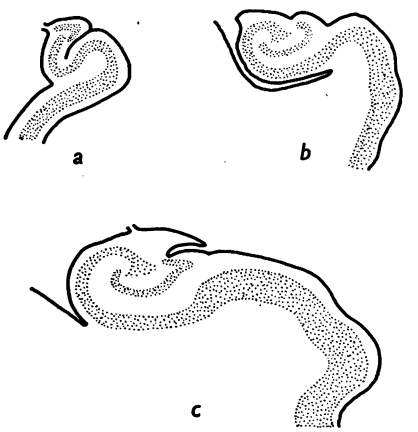
Very little can be added under this head. The alveus layer of fibres is not conspicuously different in thickness from the similar layer in man and in the sheep. The fimbria in Pl. 1, fig. 4, is very small, but this section is taken from near the anterior end of the hippocampus; more posteriorly it is much larger (Pl. 1, fig. 5). This apparent increase in size is partly due to some obliquity in the plane of section, and without counting the number of fibres it is not possible to make reliable comparisons with the size in other mammals. As the fornix, beneath the corpus callosum, it appears to be little smaller than in man, but the fibres which descend behind the anterior commissure to the mammillary region are comparatively few in number. A rather large proportion of fornix fibres take a pre-commissural course in the porpoise (Breathnach, 1953).

The dimensions of the hippocampal formation

Clearly the most satisfactory dimension for comparative purposes would be the total volume of the hippocampal formation. Attempts to estimate this were made using the same planimetric methods as for the amygdala, but were not found satisfactory. The indefiniteness of the boundary, particularly along the subicular margin, was found to introduce quite a large uncertainty into the estimate of the sectional area of the hippocampus; moreover, one could have no confidence that a point selected as the boundary in the porpoise really corresponded with any precision to a point similarly selected in another mammal. In such circumstances it became clear that only large differences of size could be considered significant, and that approximate estimates obtained by simpler means would not be improved by planimetry of a large number of sections.

Another difficulty was caused by the extent of the so-called vestigial part of the hippocampus in the porpoise, i.e. that part in which no differentiated dentate gyrus accompanies the small cornu ammonis and subiculum. Much of this is in the induseum, but a considerable amount is found in the posterior part of the subcallosal hippocampus. In the account which follows we have not attempted any quantitative comparison with other mammals so far as this part of the hippocampal formation is concerned. It appears to form rather a larger proportion of the formation in the porpoise than in most mammals, but, partly because of its shape and lack of differentiation, it is difficult to obtain measurements which could be used for comparison. Attempts at quantitative comparison have therefore been limited to that part of the subcallosal hippocampus in which a definite granular lamina of the dentate gyrus could be recognized in addition to a cornu ammonis and subicular region.

It was found that the antero-posterior extent of the hippocampus in which a dentate gyrus could be recognized either macro- or microscopically, was 12 mm. The corresponding measurement in the sheep is 31 mm. and in the human brain 50 mm. Text-fig. 9 illustrates transverse sections of the hippocampus of the porpoise, sheep and man, all drawn at the same magnification and taken from the region where the cross-sectional area appears largest. It is obvious that this area in the porpoise is much the smallest of the three. Estimates, which must be approximate on account of the uncertainty of the exact position of the subicular border, show that the area in the sheep is about twice and in man about 4 times that in the porpoise. When one



Text-fig. 9. Tracings, made to a uniform scale, of cross-sections through the hippocampal formation in (*a*) the porpoise, (*b*) the sheep, and (*c*) man. The sections were selected in each case from the region of maximal development.

considers also that the length of the fully differentiated hippocampus in the sheep is 2½ times and in man 4 times that in the porpoise, it becomes obvious that the differences in total volume must be very large indeed. One can indicate the order of these differences by saying that the hippocampus in the sheep must be about 5 times and in man more than 10 times, as voluminous as in the porpoise, and these figures are not likely to be significantly altered by any probable error in the measurements. They become particularly striking when one remembers that the total volume of the sheep brain is about a quarter of that of the porpoise and that human brain is only about 3 times larger. One can conclude that the fully differentiated part of the hippocampus is absolutely smaller and relatively very much smaller than in the sheep or man.

While statements that the hippocampus of the Cetacea is small are common in the literature, the only other measurements we have found are those of Hill (1893). In a brain of *Phocaena* he gives figures only for the lengths of certain parts of the hippocampal formation, e.g. 10 mm. for the 'length of the folded portion of the cortex, the hippocampus proper', which corresponds reasonably well with our estimate of 12 mm. for the length of that part of the hippocampus in which the granular lamina of the dentate gyrus could be recognized. The other dimensions given by Hill do

not differ significantly from measurements which could be made in our specimens, and do not need further discussion.

One may sum up this account of the hippocampal formation in the porpoise as follows. Qualitatively, in Weigert and Nissl preparations, it does not differ significantly from the hippocampus of other mammals; the absence of a hippocampal flexure cannot be regarded as an important point. It might be a result of the unusual shape of the skull and brain in the Cetacea, or possibly of the relatively small size of the hippocampus. The fact that cells in the stratum granulare and stratum pyramidale of the dentate gyrus and cornu ammonis respectively are rather less closely packed than usual, and the strata themselves somewhat less clearly defined, gives an impression of deficient differentiation. Rose's figures (1926), however, show that there is a considerable variation in this respect among mammals in general, and the significance of a somewhat superficial observation of this kind is doubtful. The wider spacing of cell bodies might result from a better development of the dendritic field, and if so, could be evidence of higher differentiation rather than regression.

There remains as its outstanding characteristic the very small size of the hippocampus, both absolute and relative to the size of the brain as a whole. At a very conservative estimate it cannot be more than a half, and probably much less than a half the volume of the hippocampus in mammalian brains of comparable size. In making this statement, however, one must remember that we have very little knowledge of the relative size of the hippocampus in some of the larger mammals with highly convoluted cortices. The relatively large amount of the hippocampus contained in the induseum, etc., where no dentate gyrus is differentiated, is also striking; the total length of the subcallosal hippocampus, for example, is 21 mm., but a dentate gyrus is recognizable even microscopically, for no more than 12 mm. of this distance. It should be added that the fibre system formed by the fimbria and fornix does not seem to be reduced in proportion to the hippocampus as a whole, but more precise methods for estimating its size, or the number of fibres it contains are necessary before any more definite statement can be made.

THE PREPYRIFORM AND ENTORHINAL CORTICAL AREAS

Several previous workers (Kukenthal & Ziehen, 1889; Riese, 1924; Langworthy, 1932) are agreed that the organization of the cetacean cortex differs considerably from that of other mammals. It is therefore even more difficult than usual to establish homologies for cortical areas in these animals. It is possible, however, to define the general position (but not the precise boundaries) of the areas under consideration by macroscopic, topographical criteria, and it becomes of interest to determine whether the cortex found in these positions shows a characteristic structure, and if that structure resembles in any way that of similarly placed cortex in other mammals.

Prepyriform area. The frontal part of the prepyriform area has already been described (Breathnach, 1953); it can be followed posteriorly into the Sylvian fossa (Text-figs. 1–5), where it becomes increasingly difficult to identify, being represented only by a molecular layer deep to which are a few scattered cells with no definite evidence of lamination. Beyond this point it bends on itself to become the temporal prepyriform area on the upper surface of the temporal operculum

(Text-figs. 3, 4). Throughout, the molecular or zonal layer contains myelinated fibres, and this is in fact the main structural criterion by which this cortex can be defined. If olfactory bulbs were present, such fibres would be identified as belonging to the lateral olfactory tract.

It is clear that the prepyriform cortex of the porpoise is very similar to that of the lateral olfactory gyrus of man, and that it extends to a position corresponding to the limen insulae and then turns forward on the upper surface of the temporal lobe towards the amygdala. While the anterior or frontal portion is moderately well represented, the temporal extension is extremely rudimentary.

Entorhinal cortex. In most mammals this cortex occupies the posterior part of the pyriform lobe (the area pyriformis posterior or post-pyriform cortex) where it is separated from isocortex by the posterior part of the rhinal fissure. An intervening area peri-rhinalis is distinguished by some authors (e.g. Rose, 1926). Medially and anteriorly it is separated from the cortical amygdaloid nucleus by the cortico-amygdaloid transition area (periamygdala of Rose, 1926) and medially and posteriorly by the subiculum from the cornu ammonis.

A well differentiated cortical area with these relationships can be seen in the porpoise, and part of its extent is shown in Text-figure 8. To low-power examination it presents a characteristic appearance as two well-defined cellular laminae separated from each other by a relatively cell-free zone (Text-figs. 1–7). More detailed examination shows that six laminae can be distinguished as follows (Pl. 1, fig. 2): (1) molecular, containing an occasional nerve cell; (2) a layer of pyramidal cells which are closely packed and in places arranged in clusters or islands; (3) a broader layer containing similar cells but much more widely spaced; (4) a narrow layer containing comparatively few small polygonal cells; (5) a closely packed layer of large polygonal cells; (6) an ill-defined 'polymorphous' layer with rather widely scattered cells of varying shape.

A similar pattern can be distinguished in all parts of the entorhinal area, although there are obvious regional variations. For example, a section taken from the upper surface of the temporal lobe (Pl. 1, fig. 3) is superficially very different from the section (Pl. 1, fig. 2) taken from the hippocampal gyrus. The same laminae can be recognized, but they are less clearly defined; cells are in general more widely separated and the total depth of the cortex is much greater. To what extent these differences can be attributed to differences in the plane of section it is difficult to say; the greater apparent depth, the broadening of the laminae and their loss of clear definition might well be due to this. The spacing of the cells would probably not be greatly affected by the plane of section, but no useful purpose would be served by attempting to define subdivisions in the entorhinal area without the use of more critical histological methods.

The six laminae described can be made to correspond reasonably well with those described by Lorento de No (1933). It is also true to say that the description in four laminae adopted by Rose (1926) can be fitted to the condition in the porpoise; but it is clear that the actual number of laminae distinguished in almost any part of the mammalian cortex is to some extent arbitrary, especially when only Nissl material is available. Our findings demonstrate that, in the porpoise, there is a well differentiated and extensive cortical area which occupies the same topographical position

as the entorhinal cortex of other mammals. Its intrinsic structure, so far as this can be studied in Nissl material, is similar to that of the entorhinal cortex, and the differences in detail which exist are probably no greater than could be found between any two mammals of widely different species. In other words, the evidence for the identification of this area as entorhinal is as good as in many other mammals, and it may be pointed out in addition that its extent and high degree of differentiation in the porpoise is in striking contrast to the rudimentary condition of the prepyriform cortex.

THE RETROSPLENIAL AND CINGULATE CORTICAL AREAS

The remaining cortical areas and certain parts of the diencephalon will be described very briefly. A more detailed account could be justified only as part of a wider survey of the cortex or thalamus as a whole; here only features relevant to their possible relationship to the rhinencephalon need be considered.

Retrosplenial area. In the retrosplenial region a small area of cortex having the structure illustrated in Pl. 2, fig. 9, can be identified. It lies along the subicular border of the induseum, and could with some justification be referred to as a 'granular' cortex. In general its cellular elements are smaller than in most regions of the isocortex of the porpoise (compare Pl. 2, fig. 11, cingulate cortex, and Pl. 2, fig. 12, from the isocortex of the frontal lobe), and a considerable number are of the 'granule' type. A somewhat similar cortex extends in a subsplenial position along the hippocampal gyrus towards the entorhinal area (Pl. 2, fig. 10). Here there is also a predominance of small elements so that one is reminded of the 'koniocortex' of von Economo (1929).

The retrosplenial cortex is obviously more distinctly laminated than the cortex in a subsplenial position, but it is very doubtful if an attempt to define these laminae and compare them in detail with those of other mammals could be justified. It is enough for our present purpose to point out that a cortex in which small or 'granular' elements are prominent is characteristic of this situation in many other mammals, including man.

Cingulate area. The cingulate gyrus is well developed, and the histology of its cortex is illustrated in Pl. 2, fig. 11. It is fairly clearly laminated, and there is a marked absence of granule cells. The lamination is rather similar to that of the frontal cortex (Pl. 2, fig. 12) and each could be fitted to either of the two slightly different schemes of lamination proposed by Riese (1924) and Langworthy (1932). The cingulate cortex is uniform throughout the length of the gyrus; there is no differentiation of granular and agranular regions as in other mammals.

DIENCEPHALIC STRUCTURES

The hypothalamus. Only the mamillary region need be considered here, though it may be said in passing that the hypothalamic nuclei in general conform to the usual mammalian pattern. The mamillary bodies are represented by slight accumulations of small cells on each side of the midline close to the floor of the third ventricle. A medial nucleus can be recognized, but more on account of the position of the cells medial to the fibres of the fornix than because they form a distinct group. No other cell groups could be recognized, so that in this respect the

mamillary region is relatively undifferentiated. It has already been noted that the fornix fibres which reach the mamillary region are few in number, and it can be added that in our material no clearly defined mamillo-thalamic tract can be recognized. Hatschek & Schlesinger (1902) also had difficulty in identifying this tract in *Delphinus delphis* though Langworthy (1932) was able to follow it to the anterior thalamic nuclei in *Tursiops truncatus*.

The thalamus. Only the anterior group of nuclei have been examined in detail, and these are illustrated in Pl. 2, fig. 7. The identifications must be regarded as tentative, since the groups of cells found in the anterior tubercle of the thalamus are very irregular and quite unlike the well-defined cell groups found, for example, in the sheep. They extend in the series only through about 0·7 mm. in a cranio-caudal direction, after which they are replaced by a large dorso-medial nucleus. It must be admitted that the posterior boundary of the cell group marked antero-ventral nucleus is very difficult to define; it may extend a little further posteriorly than appears to be the case, but even if it does the very small size and poor differentiation of the anterior group of nuclei as a whole remains a conspicuous feature of the porpoise thalamus. The absence of a defined mammillo-thalamic tract has already been noted.

Epithalamus. The remarkable development of the habenular ganglia and commissure and the fasciculus retroflexus has been noted by previous authors (Hatschek & Schlesinger, 1902). Medial and lateral nuclei are readily distinguishable; the cells of the former stain deeply and are closely packed; those of the latter are pale and are scattered on a dense plexus of fibres. Apart from its greater size, the epithalamus of the porpoise is essentially similar to that of other mammals.

DISCUSSION

The present paper completes the description of the 'rhinencephalon' of an anosmatic brain, and two main questions arise to which the findings should be relevant, namely: (i) What changes in structure can be attributed to the loss of secondary olfactory connexions? (ii) What inferences concerning the neurological aspect of olfactory function in mammals generally can be drawn from an examination of a brain in which such functions are absent?

In the rabbit and monkey Clarke & Meyer (1947) and Meyer & Allison (1949) have shown that fibres from the olfactory bulb end in a part of the anterior olfactory nucleus and olfactory tubercle, the prepyriform cortex, the nucleus of the lateral olfactory tract, and in the cortical medial and central amygdaloid nuclei. In addition a few such fibres end throughout the bed nucleus of the stria terminalis, some after crossing in the anterior commissure. It is probable that this description applies generally to osmatic mammals.

If the differences which can be observed in these structures in the porpoise can all be attributed to the loss of secondary olfactory connexions, it is at once clear that this loss is very variable in its effects. These range from almost complete regression to vestiges which cannot be recognized with confidence, as in the anterior olfactory nucleus and the nucleus of the lateral olfactory tract, to an apparent absence of any substantial change as in the cortico-medial amygdaloid nuclei or the bed nucleus of the stria terminalis. The olfactory tubercle formation and the

prepyriform cortex occupy an intermediate position, showing marked retrogression in extent but enough characteristic differentiation to be clearly recognizable.

To some extent such variations may be related to variations in the concentration of olfactory tract connexions. For example, Meyer & Allison (1949) have shown that in the monkey the temporal prepyriform cortex receives more olfactory tract fibres than the frontal, and it is the temporal part of this area in the porpoise which shows the most marked retrogression. It is obvious, however, that, to varying degrees, all the structures so far considered must play a part in olfaction in osmatic mammals, although their structural diversity shows that there must be corresponding functional differences. Some may be concerned only with the relay and reinforcement of impulses of olfactory origin, and these one would expect to disappear or become vestigial as a result of the loss of olfactory receptors. This appears to have been the fate of the olfactory bulb, the anterior olfactory nucleus and the nucleus of the lateral olfactory tract. Cortical areas or complex nuclear groups may be concerned with the discrimination and integration of impulses from many different sources, and, through efferent connexions, may have acquired control of mechanisms which are not activated solely by one type of stimulus. In this connexion it is relevant to point out that Kaada (1951), in monkeys, cats and dogs, found that 'marked inhibition of respiratory movements was produced on stimulation of points in the amygdaloid nuclei', as well as from a number of other regions most of which are included in the 'rhinencephalon' of the older literature. Inhibition of respiration in response to certain olfactory stimuli may clearly be important; in an aquatic mammal respiratory inhibition is equally or more important as a preparation for submergence, and if the amygdala is a neural mechanism capable of this function, it is not surprising that it should undergo no retrogression in spite of a lack of olfactory connexions.

One may suggest, therefore, that the anterior olfactory nucleus and the nucleus of the lateral olfactory tract should be classed with the olfactory bulb as structures concerned exclusively with the analysis, relay or reinforcement of impulses of olfactory origin, but that the amygdala, including its cortico-medial nuclei, is not primarily olfactory in function, though it may be activated by olfactory stimuli in osmatic mammals. The significance of the prepyriform cortex of the porpoise is more difficult to assess. Its great reduction in this animal, and the abundance of its connexions from the lateral olfactory tract in osmatic mammals, leave no doubt as to its primary functional association with olfaction. There is no evidence on which to base even speculations concerning the function of the remnants of this cortex in the porpoise.

It is doubtful if any of the remaining parts of the rhinencephalon receive direct connexions from the olfactory bulb in any mammal. They could not be demonstrated in the rabbit (Clark & Meyer, 1947) or the monkey (Meyer & Allison, 1949). There is no reason to think that these animals are atypical in this respect, and it is now generally accepted that statements, common in the older literature, that secondary olfactory fibres reach the septum, hippocampus and entorhinal cortex, were based on inadequate evidence.

It is, however, obvious that the absence of direct connexions from the olfactory bulb does not exclude the possibility of olfactory function. The entorhinal cortex,

for example, is very closely associated with the prepyriform cortical area, and might well receive tertiary olfactory connexions from that source. Such fibres, however, have been shown to be few in number (Allison, 1953), and comparative studies suggest that the entorhinal cortex reaches its greatest extent and highest degree of differentiation in the microsmatic Primates (Rose, 1927; Allison, 1953). That the entorhinal area does receive some impulses of olfactory origin in macrosmatic mammals is therefore likely, but it is clear that its structural differentiation is not dependent on these connexions, a conclusion which receives confirmation from the observation that it is extensive and well differentiated in the anosmatic porpoise. It may be that the entorhinal cortex is in some respects similar to the amygdala, capable of activation by olfactory impulses when these are present, but performing functions which lose none of their importance when they are absent. If so, the fact that the entorhinal cortex is well developed in the porpoise, in spite of the absence of an olfactory bulb is not surprising. In other mammals, however, the entorhinal cortex is thought to give origin to the majority of the afferent fibres to the hippocampus. It is worth noting, therefore, that a small and apparently retrogressive hippocampus need not be associated with a corresponding reduction in the entorhinal cortex.

One of the most striking features of the porpoise brain is the remarkably small size of the hippocampal formation. Some authors (e.g. Addison, 1915) have associated this with the loss of the sense of smell, as was reasonable when the hippocampus was thought to serve predominantly olfactory functions. Now, since the older evidence for olfactory function in the hippocampus has been found to be inadequate (Brodal, 1947*a*), the mere presence of a recognizable hippocampus in an anosmatic mammal is taken as additional proof that it is not concerned with olfaction in any mammal. While one cannot avoid being impressed by the coincidence that a structure which has for many years been regarded as olfactory in function, should be so poorly developed in an anosmatic mammal, it is nevertheless clear that the condition in the porpoise can be used to support either hypothesis, olfactory or non-olfactory, for hippocampal function. However, since the amygdala, which undoubtedly receives olfactory connexions in most mammals, is not substantially reduced in the porpoise, it is clearly reasonable to look elsewhere for the cause of the reduction which has occurred in the hippocampus.

This reduction is the more striking since it is accompanied by such marked lack of differentiation in the mamillary region and in the anterior thalamic nuclei, regions which owed their inclusion in the rhinencephalon to their connexion, direct or indirect, with the hippocampus. The cingulate cortex does not show a corresponding reduction, though the absence of any 'granular' area is suggestive. It is difficult to avoid the conclusion that we have here a complex neural mechanism the interconnected parts of which serve a common function which has become much less important in aquatic mammals. What this function may be is at present almost entirely a matter of speculation. It has been suggested that it is related to the control of emotional reactions (Papez, 1937; Bard & Mountcastle, 1948, and others) and the fact that the hypothalamus is included in the complex suggests a relationship to autonomic function. It is perhaps relevant to point out that an aquatic environment is very uniform so far as conditions of temperature and humidity are concerned,

and this may make a number of autonomic adjustments, vital for a terrestrial mammal, unnecessary. A detailed study of the whole hypothalamus might throw some light on this question.

The large size of the habenular nuclei has been noted; it is therefore unlikely that these are exclusively olfactory in function in any mammal, but more than that it is not possible to say. In fact, the main general conclusion which can be drawn from this whole study is that investigations of the comparative anatomy of the brain, especially when they are based on the rather superficial evidence of Nissl and Weigert preparations, are very rarely capable of precise or reliable functional interpretation. They may provide hypotheses or suggestions which indicate fruitful lines for investigation, in which it will be necessary to use quantitative, experimental or physiological methods. They may provide useful corroborative evidence, although, as in the case of the porpoise hippocampus, this will often be equivocal, and capable of supporting more than one hypothesis. Their main purpose must remain to outline the structural background and to provide ideas and suggestions which may be tested and modified by the more precise methods indicated above.

SUMMARY

The amygdaloid nuclei, hippocampal formation, and entorhinal cortical area of the anosmatic porpoise (*Phocaena phocaena*) has been described on the basis of Nissl and Weigert stained serial sections. A less detailed description is given of the cingulate and retrosplenial cortical areas, the mamillary region of the hypothalamus, the anterior thalamic nuclei, and the habenular ganglia.

The amygdaloid nuclei resemble very closely those of other mammals, except for the probable absence of the nucleus of the lateral olfactory tract. Estimates of volume show that the cortico-medial group forms approximately the same proportion of the whole complex as in the sheep.

The hippocampal formation, while showing all the parts characteristic of this formation in mammals in general, is very small. Approximate estimates indicate that the part of the formation in which both a cornu ammonis and a dentate gyrus can be recognized has about one-fifth of the volume of the corresponding structures in the sheep, and one-tenth those in man. The vestigial parts of the hippocampus (e.g. induseum griseum), in which no differentiated dentate gyrus can be recognized, appear to form a larger proportion of the whole formation than in other mammals, and a considerable part of the subcallosal hippocampus is in this condition. There is no hippocampal flexure; the fornix is well developed, but comparatively few of its fibres reach the mamillary region.

The entorhinal cortex shows no signs of regression; it is characteristically differentiated, and extensive.

Of the remaining structures examined, only the mamillary region and anterior thalamic nuclei show conspicuous differences from other mammals; in both, nuclear differentiation is very poor as compared, for example, with the sheep, and a mamillothalamic tract is not recognizable as a defined bundle of fibres.

Taking into account the observation previously reported (Breathnach, 1953) it is concluded that the only structures whose loss or regression can be related to the loss of olfactory function are the olfactory bulb, the anterior olfactory nucleus, the

prepyriform cortex, the nucleus of the lateral olfactory tract, and possibly the cortex of the olfactory tubercle. The cortico-medial amygdaloid nuclei show no significant change, and probably do not owe their primary functional significance to olfactory connexions, although these are present in osmatic mammals. Regression in the hippocampal formation and in the related mamillary and anterior thalamic nuclei is a characteristic feature of the porpoise brain, but there is no evidence to suggest that this is the result of the loss of olfactory function.

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EXPLANATION OF PLATES

All photographs are of celloidin sections 20 μ thick, stained with thionin.

PLATE 1

Fig. 1. An oblique section through the amygdala in which all the nuclei are represented. × 8.

Fig. 2. The cortex of the entorhinal area on the hippocampal gyrus. × 32.

Fig. 3. The cortex of the entorhinal area on the upper surface of the temporal lobe. × 32.

Fig. 4. The hippocampal formation cut at the region of maximal development. *X* marks the break in the cell layer referred to in text (p. 278). The arrow indicates the probable point of transition between cornu ammonis and subicular cortex. × 23.

Fig. 5. A section through the posterior part of the hippocampal formation about 10 mm. anterior to the splenium. × 16.

Fig. 6. The induseum griseum. × 16.

PLATE 2

Fig. 7. A section through the anterior part of the thalamus. × 12.

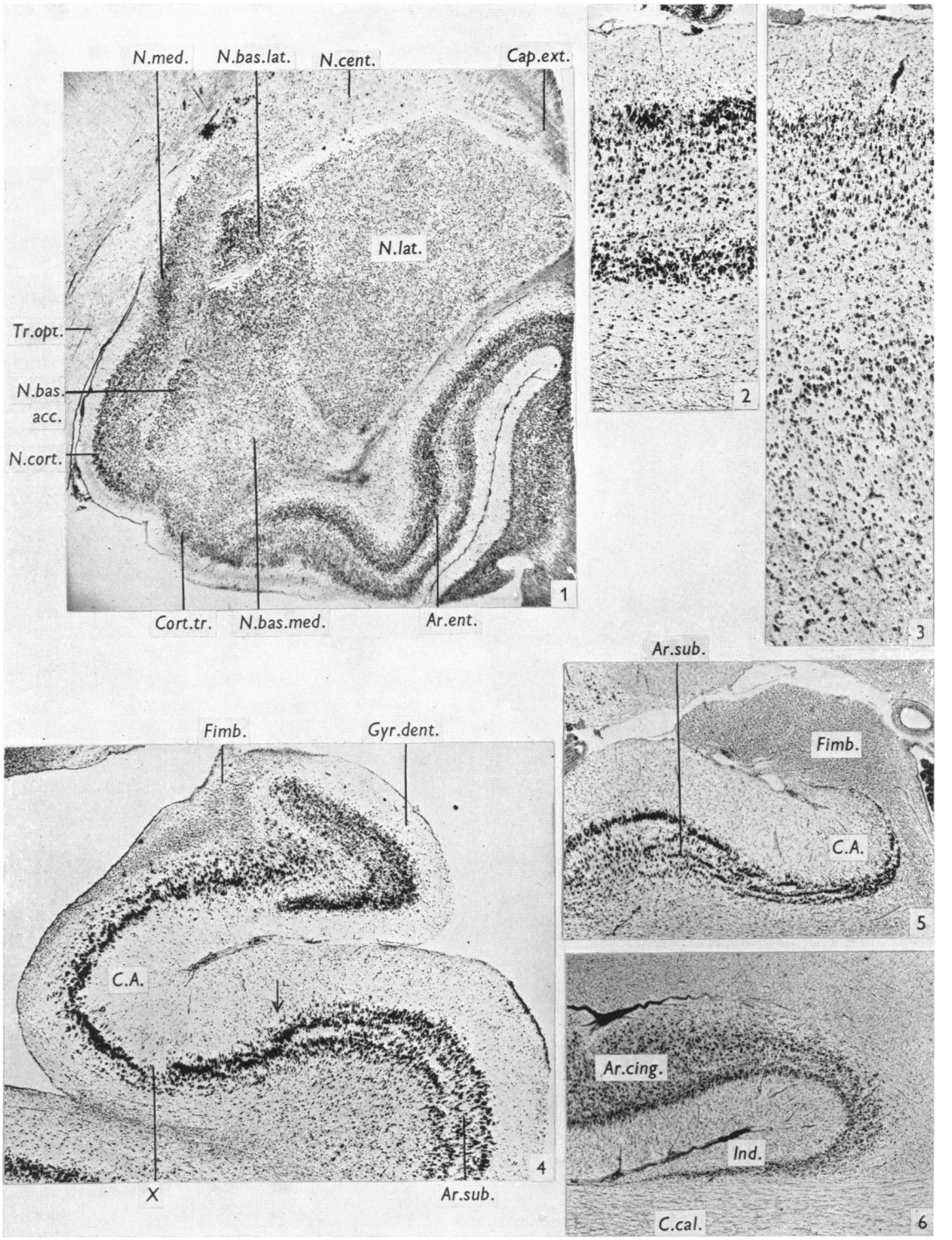
Fig. 8. The subicular cortex. × 32.

Fig. 9. The cortex of the retrosplenial area. × 32.

Fig. 10. The cortex of the hippocampal gyrus posterior to the entorhinal area. × 32.

Fig. 11. The cortex of the cingulate gyrus. × 32.

Fig. 12. A section of the cortex on the dorso-lateral aspect of the anterior part of the frontal lobe, close to the mid-dorsal line. × 32.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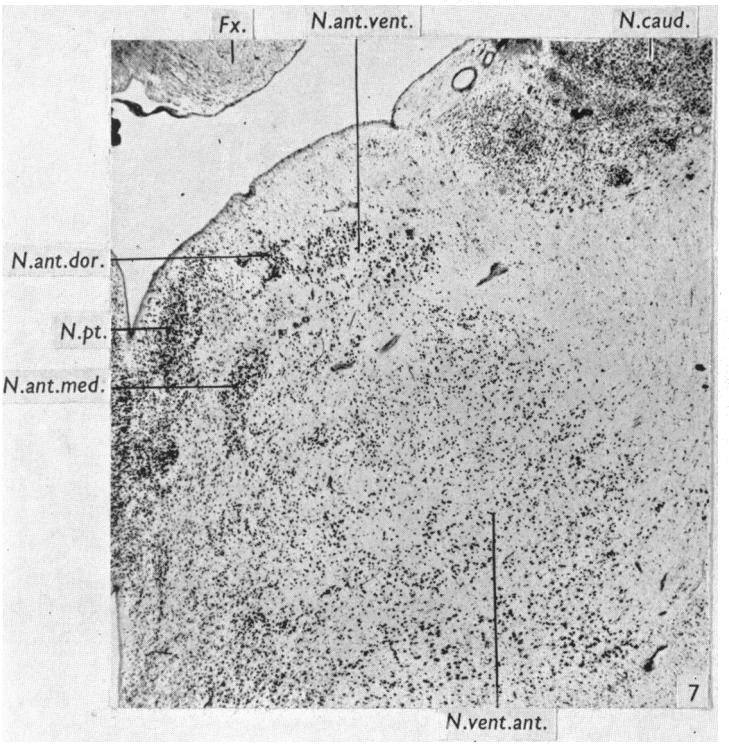
N.bas.med.
Ar.ent.
1
2
3
Ar.sub.
Fimb.
Gyr.dent.
C.A.
X
Ar.sub.
4
Fimb.
C.A.
5
Ar.cing.
Ind.
C.cal.
6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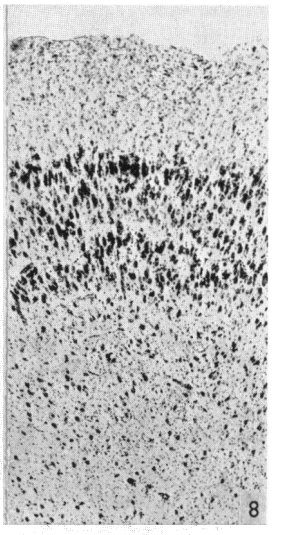
7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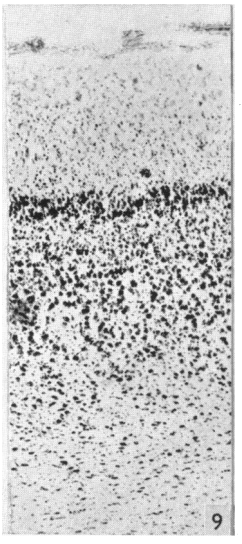
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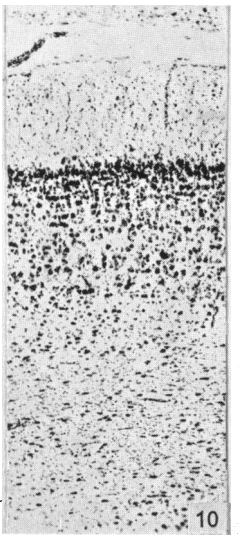
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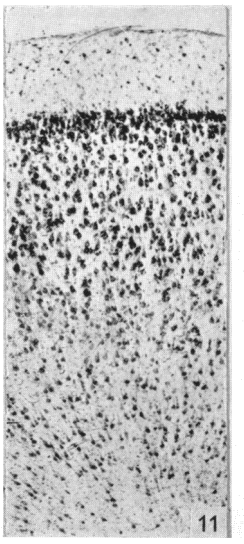
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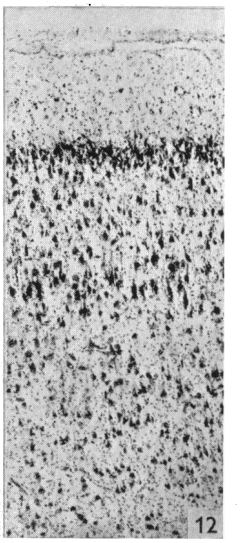
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LIST OF ABBREVIATIONS USED IN TEXT-FIGURES AND PLATES

Ar.ant.	Anterior amygdaloid area
Ar.cing.	Cingulate area
Ar.ent.	Entorhinal area
Ar.ins.agr.	Agranular insular area
Ar.prep.	Prepyriform area
Ar.sub.	Subicular area
C.A.	Cornu Ammonis
C.cal.	Corpus callosum
Cap.ext.	External capsule
Cort.tr.	Cortico-amygdaloid transition area
F.am.	Amygdaloid fissure
Fimb.	Fimbria
Fx.	Fornix
Gyr.dent.	Dentate gyrus
Ind.	Induseum griseum
Mass.int.	An intercalated cell mass
N.bas.acc.	Accessory basal amygdaloid nucleus
N.bas.lat.	Lateral part of basal amygdaloid nucleus
N.bas.med.	Medial part of basal amygdaloid nucleus
N.cent.	Central amygdaloid nucleus
N.cort.	Cortical amygdaloid nucleus
N.lat.	Lateral amygdaloid nucleus
N.med.	Medial amygdaloid nucleus
N.ant.dors.	Antero-dorsal thalamic nucleus
N.ant.med.	Antero-medial thalamic nucleus
N.ant.vent.	Antero-ventral thalamic nucleus
N.caud.	Caudate nucleus
N.lent.	Lentiform nucleus
N.pt.	Parataenial nucleus
N.tr.ol.	Nucleus of lateral olfactory tract
N.vent.ant.	Anterior ventral thalamic nucleus
Str.ter.	Stria terminalis
Tr.opt.	Optic tract